113

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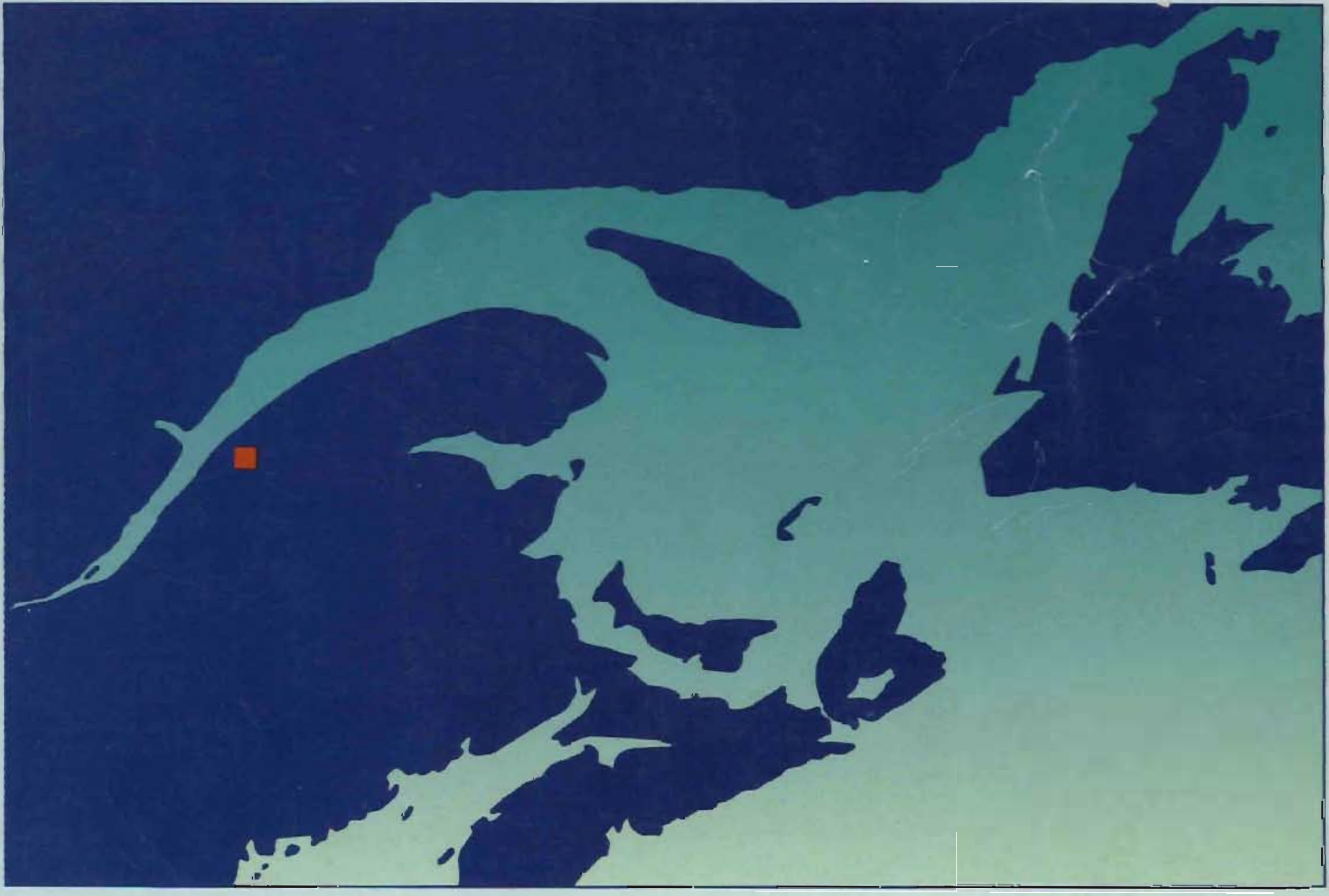
sciences halieutiques et aquatiques 113

Canadian Special Publication of
Fisheries and Aquatic Sciences 113

Le Golfe du Saint-Laurent : petit océan ou grand estuaire?

The Gulf of St. Lawrence: Small Ocean or Big Estuary?



Rédaction : Jean-Claude Therriault

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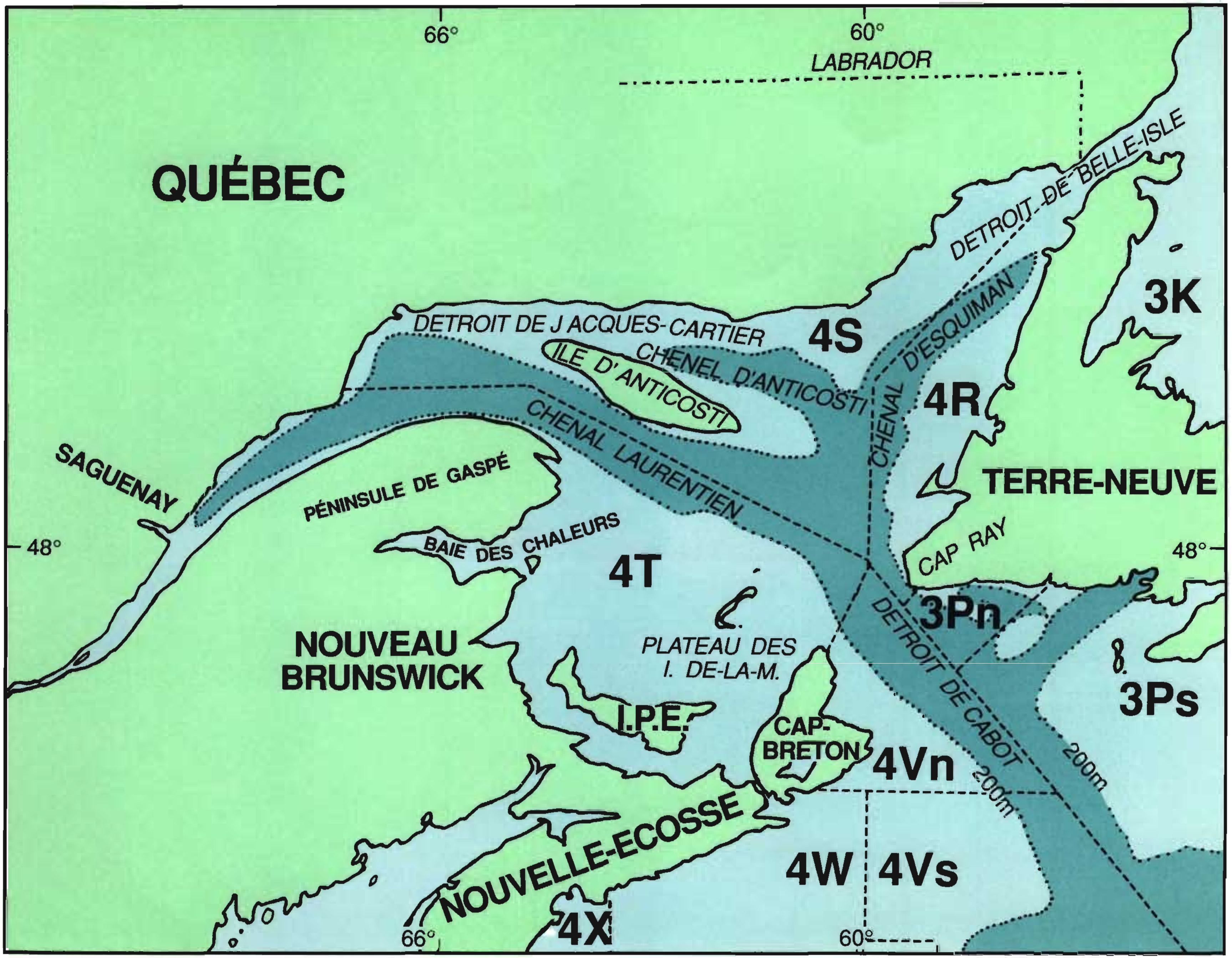
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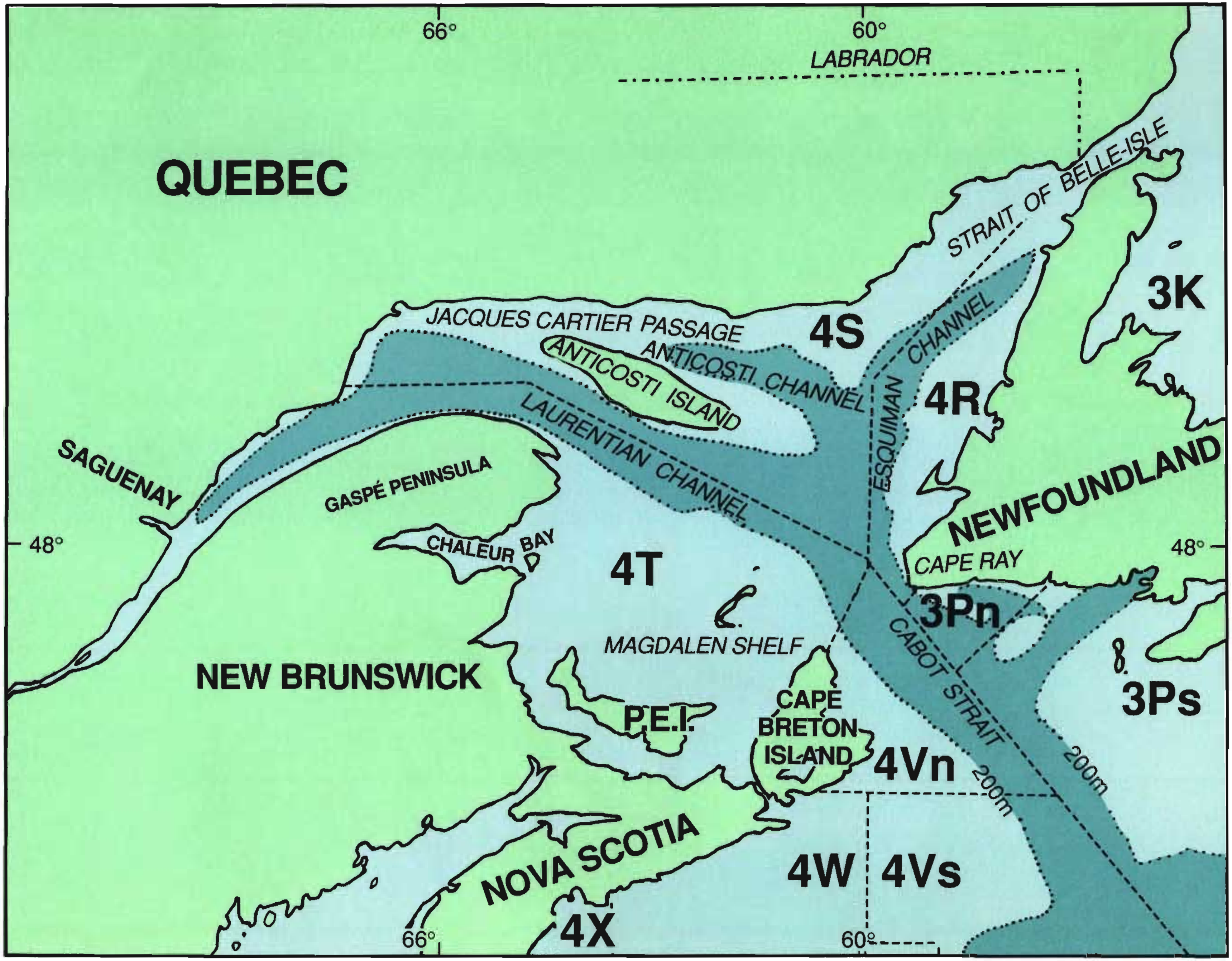
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Le Golfe du Saint-Laurent : petit océan ou grand estuaire?

*Compte-rendus d'un atelier/symposium
tenu à l'Institut Maurice-Lamontagne
(Mont-Joli) du 14 au 17 mars 1989*

Rédaction : Jean-Claude Therriault

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Institut Maurice-Lamontagne
C.P. 1000
Mont-Joli (Québec) G5H 3Z4*

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Ottawa 1991

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Fisheries and Aquatic Sciences 113

The Gulf of St Lawrence: Small Ocean or Big Estuary?

*Proceedings of a Workshop/Symposium
held at the Maurice Lamontagne
Institute, Mont-Joli, 14-17 March 1989*

Edited by Jean-Claude Therriault

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Maurice Lamontagne Institute
P.O. Box 1000
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THERRIAULT, J.-C. [ÉD.]. 1991. Le golfe du Saint-Laurent : Petit océan ou grand estuaire? Publ. spéc. can. sci. halieut. aquat. 113 : 359 p.

Cette publication fait le compte rendu des rapports d'atelier, des revues et des articles scientifiques qui ont été présentés lors d'un Atelier/Symposium sur l'Océanographie et les Pêcheries du Golfe du Saint-Laurent, qui s'est tenu à l'Institut Maurice-Lamontagne (Mont-Joli) du 14 au 17 mars 1989.

Le premier chapitre situe le contexte de cet Atelier/Symposium en présentant un bref historique de la recherche marine dans le Golfe du Saint-Laurent.

Le second chapitre rapporte les délibérations, conclusions et recommendations des ateliers de travail qui ont été organisés en océanographie (physique, biologie, chimie et sédimentologie) et en pêcherie (poissons et invertébrés). Ces ateliers pluridisciplinaires avaient pour mandat d'examiner «Comment on peut utiliser le système du Saint-Laurent, région type du plateau continental, comme laboratoire naturel pour contribuer à la solution du grand problème que constitue la conservation à long terme des ressources et de la qualité du milieu (changements à l'échelle du globe, contaminants, etc...)?».

Le troisième chapitre met en valeur les revues réalisées sur invitation dans lesquelles des auteurs ou des groupes d'auteurs choisis y expriment leurs vues et leurs recommandations personnelles.

Le quatrième chapitre rapporte la contribution des participants au Symposium sous forme d'articles scientifiques originaux tirés de leur travaux récents portant sur le Golfe.

Finalement, un recueil de références en océanographie biologique complète le dernier chapitre de ce livre.

Abstract

THERRIAULT, J.-C. [ED.]. 1991. The Gulf of St. Lawrence: Small Ocean or Big Estuary? Can. Spec. Publ. Fish. Aquat. Sci. 113: 359 p.

This publication contains the proceedings of the workshop, the scientific reviews and the contributed papers which were presented at a Symposium on the Oceanography and Fishery of the Gulf of St. Lawrence, held at the Maurice Lamontagne Institute (Mont-Joli) from 14 to 17 March 1989.

The first chapter establishes the context of this Workshop/Symposium, by presenting a brief historic summary of the marine research in the Gulf of St. Lawrence.

The second chapter reports the discussions, conclusions and recommendations of the different working groups on Oceanography (physics, biology, chemistry and sedimentology) and on the Fishery (fish and invetebrates). The discussions of each multidisciplinary working group were centered around the following mandate: "How may the St. Lawrence system, as a representative shelf area, be usesd as a natural laboratory which will contribute to the solution of major long-term problems of conservation of natural resources and of the quality of the environment (global changes, pollution, etc.)?"

The third chapter contains the invited reviews in which chosen authors or groups of authors present their personal views and recommendations.

The fourth chapter reports the contributions of Symposium participants who presented original scientific papers derived from their recent studies on the Gulf.

Finally, a list of references on biological oceanography completes the last chapter of this volume.

Préface

Du 14 au 17 mars 1989, s'est tenu à l'Institut Maurice-Lamontagne un Atelier/Symposium intitulé «Le Golfe du Saint-Laurent : Petit Océan ou Grand Estuaire?» Ce Symposium a permis à plus de 150 scientifiques des universités et organismes gouvernementaux des provinces de l'Atlantique de faire le point sur la recherche sur cette étendue d'eau qui comporte à la fois des caractéristiques estuariennes et océaniques. Cette rencontre a été parrainée par le Ministère des Pêches et des Océans et a été organisée par la région du Québec avec la participation des chercheurs des régions du Golfe, de Scotia-Fundy et de Terre-Neuve.

Les objectifs de cette rencontre étaient les suivants :

1) Établir l'état actuel des connaissances en sciences des pêches, en océanographie (physique, chimique, biologique et géologique) et en hydrographie dans le golfe du Saint-Laurent,

2) Promouvoir l'échange d'information entre ces disciplines,

3) Faire des recommandations pour l'orientation future de la recherche en océanographie et en pêcherie.

Pour atteindre ces objectifs, le comité scientifique formé de G. Bugden (Bedford), M. Chadwick (Moncton), D. Gascon (IML), B. Sundby (IML) et présidé par J.-C. Therriault (IML) a choisi trois moyens principaux soit : (1) des revues sur invitation couvrant les disciplines principales en océanographie et en pêcherie, (2) des sessions ouvertes à tous les participants du Symposium pour présenter des communications de leur travaux inédits et finalement, (3) la tenue d'ateliers de travail à participation pluridisciplinaire pour discuter et faire des présentations orales et des affiches traitant de la recherche en océanographie biologique (atelier présidé par L. Legendre : Université Laval), en océanographie, chimique et sédimentologie (atelier présidé par B. Sundby : Institut Maurice-Lamontagne), en océanographie physique (atelier présidé par P. Leblond : Université Colombie-Britannique), en recherche sur les pêches (atelier présidé par M. Sinclair : Institut océanographique de Bedford), et finalement, en recherche sur les invertébrés marins (atelier présidé par G. Ennis : MPO, Terre-Neuve). Chacun des ateliers avait pour mandat d'examiner «comment on peut utiliser le système du Saint-Laurent, région type du plateau continental, comme laboratoire naturel pour contribuer à la solution du grand problème que constitue la conservation à long terme des ressources et de la qualité du milieu (changements à l'échelle du globe, contaminants, etc.)? «Les ateliers ont attaqué leur mandat avec enthousiasme et ont suggéré des voies futures intéressantes pour la recherche dans leur domaine respectif.

Le succès de cet Atelier/Symposium sur le golfe du Saint-Laurent est en grande partie dû aux auteurs invités et au nombreux participants qui ont consacré temps et efforts à la préparation de communications orales,

Preface

From 14 to 17 March 1989, the Maurice Lamontagne Institute hosted a Workshop/Symposium entitled "The Gulf of St. Lawrence: Small Ocean or Big Estuary?" This symposium allowed more than 150 research scientists from universities and governmental departments of the Atlantic provinces to evaluate their state of knowledge on this aquatic environment which has both estuarine and oceanic characteristics. This meeting was sponsored by the Department of Fisheries and Oceans and organized by the Quebec Region with the participation of research scientists from the Gulf, Scotia-Fundy and Newfoundland Regions.

The objectives of this meeting were as follow:

1) To establish the current state of knowledge in fisheries sciences, in oceanography (physical, chemical, biological and geological) and in hydrography in the Gulf of St. Lawrence,

2) To promote exchange of information between these disciplines,

3) To make recommendations for the future orientation of oceanographic and fisheries research.

To accomplish these objectives, the scientific committee formed by G. Bugden (Bedford), M. Chadwick (Moncton), D. Gascon (IML), B. Sundby (IML) and chaired by J.-C. Therriault (IML) chose three main avenues: (1) invited reviews covering the main disciplines in oceanography and in fishery; (2) open sessions for oral and poster contributions from participants to present original results; and (3) multidisciplinary working group sessions to tackle specific questions, identify gaps in knowledge and recommend future directions for research in different fields. These workshops dealt with biological oceanography (chaired by L. Legendre, Laval University), chemical oceanography and sedimentology (chaired by B. Sundby, Maurice Lamontagne Institute), physical oceanography (chaired by P. Leblond, University of British Columbia), fish research (chaired by M. Sinclair, Bedford Institute of Oceanography) and invertebrate research (chaired by G. Ennis, Fisheries and Oceans, Newfoundland). Each working group had the mandate to examine "How the St. Lawrence system, as a representative shelf area, may be used as a naturel laboratory which will contribute to the solution of major long-term problems of conservation of natural resources and of the quality of the environment (global changes, pollution, etc.)?" The working group worked with enthousiasm and made interesting suggestions concerning the future research avenues in their respective field.

The success of this Workshop/Symposium on the Gulf of St. Lawrence is largely due to invited authors and participants of the Symposium who spent much time and effort preparing reviews, oral communications, posters d'affiches et de manuscrits faisant le point sur un sujet en particulier ou présentant des résultats inédits. Je désire également souligner le concours et la coopération des présidents d'atelier qui ont mené les débats avec doigté et qui ont fourni d'excellents rapports contenant le sommaire des discussions ainsi que des recommandations réalistes et intéressantes pour la recherche future dans le Golfe.

Suite au Symposium, les manuscrits scientifiques ainsi que les rapports d'atelier ont tous fait l'objet d'une révision indépendante par au moins deux (normalement trois) arbitres reconnus pour leur compétence dans le domaine avant d'être acceptés pour publication dans le présent volume. Je tiens à remercier spécialement ces arbitres dont les commentaires et suggestions ont permis de clarifier et d'améliorer les manuscrits originaux et les rapports d'atelier. Je remercie également la Direction générale des Communications, Publications scientifiques de Pêches et Océans, à Ottawa pour son aide technique dans la réalisation de ce volume.

Si ce Symposium n'a pu répondre spécifiquement à la question de savoir si le golfe du Saint-Laurent doit être considéré comme un petit océan ou un grand estuaire, il a tout de même permis d'ajouter des connaissances nouvelles à notre compréhension de l'écosystème du golfe du Saint-Laurent. Cependant, force est de constater qu'en 15 ans, soit depuis le dernier symposium sur le Golfe qui s'était tenu à Rimouski en 1973, relativement peu a été accompli et qu'il reste encore beaucoup à faire! Comme le Golfe constitue un laboratoire immense et complexe, un groupe, un institut (ou université) ou même un gouvernement ne peut penser s'attaquer seul aux problèmes de recherche qui ont été identifiés durant ce colloque. De plus, il y a maintenant un fort concensus pour dire qu'une approche pluridisciplinaire est essentielle.

Somme toute, la plus grande utilité de cette réunion aura probablement été de favoriser la communication entre les chercheurs de différentes disciplines et nous ne pouvons qu'espérer que de ce mélange d'idées sortiront des travaux originaux et intéressants qui seront au menu lors d'un prochain symposium.

J.-C. Therriault

and manuscripts on their original data. I also want to acknowledge the assistance and cooperation of the chairmen of working groups who conducted the discussions with tact and who provided excellent reports summarizing those discussions and proposing realistic and interesting avenues for future research in the Gulf.

Following the symposium, the scientific manuscripts and working groups reports have all been reviewed by at least two (normally three) referees recognized for their competence in the particular field of research before being accepted for publication in this book. I express particular thanks to these referees for their comments and suggestions which contributed to clarify and improve the original manuscripts and reports. I also thank the Communications Directorate, Scientific Publications of Fisheries and Oceans in Ottawa for their technical help in the realization of this book.

If this Symposium has not been able to tell us specifically if the Gulf of St. Lawrence is a big ocean or a small estuary, it nevertheless allowed to add new knowledge to our comprehension of the Gulf ecosystem. However, it must be admitted that in more than 15 years, since the last Symposium held at Rimouski in 1973, relatively little has been accomplished and that a lot still remains to be done! As the Gulf represents an immense and complex laboratory, one research group, one institute (or university) or even one government cannot possibly think that it can tackle alone the numerous research problems identified during this meeting. Moreover, there is now a strong concensus for the necessity of a multidisciplinary approach of these research problems.

To conclude, I believe the greatest benefit of this meeting has probably been the communication between research scientists from different fields in marine sciences and I can only hope that original and interesting studies will come out of this exercice. These should be on the menu of the next Symposium.

J.-C. Therriault

Remerciements spéciaux

En tant que président du comité d'organisation de l'Atelier/Symposium sur le golfe du Saint-Laurent, j'aimerais souligner que le succès de cet événement n'aurait pu être assuré sans le travail exceptionnel réalisé par la Coordonatrice Mad. R. Camirand. L. Maurice (secrétaire) et V. Haeberlé (agente de communication) ont également fourni une contribution digne de mention. Finalement, j'aimerais mentionner la contribution spéciale et importante de N. Aubut, L. Corriveau et F. Roy.

Special Acknowledgements

As chairman of the organizing committee of the Workshop/Symposium on the Gulf of St. Lawrence, I would like to emphasize that the great success of this meeting is largely due to the exceptionnal work done by the coordinator Mrs. R. Camirand. L. Maurice (secretary) and V. Haeberlé (Communication officer) have also made contributions that should be underscored. Finally, I would like to mention the special and important contribution offered by N. Aubut, L. Corriveau and F. Roy.

CHAPITRE I.
ALLOCUTION D'OUVERTURE

CHAPTER I.
INTRODUCTORY ADDRESS

Bref historique de la recherche marine dans le golfe du Saint-Laurent

J. Boulva

Directeur, Institut Maurice-Lamontagne,
Ministère des Pêches et des Océans,
C.P. 1000, Mont-Joli (Québec), Canada G5H 3Z4

Au nom du ministère des Pêches et des Océans, je suis heureux de vous accueillir à l'Institut Maurice-Lamontagne à l'occasion de ce premier symposium à être tenu dans nos murs. Alors que nous sommes encore à mettre en place les équipes de recherche, il nous est apparu important de réunir les spécialistes dans le cadre de ce colloque, en vue de faire le point sur l'état des connaissances concernant le golfe du Saint-Laurent et de tracer les orientations de la recherche des prochaines années. Pour ce faire, j'ai pensé qu'un bref rappel de l'historique de la recherche dans le Golfe serait à propos afin de bien situer le contexte de cette réunion.

Les assises scientifiques qui s'ouvrent aujourd'hui représentent un événement important puisque c'est la quatrième réunion du genre qui regroupe les experts des différentes disciplines intéressés aux sciences de la mer, et au golfe du Saint-Laurent en particulier. Cependant, les trois réunions précédentes remontent à quelque 20 ans, soit en 1968 et 1970, à Halifax et en 1973 à Rimouski, alors que l'on souhaitait mettre sur pied un grand projet d'étude du golfe du Saint-Laurent qui malheureusement ne vit jamais le jour. Encore aujourd'hui, les rapports de ces trois ateliers représentent pour nous une mine précieuse de renseignements sur ce qui était connu et sur la perception des besoins de recherche qu'on avait à l'époque. Force nous est d'admettre que l'état de nos connaissances n'a pas tellement changé puisque plusieurs des questions posées alors sont encore aujourd'hui d'une grande actualité.

D'ailleurs, voici quelques exemples pour illustrer combien est jeune l'étude du Golfe :

— en 1946, Georges Préfontaine de l'Université de Montréal rappelle l'idée que les remontées d'eaux profondes dans l'Estuaire, à la hauteur du Saguenay peuvent avoir une influence sur la productivité des pêches gaspésiennes;

— les premières mesures publiées des concentrations d'oxygène à l'est de l'Estuaire remontent à la croisière du Theta en 1966;

— l'étude systématique de la production primaire n'a été entreprise qu'à la fin des années 60 et au début des années 70 dans le cadre du Programme biologique international par l'équipe du D^{r} Steven de l'Université McGill.

En fait, on peut mieux cerner le début des recherches scientifiques dans le Golfe sur une base qu'on peut qualifier de régulière, lorsqu'on examine la création des différents centres de recherche.

La première station marine fut construite sur un chaland pour pouvoir mieux être déplacée et fut associée à

Brief History of the Marine Research in the Gulf of St. Lawrence

J. Boulva

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On behalf of the Department of Fisheries and Oceans, it is my pleasure to welcome you to the Maurice Lamontagne Institute for the first symposium to be held inside our walls. While we are still in the process of setting up our research teams, we felt it was important to bring together scientists for this symposium to take stock of our present state of knowledge regarding the Gulf of St. Lawrence and to define orientations for the research to be conducted in the years to come. I thought that recalling some of the landmarks of research in the Gulf would be appropriate to set the context for this meeting.

The scientific sessions which start today represent an important event. This is in fact the fourth such meeting regrouping experts from various fields interested in marine sciences related to the Gulf of St. Lawrence. However, the three others date back some 20 years, namely to 1968 and 1970 in Halifax and to 1973 in Rimouski. The objective at that time was to set up a major project to study the Gulf. Unfortunately, this project never materialized. Even today, the reports of these three workshops still represent a precious source of information on what was known and on the perception of research needs at that time. We have no alternative but to admit that our knowledge has not changed much, since several of the questions raised then are still very pertinent today.

Here are a few examples to illustrate how young is the study of the Gulf:

— in 1946, Georges Préfontaine of the University of Montréal, put forward the hypothesis that upwelling of deep waters in the Estuary near the Saguenay may be important for the productivity of the fisheries in the Gaspé region;

— the first published measurements of oxygen concentrations for the eastern part of the Estuary came from the THETA cruise in 1966;

— the systematic study of primary production in the Gulf was only undertaken in the late sixties and early seventies within the framework of the International Biological Program (IBP) managed by Dr. Steven from McGill University.

However, we can better determine when scientific research in the Gulf started on a regular basis, by examining the creation of the various research centers.

The first station, constructed on a scow to facilitate displacement, was associated with the creation of the now la création du défunt Office des Recherches sur les Pêcheries du Canada (ORPC) en 1898. Après des débuts à St. Andrews et à Canso, la station fit un séjour à Malpèque pour l'étude des huîtres et puis à Gaspé pour des travaux en écologie marine et sur les poissons appâts, avant de faire naufrage à Grande-Vallée en 1907. En 1928, l'ORPC aménagea à Ellerslie, Île-du-Prince-Édouard, une station de recherche liée à l'aquiculture des huîtres.

Peu après, un groupe de professeurs de l'Université Laval convaincus du besoin de recherche en biologie marine au Québec, obtint des fonds pour la construction en 1931 de la Station Biologique du Saint-Laurent à Trois-Pistoles sur la rive sud de l'Estuaire. Les rapports annuels de la Station de 1931 à 1939 contiennent, parmi d'autres résultats, les premières publications sur la chimie des eaux de l'estuaire en particulier les phosphates, nitrites, nitrates, silicates, et oxygène.

Cette station fut déménagée à Grande-Rivière en 1938 et éventuellement transférée au gouvernement provincial qui en fit la station de biologie marine, bien connue pour son activité scientifique intense jusqu'à la fin des années 60.

Il faut aussi rappeler qu'en recherche sur les pêches, certains travaux mémorables furent réalisés tels que (1) les observations du D^{r} Pierre Fortin qui, de 1852 à 1867, fit des études sur les pêcheries du Golfe, alors eaux internationales, (2) l'expédition des pêches de 1915 organisée par l'Office des Recherches sur les Pêcheries du Canada, sous la direction de Johan Hjort qui couvrit l'ensemble du Golfe et finalement (3) la contribution importante à la connaissance des espèces exploitées résultant des travaux du centre de recherche de Pêches et Océans à St – Jean, Terre-Neuve.

La recherche dans l'estuaire et le golfe du Saint-Laurent ne prit cependant un essor majeur qu'au début des années 70 avec l'apparition de nouveaux groupes de recherche dont :

— le GIROQ (Groupe Interuniversitaire de Recherche Océanographique du Québec) en 1970 regroupant des professeurs des Universités de Montréal, Laval et McGill;
— l'INRS-océanologie (Institut National de la Recherche Scientifique) en 1972 à Rimouski;
— le groupe d'océanographie de l'Université du Québec à Rimouski en 1973;
— le Centre Champlain des Sciences de la Mer, le prédécesseur de l'Institut Maurice Lamontagne de notre ministère, à Québec, en 1976;
— le Centre des Pêches du Golfe du MPO à Moncton en 1982;
— le laboratoire de Gaspé du MAPA (Ministère de l'Agriculture, des pêcheries et de l'Alimentation) en 1983;
— et enfin, l'Institut Maurice-Lamontagne à Mont-Joli, en 1986.

Si l'on ajoute l'intérêt maintenu par l'Institut Océanographique de Bedford (MPO) pour l'étude de cette importante région maritime, on réalise l'ampleur des moyens de recherche présentement disponibles pour accroître les connaissances de cette mer intérieure extrêmement productive et ainsi affermir la base scientifique des mesures de gestion, lesquelles visent avant tout à con-

defunct Fisheries Research Board of Canada (FRBC) in 1898. After spending some time at St. Andrews and Canso, the station was moved to Malpèque to study oysters, then to Gaspé for work on marine ecology and bait fish, before sinking at Grande-Vallée in 1907. In 1928, the FRBC set up a research station related to oyster aquaculture at Ellerslie, Prince Edward Island.

Shortly after (1931), a group of professors from Laval University, convinced of the need to initiate research in marine biology in Quebec, managed to raise enough funds to build the "Station biologique du Saint-Laurent" in Trois-Pistoles on the south shore of the Estuary. Annual reports published by this station from 1931 to 1939 contain among many other scientific findings, the first data on the chemistry of the estuarine waters, particularly phosphates, nitrites, nitrates, silicates and oxygen.

This station was moved to Grande-Rivière in 1938 and later transferred to the provincial government. This station then became recognized for its intense research activity in marine biology which lasted until the late 60's.

Fisheries research has been characterized by a number of memorable studies such as (1) the observations of Dr. Pierre Fortin who, from 1852 to 1867, studied the fisheries of the Gulf, then considered international waters, (2) the 1915 fishing expedition organized by the Fisheries Research Board of Canada, under the direction of Johan Hjort, which covered the entire Gulf, and finally (3) the works of the Fisheries and Oceans Research Centre in St. John's, Newfoundland, which contributed greatly to our knowledge of harvested species in the Gulf.

Research in the Estuary and the Gulf gained further momentum in the early 70's with the creation of new research organizations:

— the GIROQ (Groupe Interuniversitaire de Recherche Océanographique du Québec) founded in 1970 by professors from three Quebec universities: Montreal, Laval and McGill;
— the INRS-océanologie (Institut National de la Recherche Scientifique) in Rimouski in 1972;
— the Oceanography Section at University of Quebec at Rimouski in 1973;
— the Champlain Centre for Marine Sciences, the predecessor of the Maurice Lamontagne Institute, in Québec City in 1976;
— the Gulf Fisheries Center of DFO in Moncton in 1982;
— the laboratory of the provincial Department of Agriculture, Fisheries and Food in Gaspé in 1983;
— and finally, the Maurice Lamontagne Institute in Mont-Joli in 1986.

If we add the sustained interest of the Bedford Institute of Oceanography (MPO) for the study of this important marine area, we now have a vast array of research tools to increase our knowledge of this extremely productive inland sea and thus to strengthen the scientific basis for management measures aimed, first and foremost, at conserving resources and maintaining the production server les ressources et à maintenir la capacité de produire du milieu aquatique.

De cet examen rapide, certaines forces ressortent, ainsi que certaines faiblesses. Au cours des 20 dernières années, l'Estuaire a été l'objet d'études océanographiques beaucoup plus intensives que le Golfe. Par ailleurs, bien que le nord-est du Golfe semble avoir une productivité primaire faible comparée au sud-ouest, c'est là que l'on retrouve pourtant d'importantes ressources dont la crevette, la morue et le sébaste; ce paradoxe demeure encore inexpliqué. Nos connaissances de l'abondance des stocks exploités sont généralement bonnes alors que notre compréhension de la biologie de la majorité des espèces d'importance commerciale demeure souvent marginale. Ainsi, la reproduction et la période de vie avant l'entrée dans la pêche demeurent mal connues chez la plupart des espèces exploitées.

Voilà pourquoi vos débats à l'occasion de ce symposium sont importants. Si on ne comprend pas bien les processus océanographiques, qu'ils soient de nature physique, chimique ou biologique, on ne peut espérer affiner nos prédictions quant à l'avenir des ressources vivantes. Si on ne peut expliquer les mécanismes qui font vivre le Golfe, les processus qui en assurent la richesse faunique remarquable, comment espérer le protéger adéquatement?

Car qu'il soit petit océan ou grand estuaire, le Golfe demeure fragile face aux progrès de la technologie, aux menaces environnementales, à l'exploitation intensive de ses ressources et aux changements climatiques.

Nous savons que ces 4 journées de travail passées ensemble n'apporteront pas toutes les réponses. A peine aurons nous le temps d'effleurer les principaux sujets d'étude. Par contre, l'on répondra aux attentes en traçant la voie à suivre pour les prochaines années, en dégageant les axes de recherche à privilégier. Les chercheurs impliqués attendent ce moment depuis plusieurs années. Et ne perdons pas de vue l'objectif de nos travaux : obtenir les connaissances qui nous permettront d'assurer pour les générations futures la conservation du Golfe et de ses ressources.

En guise de conclusion, je voudrais rappeler les propos du Dr Joseph Risi, un des fondateurs de la Station biologique du Saint-Laurent, à l'occasion d'un discours qu'il donnait lors du premier symposium sur l'estuaire du Saint-Laurent à Rimouski, en 1976 :

> «Si vos prédécesseurs en océanologie laurentienne vous ont légué en somme assez peu, c'est qu'en amateurs, ils ne pouvaient faire davantage avec l'équipement plutôt rudimentaire dont ils disposaient au début. A vous, par contre, il vous sera demandé beaucoup, vous qui avez des équipes merveilleuses de spécialistes hautement qualifiés, vous qui avez des beaux laboratoires, des appareils et des instruments sophistiqués, vous qui avez même des budgets... insuffisants!»

Je souhaite à tous des discussions enrichissantes et vous remercie à l'avance pour votre participation qui je n'en doute pas sera des plus enthousiaste.

potential of this aquatic environment.

This rapid overview underscores both certain strengths and weaknesses. Over the past 20 years, oceanographic studies have been more intensive in the Estuary than in the Gulf. Moreover, while the north-eastern part of the Gulf seems to offer a lower primary productivity than the south-western part, it is there that we find important species such as shrimp, cod and redfish; this paradox has yet to be explained. Our knowledge of the size of harvested stocks is generally good while our understanding of the biology of most species of commercial importance is often limited. Reproduction and the life stages before reaching commercial size are still not well known in the case of most harvested species.

This is why your discussions within this symposium are important. If we do not understand the oceanographic processes, be they physical, chemical or biological, we have little hope of refining our forecast of the future of living resources in the Gulf. If we cannot explain the mechanisms which account for its remarkably rich wildlife, how then can we expect to offer it adequate protection?

I do not know if the Gulf is a small ocean or a big estuary, but I do know that it will remain fragile in view of the technological progresses, environmental threats, intensive exploitation of its resources and climatic change.

We are aware that these 4 days spent together will not provide all the answers. We will hardly have time to scratch the surface of the main subjects of study. However, our efforts will be appreciated as we determine the course to follow over the next few years by defining priority research areas. Researchers actively involved have been waiting for this event for several years now. And let us not loose sight of the goal of our work: to obtain the knowledge that will enable us to insure the preservation of the Gulf and its resources for future generations.

To conclude I would like to quote the final remark given by Dr. Joseph Risi, one of the founding members of the Station biologique du Saint-Laurent, as he was addressing the first Symposium on the St. Lawrence Estuary at Rimouski, in 1976:

> "If your predecessors in Laurentian oceanology left you in fact so little, it is that as amateurs, they could do little more with the somewhat rudimentary equipment at their disposal. However, in your case, expectations are high, you who have such marvelous teams of highly skilled specialists, you who occupy beautiful laboratories, use sophisticated equipment and instruments, you who even have budgets that are... insufficient!"

I wish everyone enriching discussions and thank you in advance for your enthusiastic participation in this symposium.

CHAPITRE II.
RAPPORTS DES ATELIERS

CHAPTER II.
WORKING GROUP REPORTS

Rapport de l'atelier de travail sur l'océanographie physique[1]

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Introduction

Dans le cadre du mandat général proposé aux ateliers de travail, celui d'océanographie physique a abordé les trois questions suivantes :

a) Les connaissances actuelles de la circulation dans le Golfe et de l'influence des mécanismes qui en sont responsables sont-elles suffisantes pour établir des budgets de chaleur, de sel, d'eau douce et de substances dissoutes ou en suspension?
b) Quelles méthodes, programmes d'observation ou techniques d'analyse pourraient augmenter nos connaissances du milieu physique et des mécanismes qui régissent ses variations dans le temps et l'espace?
c) Pourra-t-on reconnaître dans les propriétés des eaux du Golfe les conséquences d'un hypothétique réchauffement associé à l'effet de serre?

C'est donc par l'intermédiaire de ces questions plus précises que le groupe de travail s'est penché sur le mandat général des ateliers : «Comment peut-on utiliser le système du Saint-Laurent, région type du plateau continental, comme laboratoire naturel pour contribuer à la solution du grand problème que constitue la conservation à long terme des ressources et de la qualité du milieu (changements à l'échelle du globe, contaminants, etc...?).»

Connaissances actuelles et lacunes

1. Les marées

Presque partout dans le Golfe, comme dans la plupart des régions côtières, les phénomènes de marée sont responsables pour la plus grande partie des variations des niveaux d'eau et des courants :

Niveaux d'eau

Un modèle barotropique à résolution de 4′ existe déjà (D.A. Greenberg, Institut Océanographique de Bedford,

Report of the Workshop on Physical Oceanography[1]

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Introduction

Within the framework of the general mandate proposed for the workshops, the physical oceanography workshop dealt with the following three questions:

a) Do we currently know enough about circulation in the Gulf and the influence of the mechanisms responsible for this circulation to establish budgets of heat, salt, fresh water and dissolved substances or substances in suspension?
b) What methods, observation programs or analytical techniques could increase our knowledge of the physical environment and the mechanisms that govern its temporal and spatial variations?
c) Do the properties of the Gulf waters show evidence of a supposed warming associated with the greenhouse effect?

The working group used these more specific questions to deal with the general mandate of the workshops: "How can we use the St. Lawrence system, a continental shelf type area, as a natural laboratory to help solve the major problem of long-term conservation of resources and environmental quality (global changes, contaminants, and so on)?"

Present Knowledge and Gaps

1. Tides

Almost everywhere in the Gulf, as in most coastal regions, tidal phenomena are primarily responsible for variations in water levels and currents:

Water levels

A barotropic model with a resolution of 4′ already exists (D.A. Greenberg, Bedford Institute of Oceanog-

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[1] Ce rapport fait partie des Comptes rendus d'un atelier/symposium tenu à l'Institut Maurice-Lamontagne, Mont-Joli (Québec) du 14 au 17 mars 1989.

[1] This report forms part of the Proceedings of a Workshop/Symposium held at the Maurice Lamontagne Institute, Mont-Joli, Quebec, 14–17 March 1989.

Dartmouth, N.-E. et D.L. DeWolfe, données inédites, 1989) pour la composante M_2 et sera sous peu utilisé pour calculer les principales autres composantes. Les résultats sont d'une précision moyenne de 3,5 cm pour les déplacements du niveau d'eau associés à la composante M_2 et de 1 degré pour leur phase. On peut s'attendre à une précision du même ordre pour la somme des principales composantes. Quelques améliorations devront probablement être apportées à ce modèle en le calibrant contre des mesures de marégraphes mouillés au large en quelques points stratégiques (détroit de Northumberland, détroit de Cabot). Ce modèle suffira à caractériser la distribution des niveaux d'eau dans l'ensemble du Golfe et pourra servir de base à des modèles de plus haute résolution adaptés à des régions restreintes (la baie des Chaleurs, par exemple).

Courants

Un modèle purement barotropique ne suffit pas pour décrire les courants de marée : la friction au fond ainsi que les phénomènes baroclíniques associés à la stratification de densité nécessitent une description ou du moins une caractérisation du cisaillement vertical. Parmi les effets produits par les courants de marée, mentionnons la génération d'ondes internes, le mélange vertical et la création de fronts entre zones homogénéisées et zones stratifiées ainsi que de courants résiduels dans les zones peu profondes.

En un premier temps, un modèle barotropique pourrait servir à produire une carte des régions où la marée est susceptible de créer des ondes internes importantes. La présence de ces dernières cause des variations horizontales des courants de marée ainsi que des ondes plus courtes qui contribuent au mélange vertical. Un modèle hydrodynamique en trois dimensions des phénomènes de marée permettra éventuellement de représenter les marées internes et le cisaillement des courants dans tout le Golfe. Quoiqu'une modélisation de cet ordre de complexité nécessite encore un effort de recherches considérable, on peut entrevoir qu'elle pourrait commencer à être possible d'ici environ cinq ans. Il faudrait commencer dès maintenant, en s'inspirant par exemple des travaux de Simons (1980) et de Crean *et al.* (1988), à s'initier à cette modélisation. Les valeurs de courant, et particulièrement du cisaillement, au fond sont importantes pour estimer les échanges de substances dissoutes entre la masse d'eau et les sédiments.

Fronts

Les fronts que l'on rencontre entre des régions verticalement uniformes, où le mélange dû aux courants de marée l'emporte sur les effets de stratification, et d'autres régions bien stratifiées, aux courants relativement plus faibles, sont des transitions dont l'importance biologique est reconnue. Une caractérisation plus poussée de ces fronts, de leur dynamique, de leur distribution géographique, et de leur variation saisonnière est d'une importance primordiale pour nombre de questions en biologie marine : ces fronts constituent une barrière pour beaucoup d'organismes marins, du plancton jusqu'aux baleines!

raphy, Dartmouth, N.S., and D.L. DeWolfe, unpubl. data, 1989) for the M_2 component and will soon be used to calculate the other principal components. The results have an average accuracy of 3.5 cm for water level displacements associated with the M_2 component and of 1 degree for their phase. The same accuracy can be expected for all of the principal components. Some improvements will probably have to be made to this model by calibrating it with the measurements of tide gauges moored offshore at several strategic points (Northumberland Strait, Cabot Strait). This.model will be adequate to characterize the distribution of water levels throughout the Gulf and can be used as a basis for higher resolution models adapted to limited areas (Chaleur Bay, for example).

Currents

A purely barotropic model is insufficient to describe the tidal currents: the bottom friction and the baroclinic phenomena associated with the stratification of density require a description or at least a characterization of the vertical shear. Among the effects produced by the tidal currents are the generation of internal waves, vertical mixing and the creation of fronts between homogeneous mixed areas and stratified areas; residual currents also occur in shallow areas.

First, a barotropic model could be used to produce a chart of areas in which the tide may create sizable internal waves. The presence of the latter causes horizontal variations in the tidal currents as well as shorter waves that contribute to vertical mixing. A three-dimensional hydrodynamic model of tidal phenomena will eventually make it possible to represent internal tides and current shear throughout the Gulf. Although a considerable amount of research is still required before modelling of this complexity can be carried out, it may begin to become possible within about five years. We must begin now to familiarize ourselves with this type of modelling, drawing inspiration from the work of Simons (1980) and Crean et al. (1988). The current values and, particularly, the shear values at the bottom are important for estimating the exchanges of dissolved substances between the water mass and sediments.

Fronts

The fronts, found between vertically uniform areas (where mixing due to tidal currents overrides the effects of stratification) and other well-stratified areas (with relatively weaker currents), are transitional areas with recognized biological importance. A more thorough characterization of these fronts, their dynamics, their geographical distribution and their seasonal variation is of prime importance for a number of matters relating to marine biology: these fronts constitute a barrier for many marine organisms, ranging from plankton to whales!

2. «Forcing» atmosphérique

On sait que le vent et les gradients de pression atmosphérique causent des courants marins importants (e.g. le Gulf Stream). Les vents mesurés aux stations côtières sont souvent déviés par la topographie locale et correspondent mal à ceux qui soufflent au-dessus de la mer; ils peuvent donc rarement servir d'«input» fiable à la modélisation. Malgré le succès partiel de quelques modélisations locales (e.g. M. Couture et Y. Gratton, Université du Québec à Rimouski, données inédites, 1989), il est clair que pour comprendre et prédire les dérives des couches de surface (et des objets qui y flottent ... glaces, naufragés) ainsi que les phénomènes de remontées d'eau induits par le vent, des mesures de vent en réseau assez serré et sur bouées amarrées seront nécessaires. Les modélisations devront en général porter sur l'ensemble du Golfe, vu qu'il est impossible d'en isoler les parties.

Comme les distributions de pression atmosphérique sont beaucoup plus lisses que celles des vents, les cartes de pression maintenant disponibles suffiront à calculer les effets de pression. Après étalonnage de stations anémométriques en mer, ces mêmes cartes de pression pourront servir à calculer les vents au-dessus du Golfe et finiront ainsi par éliminer les mouillages de stations météorologiques.

Les effets du «forcing» atmosphérique portent sur une large gamme d'échelles de temps et d'espace. À court terme, de fortes tempêtes causent des dérives brusques et importantes pour des populations planctoniques (par exemple, les larves de homards), un mélange vertical qui influe sur le benthos, et des phénomènes d'érosion rapide. Pour des phénomènes à réponse non-linéaire, quelques courtes mais violentes bourrasques peuvent avoir plus d'influence que de longues périodes de vents modérés. On devra donc se souvenir que la réponse à long terme du Golfe aux forces météorologiques (et autres) ne peut être calculée simplement à partir d'un lissage passe-bas de ces forces.

On observe d'importantes variations interannuelles des vents et de la fréquence des tempêtes: les hivers se suivent et se ressemblent peu. Des phénomènes éloignés, comme El Niño, peuvent influer par téléconnections sur les patrons climatiques du Golfe. Il est essentiel d'établir une base de comparaison entre la variabilité météorologique interannuelle et les variations océanographiques, tant physiques que chimiques et biologiques, observées dans le Golfe. On ne pourra espérer reconnaître les changements à long terme associés à un réchauffement global anticipé sans avoir d'abord exploré la gamme de variations naturelles.

3. Circulation générale

Il existe à l'intérieur du Golfe une circulation moyenne, cohérente sur des échelles de temps de 20 jours ou plus et de centaines de kilomètres. Les membres de l'atelier se sont trouvés d'accord pour penser que cette circulation est assez bien connue dans ses grandes lignes, mais que sa variabilité saisonnière et les relations causales qui la relient aux forces du vent, aux débits d'eau douces et aux influences océaniques restent mal comprises.

C'est dans cette optique que les scientifiques devront continuer à se pencher sur les effets encore mal connus

2. Atmospheric Forcing

It is known that the wind and atmospheric pressure gradients cause sizable ocean currents (such as the Gulf Stream). The winds measured at coastal stations are often deflected by local topography and do not correspond very closely to those that blow over the ocean; thus, these measurements can rarely be used as reliable input for modelling. In spite of the partial success of some local modelling (such as the work of M. Couture and Y. Gratton, University of Quebec at Rimouski, unpubl. data, 1989), it is clear that in order to understand and predict surface drift (and the drifting of objects, such as ice and wreckage), as well as the phenomena of wind-induced upwelling, it will be necessary to take wind measurements in a fairly close-meshed network and from moored buoys. The modelling should include the entire Gulf, since it is impossible to isolate parts of it.

Since the distribution of atmospheric pressure is much more even than that of the wind, the pressure charts now available will be adequate for calculating the effects of pressure. After calibration of anemometric ocean stations, these same pressure charts can be used to calculate the winds over the Gulf and will eventually eliminate the mooring of meteorological stations.

The effects of atmospheric forcing relate to a wide range of temporal and spatial scales. In the short term, severe storms cause sudden and significant drifting of planktonic populations (such as lobster larvae), vertical mixing that affects the benthos, and rapid erosion. For nonlinear response phenomena, a few short but violent squalls can have more effect than long periods of moderate wind. It should be remembered that the Gulf's long-term response to meteorological and other forces cannot be calculated simply by a low-pass smoothing of these forces.

Significant interannual variations in wind and the frequency of storms have been observed: succeeding winters are not much alike. Distant phenomena, such as El Niño, can effect the climatic patterns of the Gulf through teleconnections. It is essential to establish a basis of comparison between interannual meteorological variability and physical, chemical and biological oceanographic variations observed in the Gulf. One cannot hope to recognize long-term changes associated with an anticipated global warming without having first explored the range of natural variations.

3. Overall Circulation

The Gulf has a mean circulation that is consistent over 20 days or more and hundreds of kilometres. The members of the workshop agreed that the general principles of this circulation are quite well known, but that its seasonal variability and the causal relationships that link it to wind strengths, freshwater flow rates and oceanic influences are still poorly understood.

It is from this perspective that scientists must continue to study the still little known effects of harnessing rivers du harnachement des rivières sur la circulation du Golfe. Quel serait, par exemple, l'effet d'un harnachement des rivières de la côte nord du Golfe sur l'intensité de la gyre nord-ouest, sur le courant de Gaspé et sur la production biologique du plateau Madelinien?

Les détails de la circulation générale restent en particulier trop peu sûrs pour pouvoir fermer des budgets de masse ou d'autres propriétés à l'intérieur du Golfe ou de l'une de ses parties.

Plusieurs suggestions ont été faites visant à améliorer nos connaissances de la circulation moyenne : l'utilisation de méthodes inverses pour extraire à partir des champs de données scalaires des estimés objectifs du transport d'eau et d'autres propriétés; le mouillage d'instruments en plusieurs points du Golfe pour une période de plusieurs années; l'utilisation des modèles numériques tri-dimensionnels comme outils exploratoires permettant d'intégrer les effets du vent et du flux de chaleur à la surface; l'exploitation de données de la topographie de surface provenant du satellite TOPEX; l'utilisation systématique des images thermiques obtenues par les satellites NOAA; le calcul des transports nets à l'aide de câbles sous-marins.

Les membres de l'atelier n'ont pas cru qu'un effort massif pour obtenir des données de température et de salinité en un réseau serré et synoptique soit utile pour préciser nos connaissances de la circulation: un tel effort ne révélerait les courants géostrophiques baroclinique qu'à un seul instant. Une utilisation judicieuse de moyens comme ceux énumérés ci-haut donnera des résultats plus valables et de façon plus économique. Il serait bon, cependant, de coordonner autant que possible les prises de mesures (CTD, mouillages) faites à partir des différentes croisières dans le Golfe pour en arriver à un certain degré de synopticité qui permettra de vérifier les travaux de modélisation.

Pour faire avancer les connaissances de la circulation moyenne, on reconnaît que le Golfe doit être considéré comme un système entier et cohérent: ce qui se passe dans le courant de Gaspé, par exemple, ne peut être entièrement isolé de phénomènes qui se passent ailleurs. Le degré d'interdépendance des diverses régions reste encore à explorer. Ce sera là une des tâches principales de l'océanographie physique au cours de la prochaine décennie.

4. Budgets de quantités

Connaît-on la circulation assez bien pour établir des budgets de chaleur ou d'autres quantités à l'intérieur du Golfe ou de ses parties? Les études de processus, par exemple ceux associés au cycle du carbone ou à la formation des glaces, supposent souvent qu'on puisse identifier les contributions de divers mécanismes à l'intérieur d'un volume d'eau. Les courants qui entrent ou sortent de ce volume charrient des quantités considérables des propriétés étudiées, à un tel point que la divergence du flux horizontal peut représenter une très importante contribution au budget de ces propriétés. Toute erreur dans ce flux deviendra aussi une erreur dans les estimés obtenus par différence.

Des essais de budgets de volume ou de sel par intégration des transports aux embouchures d'un bassin plus

on Gulf circulation. For example, how would the harnessing of the rivers of the North Shore of the Gulf affect the intensity of the northwest gyre, the Gaspé current and the biological production of the Magdalen shelf?

Details of the general circulation remain too uncertain to permit the completion of budgets of mass or other properties in the Gulf or in any portion of it.

Several suggestions have been made in order to improve our knowledge of mean circulation: the use of inverse methods to extract from scalar fields objective estimates of water transport and other properties; instrument mooring at several points in the Gulf for a period of several years; the use of three-dimensional numerical models as exploratory tools enabling integration of the effects of the wind and of heat flux at the surface; the use of surface topography data from the TOPEX satellite; the systematic use of thermal images obtained by the NOAA satellites; the calculation of net transports using underwater cables.

The members of the workshop did not think that a massive effort to obtain temperature and salinity data in a close-meshed synoptic network would be useful in improving our knowledge of circulation: such an effort would show the baroclinic geostrophic currents for only a single moment. Judicious use of methods such as those listed above will produce more valid results, in a more economical manner. However, it would be a good idea to co-ordinate — as much as possible — the taking of measurements (CTD, instrument moorings) during different cruises in the Gulf in order to ensure that the measurements are, to a certain degree, synoptic; this will make it possible to verify the modelling work.

In order to advance our knowledge of mean circulation, the Gulf must be considered a complete and coherent system: for example, what happens in the Gaspé current cannot be completely isolated from the phenomena that occur elsewhere. The degree of interdependence of the various areas remains to be explored. This will be one of the main tasks of physical oceanography during the next decade.

4. Quantity Budgets

Do we know enough about circulation to establish heat or other quantity budgets for the Gulf or portions of it? Process studies, such as those associated with the carbon cycle or ice formation, often assume that the contributions of various mechanisms in a volume of water can be identified. The currents that enter or leave this volume carry considerable quantities of the properties studied, to the point that the divergence of the horizontal flux can represent a very important contribution to the budget of these properties. Any error in this flux will also become an error in the estimates obtained by calculating the difference.

Tests of volume or salinity budgets by integrating the transports to the mouths of a smaller basin, the Georgia petit, le détroit de Georgie (Godin *et al.* 1981), ont échoué devant l'erreur associée à la divergence des flux. Il peut être possible de mieux faire en certains cas, selon les profils verticaux des courants ou de la propriété étudiée, mais il reste que les mouillages les plus denses, aptes à bien décrire les courants et même les flux de certaines quantités, ne peuvent souvent en résoudre la divergence avec une précision suffisante.

Méthodes et techniques

1. Observations

Nous avons déjà fait référence plus haut à un nombre de méthodes d'observation (satellites, câbles sous-marins, mouillages, dériveurs, XBT aéro-déployés) auxquels on pourra avoir recours pour ajouter aux connaissances de l'océanographie physique du Golfe.

Sans vouloir entrer dans les détails, nous recommandons cependant qu'un effort soit fait pour augmenter le degré de synopticité des mesures prises dans le Golfe : qu'il y ait concertation, autant que possible entre divers chercheurs ou instituts pour récolter des données à peu près en même temps et les rendre facilement disponibles à tous. Il y a carence notable de mesures hivernales et il faudrait plutôt instaurer qu'annuler des programmes de mesures à cette saison.

À l'heure des changements aux périodes climatiques, il faudra aussi assurer la continuation ou même la reprise de séries chronologiques à long terme qui permettent le monitoring des conditions du Golfe. Ce n'est qu'à l'aide de longues séries qu'on pourra reconnaître les fluctuations ou dérives lentes des propriétés du Golfe et les comparer à celles du milieu externe sur des périodes de temps de même ordre.

2. Modélisation

Ce qui compte le plus, c'est de comprendre les mouvements et les variations des propriétés des eaux du Golfe. Cette compréhension viendra d'abord de l'approfondissement des connaissances théoriques des mécanismes océanographiques. Le Golfe présente une grande variété de phénomènes, tels que génération d'ondes internes, remontées d'eau, pénétration d'influences océaniques, dérive et formation de couvert de glace saisonnière, dont une étude plus poussée pourra mener à d'intéressantes contributions aux connaissances océanographiques. De mieux connaître ces phénomènes permettra de mieux comprendre ce qui se passe dans le Golfe et aussi de participer avantageusement au dialogue avec les océanographes qui étudient d'autres systèmes côtiers. Ce premier stage de compréhension est nécessaire, mais il ne suffira pas à maîtriser le Golfe!

En effet, pour comprendre le Golfe lui-même, en tant que système spécifique et complexe, il faudra développer des méthodes suffisamment puissantes pour en examiner la totalité. Comme une horloge dont le fonctionnement transcende la somme de ses pièces, la dynamique du Golfe dépasse une description de ses parties. Il y a connection, par transport d'eaux, par propagation d'ondes longues, par interactions avec l'atmosphère, entre les diverses parties du Golfe, et la

Strait (Godin et al. 1981), failed because of the error associated with flux divergence. It may be possible to do better in some cases, depending on the vertical profiles of the currents or of the property studied; but the fact remains that the most dense instrument moorings, capable of satisfactorily describing the currents and even the flux of certain quantities, often cannot resolve the divergence with sufficient accuracy.

Methods and Techniques

1. Observations

We have already made reference above to a number of observation methods (such as satellites, underwater cables, instrument moorings, drifters and air-deployed XBTs) which can be used to add to our knowledge of physical oceanography in the Gulf.

Without going into detail, we do, however, recommend that an effort be made to make the measurements taken in the Gulf more synoptic: there should be as much cooperation as possible between various researchers or institutes so that data can be collected at almost the same time and can be made easily available to everyone. There is a significant lack of winter measurements and it is necessary to set up rather than cancel measurement programs for that season.

At the time of changes in climatic periods, it will also be necessary to ensure the continuation or even the resumption of long-term time series that permit the monitoring of Gulf conditions. It is only with the help of long series that we will be able to recognize slow drifts or fluctuations in Gulf properties and compare them to those of the external environment for similar time periods.

2. Modelling

The most important thing is to understand the movements and variations in the properties of the Gulf waters. This understanding will come, first of all, from greater theoretical knowledge of oceanographic mechanisms. The Gulf presents a wide variety of phenomena, such as the generation of internal waves, upwellings, penetration of ocean influences, seasonal ice formation and drift; a more thorough study of these phenomena may bring interesting contributions to oceanographic knowledge. By becoming more familiar with these phenomena, we will be able to better understand what happens in the Gulf and, also, to participate fruitfully in the dialogue with oceanographers who study other coastal systems. This initial stage of understanding is necessary, but it will take more than this to master the Gulf!

In fact, in order to understand the Gulf as a specific and complex system, it will be necessary to develop sufficiently powerful methods to examine it in its entirety. Like a clock whose operation transcends the sum of its parts, the dynamics of the Gulf go beyond a description of its components. The various parts of the Gulf are connected by the transport of waters, by the propagation of long waves and by interactions with the atmosphere; the response of the entire system to atmospheric forcing, réponse du système entier aux «forcings» atmosphériques, aux épanchements d'eau douce ou aux intrusions Atlantiques ne sera pas simplement celle de ses parties prises séparément.

Le seul outil apte à explorer la réponse du Golfe aux forces externes en un tout aussi bien qu'en ses parties, c'est un modèle numérique, véritable laboratoire dont on peut contrôler les conditions à volonté. Ce modèle devra être à trois dimensions et nécessitera plusieurs années d'élaboration avant de fournir des résultats utiles. Il devra être assez souple pour s'adapter aux connaissances nouvelles, assez robuste pour fonctionner en parties détachées ou sous conditions physiquement peu réalistes. Le Golfe est un bassin dont les dimensions sont assez réduites pour qu'on puisse entrevoir la modélisation serrée avec des moyens bientôt disponibles. Comme en simulation météorologique, un modèle numérique à trois dimensions du Golfe pourra apporter autant sinon plus de connaissances sur la dynamique du système que les observations directes.

L'élaboration de ce modèle nous apparaît comme une priorité scientifique de première importance. Le développement du modèle apportera un support significatif à l'étude des mécanismes locaux et fondamentaux; son application au Golfe permettra enfin d'appliquer les résultats de l'océanographie physique aux problèmes de pêcheries. Ce sera le modèle et non le Golfe lui-même qui sera le laboratoire, le milieu contrôlable dans lequel on pourra évaluer avec confiance les conséquences de modifications ou des variations du milieu externe.

Changements climatiques

L'augmentation observée dans l'atmosphère du bioxyde de carbone se traduira, selon tous les modèles, par un réchauffement de l'atmosphère d'ici une cinquantaine d'années. La valeur de l'augmentation de température reste encore incertaine. Étant donné la grande variabilité interannuelle observée dans le «forcing» météorologique ainsi que dans les eaux profondes du Golfe (Bugden 1991), il semble difficile de pouvoir détecter directement les effets d'une lente augmentation de la température de l'atmosphère. Comment aussi séparer les fluctuations naturelles considérables, même à long terme, du signal anthropogénique?

Nous proposons d'abord un monitoring à long terme de propriétés critiques des eaux du Golfe (à définir), comme nous l'avons mentionné ci-haut. En plus, il serait utile d'examiner les données météorologiques afin d'identifier les années extrêmes (hivers les plus chauds et les plus froids) et de voir si les propriétés des eaux du Golfe et de son couvert de glace reflètent une réponse à ces variations climatologiques. Il s'agirait là d'une première mesure de la sensibilité du Golfe aux variations climatiques.

Conclusions

Les délibérations du groupe de travail sur l'Océanographie Physique nous ont permis d'identifier plusieurs points saillants vers lesquels orienter la recherche en océanographie du Golfe. Nous les résumons ici de façon très générale :

freshwater extrusions or Atlantic intrusions will not be simply that of its parts taken separately.

The only tool suitable for exploring the response of the Gulf (in whole or in part) to external forces is a numerical model — a veritable laboratory in which conditions can be controlled at will. This model must be three-dimensional and will require several years of development before it can provide useful results. It must also be fairly flexible in order to adapt to new knowledge and fairly robust in order to function in separate parts or under physically unrealistic conditions. The Gulf is a basin of quite small dimensions; we can thus envisage close-set modelling with the means that will soon be available. As in meteorological simulation, a three-dimensional numerical model of the Gulf will produce as much knowledge of the dynamics of the system as direct observations, if not more.

We believe that development of this model is a scientific priority of great importance. Development of the model will provide significant support for the study of basic local mechanisms; its application to the Gulf will finally make it possible to apply the results of physical oceanography to fisheries problems. It will be the model and not the Gulf itself that will be the laboratory — the controllable environment in which it will be possible to assess with confidence the consequences of modifications or variations in the external environment.

Climatic Changes

The observed increase of carbon dioxide in the atmosphere will be translated — according to all models — into a warming of the atmosphere within about 50 years. The value of the temperature increase is still uncertain. Given the wide interannual variability observed in meteorological forcing, as well as in the deep waters of the Gulf (Bugden 1991), it seems difficult to directly detect the effects of a slow increase in atmospheric temperature. Also, how does one separate the natural fluctuations, which are considerable even in the long term, from the anthropogenic signal?

We propose, first of all, long-term monitoring of the critical properties of the Gulf waters (to be defined), as mentioned above. It would also be useful to examine meteorological data in order to identify extreme years (the warmest and coldest winters) and to see whether the properties of the Gulf waters and of its ice cover reflect a response to these variations in climate. This will constitute an initial measurement of the Gulf's sensitivity to climatic variations.

Conclusions

The discussions of the working group on physical oceanography enabled us to identify several directions for research on Gulf oceanography. They are listed here in a very general manner:

a) Un raffinement des techniques de modélisation des marées, qui permettra d'approfondir les connaissances de la physique des fronts, des courants résiduels, des ondes internes et du mélange, et d'appliquer ces connaissances aux problèmes biologiques et géologiques.
b) Une modélisation plus poussée qui permettra éventuellement de distinguer les effets des impulsions météorologiques, du débit d'eau douce et des influences océaniques sur la circulation à grande échelle des eaux du Golfe. Ces travaux devront tenir compte des interactions entre les différentes parties du Golfe et considérer ce dernier comme un système hydrodynamique non-linéaire dont la complexité dépasse celle de la somme de ses parties.
c) Une amélioration des systèmes de mesures, permettant d'obtenir des données mieux adaptées aux études de simulation numérique, une vue plus synoptique des propriétés des eaux du Golfe, et une perspective à long terme de leur variation temporelle d'où on pourra espérer détecter les conséquences de l'effet de serre.
d) Un effort concentré et soutenu de modélisation numérique en trois dimensions de la dynamique du Golfe, en son tout comme en ses parties. L'élaboration de ce modèle sera l'axe principal de l'océanographie physique de la prochaine décennie, autour duquel s'organiseront les études d'exploration et de vérification sur le terrain, les travaux théoriques visant à élucider les mécanismes physiques, et les prédictions de l'évolution du milieu marin.

Pour répondre enfin à la question-mandat, il nous a paru clair que le Golfe du Saint-Laurent est loin d'être une «région type du plateau continental»; il s'agit plutôt d'une mer marginale où se rencontrent une large gamme de phénomènes océanographiques, beaucoup plus qu'on puisse en trouver sur le plateau continental type. Si l'on s'entend pour définir comme «laboratoire» un système dont on peut contrôler les conditions, ou du moins comprendre la variabilité, on ne pourra parler du Golfe comme d'un «laboratoire naturel» que de façon métaphorique. Ce n'est pas le Golfe lui-même, mais son simulacre, un modèle numérique tridimensionnel qui servira de laboratoire et qui, lui, pourra contribuer à la solution des grands problèmes de la qualité des ressources et la conservation du milieu.

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a) Refinement of tide modelling techniques; this will enable us to improve our knowledge of the physics of fronts, residual currents, internal waves and mixing, and to apply this knowledge to biological and geological problems.
b) More detailed modelling, which will eventually make it possible to identify the effects of meteorological forces, freshwater flow rate and oceanic influences on the large-scale circulation of Gulf waters. This work must take into account the interactions between various parts of the Gulf and consider the latter as a nonlinear hydrodynamic system, the complexity of which exceeds that of the sum of its parts.
c) Improvement of the systems of measurement, making it possible to obtain data that is better adapted to numerical simulation studies, a more synoptic view of the properties of Gulf waters and a long-term view of their temporal variation; from this information, it may be possible to detect the consequences of the greenhouse effect.
d) A concentrated and sustained effort toward the three-dimensional numerical modelling of the dynamics of the Gulf, as a whole as well as in its parts. Development of this model will be the principal focus of physical oceanography during the next decade, around which will be organized exploratory and field verification studies, theoretical work aimed at clarifying the physical mechanisms, and work aimed at predicting the evolution of the marine environment.

With regard to our mandate, it seemed clear to us that the Gulf of St. Lawrence is far from being a "continental shelf type area"; rather, it is a marginal sea where one encounters a wide range of oceanographic phenomena, many more that one could find on the typical continental shelf. If one defines a "laboratory" as a system in which conditions can be controlled, or at least the variability understood, one cannot describe the Gulf as a "natural laboratory" except in a metaphorical manner. It is not the Gulf itself, but its image, a three-dimensional numerical model, that will serve as the laboratory and will be able to help solve the major problems of resource quality and conservation of the environment.

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Rapport de l'atelier de travail sur l'océanographie chimique et la sédimentologie[1]

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Introduction

Dans une rétrospective récente de l'océanographie chimique du golfe du Saint-Laurent, Strain (1990) en est venu à la conclusion que «Le bilan actuel de la chimie dans le Golfe décrit souvent seulement les échelles temporelles et spatiales les plus grossières et les éléments chimiques les plus évidents. . . La description des propriétés variables dans le temps a été limitée aux propriétés observables par des programmes d'échantillonnage qui auraient généralement nécessité deux semaines pour faire le relevé d'une grande superficie, qui, en moyenne, auraient pu être faits au cours de deux saisons différentes, et qui auraient pu être répétés ou non pour la même saison au cours de différentes années. Toutes ces mesures ne peuvent cependant pas révéler bien des choses au sujet des interactions entre la chimie de surface et les proliférations planctoniques, ni évaluer l'influence de la crue nivale printanière sur toutes les parties du golfe, ni distinguer entre les tendances à long terme et la variabilité interannuelle.»

Le Groupe de travail sur l'océanographie et la sédimentologie chimiques, qui représentait une gamme variée de spécialités et une vaste expérience en chimie marine, en géologie marine, en biologie marine et en océanographie physique, s'est dit d'accord avec cet énoncé. Le Groupe a estimé que, si des progrès devaient être accomplis en matière de connaissance de la chimie du Golfe, les recherches à venir devraient porter essentiellement sur la dynamique des processus contrôlant la répartition des espèces chimiques, plutôt que sur des descriptions statiques. En concentrant notre attention sur les cycles du carbone, les

Report of the Workshop on Chemical Oceanography and Sedimentology[1]

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Introduction

In a recent overview of the chemical oceanography of the Gulf of St. Lawrence, Strain (1988) concluded that "The existing picture of chemistry in the Gulf describes only the coarsest and most obvious time and space scales and frequently only the most obvious chemical components. . . The description of properties varying in time has been restricted to those that could be observed by sampling programs which would have typically required two weeks to survey a large area, which on average might have been conducted during two different seasons, and which might or might not have been repeated for the same season in different years. Obviously, such measurements cannot reveal much about the interactions between surface chemistry and plankton blooms, cannot evaluate the influence of the spring freshet on all parts of the Gulf, cannot distinguish between long term trends and interannual variability."

The Working Group on Chemical Oceanography and Sedimentology, which represented a broad variety and diversity of expertise and experience in marine chemistry, marine geology, marine biology and physical oceanography, agreed with this assessment. It felt that, if progress is to be made in furthering the understanding of chemistry in the Gulf, future research must focus on the dynamics of the processes that control the distribution of chemical species, rather than on static descriptions. By focusing on the cycles of carbon, trace metals and stable organic compounds, on paleoceanography,

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[1] Ce rapport fait partie des Comptes rendus d'un atelier/symposium tenu à l'Institut Maurice Lamontagne, Mont-Joli (Québec) du 14 au 17 mars 1989.

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métaux traces et les composés organiques stables, sur la paléocéanographie et sur la conceptualisation mathématique des processus géochimiques, nous devrions finir par comprendre les processus actuels, par pouvoir les relier au passé et par pouvoir faire des prédictions pour l'avenir.

L'environnement du golfe du Saint-Laurent

L'environnement du golfe du Saint-Laurent offre une gamme variée de laboratoires naturels se prêtant bien aux études en océanographie chimique. Chacun d'eux représente un ensemble particulier de conditions environnementales. L'estuaire supérieure du Saint-Laurent est un estuaire à haute énergie, partiellement mélangé, à forte gradients de salinité et de température. Il possède une zone de turbidité maximale bien développée dans laquelle les particules fines participent à des échanges avec les slikkes saisonnières; de manière générale, le fond de l'estuaire est recouvert de sédiments graveleux et sablonneux. Il ne semble y avoir aucune accumulation nette de sédiments à grain fin.

La tête du chenal Laurentien marque le début de l'estuaire maritime. Dans ce profond chenal, bordé par d'étroites plates-formes de 30 à 40 m de profondeur, les gradients horizontaux de salinité sont faibles. Le transport par advection l'emporte sur la diffusion turbulente et le lent écoulement compensatoire net des eaux profondes vers la tête du chenal font de cette région le principal site de sédimentation de particules fines terrigènes. La vitesse d'accumulation des sédiments se compte en millimètres par année. Les échanges entre les eaux profondes et les eaux de surface sont vigoureux à la tête du chenal. Les fleuves et rivières de la côte nord déversent une quantité substantielle d'eau douce et la circulation estuarienne générale est modifiée par des structures mésoscalaires variables. La production primaire de matières organiques marines est limitée surtout aux mois d'été.

Le chenal Laurentien traverse complètement le golfe du Saint-Laurent, servant de voie privilégiée pour les échanges d'eaux profondes et de surface avec l'océan Atlantique. La distance croissante à partir des principales sources de matériaux terrigènes et l'ordre de grandeur plus faible des vitesses d'accumulation des sédiments dans le Golfe augmentent l'importance relative des constituants biogènes marins dans les sédiments, malgré la productivité primaire plus basse au-dessus des portions profondes du Golfe.

La partie sud du golfe du Saint-Laurent est dominée par les eaux peu profondes du plateau madelinien qui sont périodiquement mélangées par les tempêtes. La productivité biologique est élevée, comme c'est le cas de la diversité des espèces d'organismes tant pélagiques que benthiques. Les sédiments de fond sont constitués surtout de sables remaniés et l'accumulation semble à peu près inexistante.

Le fjord du Saguenay constitue une partie relativement petite, mais particulièrement utile du système du Golfe. Le fjord est relativement isolé et possède des dimensions qui le rendent particulièrement propice à l'étude des processus océanographiques fondamentaux.

and on mathematical conceptualization of geochemical processes, we will eventually be able to understand present-day processes, relate these to the past, and make predictions about the future.

The Gulf of St. Lawrence Environment

The Gulf of St. Lawrence environment offers a variety of natural laboratories for chemical oceanography studies. Each of these represents a particular set of environmental conditions. The Upper St. Lawrence Estuary is a high-energy partially-mixed estuary with strong salinity and temperature gradients. It possesses a well-developed turbidity maximum where particulate matter exchanges with seasonal mud flats, and is mainly floored with gravelly and sandy bottom sediments. There appears to be no net accumulation of fine-grained deposits.

The head of the Laurentian Trough marks the beginning of the Lower (or Maritime) Estuary. In this deep channel, bordered by 30–40 m deep, narrow platforms, horizontal salinity gradients are weak. Advective transport dominates over turbulent diffusion, and the slow compensatory net landward flow of the deep waters makes this region the principal site of deposition of terrigenous particulate matter. Sediment accumulation rates are on the order of mm/yr. Exchanges between the deep waters and the surface water are vigorous at the head of the Trough. Rivers on the north shore contribute significant amounts of fresh-water, and the overall estuarine circulation is modified by variable mesoscale structures. Primary production of marine organic matter is limited mainly to the summer months.

The Laurentian Trough extends right across the Gulf of St. Lawrence, providing a conduit through which deep and surface waters exchange with the Atlantic Ocean. The increasing distance from major sources of terrigenous material and the order-of-magnitude lower sediment accumulation rates in the open Gulf increase the relative importance of the marine biogenic component in sediments, in spite of the lower primary productivity over the deep portions of the Gulf.

The southern Gulf of St. Lawrence is dominated by the periodically storm-mixed shallow waters of the Magdalen shelf. Biological productivity is high, as is species diversity of both pelagic and benthic organisms. Bottom sediments consist mainly of reworked sands and accumulation is apparently nil.

A small but particularly useful part of the Gulf system is the Saguenay Fjord. It is relatively isolated and has dimensions that make it uniquely suitable for the study of fundamental oceanographic processes.

Les cycles du carbone et des sels nutritifs à l'intérieur du Golfe

La compréhension du cycle du carbone constitue un problème-clé en océanographie chimique. S'il en est ainsi, c'est surtout parce que tant la production que la destruction de la matière organique modifient la composition de l'eau de mer, respectivement en extrayant le carbone organique et les autres espèces chimiques de l'eau de mer et en les libérant dans l'eau. Lorsque la production et la destruction de la matière organique sont séparées dans l'espace, des gradients de concentration chimique se développent.

La balance de masse de la matière organique du golfe du Saint-Laurent est dominée par des cycles internes dans lesquels la production autochtone ne dépasse que légèrement l'oxydation-reminéralisation *in situ*. Bien que quelques tentatives aient été faites pour déterminer les principaux éléments de ces cycles internes, une image quantitative du mouvement du carbone et des espèces connexes reste encore à définir.

La quantification des cycles du carbone et des sels nutritifs est gênée par l'absence de connaissances quantitatives de l'environnement physique, géologique et biologique du Golfe. Les biologistes émettent l'hypothèse que le Golfe constitue une mosaïque de milieux biologiquement différents et soutenus par différents réseaux trophiques. Il reste toutefois que la distribution des espèces, particulièrement en ce qui concerne les producteurs primaires, n'a pas encore été identifiée dans ces différents réseaux trophiques. La distribution des espèces est essentielle à la détermination des apports relatifs de carbone organique et inorganique aux sédiments. On sait encore peu de choses au sujet de ces apports, mais on peut présumer que le couplage spatio-temporel de la production et de la consommation est complexe. L'importance relative de la colonne d'eau et des sédiments pour la minéralisation de la matière organique dépend de la profondeur de l'eau, mais une simple relation de profondeur ne peut être prévue parce que la profondeur variable de la colonne d'eau crée des milieux de fond fortement contrastants, p. ex. le fond sablonneux qui règne sur le plateau madelinien et le fond vaseux du profond chenal Laurentien. Les courants forts existent dans certaines régions, p. ex. le courant de Gaspé, tandis qu'ils sont complètement absents dans d'autres, ce qui rend difficile l'évaluation du transport de la matière organique.

Les détails concernant le cheminement physique et biochimique du carbone et des sels nutritifs ainsi que les flux en cause n'ont pas été suffisamment approfondis. On ne sait pas encore très bien où et quand la reminéralisation se produit par rapport à la production. La matière organique se minéralise-t-elle à proximité de l'endroit où elle est formée, ou encore est-ce que l'advection ou la dispersion créent des séparations spatiales importantes de la production et de la minéralisation? Quelle est le délai entre la production et la minéralisation, soit le temps de résidence de la matière organique? Comment la reminéralisation réagit-elle aux variations temporelles de production? Si la production et la régénération sont latéralement séparées, comment le sels nutritif limitant revient-il et selon quelle échelle de temps? Quels sont les

Cycling of Carbon and Nutrients within the Gulf

Understanding the carbon cycle is a key problem in chemical oceanography. The principal reason for this is that both production and destruction of organic matter change the composition of sea water by respectively extracting inorganic carbon and other chemical species from seawater and releasing them back to the water. When production and destruction of organic matter are separated in space, chemical concentration gradients develop.

The organic matter mass-balance of the Gulf of St. Lawrence is dominated by internal cycling wherein autochthonous production only slightly exceeds *in situ* oxidation/remineralization. Although some attempts have been made to determine the principal features of this internal cycling, a quantitative picture of the movement of carbon and related species has yet to emerge

Quantifying the carbon and nutrient cycles is impeded by the lack of quantitative knowledge of the physical, geological and biological environment of the Gulf. Biologists hypothesize that the Gulf is a mosaic of biologically different environments sustained by different food webs. However, the species distribution, particularly of the primary producers, has not been identified in these different food webs. The species distribution is essential in determining the relative fluxes of organic and inorganic carbon to the sediments. Little is known about these fluxes, but one can expect the spatial and temporal coupling of production and consumption to be complex. The relative importance of water column and sediments for the mineralization of organic matter will depend on water depth, but a simple depth relationship can not be expected because the variable depth of the water column creates highly contrasting bottom environments, e.g. the sandy bottom on the shallow Magdalen Shelf and the muddy bottom in the deep Laurentian Trough. Strong currents exist in some regions, e.g. the Gaspe Current, but are absent in others, making it difficult to evaluate transport of organic matter.

The details of the physical and biogeochemical pathways of carbon and nutrients and the fluxes involved have not been sufficiently elucidated. It is not clear where and when remineralization occurs relative to production. Is organic matter mineralized close to where it is formed, or do advection and dispersion create important spatial separations of production and mineralization? What is the time delay between production and mineralization, i.e. the residence time of the organic matter? How does remineralization respond to temporal variations of production? If production and regeneration are laterally separated, how does the limiting nutrient return and on what time scale? What are the magnitudes of the fluxes involved in these processes? What are the relative contributions of sediment and water column regeneration in ordres de grandeur des flux qui sont associés à ces processus? Quelles sont les contributions relatives de la régénération dans les sédiments et dans la colonne d'eau dans les zones peu profondes et profondes?

Le recyclage de la matière organique et la régénération des sels nutritifs dans les sédiments sablonneux ont sûrement été négligés par les géochimistes et bien souvent écartés *a priori*. Nous contestons une telle négligence et nous proposons au contraire de réévaluer le rôle des vastes dépôts de sable recouvrant le plateau madelinien dans la transformation de la matière organique. En outre, on sait bien que l'activité des organismes benthiques affecte les échanges qui se produisent à travers l'interface sédiments-eau. Comment alors cette activité influence-t-elle la dynamique du carbone dans le sédiment du Golfe?

Sans perdre de vue le fait que nous considérons le golfe du Saint-Laurent comme un archétype de mer marginale, nous suggérons aussi de faire des comparaisons entre la dynamique du carbone dans le chenal Laurentien et le plateau madelinien, d'une part, avec celle qui règne dans des systèmes analogues comme ceux du chenal Norvégien et de la partie sud de la mer du Nord afin d'évaluer les différences découlant des interventions anthropiques sur cette dernière.

Le cheminement des métaux traces dans le Golfe

Dans le golfe du Saint-Laurent, nous possédons déjà une assez bonne idée de la distribution générale des métaux traces dans la colonne d'eau et de l'apport fluvial en métaux-traces dans le Golfe. Nous savons aussi que les métaux-traces sont suffisamment mobiles pour qu'une grande proportion de leur apport ne soit pas piégée à l'intérieur du Golfe, mais qu'elle puisse être exportée vers l'océan profonde. Nous en savons maintenant pas mal au sujet de la distribution des métaux-traces dans les sédiments ainsi qu'au sujet des réactions chimiques et des processus de transport qui agissent sur ces métaux. Nous en savons toutefois beaucoup moins concernant les variations spatio-temporelles dans la distribution des métaux traces, mais des indications existent comme quoi ces variations seraient effectivement très importantes.

Les métaux-traces constituent des sujets intéressants pour les études de cheminement. Certains d'entre eux sont soupçonnés d'être étroitement liés à l'activité des organismes vivants et leur cheminement semble suivre parallèlement celui des principaux sels nutritifs. On ne sait pas encore toutefois si cette situation est due au fait que ces métaux sont directement impliqués dans le cycle du carbone, ou s'il existe d'autres raisons expliquant ce parallélisme. Le cadmium constitue un bon exemple de métal-trace semblant suivre le cycle du carbone. Il semble être extrait de l'eau de mer sur des particules dans la couche superficielle de la mer. L'extraction est peut-être faite par des organismes vivants, mais nous ne connaissons pas le mécanisme qui opère dans ce cas. Le cadmium est transporté en dehors de la couche de surface sur des particules biogènes et il se dissout de nouveau dans la colonne d'eau et dans les sédiments quand ces particules sont détruites par voie aérobique. Il est possible de tracer un schéma grossier du cheminement emprunté par le cadmium en

shallow and deep regions?

Recycling of organic matter and regeneration of nutrients in sandy sediments has surely been neglected by geochemists and oftentimes dismissed a priori. We question this neglect, and propose that the role of the extensive Magdalen Shelf sands in processing organic matter be re-evaluated. Additionally, the activity of benthic organisms is well known to affect exchanges across the sediment-water interface. How does this activity influence carbon dynamics in Gulf sediments?

In keeping with our view of the Gulf of St. Lawrence as an archetypical marginal sea, we also suggest that comparisons be made between carbon dynamics in the Laurentian Trough and the Magdalen Shelf with those in similar systems such as the Norwegian Trough and the southern North Sea to assess the differences made by man's impact on the latter.

Trace Metal Pathways in the Gulf

In the Gulf of St. Lawrence we already have a fair picture of the overall distribution of trace metals in the water column, and of the river input of trace metals to the Gulf. We also know that trace metals are sufficiently mobile that a large proportion of their input is not trapped within the Gulf but is exported to the deep sea. We now know quite a bit about the distribution of trace metals in sediments and the chemical reactions and transport processes that act upon them. However, we do not know much about temporal and spatial variations in the distribution of trace metals, but there are indications that they are indeed very important.

Trace metals are interesting candidates for pathway studies. Some of them are suspected to be closely tied to the activity of living organisms, and their pathways appear to parallel those of the major nutrient salts. It is not known, however, if this is because these metals are directly involved in the carbon cycle, or if there are other reasons for the parallel. Cadmium is a good example of trace metals that seem to follow the carbon cycle. It appears to be extracted from seawater in the surface layer of the sea onto particles. The extraction may be carried out by living organisms, but we don't know the mechanism involved. Cadmium is transported out of the surface layer on biogenic particles, and dissolve again in the water column and the sediments when these particles are destroyed aerobically. It is possible to sketch out a rough scheme for the pathways of cadmium with existing knowledge, but the essential information about the reaction rates for extraction of cadmium from seawater and the subsequent release is missing.

recourant aux connaissances existantes, mais les informations essentielles concernant les vitesses de réaction pour l'extraction du cadmium à partir de l'eau de mer ainsi que pour la libération qui s'ensuit font encore défaut.

Certains métaux-traces ne sont pas impliqués de façon directe avec les organismes vivants, mais réagissent aux variations dans les propriétés chimiques du milieu induit par les organismes. Le manganèse constitue un bon exemple de cet état de fait, puisqu'il se dissout aux endroits où une activité microbienne a enlevé l'oxygène et créé un milieu réducteur. Actuellement, le cheminement du manganèse est bien décrit sur le plan qualitatif, et on en sait à ce moment de plus en plus au sujet de la cinétique des réactions chimiques qui se produisent. Le manganèse constitue par conséquent un sujet de premier choix lorsque l'on veut quantifier des cheminements.

Le manganèse et le cadmium illustrent deux propriétés contrastantes des métaux-traces et peuvent logiquement servir de centre d'intérêt pour approfondir nos connaissances au sujet des cheminements. Que nous reste-t-il donc à découvrir et à approfondir? Puisque les cheminements des métaux-traces sont si intimement liés à l'activité biologique et au cycle du carbone, l'étude de ces métaux doit être menée parallèlement aux études portant sur le cycle du carbone. Les questions qu'il faut se poser sont analogues : Où et quand les métaux-traces sont-ils extraits de la solution? Quels sont les mécanismes et quelle est la cinétique en cause? Où et quand les métaux sont-ils remis en solution? Par quelles réactions et par quelle cinétique? Quel est le rôle joué par les colloïdes dans l'extraction des métaux à partir de l'eau de mer? La question posée au sujet des milieux peu profonds et riches en énergie comme celui du plateau madelinien s'applique aussi aux métaux-traces.

Le cheminement des constituants organiques stables dans le Golfe

Pour des raisons pratiques, la discussion portant sur les produits chimiques organiques traces a été limitée aux produits stables et dont les réactions peuvent être décrites en recourant aux principes de la chimie physique. Il existe de nombreuses questions intéressantes qui peuvent être posées concernant les matières organiques métabolisables (p. ex. les vitesses de réaction, les intermédiaires métaboliques, les produits finaux du métabolisme, la stabilisation par formation de complexes métalliques), mais ces sujets entrent davantage dans le champ de la biochimie que dans celui de la chimie marine. Les produits chimiques organiques stables, c'est-à-dire ceux qui ne sont pas affectés ou transformés de façon significative par le métabolisme, la photodégradation ou d'autres réactions chimiques, comprennent la plupart des HAP pyrogènes et biogènes, la plupart des BPC ainsi que d'autres composés halogènes, de même que certains complexes organo-métalliques comme les composés organiques du plomb. En raison de la faible solubilité de la plupart de ces composés dans l'eau, leur répartition entre les phases solides et aqueuses est extrêmement favorable aux phases solides et il arrive souvent de trouver de fortes concentrations associées aux lipides. Pour cette raison,

Some trace metals are not involved directly with living organisms, but respond to changes in chemical properties of the environment induced by organisms. A good example of this is manganese, which dissolves in places where microbial activity has removed oxygen and created a reducing environment. The pathways of manganese are now qualitatively well described, and information on the kinetics of the chemical reactions involved is presently emerging. Manganese is therefore a prime candidate for an attempt to quantify the pathways.

Manganese and cadmium illustrate two contrasting properties of the trace metals, and can logically serve as the focus of attention to develop pathway information. What is then the information that is missing and that needs to be developed? Since the pathways of trace metals are so intimately tied in with biological activity and the carbon cycle, the study of trace metals must be carried out in parallel with the studies of the carbon cycle. The questions to be asked are similar: Where and when are trace metals extracted from solution? Which are the mechanisms and what is the kinetics involved? Where and when are they released to solution again? By which reactions and kinetics? What is the role of played by colloids in the extraction of metals from seawater? The question asked about shallow energy-rich environments such as the Magdalen Shelf applies to trace metals as well.

Pathways of Stable Organic Compounds in the Gulf

For practical reasons, the discussion of organic trace chemicals was limited to those that are stable and whose reactions can be described with the principles of physical chemistry. There are many interesting questions that can be asked about metabolizable organics (e.g. reaction rates, metabolic intermediates, metabolic end products, stabilization by metal complexing), but these fall more within the scope of biochemistry than marine chemistry. Stable organic chemicals, i.e. those which are not significantly affected or transformed by metabolism, photodegradation, or other chemical reactions, include most pyrogenic and biogenic PAHs, most PCBs and other halogenated compounds, and some organo-metallic complexes such as organo-lead. Because of the low solubility of most of these compounds in water, their partitioning between solid and aqueous phases is overwhelmingly in favour of the solid phases, and one often finds high concentrations in association with lipids. For this reason, their pathways in the marine environment should be related to the pathways of lipid containing solids.

leurs cheminements dans le milieu marin devraient être rapprochés des cheminements des solides qui contiennent des lipides.

On en sait beaucoup moins au sujet de la distribution et du cheminement de ces composés organiques qu'au sujet des métaux-traces. Il reste que nous soupçonnons que certains des principes qui s'appliquent aux métaux-traces peuvent aussi s'appliquer aux matières organiques, à l'exception des réactions chimiques en cause. L'approche adoptée pour les matières organiques devrait comprendre des études sur leur distribution et les réactions de répartition entre l'état de solution, les phases solides et l'atmosphère.

Un certain nombre de questions précises peuvent être posées concernant les matières organiques stables, comme les suivantes : Qu'est-ce qui contrôle la répartition des matières organiques hydrophobiques entre la solution et les organismes vivants? Quel est le mécanisme et la cinétique de l'absorption à partir de la solution. Le processus est-il réversible? Comment les HAP et les BPC atteignent-ils le sommet de la chaîne alimentaire de façon apparemment très efficace si l'on en juge par leurs fortes concentrations chez les mammifères marins? Existe-t-il une possibilité de court-circuit dans la chaîne trophique?

Quelle est l'importance du transport atmosphérique des matières organiques et hydrophobiques anthropogènes jusqu'au large du Golfe comparativement au transport sur des particules en suspension fluviale? Est-il possible de distinguer entre ces deux modes de transport pour les principaux HAP pyrogènes? Est-il possible d'établir une relation entre la distribution de certaines matières organiques anthropogènes dans les sédiments récents qui se trouvent dans le Golfe et le patron de circulation des eaux et de l'atmosphère? L'emploi d'une nouvelle famille de contaminants organo-métalliques se répandra probablement rapidement au cours des prochaines années. Quelles sont les propriétés chimiques importantes qui contrôlent leur répartition entre les particules et la solution?

Les chimistes ont été appréciés par leurs collègues dans d'autres disciplines depuis les débuts de l'océanographie en raison de leur capacité de fournir des traceurs. Des traceurs chimiques sont en effet employés, par exemple, pour étudier le mouvement des masses d'eau et les vitesses de mélange, le transport des sédiments et leur vitesse de mélange, la paléotempérature et la productivité. Le domaine des traceurs chimiques se développe rapidement grâce à l'introduction de nouvelles méthodes analytiques en chimie organique. Par exemple, certaines espèces d'organismes synthétisent souvent des molécules organiques uniques et stables, dont la présence dans l'environnement rappelle sans équivoque celle de ces organismes. Il arrive parfois que l'on puisse établir une relation entre certains facteurs environnementaux, comme la température et les composés synthétisés. De récents travaux ont permis de mettre en évidence la composition de lipides génétiquement contrôlés chez certains poissons et mammifères marins et cette composition peut servir à identifier et à distinguer des populations ou des stocks de tels animaux. Les progrès accomplis dans ce domaine reposent sur des interactions étroites entre la chimie et d'autres disciplines. Il existe peut-être des composés anthropogéniques stables et hydrosolubles pouvant servir de traceurs de masse d'eau dans les processus côtiers à petite échelle.

Far less is known about the distribution and the pathways of these organic compounds than about the trace metals. Yet, we suspect that some of the principles that apply to trace metals may also apply to the organics, with the exception of the chemical reactions involved. The approach to organics should include studies of their distribution and the partitioning reactions between solution, solid phases and air.

A number of specific questions can be asked about stable organics, such as: What controls the partitioning of hydrophobic organics between solution and living organisms? What is the mechanism and kinetics of the uptake from solution. Is it reversible? How do PAHs and PCBs reach the top of the food chain so efficiently as it appears from their high concentrations in marine mammals? Is there a possibility of a short circuit in the trophic chain?

What is the importance of atmospheric transport of anthropogenic hydrophobic organics to the open Gulf compared to transport on river-borne suspended particles? Is it possible to distinguish between these two transportation modes for major pyrogenic PAHs? Is it possible to establish a relationship between the distribution of some anthropogenic organics in recent sediments in the Gulf and the circulation pattern of water or atmosphere? The use of the new family of organo-metallic contaminants will probably expand rapidly in the next few years. Which important chemical properties will control their partitioning between particles and solution?

Chemists have been appreciated by their colleagues in other marine disciplines since the beginning of oceanography for their ability to supply tracers. Chemical tracers are used, for example, to study water mass movement and mixing rates, sediment transport and mixing rates, paleotemperature and productivity. The field of chemical tracers is in rapid development thanks to the introduction of new analytical methods in organic chemistry. For example, individual species of organisms often synthesize unique and stable organic molecules, the occurrence of which in the environment points unequivocally to those organisms. Sometimes one can establish a relationship between environmental factors, such as temperature, and the compounds that are synthesized. Recent work has pointed to a genetically controlled lipid composition in certain marine fish and mammals that may be used to identify and distinguish populations or stocks of these animals. Developments in this field depend on close interactions of chemistry with other disciplines. Perhaps there are stable, water-soluble anthropogenic compounds that could be used as water mass tracers in small-scale nearshore processes.

Paléocéanographie du Golfe

La productivité biologique et la présence ou l'absence d'espèces importantes de poissons dans le golfe du Saint-Laurent sont des fonctions sensibles découlant des conditions environnementales. Ces conditions ont été modifiées dans le passé, comme elles le seront dans l'avenir. C'est dans les sédiments que l'on trouvera la clé des liens existant entre l'environnement et la biologie du Golfe, parce que ce sont ces mêmes sédiments qui renferment les indicateurs chimiques et biologiques des conditions qui régnaient à l'époque de leur accumulation. La vulnérabilité du système aux influences d'origine anthropique et climatologique pourrait être évaluée à condition de pouvoir réunir une solide documentation concernant la façon dont ces indicateurs ont évolué dans le passé. Une telle documentation pourrait à son tour être utile dans la prévision des variations à venir.

Des techniques paléocéanographiques peuvent être employées pour étudier les liens environnementaux sur une gamme étendue d'échelles de temps, pourvu que la stratigraphie sédimentaire soit assez épaisse pour permettre de résoudre les unités de temps désirées. Les sous-régions du Golfe offrent cette possibilité. Ainsi, la tête du fjord du Saguenay est particulièrement propice à l'examen de l'histoire des apports industriels récents dans l'environnement. En raison de l'accumulation rapide des sédiments, ponctuée par des horizons datables, les matériaux déposés au cours du siècle dernier peuvent être datés à moins d'une année près. À l'autre extrême de l'échelle de temps, les vitesses de sédimentation continues, mais relativement faibles, dans la partie est du chenal Laurentien feraient de cette région une région idéale pour l'examen des variations climatiques associées à la fin du Wisconsinien. S'il en est ainsi, c'est parce que l'est du golfe du Saint-Laurent serait resté une zone d'eau libre même pendant la dernière glaciation.

La contrainte climatologique des processus biogéochimiques dans le Golfe est influencée par les modulations dans les apports des trois principales masses d'eau : les déversements d'eau douce du fleuve Saint-Laurent, les apports de surface des eaux de la mer du Labrador par le détroit de Belle-Isle et les apports d'eaux atlantiques par le détroit de Cabot. Les vitesses de sédimentation intermédiaires à l'intérieur de l'estuaire maritime conviennent peut-être à l'examen de telles variations d'échelle intermédiaire sur plusieurs décennies ou plusieurs siècles.

Le type de questions pouvant être abordées par les études paléocéanographiques comprend ce qui suit : Dans quelle mesure les interventions d'origine anthropique ont-elles modifié le régime biogéochimique du Golfe et selon quelles échelles de temps ces variations se sont-elles produites? Quelles ont été les principales variations climatiques et dans quelle mesure l'environnement tempéré actuel du Golfe a-t-il subi de fortes influences arctiques? Comment ces variations ont-elles exercé une influence sur leur productivité? Comment le cycle hydrologique du fleuve Saint-Laurent a-t-il varié aux échelles intermédiaires de temps (100–1000 ans)? De telles variations nous renseignent-elles au sujet des régimes dominants de température et de précipitation?

Paleoceanography of the Gulf

Biological productivity and the presence or absence of important species of fish in the Gulf of St. Lawrence are sensitive functions of environmental conditions. These conditions have been changing in the past, as they will in the future. Sediments hold the clues to the relationship between the environment and the biology of the Gulf, because they preserve chemical and biological indicators of the conditions prevailing during the time of their deposition. The sensitivity of the system to anthropogenic and climatological influences may be assesses if well-documented records of how these indicators have been changing in the past can be established. These records may in turn be helpful in predicting future changes.

Paleoceanographic techniques can be used to investigate environmental relationships on a variety of time scales, provided that the sedimentary record is thick enough to permit resolution of the desired time units. The sub-regions of the Gulf offer this possibility. Thus, the head of the Saguenay Fjord is particularly well-suited for examining the history of recent industrial inputs to the environment. Because of the rapid accumulation of sediment, punctuated by datable horizons, material deposited during the past century can be dated with a resolution of less than a year. At the other extreme of the time scale, the continuous but relatively low sedimentation rates in the eastern part of the Laurentian Trough would make this region ideal for examining the climate change associated with the end of the Wisconsinan. This is because the eastern Gulf of St. Lawrence was apparently open water even during the last glacial period.

The climatological forcing of biogeochemical processes in the Gulf is influenced by modulations in the inflows of three major water masses: freshwater discharge from the St. Lawrence River, surface inflow of Labrador Sea water through the Strait of Belle Isle, and inflow of Atlantic water through Cabot Strait. The intermediate sedimentation rates within the Maritime Estuary might perhaps be well-suited for examining such intermediate-scale changes over several decades or centuries.

The kind of questions that can be addressed with paleoceanographic studies include the following: To what extent have anthropogenic inputs modified the biogeochemical regime of the Gulf and on what time scales have these changes occurred? What have been the major changes in climate and to what extent has the present temperate Gulf environment undergone strong Arctic influences. How has this impacted on its productivity? How has the hydrological regime of the St. Lawrence River varied on intermediate time scales (100–1000 yr)? Do these changes reveal information about the prevailing temperature and precipitation regimes?

Suivant les questions posées, une vaste gamme de paramètres sédimentologiques s'offre à nous. Parmi les marqueurs d'origine anthropique, on trouve les contaminants inorganiques et organiques (Hg, Pb, Cd, HAP, BPC, etc.), les radionucléides (Cs-137, Pu-239,240, etc.) ainsi que les indicateurs de pluies acides (microfossiles, etc.). Au nombre des marqueurs climatologiques, on trouve la matière organique (la lignine, les isotopes stables, des proportions relatives de C, H, N et S), des indicateurs palynologiques et paléontologiques tels que les microfossiles et les rapports des isotopes d'oxygène des radionucléides comme le C-14, les traceurs hydrologiques, les indicateurs de texture des sédiments (granulométrie, minéralogie) ainsi que les indicateurs sismiques (discordances, surfaces d'érosion).

Les anciennes échelles de temps étaient considérablement différentes en ce qui concerne les variations d'origine anthropique (10 à 100 ans) et climatologique (> 100 ans). Toutefois, l'étroit couplage actuel des influences anthropiques et climatologiques par le biais de phénomènes comme les augmentations du CO_2 dans l'atmosphère, l'amincissement de la couche d'ozone dans la stratosphère et les cycles océano-atmosphériques du méthane a modifié les deux échelles de temps. La reconstruction de l'évolution des effets séparées de ces deux influences sur les paramètres biogéochimiques constitue un élément clé dans l'explication des aspects dynamiques du couplage.

La conceptualisation mathématique des processus géochimiques pour les besoins de la quantification et de la prédiction

La modélisation des processus géochimiques peut être utile à plusieurs points de vue : un modèle correctement formulé peut permettre d'extraire des informations qui seraient autrement difficiles à mesurer, comme les flux. Les modèles peuvent fournir des prédictions (fantaisistes ou réelles) de l'évolution temporelle d'un système. Les modèles peuvent aussi permettre de déterminer l'endroit et le moment où des processus choisis dominent dans une collection de processus concurrents. Des études de sensibilité peuvent aussi indiquer quelles sont les informations qui sont pertinentes et quels sont les paramètres qui doivent être mesurés avec précision, tout en permettant de tester la valeur du mode de création des paramètres.

L'effort de modélisation devrait être envisagé en tant que composant essentiel de toute étude portant sur le Golfe puisqu'un tel effort pourrait fournir à la fois des informations scientifiques fondamentales et servir d'instruments privilégiés dans la gestion et l'analyse de l'environnement.

Dans le contexte des thèmes de recherche que nous avons identifiés ici, la modélisation doit être considérée comme élément essentiel si nous espérons en arriver à une compréhension quantitative de la géochimie du Golfe tout en faisant des prédictions au sujet des effets de la perturbation d'origine anthropique. De façon plus spécifique, dans l'étude du cycle du carbone, il serait nécessaire de calculer les flux de carbone et de sels nutritifs à partir des profils de concentration dans les eaux interstitielles des sédiments lorsque les flux ne peuvent être mesurés

Depending on the questions that are asked, a wide variety of sedimentological parameters is available to us. Among the anthropogenic markers are inorganic and organic contaminants (Hg, Pb, Cd, PAH, PCB, etc.), radionuclides (Cs-137, Pu-239,240, etc.) and acid rain indicators (microfossils, etc.). Among the climatological markers are organic matter (lignin, stable isotopes, relative proportion of C,H,N and S), palynological and paleontological indicators such as microfossils and oxygen isotope ratios, radionuclides such as C-14, hydrological tracers, sediment texture signals (grain size, mineralogy), and seismic signals (unconformities, erosional surfaces).

The past time scales have been greatly different for anthropogenic (10–100 yr) and climatological changes (> 100 yr). However the present close coupling of anthropogenic and climatological influences through phenomena such as atmospheric increases of CO_2, ozone depletion in the stratosphere, and atmospheric-oceanic cycling of methane, has modified both time scales. A key element to understanding the dynamic aspects of this coupling lies in the past reconstruction of their separate influences on biogeochemical parameters.

Mathematical Conceptualization of Geochemical Processes for Quantification and Prediction

Modelling geochemical processes can be useful in a number of ways: A correctly formulated model can be used to extract information that is otherwise difficult to measure, such as fluxes. Models can provide predictions (fanciful or real) of the time evolution of a system. Models can identify where and when selected processes dominate among a collection of competing processes. Sensitivity studies also indicate what information is relevant and which parameters must be measured accurately, and test the value of the parameterization scheme.

The modelling effort should be considered an essential component of any Gulf study because it can supply both fundamental scientific information and provide a tool for environmental management and analysis.

Within the context of the research themes we have identified, modelling must be considered an essential component if we hope to achieve a quantitative understanding of the geochemistry of the Gulf and make predictions about the effects of anthropogenic perturbation. Specifically, in the carbon cycle study, it will be necessary to calculate the carbon and nutrient fluxes from sediment porewater profiles if they cannot be measured directly. This will require a diagenetic model that incorporates realistic organic matter decay kinetics and the directement. Cela nécessitera un modèle diagénétique incorporant une cinétique réaliste de la décomposition de la matière organique ainsi qu'une description appropriée des processus de transport qui affectent les sédiments (p. ex. la diffusion, la bioturbation, l'irrigation, les écoulements imposés par la pression, et les mouvements de sédiments). Si les données indiquent que le site de la régénération primaire est éloigné des zones de production, il faudra un modèle pour explorer la dynamique et les échelles de temps du transport entre les zones de production et les zones de reminéralisation. Le tout pourrait commencer par un simple modèle en forme de boîte couplé à un modèle benthique (diagénétique), mais il faudra un jour établir une liaison entre les modèles de circulation et de transport tridimensionnels et un modèle benthique variant dans l'espace.

Les diverses cheminements identifiés dans les études portant sur les métaux traces et les produits chimiques organiques peuvent être comparés en faisant appel à une simulation mathématique. Une telle démarche mettra en évidence les composantes plus importantes des balances de masse et elle permettra de calculer les flux au système. Un tel modèle permettra aussi de prédire l'évolution et le sort des perturbations de contaminants dans le Golfe.

Les études paléocéanographiques fourniront des données permettant d'établir les modèles prédictifs de l'évolution du Golfe. À cette fin, il sera nécessaire d'élaborer des méthodes mathématiques permettant d'interpréter correctement ces données du point de vue des variables environnementales.

La dimension internationale des recherches effectuées dans le golfe du Saint-Laurent

Le golfe du Saint-Laurent ressemble à plusieurs égards au milieu de la mer du Nord en Europe. Ainsi, la partie méridionale de la mer du Nord, dont les eaux peu profondes ont une forte productivité et reposent sur des sédiments sablonneux et graveleux, ressemble à la zone du plateau madelinien dans le Golfe. La partie nord de la mer du Nord, dominée par la fosse de Norvège (un chenal atteignant une profondeur de 400 à 600 m qui longe la côte sud de la Norvège et se fraie un chemin à travers la bordure de la plate-forme continentale dans la mer de Norvège), correspond aux parties les plus profondes du Golfe. La tête du chenal norvégien se trouve dans le Skagerrak, où les eaux douces de la Baltique pénètrent dans la mer du Nord. La ressemblance avec la partie supérieure du chenal Laurentien dans l'estuaire maritime du Saint-Laurent est frappante. Tant dans la mer du Nord que dans le Golfe, les bassins au chenaux sont le site d'une sédimentation contemporaine. Les modes de circulation dans les deux mers sont aussi analogues en ce qu'elles connaissent une circulation nette à l'inverse des aiguilles d'une montre dans les parties moins profondes et des écoulements stratifiés dans les chenaux. Les principales voies existant entre la mer du Nord et l'Atlantique sont la section Norvège–Shetland–Écosse et la Manche, lesquels correspondent respectivement au détroit de Cabot et au détroit de Belle-Isle dans le Golfe.

Les scientifiques canadiens travaillant dans le golfe du Saint-Laurent sont avantagés à plusieurs points de vue

proper description of transport processes in sediments (e.g. diffusion, bioturbation, irrigation, pressure driven flows and sediment movement). If the data indicate that the location of primary regeneration is removed from the areas of production, a model will be needed to explore the dynamics and time scales of the transport between production and remineralization areas. This might begin with a simple box model coupled to a benthic (diagenetic) model, but will eventually demand the linkage of three-dimensional circulation and transport models to a spatially-varying benthic model.

The various pathways identified in the trace metal and organic chemical studies should be compared using a mathematical simulation. This will highlight the more important components of the balances, and allow calculation of the fluxes to the system. Such a model will also permit prediction of the evolution and fate of contaminant perturbations in the Gulf.

The paleoceanographic studies will provide data to establish the utility of the predictive evolutionary models of the Gulf. To this end it will be necessary to develop mathematical methods to properly interpret this data in terms of environmental variables.

International Aspect of Research in the Gulf of St. Lawrence

The Gulf of St. Lawrence resembles in many ways the North Sea system in Europe. Thus the southern part of the North Sea, which is shallow with sandy and gravelly sediments and high productivity, resembles the Magdalen Shelf area of the Gulf. The northern part of the North Sea, which is dominated by the Norwegian Trough, a 400–600 m deep channel which swings around the coast of southern Norway and cuts through the edge of the continental shelf in the Norwegian Sea, corresponds to the deeper parts of the Gulf. The head of the Norwegian Trough is in the Skagerrak, where freshwater from the Baltic enters the North Sea. The resemblance with the head of the Laurentian Trough in the Maritime estuary of the St. Lawrence is striking. In both the North Sea and the Gulf the trough systems are the site of modern sedimentation. The circulation patterns in the two seas are also similar with a net counter clockwise circulation in the shallower parts and stratified flows in the troughs. The major connections of the North Sea with the Atlantic are the Norway-Shetland-Scotland section and the Strait of Dover, which correspond to the Cabot Strait and the Strait of Belle Isle, respectively, in the Gulf.

Canadian scientists working on the Gulf of St. Lawrence have several advantages over their European par rapport à leurs vis-à-vis européens. Comme le Golfe relève entièrement d'une même juridiction, il y est plus facile de déployer des efforts concertés que ce n'est le cas pour la mer du Nord. Le Golfe étant plus petit, il y est plus facile de mener une étude intégrée. Finalement, le Golfe est relativement peu pollué comparativement à la mer du Nord et, de ce fait, il peut être considéré comme un exemple d'un système côtier ayant conservé un état presque naturel. Cela n'est cependant pas un motif pour mener isolément nos études dans le Golfe, puisqu'il y a des raisons de croire que les connaissances acquises dans l'un des deux systèmes sont susceptibles de s'appliquer directement dans l'autre, et que des liens solides entre les scientifiques canadiens et européens contribueront à accélérer l'approfondissement des connaissances relatives aux deux systèmes.

Dans un contexte plus vaste, le golfe du Saint-Laurent peut être considéré comme un prototype d'environnement côtière sous des latitudes tempérées telles que le plateau continental de l'Est canadien, la mer du Nord, la mer d'Okhotsk ainsi que la mer de Chine. Il existe donc ici une possibilité pour les scientifiques canadiens de jouer un rôle de premier plan dans l'étude de la chimie des environnements à plateau et pente continentale.

Références

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counterparts. Since the Gulf is entirely within the jurisdiction of a single country, it is easier to mount a concerted effort here than is possible for the North Sea. The Gulf is also smaller, which makes it more manageable to study as a complete system. Finally, it is relatively unpolluted compared to the North Sea, and can be considered as an example of a coastal system in a nearly natural state. We should not carry out studies in the Gulf in isolation, however, for there is reason to believe that the knowledge developed in one of these systems may be directly applicable in the other, and that strong links between Canadian and European scientists will accelerate the development of knowledge of both systems.

In a broader context, the Gulf of St. Lawrence may be seen as a prototype for shelf-slope environments in temperate latitudes such as the eastern Canadian continental shelf, the North Sea, the Sea of Okhotsk, and the Yellow Sea. There is thus an opportunity for Canadian scientists to play a leading role in the study of the chemistry of the shelf-slope environment.

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Rapport de l'atelier de travail sur l'océanographie biologique[1]

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Le rôle des océans dans le cycle du carbone (changements à l'échelle du Globe)

Le défi de taille qu'auront à relever les milieux scientifiques canadiens durant les prochaines décennies sera de prévoir les effets des changements touchant l'atmosphère de la planète (Transformation du Globe), et plus particulièrement l'augmentation de la concentration du gaz carbonique de l'atmosphère et «l'effet de serre» qui en résulte. L'océan constitue l'un des réservoirs pouvant absorber le gaz carbonique d'origine anthropogénique. Le processus peut être accéléré par la fixation de carbone dans la biomasse phytoplanctonique (la «pompe biologique») et par l'exportation subséquente de ce carbone fixé biologiquement vers les eaux profondes et les sédiments (fig. 1). Ce processus élimine effectivement le gaz

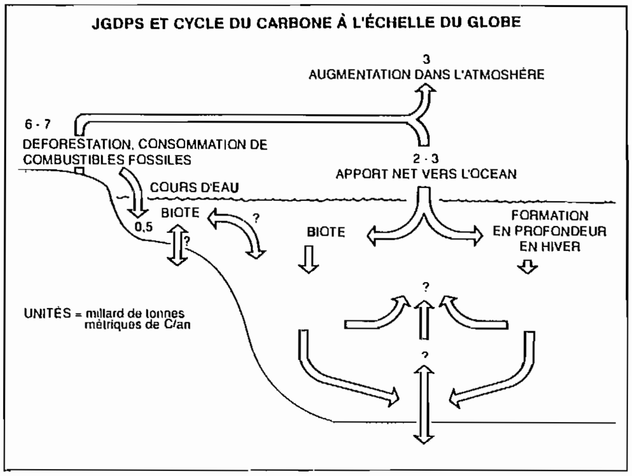

FIG. 1. Modèle théorique simplifié du rôle des océans dans le cycle du carbone (d'après Platt *et al.*, 1989).

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[1] Ce rapport fait partie des Compte rendus d'un atelier/symposium tenu à l'Institut Maurice-Lamontagne, Mont-Joli (Québec) du 14 au 17 mars 1989.

Report of the Workshop on Biological Oceanography[1]

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Role of Oceans in the Global Carbon Cycle (Global Change)

A major challenge for Canadian science in the next decades will be the prediction of the effects of global atmospheric changes (Global Change), especially the increasing concentration of carbon dioxide in the atmosphere and the resulting "greenhouse effect". One ultimate fate of anthropogenic carbon dioxide is absorption in the oceans, a process which can be accelerated by carbon fixation into phytoplankton biomass (the "biological pump") and the subsequent export of this biologically-fixed carbon into deep waters and sediments (Fig. 1). This process effectively removes carbon dioxide from the global system for a time scale of decades to centuries, which corresponds to the time scale of present

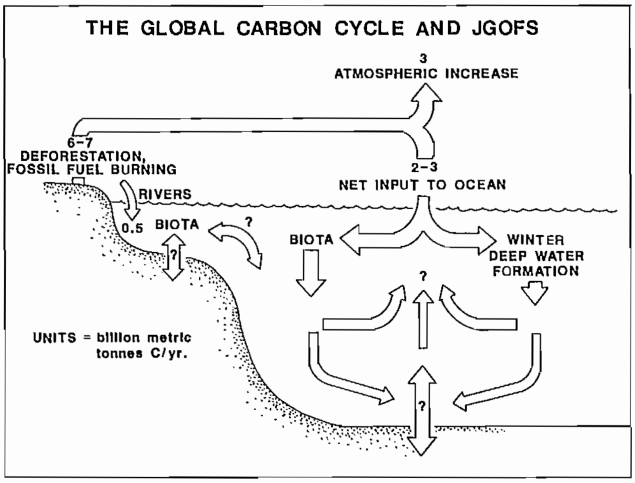

FIG. 1. Simplified conceptual model of the role of the oceans in the global carbon cycle (from Platt et al. 1989).

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[1] This report forms part of the Proceedings of a Workshop/Symposium held at the Maurice Lamontagne Institute, Mont-Joli, Quebec, 14–17 March 1989.

carbonique de l'atmosphère de la planète pour une période pouvant aller de plusieurs décennies à quelques siècles, période qui correspond à la vitesse actuelle des changements à l'échelle planétaire. À partir des années 1990, le Canada participera à l'effort international de recherche consacré à l'étude du flux des composés du carbone dans l'océan et à l'importance du rôle que jouent les océans dans le changement climatique en absorbant le gaz carbonique de l'atmosphère (JGOFS: *Joint Global Ocean Flux Study*; Brewer *et al.* 1986). Nos discussions au sein du groupe de travail sur l'océanographie biologique ont porté sur l'examen des moyens qui pourraient être mis en oeuvre pour étudier, à l'intérieur du système qu'est le golfe du Saint-Laurent, les points énumérés ci-dessous qui font partie du programme national canadien pour JGOFS (Platt *et al.* 1989).

1) Études comparatives sur les relations de phase (synchronisme) dans la dynamique du réseau alimentaire pour divers régimes de la partie supérieure de l'océan, en ce qui concerne l'exportation de matériel biogène de la zone photique.
2) Études de processus visant à dégager les voies majeures de circulation du carbone, en ce qui concerne son exportation de la zone photique.
3) Mesure des flux verticaux d'éléments nutritifs dans la zone photique et de l'exportation de matières biogènes de cette même zone, autant dans des conditions stables que dans des conditions perturbées et ce, dans des régimes océaniques différents.
4) Études sur la reminéralisation de la matière organique dans la couche benthique, menées dans des environnements différents.
5) Études de processus visant à déterminer les relations entre la production autotrophe de carbone réduit dans la zone photique et son transport vers la couche benthique.

Pourquoi le golfe du Saint-Laurent?

Le programme international pour JGOFS étudiera le flux océanique de carbone en calculant des bilans planétaires et en effectuant des études axées sur les processus. Étant donné la nature limitée des ressources scientifiques canadiennes, le programme national canadien pour JGOFS recommande qu'une importante partie de notre effort national soit orientée vers les études de processus (Platt *et al.* 1989). Comme les études portant sur les processus sont difficiles à réaliser aux grandes échelles horizontales et verticales de l'océan, nous devrions nous concentrer sur les mécanismes-clés qui peuvent être étudiés dans des systèmes à échelle réduite tels que le golfe du Saint-Laurent. Par exemple, le contrôle hydrodynamique du flux de carbone (Legendre et Demers 1984; Taggart et Leggett 1987) ainsi que les aspects saisonniers du flux de ce carbone, sont plus faciles à étudier près des côtes qu'en pleine mer. De plus, la logistique du calibrage *in situ* des données de télédétection s'avère beaucoup plus simple lorsque les régions étudiées sont plus près du littoral (pour exemples, consulter Falkowski 1988; Platt et Sathyendranath 1988). En plus de fournir des systèmes à échelle réduite qui sont faciles d'accès pour l'étude des processus océaniques, les plateaux continentaux sont, en ce qui concerne la sédimentation, la production

day Global Change. During the 1990's, Canada will join an international effort devoted to investigating the flux of carbon compounds in the ocean and the extent to which the oceans may affect climatic change by absorbing carbon dioxide from the atmosphere (JGOFS: Joint Global Ocean Flux Study; Brewer et al. 1986). Discussion of the biological oceanography working group were focussed on exploring how the following points from the Canadian National Programme for JGOFS (Platt et al. 1989) might be studied within the Gulf of St. Lawrence System:

1) Comparative studies of phase (relative timing) relationships in food web dynamics in different upper ocean regimes as they relate to export of biogenic material from the photic zone.
2) Process studies aimed at the elucidation of major pathways of carbon as they relate to export from the photic zone.
3) Measurement of vertical fluxes of nutrients into and export of biogenic material from the photic zone under stable and perturbed conditions in contrasting oceanic regimes.
4) Studies of remineralization of organic matter at the benthic boundary layer in contrasting environments.
5) Process studies aimed at determining the relationship between autotrophic production of reduced carbon in the photic zone and its delivery to the benthic boundary layer.

Why the Gulf of St. Lawrence?

The international JGOFS programme will address oceanic carbon flux by developing global scale budgets and conducting process-oriented studies. Given the limited nature of Canadian scientific resources, the Canadian National Programme for JGOFS recommends that an important part of our national effort be directed at process studies (Platt et al. 1989). Because process studies are difficult to carry out at the large horizontal and vertical scales of the open ocean, we should concentrate on key mechanisms which can be studied within reduced-scale systems such as the Gulf of St. Lawrence. For example, hydrodynamic control of carbon fluxes (Legendre and Demers 1984; Taggart and Leggett 1987) and seasonal aspects of carbon flux are easier to study in a nearshore setting than offshore. Furthermore, *in situ* calibration of remote sensing information is also much simpler, in logistic terms, when study areas are located closer to shore (e.g. Falkowski 1988; Platt and Sathyendranath 1988). In addition to providing convenient reduced-scale systems for the study of oceanic processes, continental shelves are themselves important to global carbon flux, in terms of sedimentation, primary production and sequestration of carbon (Hargrave 1986; Holser et al. 1988). Moreover, the largest anthropogenic impacts primaire et la fixation du carbone, importantes en elles-mêmes dans le flux du carbone à l'échelle de la planète (Hargrave 1986; Holser *et al.* 1988). D'ailleurs, les plus grands impacts anthropogéniques sur l'océan mondial ont lieu et continueront d'avoir lieu sur les marges continentales.

Le golfe du Saint-Laurent possède une grande variété de conditions hydrodynamiques, notamment une couverture saisonnière de glace, des polynies, des fronts, tourbillons, des apports d'eau douce et les influences qui s'y rattachent, ainsi que de fortes variations saisonnières de la stratification verticale. Ces variations régionales et temporelles des caractéristiques physiques et chimiques du Golfe produiront des conditions différentes, i.e. différents sous-systèmes modèles de production et d'exportation de carbone biogène. Le Golfe pourrait aussi servir de modèle pour l'étude de l'influence des glaces marines sur la productivité primaire à des latitudes septentrionales. Un autre avantage à mener des études de type JGOFS dans le Golfe, est qu'il y existe une grande quantité d'informations sur les processus océanographiques physiques ainsi que sur la pêche. Cependant, l'information sur l'océanographie biologique est actuellement incomplète ou limitée à des variables d'état (ex. la biomasse).

Certains processus de transfert de carbone sur le plateau continental peuvent être différents de ceux qui se produisent en haute mer. En haute mer, on croit généralement que l'exportation de carbone (de la surface de la mer) résulte de la sédimentation de particules biogènes et peut-être aussi de la convection, à grande échelle, de matière organique dissoute (Toggweiler 1989; Legendre et Gosselin 1989). De plus, la contribution des organismes effectuant des migrations verticales, à l'exportation et à la fixation de carbone, pourrait être plus élevée sur le plateau continental qu'en haute mer. L'importance de la pêche sur le flux de carbone au-dessus du plateau continental et dans les régions côtières, devrait également être examinée, au moins de façon théorique. Les migrations de poissons pourrait représenter un important transport horizontal de carbone. La pêche commerciale pourrait, quant à elle, représenter un important transport de carbone vers les systèmes continentaux.

Il est cependant important de reconnaître qu'un système côtier comme le golfe du Saint-Laurent ne peut être utilisé comme un modèle exact, à échelle réduite, des bassins océaniques, dans lesquels l'échange entre les eaux côtières et les eaux hauturières se fait généralement à la rupture du talus continental. Dans le golfe du Saint-Laurent, un chenal profond pénètre loin dans l'Estuaire, plaçant ainsi les eaux profondes à proximité des régions côtières. Cela limite l'utilisation du Golfe comme océan en miniature, du moins en ce qui concerne les processus de transport horizontal. Il s'ensuit que les études de type JGOFS dans le Golfe devraient viser les processus qui contrôlent le flux vertical de carbone, sans perdre de vue le fait que le transport horizontal est une caractéristique importante du plateau continental et que cette caractéristique est différente à plusieurs égards de celle de la haute mer. Parmi les autres caractéristiques importantes de la haute mer qu'on ne retrouve pas dans le Golfe mentionnons les processus associés aux grandes profondeurs, comme la convection et le transport horizontaux en profondeur de carbone organique dissous (COD).

on the world ocean occur and will continue to occur on the continental margins.

The Gulf of St. Lawrence contains a wide range of hydrodynamic conditions including seasonal ice cover, polynyas, fronts, gyres, freshwater input and influences, and large seasonal variations in vertical stratification. These regional and temporal variations in physical and chemical characteristics within the Gulf will produce different conditions, i.e. different model sub-systems, for the production and export of biogenic carbon. The Gulf could also serve as a model system for studying the influence of sea-ice on primary productivity at high latitudes. Another advantage of conducting JGOFS type studies in the Gulf is that there is a wealth of background information on physical oceanographic processes and fisheries. However, biological oceanographic information is presently under-developed or limited to state variables (e.g. biomass).

Some carbon transfer processes in shelf regions may not be identical to those of the open ocean. In the open sea, it is generally assumed that the export of carbon (from the sea surface) is largely through sinking of biogenic particles and possibly by large-scale convection of dissolved organic matter (Toggweiler 1989; Legendre and Gosselin 1989). In addition, the contribution of vertically migrating organisms to export and sequestration of carbon may be greater in shelf areas than in the open ocean. The importance of fisheries to carbon flux in coastal and shelf areas should also be explored, at least in a theoretical sense. Fish migration may represent an important horizontal transport of carbon; commercial fishing may be an important transfer of carbon into continental systems.

It is important to point out, however, that nearshore systems such as the Gulf of St. Lawrence cannot be used as complete reduced-scale models of major oceanic basins, in which exchange between coastal waters and the open ocean is generally across a shelf break. In the Gulf of St. Lawrence, a deep channel penetrates directly into the estuarine region, thus placing deep waters in close proximity to coastal areas. This restrains use of the Gulf as a mini-ocean, at least as far as horizontal transport processes are concerned. It follows that JGOFS studies in the Gulf should focus on processes that control vertical fluxes of carbon, while taking into consideration the fact that horizontal transport is an important feature of shelf systems and that this feature may differ in many aspects from that of the open ocean. Other important features of the open ocean not found in the Gulf are deep-water processes such as deep convection and deep horizontal transport of DOC.

Le programme national canadien pour JGOFS: le golfe du Saint-Laurent

Le groupe de travail recommande un ensemble d'études en océanographie biologique reliées au programme national canadien pour JGOFS et tenant compte des avantages et des limitations liés au golfe du Saint Laurent déjà présentés. Ces études sont axées sur les processus qui provoquent l'exportation de carbone biogène vers les eaux profondes plutôt que de le diriger vers les mécanismes de recyclage.

1) Étant donné le manque d'information, la mesure des taux biologiques doit être privilégiée dans le golfe du Saint Laurent. Les informations existantes (ex. les fichiers de données du Programme biologique international, ou PBI; voir de Lafontaine *et al.* 1991) pourraient être utilisées ou analysées davantage afin d'orienter les études sur les processus.
2) On devrait identifier l'ensemble des conditions hydrodynamiques qui favorisent, de façon générale, l'exportation verticale par rapport au recyclage *in situ* de matières organiques (ex. Jenkins et Goldman 1985; Platt et Harrison 1985; Legendre et Le Fèvre 1989). Puisque aucune méthode unique ne permet de quantifier la production, l'exportation et le recyclage, il sera nécessaire d'utiliser plusieurs approches (ex. les bilans d'oxygène, les études fondées sur la prise de ^{15}N, les pièges à sédiments, les études de production secondaire).
3) Puisqu'une exportation significative requiert des chaînes alimentaires courtes, composées généralement de grosses cellules phytoplanctoniques (Ryther 1969), il serait avantageux de relier la production de ces grosses cellules à des conditions hydrodynamiques spécifiques. Par exemple, trois réseaux trophiques planctoniques (qui constituent autant de systèmes d'exportation de carbone), qui semblent être dépendants de la stratification de densité, ont été reconnus dans le golfe du Saint Laurent (voir de Lafontaine *et al.* 1991).
4) L'importance de la synchronisation de la production primaire et secondaire quant au contrôle de l'exportation de matière organique devrait être évaluée (par ex., Parsons et Lalli 1988). Ainsi, en absence de broutage actif par les producteurs secondaires, les poussées printanières de diatomées pourraient avoir comme résultat la sédimentation rapide des cellules au lieu de leur entrée dans les réseaux trophiques pélagiques. Par ailleurs, la transformation de la biomasse phytoplanctonique par le réseau trophique pélagique conduit à une importante reminéralisation du carbone organique par de la respiration, réduisant ainsi l'exportation nette vers les eaux profondes.
5) Comme il existe plusieurs formes de carbone, il est important d'établir comment les propriétés qualitatives de la matière organique influent sur la façon dont elle est transformée par les écosystèmes marins. Par exemple, dans les couches supérieures de l'océan, les consommateurs primaires peuvent habituellement déceler des différences d'ordre qualitatif entre des particules de taille semblable (Huntley *et al.,* 1983)

The Canadian National Programme for JGOFS: Gulf of St. Lawrence

The working group recommends a set of biological oceanographic studies relative to the Canadian National Programme for JGOFS, that take into account the above discussed advantages and limitations of the Gulf of St. Lawrence. These studies focus on processes leading to the export of biogenic carbon into deep waters rather than being directed toward recycling mechanisms.

1) Given the present paucity of information, measurement of biological rate variables in the Gulf of St. Lawrence should be emphasized. Some existing information (e.g. IBP data sets; see de Lafontaine et al. 1991) could nonetheless be used or further analysed in order to orientate process studies.
2) Sets of hydrodynamic conditions that generally favour vertical export over *in situ* recycling of organic matter should be identified (e.g. Jenkins and Goldman 1985; Platt and Harrison 1985; Legendre and Le Fèvre 1989). Since no single method allows quantification of production, export, and recycling, application of several approaches will be necessary (e.g. oxygen budgets, ^{15}N uptake studies, sediment traps, secondary production studies).
3) Since significant export requires short food chains, which are generally based on large phytoplankton cells (Ryther 1969), it would be advantageous to relate production of large phytoplankton to specific hydrodynamic conditions. For example, three planktonic food webs (and thus carbon export systems) that appear to depend on density stratification have already been identified in the Gulf of St. Lawrence (see de Lafontaine et al. 1991).
4) The importance of relative timing (phasing) of primary and secondary production in the control of organic matter export should be assessed (e.g. Parsons and Lalli 1988). For example, without active grazing by secondary producers, spring diatom blooms may result in rapid sinking of cells rather than their entry into the pelagic food web. On the other hand, processing phytoplankton biomass by the pelagic food web results in considerable remineralization of fixed organic carbon through respiration, thus reducing net carbon export to deep waters.
5) Since "all carbon is not equal", it is important to identify how qualitative properties of organic matter affect the way it is processed by the marine ecosystems. For example, in the upper ocean, primary consumers can generally detect qualitative differences between similarly sized particles (e.g. Huntley et al. 1983) and between phytoplankton cells of the same species but in different growth states (e.g.

et des cellules de phytoplancton de la même espèce mais à des stades de croissance différents (Cowles *et al.*, 1988). Les effets de la qualité de la nourriture sur l'alimentation, la croissance et les taux de reproduction devraient être étudiés pour les plus importantes espèces de zooplancton du golfe du Saint-Laurent. Il faudrait également évaluer l'importance des différentes sources de carbone organique particulaire (phytoplancton, algues macroscopiques, plantes d'origine terrestre, etc.) de même que les voies de circulation des divers types de carbone. Pour ce faire, on pourrait utiliser certains marqueurs biomoléculaires spécifiques (pigments, phytotoxines, marqueurs lipidiques) que renferme la matière organique particulaire (Gieskes et Kraay, 1986; Roy *et al.*, 1989). Dans la couche benthique, des différences qualitatives présentées par la matière organique en voie de sédimentation (cellules intactes de phytoplancton vs pelotes fécales, carbone d'origine terrestre vs carbone d'origine marine) peuvent en influencer le sort (c'est-à-dire enfouissement vs reminéralisation du carbone).

6) Legendre et Le Fèvre (1989) ont décrit différentes voies d'exportation du carbone biogène (fig. 2), y compris l'exportation des grosses cellules par l'intermédiaire des herbivores (broutage, principalement par les copépodes) et celle des petites cellules qui résulte de l'alimentation de type «baleines à fanons» (broutage par les appendiculaires). On pourrait évaluer l'importance relative de ces deux voies en examinant la production et le broutage des grosses et des petites cellules dans la zone euphotique. On pourrait compléter cette étude par un examen des cycles de reproduction et des liens trophiques avec les poissons dont les larves dépendent, pour se nourrir, de la voie herbivore (par exemple, les poissons autres que les poissons plats) et ceux dont les larves peuvent se nourrir d'appendiculaires (par exemple, les poissons plats; Last, 1980).

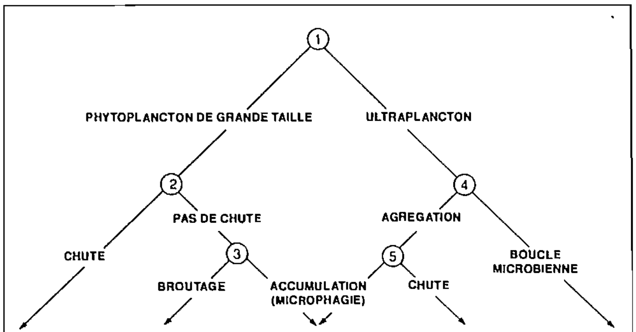

FIG. 2. Modèle à bifurcations de la production exportée (flèches vers le bas) dans les océans (d'après Legendre et Le Fèvre, 1989). Le modèle ne suppose pas de hiérarchie entre les facteurs physiques responsables des bifurcations puisque plusieurs bifurcations peuvent coexister. Figure tirée du Dahlem Workshop Report LS 44, p. 51, Chichester, John Wiley & Sons; reproduction autorisée.

Cowles et al. 1988). Effects of food quality on feeding, growth and reproductive rates should be examined for the most important zooplankton species in the Gulf of St. Lawrence. The different sources of particulate organic carbon should also be quantified (e.g. phytoplankton, macro-algae, terrestrial plants, etc.) and the pathways of quality-related carbon cycling identified. This could be accomplished by studying the fate of specific biomolecular tracers (e.g. pigments, phytotoxins, lipid markers) contained in particulate organic matter (e.g. Gieskes and Kraay 1986; Roy et al. 1989). In the benthic boundary layer, qualitative differences in sedimenting organic material (e.g. intact phytoplankton cells versus faecal pellets, terrestrial versus marine carbon) may influence its ultimate fate (i.e. carbon burial versus carbon remineralization).

6) Legendre and Le Fèvre (1989) describe various pathways for export of biogenic carbon (Fig. 2), including the export of large cells through herbivores (grazing, mainly by copepods) and that of small cells through "baleen whale" feeding (appendicularian shunt). The relative importance of these two pathways can be assessed by looking at the production and grazing of large and small cells in the euphotic zone. A complementary approach would be to examine the reproductive cycles and trophic relationships of fish whose larvae depend on the herbivory pathway (e.g. round fish) versus those whose larvae can feed on appendicularians (e.g. flatfish; Last 1980).

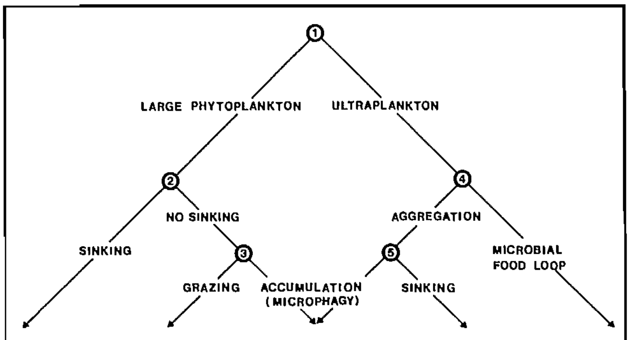

FIG. 2. Bifurcation model of export production (downward arrows) in oceans (from Legendre and Le Fèvre 1989). The model does not imply hierarchy among physical factors causing the bifurcations, since several bifurcations may take place simultaneously. Reprinted with permission from the Dahlem Workshop Report LS 44, p. 51, Chichester, John Wiley & Sons.

7) Un des effets possibles des changements climatiques serait la modification des conditions qui déterminent les voies d'exportation du carbone. On devrait étudier les effets théoriques que pourraient avoir sur les pêches commerciales un changement des voies d'exportation (par exemple, effets sur la productivité ou le déplacement des stocks). Il faudrait également étudier les effets directs que pourraient avoir les changements climatiques sur les pêches (par exemple, modification de la température de l'eau, de la salinité ou des patrons de circulation).

8) Les aspects théoriques de l'influence des pêches sur les écosystèmes (et par conséquent sur la transformation du carbone) devraient être examinés. Par exemple, si des espèces exploitées agissent sur les communautés marines par le biais de la prédation ou si elles influent sur la synchronisation relative de la production primaire et secondaire, les activités de pêche commerciale pourraient modifier cette interaction. La structure des communautés et l'existence de synchronismes peuvent être des éléments déterminants de l'exportation du carbone. De plus, la consommation de biomasse planctonique et son recyclage sont très importants pendant la phase de croissance des larves de poissons pélagiques; une modification de ce mécanisme de recyclage pourrait agir globalement sur la productivité et l'exportation.

9) Il est indispensable d'étudier l'association des processus benthiques et pélagiques pour comprendre le recyclage et l'enfouissement de la matière organique en voie de sédimentation dans le milieu benthique, particulièrement en termes d'apports saisonniers ou à plus court terme de matière organique (Eppley *et al.*, 1983; Vézina et Platt, 1987).

10) La structure des communautés benthiques peut exercer une influence importante sur la transformation de la matière organique dans les sédiments, y compris sur la relation entre la reminéralisation et l'enfouissement du carbone. Il faudrait étudier les facteurs physiques (sédimentation, régimes des courants) et biotiques (quantité et qualité de l'apport de nourriture) qui agissent sur la structure de la communauté benthique. Par exemple, on a suggéré que la sédimentation de carcasses pouvait être un facteur important expliquant la structure de certaines communautés benthiques (Rowe et Staresinic, 1979; Stockton et De Laca, 1982).

11) Il faudrait étudier le flux ascendant direct de la matière organique particulaire ou dissoute depuis le benthos jusqu'en milieu pélagique. Une étude récente a révélé l'existence d'un flux ascendant important (mesuré en profondeur) de carbone organique particulaire provenant du benthos profond, représentant de 10 à 20 pour cent de la matière qui atteint le fond de l'océan, sous la forme de masses d'oeufs et de gouttellettes de lipides (Smith *et al.*, 1989). La production de ce type de substances est vraisemblablement importante dans les systèmes du plateau continental (comme le golfe du Saint-Laurent) où les organismes benthiques sont abondants.

7) One possible effect of climate change will be to modify conditions that determine pathways of carbon export. Theoretical consideration should be given to possible effects on commercial fisheries of changing export pathways (e.g. productivity, displacement of stocks). Possible direct effects of climate change on fisheries (e.g. modification of water temperature, salinity or circulation patterns) should also be considered.

8) Theoretical consideration should be given to possible effects of fisheries on ecosystems (and thus carbon processing). For example, if exploited species affect marine communities through predation or influence relative timing of primary and secondary production, these effects could be modified by commercial fishing. Community structure and phase relationships may be important determinants of carbon export. Furthermore, considerable plankton biomass is consumed and recycled during the growth of pelagic fish larvae; alteration of this recycling mechanism could affect overall productivity and export.

9) It will be essential to study the coupling of benthic and water column processes in order to understand the recycling and burial of sedimenting organic matter in the benthic environment, particularly in terms of seasonal or shorter-term pulses of organic matter (Eppley et al. 1983; Vézina and Platt 1987).

10) Benthic community structure may have important influences on organic matter processing in the sediments, including the relationship between the remineralization and burial of carbon. Physical (sedimentation, current regimes) and biotic (quantity and quality of food supply) factors controlling benthic community structure need to be investigated. For example, carcass falls have been proposed as an important factor in the structuring of some benthic communities (Rowe and Staresinic 1979; Stockton and De Laca 1982).

11) Direct upward flux of particulate and dissolved organic matter from the benthos into the pelagic environment should be investigated. A recent study has revealed a significant upward flux (measured at depth) of particulate organic carbon from the deep-sea benthos, equal to 10–20 % of material reaching the seafloor, in the form of egg masses and lipid globules (Smith et al. 1989). Production of this type of material is likely to be important in shelf systems (e.g. the Gulf of St. Lawrence) where benthic organisms are abundant.

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Rapport de l'atelier de travail sur les poissons[1]

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Introduction

En premier lieu, le groupe de travail a examiné les deux volets de son mandat :

1. identifier les lacunes dans les connaissances touchant la biologie des populations de poissons pour les espèces du golfe du Saint-Laurent présentant une valeur commerciale;
2. envisager la possibilité d'utiliser le golfe du Saint-Laurent comme un laboratoire naturel pour l'étude des problèmes majeurs concernant la biologie des populations de poissons.

Nous recommandons d'aborder le premier volet du mandat de façon systématique en utilisant comme cadre de référence la base de données sur l'évaluation des stocks pour déceler les lacunes dans nos connaissances. Plusieurs étapes doivent être prises en considération pour l'évaluation des stocks :

1. définir les unités de gestion géographiques adéquates;
2. évaluer l'effectif des poissons pour l'unité à gérer (incluant la taille des classes d'âge responsables du recrutement);
3. effectuer le calcul du taux de mortalité par exploitation, des niveaux de prise ou de l'effort de pêche annuel pour les espèces en question, selon les objectifs de gestion halieutique (c.-à-d. $F_{0\cdot1}$, f_{msy}, maintien de la biomasse des stocks de frai, etc.);

Il existe déjà une méthodologie de routine qui est commune à plusieurs unités de gestion halieutique dans la Zone atlantique, y compris celles qui se trouvent dans le golfe du Saint-Laurent. Une liste des exigences en termes de connaissances et de données a été dressée, et les insuffisances pour chaque unité de gestion ont été évaluées. Les résultats de cette analyse sont résumés sous forme

Report of the Workshop on Fish[1]

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Introduction

The Working Group initially reviewed the two aspects of their mandate:

1. To identify gaps in knowledge in the population biology of commercially important fish species in the Gulf of St. Lawrence;
2. To consider how the Gulf of St. Lawrence can be used as a natural laboratory to study major problems in the population biology of fishes.

It was proposed that the first aspect be addressed in a systematic manner using the stock assessment framework as a structure to identify gaps in knowledge. There can be considered to be several steps in stock assessments:

1. Definition of the appropriate geographic management units;
2. Estimation of the abundance of fish in the management unit (including estimation of the size of the recruiting year classes);
3. Calculation of the appropriate fishing mortality, annual catch or effort levels for the fish species in question given the fisheries management objectives (i.e., $F_{0\cdot1}$, f_{msy}, maintenance of spawning stock biomass, etc.);

There is in place a routine methodology that is common to many fish management units in the Atlantic Zone, including those in the Gulf of St. Lawrence. A list of requirements (both knowledge and data) was drawn up and deficiencies for each of the management units were evaluated. The results of the analysis are summarized in a matrix form in Table 1. The discussion of this aspect

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[1] Ce rapport fait partie des Comptes rendus d'un atelier/symposium tenu à l'Institut Maurice-Lamontagne, Mont-Joli (Québec) du 14 au 17 mars 1989.

[1] This report forms part of the Proceedings of a Workshop/Symposium held at the Maurice Lamontagne Institute, Mont-Joli, Quebec, 14–17 March 1989.

TABLEAU 1. Sommaire des connaissances scientifiques portant sur les stocks de poissons dans le golfe du Saint-Laurent. (N.A. = non applicable; [ ] = pas de données; * = données incomplètes; ** = données satisfaisantes.)

Stock	Information statistique sur		L'effort de pêche dirigé	Échantillonnage biologique des		Études d'abondance R/V pour		Les études biologiques
	La prise nominale	La prise rejetée		Prises	Rejets	Les stocks	Les recrues	L'identification du stock
Poissons de fond								
3PN, 4RS morue	*		*	**		*		*
4T, Vn morue	*		*	**	*	**		*
4RST sébaste	**	*	**	**	*	*	*	*
4T plie canadienne	*	*	*	*	*	*		*
4RS plie grise	*			*		*		
4RST flétan atlantique	*		N.A.	*				
4RST flétan du Groenland	*			*		*		
4R merluche blanche	*		**	**		*		*
Pélagiques								
4RST capelan	*	*		*				*
4R hareng	**		**	**	*			*
4S hareng	*			*				*
4T hareng	**		**	**		*		*
Maquereau	*		*	**		*		*
Thon	**	N.A.	**	*	N.A.			N.A.
Anadromes								
Alose et gaspareau								
(Miramichi)	**		*	**		*		*
(Margaree)	**		*	**		*		*
Saumon								
(Terre-Neuve et Labr.)	**		*	**		*		*
(Restigouche)	**		*	**		*		*
(Miramichi)	**		**	**		**		**
(Margaree)	**		**	**		*		*
Éperlan	**		*					

TABLE 1. Summary of scientific knowledge on the fish stocks in the Gulf of St. Lawrence. (N.A. = Not applicable; [blank] = No data; * = Deficiencies in data; ** = Data satisfactory.)

Stock	Statistical information on		Directed fishing effort	Biological sampling of		R/V abundance surveys for		Biological studies
	Nominal catch	Discarded catch		Catches	Discards	Stock	Recruits	Stock ID
Groundfish								
3PN, 4RS Cod	*		*	**		*		*
4T, Vn Cod	*		*	**	*	**		*
4RST Redfish	**	*	**	**	*	*	*	*
4T Am. Plaice	*	*	*	*	*	*		*
4RS Witch	*			*		*		
4RST Atl. halibut	*		N.A.	*				
4RST Gr. halibut	*			*		*		
4R White hake	*		**	**		*		*
Pelagics								
4RST Capelin	*	*		*				*
4R Herring	**		**	**	*			*
4S Herring	*			*				*
4T HErring	**		**	**		*		*
Mackerel	*		*	**		*		*
Tuna	**	N.A.	**	*	N.A.			N.A.
Anadromous								
Alew. & Gasp.								
(Miramichi)	**		*	**		*		*
(Margaree)	**		*	**		*		*
Salmon								
(Nfld. & Labr)	**		*	**		*		*
(Restigouche)	**		*	**		*		*
(Miramichi)	**		**	**		**		**
(Margaree)	**		**	**		*		*
Smelt	**		*					

de matrice au tableau 1. La discussion sur cet aspect du mandat fut brève et les priorités n'ont pas été établies.

Avant d'aborder le deuxième aspect de notre mandat, nous nous sommes penchés sur les caractéristiques propres au golfe du Saint-Laurent qui font de cette mer intérieure un «lieu expérimental» de choix pour résoudre des questions de grande importance touchant la biologie des populations de poissons. Nous avons relevé les particularités suivantes :

1. Les cycles de vie de populations de plusieurs espèces se déroulent entièrement à l'intérieur des limites du golfe.
2. Il existe des différences entre les populations des espèces du golfe et celles des régions contiguës des Grands Bancs de Terre-Neuve et du plateau Néo-Écossais. Ces différences comprennent l'effectif relatif des classes d'âges, l'époque du frai et les tendances de la biomasse.
3. Ces différences entre les populations de poissons du golfe et celles qui se trouvent à l'extérieur de celui-ci impliquent que les processus qui règlent la dynamique des populations se manifestent dans les limites mêmes de cette région géographique.
4. Les caractéristiques d'ordre océanographique tout comme celles qui sont propres aux populations témoignent de l'existence d'une structure spatiale à l'intérieur du golfe. Par exemple, afin de faciliter l'analyse des tendances temporelles de la température à la surface de la mer (TSM) durant la période de 1944 à 1977, Budgen et al. (1982) ont divisé le golfe en trois zones géographiques (nord-est, nord-ouest et bancs Madeleine). Cette analyse a montré que les tendances de la TSM étaient uniformes partout dans le golfe pendant l'hiver, mais qu'au printemps et en été, des différences se manifestaient entre les zones. On a également constaté, dans les différentes parties du golfe, des différences dans les cycles saisonniers de la production primaire, dans la composition des espèces phytoplanctoniques et dans la structure par taille du zooplancton. Tout semble indiquer que, chez quelques espèces, il existe dans le golfe plusieurs populations qui se maintiennent d'elles-mêmes. Cette structure spatiale à l'intérieur du golfe pourrait servir de base à des études comparatives fructueuses.
5. Certains indices révèlent une importante variabilité interannuelle des conditions environnementales et des fluctuations de populations. Citons encore une fois Budgen *et al.* (1982) qui ont analysé la variabilité interannuelle de l'épaisseur de la couche médiane froide, les profils d'éléments nutritifs, la biomasse du phytoplancton (pour l'estuaire du Saint-Laurent seulement) et l'effectif des classes d'âges du hareng, du maquereau et de la morue. Dans chaque cas, ils ont enregistré un signal interannuel important. Koutitonsky (ce document) a montré que les particularités saisonnières ainsi que l'apport annuel d'eau douce varient considérablement d'une année à l'autre, mais les participants ont noté également que le coefficient de variabilité de l'apport annuel d'eau douce pour les années de 1950 à 1979 n'était que de 10 %.
6. Lors des migrations saisonnières, plusieurs espèces de poissons du golfe du Saint-Laurent empruntent des itinéraires bien définis. Les migrations de cycle de vie chez les poissons peuvent être plus facilement étudiées

of the mandate was short and priorities were not identified.

Prior to addressing the second component of the mandate of the Working Group, there was a discussion of the features of the Gulf of St. Lawrence that make this inland sea an attractive "experimental" area for the resolution of substantial issues in fish population biology. The features that were identifies are:

1. The life cycles of populations of several fish species are contained within the Gulf.
2. There are differences between populations of species in the Gulf compared with those in contiguous areas on the Grand Banks and the Scotian Shelf. Those differences include relative year-class strengths, timing of spawning and biomass trends.
3. The above-note differences between populations of fish species within and outside the Gulf infer that processes controlling the dynamics occur within this geographic area.
4. There is evidence of spatial structure within the Gulf in both oceanographic and fish population features. For example, Bugden et al. (1982) divided the Gulf into three geographic areas (northwest, northeast and Magdalen Shallows) to facilitate an analysis of temporal trends in sea surface temperature during the period 1944–77. The analysis indicated that there was coherence in the SST trends throughout the Gulf during the winter, but differences in the trends between the areas during spring and summer. There is also some evidence of differences in seasonal cycles of primary production, phytoplankton species composition and the size structure of zooplankton in different parts of the Gulf. For some fish species, there is convincing evidence that several self-sustaining populations exist in the Gulf. This spatial structure within the Gulf could provide a basis for fruitful comparative studies.
5. There is evidence of strong interannual variability in environmental features and in population fluctuations. Again, by way of example, Bugden et al. (1982) analyzed the interannual variability in the thickness of the intermediate cold layer, nutrient profiles, phytoplankton biomass (lower St. Lawrence Estuary only) and year-class strengths of herring, mackerel and cod. In each case a strong interannual signal was noted. The seasonal features, as well as the annual freshwater runoff, were shown to vary considerably between years by Koutitonsky (this volume); but it was also noted by the Working Group that the coefficient of variability for the annual runoff for the period 1950 to 1979 is only 10%.
6. Several fish species in the Gulf of St. Lawrence migrate seasonally in well defined patterns. Given the enclosed nature of the Gulf and the predictability of the migration patterns, fish life-cycle migrations may be more

dans le golfe que dans d'autres régions de la plateforme continentale, étant donné le caractère mi-clos que présente le golfe ainsi que la nature prévisible des patrons de migration.

7. En raison des conditions de température sur les bancs Madeleine (eau froide en hiver, eau tiède pendant les mois d'été), le golfe du Saint-Laurent est une région biogéographique complexe. Des espèces de poissons boréales côtoient des espèces habitant des eaux plus tempérées. Chacune de ces espèces se retrouve à la limite septentrionale ou méridionale de sa distribution géographique naturelle. C'est pourquoi le golfe constitue un endroit particulièrement favorable à l'étude de l'impact des changements climatiques.

En considérant ces caractéristiques du golfe du Saint-Laurent, nous avons échangé sur les sujets de recherche touchant la biologie des populations qui méritaient une attention plus particulière de la part de notre groupe de travail. Cinq sujets ont été sélectionnés :

1. relations entre les migrations associées au cycle biologique et les processus océanographiques,
2. variabilité du recrutement,
3. variabilité génétique des populations de poissons,
4. polluants chimiques et populations de poissons,
5. biogéographie des poissons et réchauffement terrestre.

Pour chacun de ces sujets, nous avons relevé les problèmes concernant la recherche sur les populations de poissons du golfe du Saint-Laurent. Nous en faisons une brève description dans les sections suivantes. Certains des sujets sont examinés en détail, et des canevas de projets de recherche sont présentés. En ce qui concerne les autres sujets, nous ne faisons qu'un simple exposé de la nature des questions qui se posent pour la recherche.

Relations entre les migrations associées au cycle biologique et les processus océanographiques

Nous avons traité de ces questions de recherche et des méthodes pour les aborder en fonction de trois aspects des migrations associées au cycle biologique :

1. l'époque des migrations de frai, par l'étude des diverses populations de hareng de l'Atlantique du golfe, dans le but de vérifier certains concepts-clés en biologie halieutique;
2. l'époque des migrations des juvéniles, par l'étude des smolts du saumon de l'Atlantique provenant de populations de différentes rivières qui se déversent dans le golfe du Saint-Laurent;
3. l'époque des migrations d'hivernage de poissons adultes, par l'étude des complexes de populations de morue des zones 4T et 4RS, afin de mettre au point des méthodes d'expérimentation.

Nous présentons ci-dessous nos premières réflexions concernant ces projets de recherche :

1. *Migrations des poissons :* hareng de l'Atlantique et saumon de l'Atlantique

   Historique : On retrouve des populations de saumon et de hareng partout dans le golfe du Saint-Laurent. Le moment des migrations de frai du hareng, au printemps et en automne, ne semble pas varier d'une région du golfe à l'autre. En revanche, le moment des migrations des smolts varie selon les régions. Puisque l'on croit que les cycles saisonniers de productivité pré-

readily studied in the Gulf compared to other shelf areas.

7. The Gulf of St. Lawrence, because of both cold water conditions during winter and warm water during the summer months on the Magdalen Shallows, is a complicated biogeographic area. Northern boreal fish species coexist with more temperate water species. Species are found both at the northern and southern limits of their geographic range. Thus the Gulf is a particularly opportune location to study the impact of climate change.

From the perspective of the above characteristics of the Gulf of St. Lawrence, there was a discussion of what research themes within the field of fish population biology should be selected for detailed discussion by the Working Group. Five themes were identified:

1. Life-cycle migrations in relation to oceanographic processes;
2. Recruitment variability;
3. Genetic variability of fish populations;
4. Chemical contaminants in fish populations;
5. Fish biogeography and global warming.

Research problems based on fish populations in the Gulf of St. Lawrence were identified for each theme. These are briefly described in the following sections. Some themes were discussed in some detail and outlines of research projects presented. For other themes, only a general statement of the nature of the research problem is defined.

Life-Cycle Migrations in Relation to Oceanographic Processes

Research problems and approaches to their study were developed for three aspects of life-cycle migration:

1. Timing of spawning migrations using the diverse Atlantic herring populations in the Gulf to test some key concepts in fisheries biology;
2. Timing of juvenile migrations using smolts of Atlantic salmon from populations of different rivers entering the Gulf of St. Lawrence;
3. Timing of overwintering migrations of adult fish using the cod population complexes of, respectively, 4T and 4RS to develop the experimental design.

Preliminary thoughts on these potential studies are provided below:

1. *Fish migrations:* Atlantic herring and Atlantic salmon.

   Background: Herring and salmon populations are found throughout the Gulf of St. Lawrence. Timing of the spring and autumn herring spawning migrations appears not to vary among different regions in the Gulf. By contrast, timing of salmon smolt migrations is variable among different regions in the Gulf. Because it is believed that seasonal productivity cycles vary spatially and temporally, the Gulf provides a sentent des variations spatiales et temporelles, le golfe offre une occasion unique pour déterminer s'il existe un lien entre les migrations du hareng et du saumon et les cycles de productivité primaire et secondaire.

Hypothèse : Les périodes de migration du hareng et du saumon sont indépendantes des cycles de production marine du golfe du Saint-Laurent. En gros, cette expérience consisterait en deux vérifications de l'hypothèse «bien assorti/mal assorti» («match-mismatch», Cushing 1975). Premièrement, on vérifiera si le frai du hareng et, subséquemment, le début de l'alimentation des larves sont synchrones avec les cycles de production primaire et secondaire; selon cette hypothèse, ces cycles coïncideraient partout dans le golfe. Deuxièmement, on effectuerait des tests pour déterminer si la période de migration des smolts et la production de zooplancton ≥ 5mm sont synchrones; selon l'hypothèse, ces cycles présenteraient des variations importantes autour du golfe. De plus, la grosseur et le taux de croissance des smolts durant leur premier été en mer seraient dépendants de la grosseur et de la production du zooplancton.

Données : Les migrations du hareng et des tacons de saumon seront examinées en quatre régions différentes du golfe. Ces régions ont été définies par de Lafontaine *et al.* (1991), selon la dynamique du réseau alimentaire. Le nombre de frayères qui pourraient raisonnablement être échantillonnées est résumé ci-dessous :

Région	Stocks de hareng		Stocks de saumon
	Printemps	Automne	
Le nord du golfe	2	3	3
Courant giratoire du nord-ouest	2	2	3
Courant de Gaspé	2	2	3
Le sud du golfe	7	6	4

Les données suivantes seront cueillies dans chaque région :

- la date médiane d'arrivée des harengs à l'aire de frai;
- la date médiane de migration des tacons;
- la mesure quotidienne de la température à la surface et au fond;
- les écailles de saumons revenant les années suivantes afin de faire un estimé de la croissance durant la première année en mer;
- la cueillette hebdomadaire de larves de hareng servirait à déterminer la période de métamorphose.

Échéancier :

a) La variabilité spatiale des périodes de migration et sa relation avec les cycles de productivité pourraient être observées durant 1 à 3 ans. Notez aussi qu'une hypothèse connexe, qui examinerait la relation entre la grosseur des tacons et la grosseur des particules de nourriture dans les différents secteurs du golfe, pourrait être examinée en même temps.

b) Il faudrait environ 10 ans pour déterminer la variabilité annuelle des migrations et de la production marine, mais ceci dépendrait entièrement des résul-

unique opportunity to test if herring and salmon migrations are linked to cycles in primary and secondary productivity.

Hypothesis: The timing of herring and salmon migrations is independent of marine production cycles in the Gulf of St. Lawrence. Essentially, this experiment would provide two tests of the match–mismatch hypothesis (Cushing 1975). First, the spawning of herring and the subsequent first feeding of larvae would be tested for synchronicity with primary and secondary production cycles; the hypothesis would predict that these cycles were concurrent throughout the Gulf. Second, the migration time of smolts would be tested for synchronicity in the production of zooplankton ≥ 5 mm; the hypothesis would predict that there is significant variation in these cycles around the Gulf. In addition, the sizes and growth rates of smolts during their first summer at sea would be compared to sizes and production in the zooplankton community.

Data: Herring and salmon smolt migrations would be examined in four different areas of the Gulf. These areas have been defined according to food web dynamics by de Lafontaine et al. (1991). The number of spawning beds that could be reasonably sampled in each area are summarized below:

Area	Herring stocks		Salmon stocks
	Spring	Fall	
North Gulf	2	3	3
Northwest Gyre	2	2	3
Gaspé Current	2	2	3
Southern Gulf	7	6	4

The following data would be collected in each area:

- median date of arrival of herring on spawning grounds;
- median date of smolt migrations;
- daily measurements of surface and bottom temperature;
- scales of salmon returning in the following years to estimate growth during the first summer at sea;
- weekly collections of herring larvae would be used to identify time of metamorphosis.

Time Frame:

a) Spatial variability in run timing and its relationship to productivity cycles could be monitored for 1–3 yr. Note also that a related hypothesis, which would examine the relationship between smolt size and food particle size in different areas of the Gulf, could also be examined in this time frame.

b) Annual variability in run timing and marine production would require a time frame of about 10 yr, but would depend entirely on the results of (a). In particular, annual variation in time of tats de la partie a) ci-dessus. En particulier, la variation annuelle de la période de métamorphose pourrait être comparée à la chronologie du cycle de production. En ce qui concerne le saumon, on pourrait faire une comparaison entre les estimations de mortalité en mer et la variation annuelle de l'ensemble «migration des tacons-cycles de production.» Selon le CIEM et le CSCPCA, la variation touchant la mortalité en mer représente la lacune la plus importante dans les connaissances de la biologie du saumon.

2. *Migration des poissons :* La morue franche

Historique : La morue entre dans le golfe et en sort de façon assez prévisible au moment de la formation des glaces, en hiver. Les caractéristiques des deux stocks (3Pn4Rs et 4TVn) sont similaires, mais les prises fluctuent considérablement d'une année à l'autre (qu'il s'agisse de pêche commerciale ou de prises destinées aux recherches), ce qui indique de grandes variations locales de la densité de population de la morue dans les aires d'hivernage. Rose et Leggett (1988) ont démontré que les déplacements et la distribution des morues dans leurs aires d'alimentation intérieures résultaient d'interactions complexes entre la dynamique des masses d'eau et la distribution des capelans, leur principale proie. Il est probable que la distribution de la morue en hiver résulte d'interactions similaires entre les facteurs physiques et biologiques.

L'hypothèse : Le but de cette étude est d'identifier les facteurs qui influencent la distribution des morues en hiver. Il n'y a pas encore d'hypothèse spécifique à vérifier. Le but de cette étude est de comparer les deux stocks durant leur migration d'hivernage. Les facteurs environnementaux immédiats qui pourraient influencer ces migrations devraient être similaires dans le cas des deux stocks.

Puisque les deux stocks ont des caractéristiques biologiques différentes (structure d'âge, croissance, proies), il serait possible de vérifier les hypothèses reliant la migration à ces variables.

Données : Les statistiques sur les prises et l'effort de pêche sont disponibles pour des zones carrées de 10 minutes de cité. Ces carrés serviront de cadre pour des études intensives mensuelles, avec stratification aléatoire, des deux côtés du détroit de Cabot. Les études seront effectuées entre novembre et mars. Durant cette période, la biomasse par classes d'âge sera estimée pour chaque carré de 10 minutes de côté. Les résultats seraient ensuite comparés aux données, structurées par classes d'âge, sur les prises des pêches commerciales pour la même période.

Un équipement hydroacoustique serait utilisé afin de savoir où se trouvent les bancs de poissons de fond à l'intérieur de ces carrés. L'emploi fréquent des chaluts de fond et des chaluts pélagiques servirait à vérifier la composition de ces bancs.

En observant les changements qui apparaissent dans la structure par classes d'âge, il serait possible de détecter une éventuelle sélectivité selon la taille pendant les

metamorphosis could be compared to timing in the production cycle. For salmon, annual variation in the match between smolt migrations and production cycles could be compared to estimates of marine mortality. Variation in marine mortality has been identified by ICES and CAFSAC as the major gap in salmon biology.

2. *Fish migration:* Atlantic cod

Background: Cod migrate in and out the Gulf as the ice forms during the winter in a reasonably predictable manner. The characteristics of the migrations for the two stocks (3Pn4RS and 4TVn) are similar, yet there are large fluctuations from year to year in catch rates (either from the commercial fishery or research surveys), reflecting large variations in local density of cod on their overwintering grounds. Rose and Leggett (1988) have shown that the movement and distribution of cod on their inshore feeding grounds was the result of complex interactions between the dynamics of water masses and the distribution of capelin, their principal prey. It is probable that the winter distribution of cod is the result of similar interactions between physical and biological factors.

Hypothesis: The purpose of this study is to identify the factors that regulate the winter distribution of cod. There are not yet any specific hypotheses to test. The basis of this study is to compare the two stocks during their overwintering migration. The proximate environmental factors which may influence these migrations should be the same for both stocks.

Since both stocks have different biological characteristics (age structure, growth, preys), it would then be possible to test hypotheses relating migrations to these variables.

Data: Catch and effort statistics are available in both areas by 10 minute squares. These squares would provide the framework for intensive, random-stratified, monthly surveys on both sides of Cabot Strait. The surveys would occur from November to March. Estimates of biomass-at-age would be calculated for each 10 minute square during this time period. The surveys would then be compared to age-structured catch rate data in the commercial fishery when it occurred during the same time period.

Acoustic gear would be used to describe the location of groundfish schools within these squares. Frequent sets with bottom or midwater trawls would be used to verify the composition of these schools.

By following any seasonal changes in the age structure, it would be possible to identify possible size selectivity in the winter fisheries. Environmental conditions pêches d'hiver. Les conditions environnementales telles que le couvert de glace et les profils de température devraient être considérées dans l'analyse.

Les remarques qui ont été formulées à la suite d'une rencontre avec J. Runge ayant porté sur la migration des poissons (sur la question de la période de la migration de frai et des migrations des tacons plus particulièrement) sont intéressantes et font partie de notre compte rendu.

Commentaires sur le projet de recherche sur la migration des poissons (J. Runge)

Le hareng de l'Atlantique et le saumon de l'Atlantique

Selon l'hypothèse formulée dans le projet de recherche, la période de migration des harengs et des saumons est indépendante des cycles de production dans le golfe du Saint-Laurent. Nous entendons par là qu'il n'y a pas de lien significatif entre le temps de migration (mesuré en jours juliens) et la période de production maximale (mesurée aussi en jours juliens), comme l'illustre la figure 1, une correction pouvant être faite pour tenir compte du rapport de dépendance entre la température et la période d'éclosion. Le projet de recherche soutient que l'hypothèse pourrait être vérifiée par une étude de la chronologie des cycles de production primaire et secondaire en relation avec la chronologie du frai du hareng ainsi que par la mesure du déroulement du cycle d'abondance des grands organismes zooplanctoniques en relation avec la migration des tacons. Comme nous allons le voir plus loin, on ne sait pas très bien ce qui peut donner une mesure adéquate des cycles de production en ce qui concerne l'aire d'alimentation des harengs larvaires et des tacons. Cette recherche pourrait toutefois être fructueuse. On trouvera dans les commentaires qui suivent des recommendations concernant la mesure des variables dans le cycle de production et des remarques sur la signification possible des résultats de cette recherche.

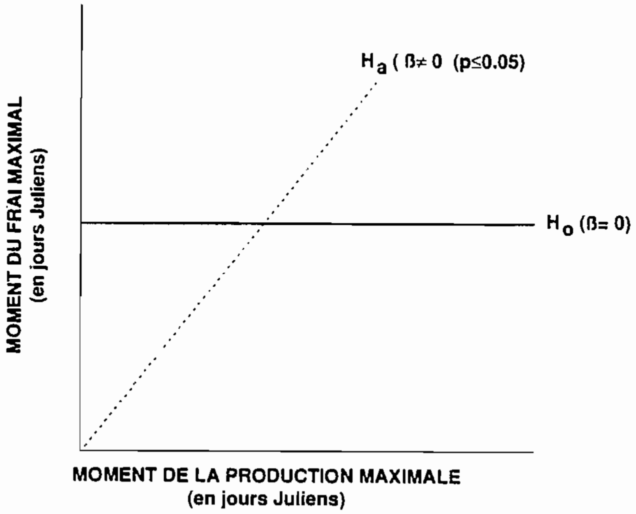

FIG. 1. Relation entre le moment du frai maximal et le moment de la production marine maximale (en jours juliens). H_o se réfère à l'hypothèse selon laquelle le moment des migrations du hareng et du saumon est indépendant des cycles de production marine dans le golfe du Saint-Laurent. H_a correspond à l'autre hypothèse.

such as ice cover and temperature profiles should be considered in the analysis.

Reflections subsequent to the meeting by J. Runge on the fish migration discussions (specifically the question of timing of spawning migrations and of smolt migrations) are of interest and are included in our report.

Comments on Working Proposal on Fish Migrations (J. Runge)

Atlantic Herring and Atlantic Salmon

The hypothesis put forward in the working proposal states that the timing of herring and salmon migrations is independent of marine production cycles in the Gulf on St. Lawrence. I interpret this to mean that there is no significant relationship between the time of the migration (measured in Julian days) and time of peak production (also measured in Julian days), as illustrated in Fig. 1, with a possible correction for temperature-dependent egg hatching time. The working proposal asserts that the hypothesis could be tested by studying the timing of primary and secondary projection cycles in relation to the timing of herring spawning and by measuring the timing in the cycle of abundance of large zooplankters in relation to the migration of salmon smolts. As I will discuss later, there is a fundamental lack of understanding of what constitutes a sufficient measure of the production cycles with regard to the prey field for larval herring and salmon smolts. Nevertheless, it may be worthwhile to pursue this line of research. The following comments make recommendations for the measurement of production cycle variables and explore the possible implications of the outcome of the research.

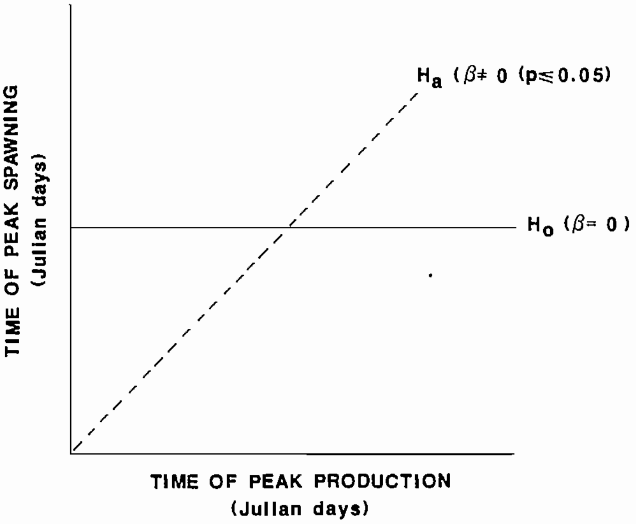

FIG. 1. Relationship between the timing of fish peak spawning and the timing of peak marine production (measured in Julian days). H_o refers to the hypothesis stating that the timing of herring and salmon migrations is independent from marine production cycles in the Gulf of St. Lawrence. H_a is the alternative hypothesis.

1. La mesure des variables dans le cycle de production

a) *Production primaire :* La mesure du stock permanent de «chlorophylle intégrée» (mg chl a m^{-2} jusqu'à 50 m de profondeur) sur une base bihebdomadaire ou, de préférence, quotidienne durant le printemps et l'été, serait, selon notre estimation, la meilleure façon d'étudier tout le cycle de production primaire. Pour évaluer la quantité .de phytoplancton directement disponible pour le macrozooplancton (copépodes), il serait bon de trier les échantillons avec un tamis de 5 μm. Si on continue d'améliorer les trappes à sédiments, le recours à des modèles (équipés d'une minuterie) qui ferment à des intervalles hebdomadaires ou bihebdomadaires pourrait être utile dans l'interprétation de la chronologie des cycles de production.

b) *Production secondaire :* Dans le cas du hareng, nous croyons que le meilleur moyen d'étudier le cycle de production secondaire est d'évaluer la biomasse (poids en matière sèche) d'échantillons de zooplancton prélevés, du fond à la surface, avec un filet à mailles de 80 μm. Les échantillons devraient être triés selon la taille avec un tamis à plus grosses mailles (l'analyse préliminaire de la diète des harengs larvaires servirait à déterminer la grosseur des mailles) afin d'enlever les plus gros spécimens de zooplancton qui augmentent beaucoup la biomasse mais qu'on ne peut considérer comme des proies. Il y a un problème potentiel dans le fait que le filet à mailles de 80 μm peut retenir du phytoplancton de grosse taille; à certaines périodes de l'année, cela peut constituer un problème grave. L'analyse optique des échantillons de zooplancton devrait être explorée comme source de données s'ajoutant aux estimations tirées du poids en matière sèche. Une autre façon d'étudier les cycles secondaires consiste à évaluer l'abondance et la composition par espèce des copépodes femelles (qui produisent la majeure partie des proies); on pourrait aussi prélever des échantillons avec des seines. Les progrès réalisés dans l'étude de la dynamique du zooplancton rendent possible une évaluation des taux de production de copépodes à partir de ces données et de celles qu'on possède sur la biomasse mesurable de chlorophylle.

Pour estimer le cycle de production des tacons, il faut d'abord déterminer la taille des proies et établir si les tacons se nourrissent d'organismes pélagiques ou épibenthiques. Une proie pélagique pourrait être échantillonnée à l'aide d'un filet à plancton à mailles de taille appropriée. En ce qui concerne toutes les variables du cycle de production, on rencontrera les problèmes habituels (mais majeurs) associés à l'élaboration d'un programme d'échantillonnage permettant d'obtenir des évaluations statistiquement valides.

c) *Échelle temporelle de l'étude :* La mesure de ces variables sur une base hebdomadaire, bihebdomadaire, ou quotidienne (selon la période de l'année) pour chaque aire de frai sélectionnée, durant une période de 5 à 10 ans.

1. Measurement of Production Cycle Variables

a) *Primary production:* Integrated chlorophyll standing stock (mg chl a m^{-2} in surface 50 m) measured semi-weekly, or preferably daily during spring and summer, would be my best guess to cover the primary production cycle. It would be useful to size fractionate the samples with a 5 μm screen to obtain a rough estimate of phytoplankton directly available to macrozooplankton (copepods). If advances in sediment trap technology continue, use of sediment traps which close (with a programmed timer) at weekly or semi-weekly intervals could be very useful for interpreting timing of production cycles.

b) *Secondary production:* My best guess to cover the secondary production cycle for herring would be biomass (dry weight) of zooplankton samples taken with a 80 μm mesh net from the bottom to the surface. The samples should be size fractionated with a larger screen (mesh size to be determined after preliminary analysis of larval herring diet) to remove large zooplankters which would contribute most to the biomass but would clearly not be prey items. There is a potential problem in that the 80 μm mesh net will pick up large phytoplankton, which may pose serious difficulties at certain times of the year. Optical image analysis of zooplankton samples should be explored as a supplement to dry weight estimates. A new proposal to measure secondary cycles would involve measurement of the abundance and species composition of copepod females (which produce the bulk of larval prey items); also samples with net tows. Advances in the study of zooplankton dynamics make it feasible to consider estimating copepod production rates with this information, coupled with data on the chlorophyll standing stock.

To estimate the production cycle for salmon smolts, it is necessary first to know the size range of prey items and whether the smolts feed on pelagic or epibenthic organisms. Pelagic prey could be sampled by plankton tows of an appropriately-selected mesh. As for all production cycle variables, there will be the usual (but major) problems of designing a sampling program to obtain statistically valid estimates.

c) *Time scale of study:* Measurement of these variables on a weekly, semi-weekly, or daily basis (depending on time of year) at each selected spawning area for a period of 5–10 yr.

2. Les résultats possibles et leur signification

Présumons que les migrations de harengs et de saumons ainsi que les cycles de production du plancton ont été mesurés avec succès durant une période de cinq ans. Pour chaque aire de frai, une analyse similaire à celle de Cushing (1975 : fig. 51) pourrait être effectuée. Une meilleure quantification devrait être possible en définissant trois variables pour chaque aire : TP_i (date maximale, en jours juliens, de la production phytoplanctonique maximale), TZ_l (date de la production maximale de zooplancton) et TM_i (milieu de la période de migration de frai). Nous pourrions ensuite vérifier l'hypothèse originale en utilisant la régression ou l'analyse de variance emboîtée. Nous pourrions, par exemple, vérifier la signification de la pente de régression de TM sur TP et de TM sur TZ (fig. 1). Si les pentes des deux analyses de régression ne sont pas significativement différentes de zéro, l'hypothèse nulle originale (c.-à-d. que le temps est indépendant des cycles de production) est acceptée. Si, toutefois, les deux pentes sont significativement plus grandes que zéro, l'hypothèse nulle originale est rejetée (ce qui viendrait appuyer l'hypothèse de Cushing). Dans un cas comme dans l'autre, nous pourrions établir (en admettant que nous ayons mesuré le cycle de production de façon appropriée) que les changements touchant la chronologie des cycles de production marine pourraient, ou non, provoquer des changements de la période de migration du hareng et du saumon (en supposant que, si la migration est reliée au cycle de production, la pression de la sélection naturelle entraînerait la population dans la même direction que le cycle de production).

Il est fort possible, toutefois, que nous obtiendrons un résultat mixte, c'est-à-dire que l'hypothèse nulle serait rejetée dans le cas de la production de phytoplancton, mais acceptée dans le cas de la production de zooplancton, ou vice versa. Nous pourrions obtenir un tel résultat si nous n'avions pas mesuré l'une ou l'autre des variables de façon appropriée ou si le lien entre les cycles de production de phytoplancton et de zooplancton n'était pas direct ou linéaire. Le modèle de Cushing (1975, 1982) pourrait ne pas convenir pour décrire les maillons de la chaîne alimentaire dans le golfe.

Quel que soit le résultat, nous n'aurions pas les moyens de prédire si les changements du niveau de production ou de la variabilité des périodes des cycles de production d'une année à l'autre pourraient influencer le rendement des pêches, sans une mesure simultanée du recrutement et (de préférence) de la croissance/mortalité des larves de hareng et des tacons.

Les observations qui précèdent font ressortir un problème fondamental, celui de la définition des cycles de production marine eu égard aux aires d'alimentation durant les premiers stades de la vie des poissons. L'insuffisance de nos connaissances, en ce qui concerne la niche alimentaire — quelle est sa composition (variable selon les espèces de poissons), quelles échelles spatiales/temporelles sont importantes, comment sa production est-elle reliée au cycle de production primaire, quels autres

2. Possible Results and their Implication

Let us assume that herring and salmon smolt migrations and plankton production cycles have been successfully measured for a period of 5 yr. For each spawning area, an analysis similar to Cushing (1975: fig. 51) could be carried out. It should be possible to be even more quantitative by defining for each site three variables: TP_i (maximum time of peak phytoplankton production, in Julian days), TZ_l (maximum time of peak zooplankton production) and TM_i (midpoint of migration or spawning period). We could then test, using regression or nested analysis of variance, the original hypothesis. We could, for example, test for the significance of the slope of the regression of TM on TP and of TM on TZ (Fig. 1). If the slopes of both regression analyses are not significantly different from zero, the original null hypothesis (i.e., that the timing is independent of production cycles) is accepted. If, however, both slopes are significantly greater than zero, the original null hypothesis is rejected (giving support to Cushing's hypothesis). In either case, we could predict (with the important assumption that we have measured the production cycle appropriately) that the changes in the timing of the marine production cycles in the Gulf would or would not result in changes in the timing of herring or salmon migrations (with the important assumption that, if the timing of migration is related to the production cycle, natural selection would drive the fish populations in the same direction as the production cycle).

It is also quite possible, however, that we may obtain a crossed result, i.e., that the null hypothesis is rejected for phytoplankton production but not for zooplankton production, or vice-versa. This could result if we have not measured on or the other variables appropriately or if the link between the phytoplankton and zooplankton production cycles is not direct or "linear". Cushing's (1975, 1982) model may be inadequate to describe the food chain linkages in the Gulf.

Whatever the outcome, we would not have the predictive capability to say whether changes in the level of production or in the variability in the timing of the production cycles from year-to-year would affect yield to the fisheries, without a concurrent measure of recruitment and (preferably) growth/mortality of herring larvae or salmon smolts.

The above considerations point to a fundamental problem in defining marine production cycles with respect to the prey field for early-life stages of fish. We don't understand the prey field well enough — what its composition is (which will vary among fish species), what spatial/temporal scales are important, how its production is linked to the cycle of primary production, what other physical and biological factors influence its productivity? — to design an efficient research program and to inter-facteurs physiques et biologiques influencent sa productivité? — nous empêche de concevoir un plan de recherche efficace et d'interpréter les résultats des études sur les interactions poisson/nourriture. La proportion qui suit laisse entendre que le modèle «bien assorti/mal assorti» de Cushing (1975, 1982), associant le concept de profondeur critique à la productivité phytoplanctonique et au recrutement de poissons, n'est pas suffisamment développé et illustre mal la relation entre les caractéristiques des populations de poissons marins (temps du frai, variabilité annuelle de recrutement, variations à long terme de l'abondance des poissons) et la productivité des niveaux trophiques inférieurs dans la chaîne alimentaire des eaux tempérées nordiques. Cette proposition laisse sous-entendre que pour comprendre ces relations il est nécessaire d'étudier la dynamique, la composition en termes d'espèces, et les maillons trophiques des réseaux trophiques locaux pour chaque population de poissons considérée.

La variabilité du recrutement

Comme le soulignent Sinclair et Tremblay (1984), l'hypothèse originale du «bien assorti/mal assorti» de Cushing relie le temps de frai, la variabilité annuelle de recrutement et les variations à long terme de l'abondance des poissons à un modèle simple reliant la dynamique du phytoplancton au concept de profondeur critique. À vrai dire, l'hypothèse relie le temps de frai des poissons au cycle de production phytoplanctonique. Pour vérifier l'hypothèse originale, ces variables doivent être mesurées. Cependant, comme l'affirme lui-même Cushing, c'est dans le cas de la production de nourriture pour les poissons larvaires (les copépodes notamment, mais aussi d'autres organismes microzooplanctoniques) que le «bien assorti/mal assorti» du frai est important.

Cushing a tenu pour acquis (1982 : page 182) que la production d'herbivores est intimement liée à celle du phytoplancton. Toutefois, une étude récente (i.e., Frost 1985; Runge 1988) laisse entendre que, selon les espèces, les proies des larves réagissent différemment à la disponibilité de nourriture, de sorte que le lien entre le cycle de production du phytoplancton et celui du zooplancton n'est pas simple. Le lien entre la production de zooplancton et la disponibilité de leur nourriture ainsi que les facteurs influançant cette relation (par exemple, tempête, fronts, boucle microbienne, bloom printanier, qualité de nourriture, la composition du phytoplancton selon la taille), est présentement l'objet d'intenses recherches. Il suffit de dire que, pour le moment, les relations entre le cycle de production phytoplanctonique, le cycle de production zooplanctonique et la réponse alimentaire des poissons larvaires ne sont pas bien comprises.

Nous sommes d'avis que le modèle «bien assorti/mal assorti» de Cushing (1975, 1982) est insuffisamment développé et qu'il ne permet pas de définir les relations entre les populations de poissons marins (période de frai, variabilité annuelle du recrutement et variations à long terme de l'abondance des poissons) et la productivité des niveaux trophiques inférieurs dans les eaux tempérées nordiques. Pour comprendre ces relations, il est nécessaire d'étudier la dynamique, la composition en termes d'espèces et les maillons des réseaux trophiques locaux pour chaque population de poissons considérée. Runge (1988)

pret results of studies of fish/food interactions. In the following proposal, it is suggested that Cushing's match/mismatch model (1975, 1982) linking the critical depth concept to phytoplankton productivity and to fish recruitment, is insufficiently developed to properly identify relationships between the characteristics of marine fish populations (timing of spawning, annual recruitment variability, and long-term changes in fish abundance) and the productivity of lower trophic levels in the marine food chain in north temperate waters. An underlying assumption of the proposal is that, in order to understand these relationships, it is necessary to study the dynamics, species composition, and trophic linkages of *local* food webs for each fish population under consideration.

Recruitment Variability

As Sinclair and Tremblay (1984) point out, the original match/mismatch hypothesis put forward by Cushing links timing of spawning, annual recruitment variability, and long-term changes in fish abundance to a simple model relating phytoplankton dynamics to the critical depth concept. Strictly speaking, the hypothesis links timing of spawning in fish to the *phytoplankton* production cycle. In order to test the original hypothesis, these variables should be measured. However, as Cushing himself has argued, it is the production of larval fish food (notably copepods, but also other microzooplankton) with which the match or mismatch of spawning is important.

Cushing assumed (1982: p. 182) that the production of herbivores is quite closely linked to that of the phytoplankton. However, recent work on production dynamics of zooplankton (e.g., Frost 1985; Runge 1988) suggests that there are species-specific differences in the response of larval prey to food availability such that the link between the phytoplankton production cycle and the zooplankton production cycle is not straightforward. The link between zooplankton production and their food availability, and the factors influencing this relationship (e.g. storm events, fronts, microbial loop, timing of spring bloom, nutritional quality, phytoplankton size composition), is currently a subject of active research. Suffice to say that, for the moment, the relationships between the phytoplankton production cycle, the zooplankton production cycle, and the feeding responses of larval fish are not well understood.

It is suggested here that Cushing's match/mismatch model (1975, 1982) is insufficiently developed to properly identify relationships between the characteristics of marine fish populations (timing of spawning, annual recruitment variability, and long-term changes in fish abundance) and the productivity of lower trophic levels in north temperate waters. In order to understand these relationships, it is necessary to study the dynamics, species composition, and trophic linkages of local food webs for each fish population under consideration. A qualitative discussion of possible "strong" and "weak" links s'est livré à une étude qualitative des liens «forts» et «faibles» possibles entre la productivité phytoplanctonique et la niche alimentaire des poissons larvaires. Le golfe du Saint-Laurent est un bon terrain d'essai pour l'étude quantitative des liens trophiques étant donné la diversité des interactions qu'on y observe, dans le réseau trophique, entre différentes espèces de poissons et aussi, potentiellement, entre les différents stocks d'une même espèce.

Notre but, en formulant ce point de vue, est de faire ressortir une lacune dans notre connaissance des écosystèmes du golfe du Saint-Laurent en ce qui a trait aux stocks de poissons. Il n'y a pas une seule hypothèse précise à vérifier en ce moment. Puisque les recherches proposées permettront une mesure plus précise des variables du cycle de production reliées directement à la croissance des poissons larvaires, elles sont en rapport avec la vérification de l'hypothèse selon laquelle la période de migration des poissons est indépendante des cycles de production marine. Dans les objectifs suivants, on trouve des hypothèses spécifiques implicites (par exemple : la distribution verticale et l'alimentation des sébastes larvaires sont déterminées par la distribution verticale et la concentration des oeufs de *Calanus finmarchicus :* Runge et de Lafontaine, en préparation); l'examen de ces hypothèses mènerait peut-être à une révision de la théorie du «bien assorti/mal assorti» proposée originairement par Cushing.

Objectifs

1. Les observations portant sur la structure du réseau trophique local (c.-à-d. à l'intérieur de chaque aire d'alevinage ou de rétention) et concernant les stades de développement précoce de chaque stock étudié (hareng, sébaste, maquerau, tel qu'examiné ci-dessous). Les observations comprennent : le cycle de production phytoplanctonique, la composition en termes d'espèces et la succession saisonnière du phytoplancton et du zooplancton; la composition de la diète durant les stades de développement précoces des populations de poissons.
2. Des recherches visant à comprendre les liens entre la productivité des niveaux trophiques inférieurs à l'alimentation, la croissance et la survie des poissons larvaires, incluant la distribution verticale, les comportements d'alimentation et la composition de la diète des larves ainsi que la variabilité et les facteurs qui influencent la productivité de sa proie.
3. Un développement théorique de l'hypothèse «bien assorti/mal assorti» originale pour y intégrer les données récentes sur les liens entre les cycles de production zooplanctonique et phytoplanctonique. Des prévisions spécifiques aux stocks individuels de poissons dans la région du golfe.

Recommandations concernant l'étude des stocks de poissons et des réseaux trophiques locaux

1. Le sébaste atlantique dans le nord du golfe : Le réseau trophique auquel le sébaste larvaire appartient peut être relativement simple; il inclut de grands organismes phytoplanctoniques, des oeufs de Calanus et des nauplii (Runge, communication personnelle).

between phytoplankton productivity and the prey field for larval fish has been put forward (Runge 1988). The Gulf of St. Lawrence is a good testing ground for the quantitative study of trophic linkages because of the diversity of food web interactions among fish species and also potentially within a single species among different stocks.

The purpose of this proposal is to highlight a gap in our knowledge of Gulf of St. Lawrence ecosystems in relation to fish stocks. There is no single, focused hypothesis to test at this time. Because the proposed research will allow a more precise measurement of production-cycle variables directly related to larval fish growth, it does have a bearing on the test of the hypothesis that timing of fish migrations are independent of marine production cycles. Implicit in the following objectives are specific hypotheses (for example: vertical distribution and feeding of redfish larvae are determined by vertical distribution and concentration of eggs of *Calanus finmarchicus:* Runge and de Lafontaine, in prep.), the examination of which may lead to a revision of the match/mismatch theory originally proposed by Cushing.

Objectives

1. Observations of local (i.e., within each nursery or retention area) food web structure involving early life stages of each fish stock under study (herring stocks, redfish, mackerel, as discussed below). Observations include: phytoplankton production cycle, phytoplankton and zooplankton species composition and seasonal succession; dietary composition of early life stages of fish populations.
2. Process-oriented studies designed to understand linkages between lower trophic level productivity and larval fish feeding, growth, and survival, including vertical distribution, feeding behaviour, and dietary composition of larvae, variability and factors influencing productivity of its prey.
3. Theoretical development of the original match/mismatch hypothesis to include the emerging understanding of linkages between phytoplankton and zooplankton production cycles. Predictions specific to individual fish stocks in the Gulf Region.

Recommend Fish Stocks/Local Food Webs for Study

1. Redfish in the northern Gulf: The food web involving larval redfish may be relatively simple, involving large phytoplankton and *Calanus* eggs and nauplii (Runge, pers. Comm.).

2. Le hareng dans le sud du golfe : Il peut exister d'importantes différences entre des réseaux trophiques locaux auxquels se rattachent les larves de hareng de différents stocks (c.-à-d. les Îles de la Madeleine vs Escuminac [au printemps]; Pictou vs Northumberland [à la fin de l'été]).
3. Le maquerau dans le sud du golfe (la vallée du Shediac) : Puisque la diète du maquerau est si variée, le lien entre les caractéristiques de recrutement et les cycles de production à des niveaux trophiques inférieurs pourrait être plus faible que pour les stocks de harengs ou de sébastes. Le rôle des prédateurs est particulièrement important dans la détermination de la variabilité du recrutement.
4. Les complexes de populations de morues de chaque côté du chenal Laurentien : Bien qu'il y ait des similarités dans l'évolution de la taille des classes d'âge pour les deux complexes de population, il y a aussi des différences intéressantes.

La variabilité génétique dans les populations de poissons

La structure des populations de poissons est définie par leurs caractéristiques biologiques et par leur environnement physique. Le golfe du Saint-Laurent est un milieu exceptionnel pour étudier l'influence de ces différents facteurs sur la structure des populations de poissons marins. Le golfe contient un rassemblement de diverses espèces dont les cycles biologiques et les modèles de distribution sont très variés. De plus, à cause de la configuration du golfe, il y a des barrières potentielles au flux de gènes, à grande échelle (à l'intérieur et à l'extérieur du golfe) et à une échelle moyenne (au nord et au sud du chenal Laurentien, entre les réseaux trophiques). On pourrait aussi déterminer la structure des stocks à une échelle réduite correspondant à des caractéristiques océanographiques et géographiques locales. La distribution des espèces commerciales permet une étude comparative de la variation génétique à chaque niveau de la structure physique. La différentiation génétique des populations de poissons du golfe n'a pas encore été étudié en détail. Du point de vue de la gestion halieutique, il est important de comprendre les interactions entre populations.

Méthodes

Le plan d'échantillonnage sur le terrain devrait être assez détaillé pour tenir compte à la fois des variations biogéographiques et de celles qui touchent le cycle de vie des espèces qui nous intéressent et pour déceler de possibles variations de caractères. Ce schéma d'échantillonnage devrait aussi reconnaître la possibilité de l'intégrité de populations à l'intérieur de petites aires géographiques. Pour déterminer précisément la structure de la population, les traits génétiques biochimiques (ADN mitochondrial, analyse par électrophorèse, etc.) et les caractères utilisés dans l'étude classique de la discrimination des stocks (caractères concernant la morphologie, la physiologie et le comportement) devraient être mesurés, de préférence, sur le même individu. Lorsque c'est possible, il faudrait faire une analyse de la contribution relative de la génétique et de la variabilité environnementale à la

2. Herring in southern Gulf: There may be important differences in local food webs involving larvae of herring of different stocks (e.g., Magdalen Islands vs Escuminac [spring]; Pictou vs Northumberland [late summer]).

3. Mackerel in southern Gulf (Shediac Valley): Because mackerel are such eclectic feeders, the link between recruitment characteristics and production cycles at lower trophic levels may be weaker than either redfish or herring stocks. Role of predators is especially important in determining recruitment variability.

4. Cod population complexes on each side of the Laurentian Channel: Although there are similarities in the trends in year-class sizes for both population complexes, there are also interesting differences.

Genetic Variability in Fish Populations

The population structure of fishes is defined by their biological characteristics and by their physical environment. The Gulf of St. Lawrence represents a unique opportunity to study the influence of these different factors on the population structure of marine fishes. The Gulf contains a diverse assemblage of species with a variety of life history and dispersal patterns. In addition, the physical structure of the Gulf is such that there are potential barriers to gene flow at a large scale (inside and outside the Gulf) and at a medium scale (north and south of the Laurentian Channel, between food webs). Stock structure can also be determined at a finer scale defined by local oceanographic and geographic features. The distribution patterns of commercial species allows comparative study of genetic variation at each level of physical structure. The genetic differentiation of fish populations in the Gulf has not been studied in much detail to date. From a fisheries management point of view, it is important to understand the interactions between the populations.

Methods

The field sampling scheme should be fine grained enough to take into account biogeographic and life-history variations of the species of interest and to detect possible clinal variation of characters. This sampling scheme should also recognize the possibility of integrity of populations within small geographic areas. To determine the population structure precisely, biochemical genetic traits (mt DNA, electrophoretic analysis, etc.) and traits used in classical studies of stock discrimination (morphological, physiological, and behavioural characters) should be preferably measured on the same individual. Where possible, analysis of the relative contributions of additive genetic on environmental variance to the variation in polygenic traits should be done. In all cases, it is necessary to determine the interannual variations. It may be worthwhile to establish a long-term provariance des traits polygéniques. Dans tous les cas, il est nécessaire de déterminer les variations interannuelles. Il pourrait être utile de mettre sur pied un programme d'observation à long terme de la variabilité génétique de certaines espèces de valeur commerciale; il serait préférable de choisir une pêche en développement afin d'évaluer l'impact de l'exploitation et des changements d'ordre environnemental sur la diversité génétique. Un tel programme pourrait aussi servir à évaluer la variabilité temporelle de l'intégrité de la population.

Les polluants chimiques dans les populations de poissons

Le golfe du Saint-Laurent est un laboratoire important pour les recherches sur les transformations et les effets des substances chimiques dans les écosystèmes estuariens et marins. En matière de contamination, le golfe occupe une position intermédiaire entre les Grands Lacs et l'océan Atlantique lorsque l'on considère l'importance, la complexité, la gravité, l'échelle et l'intensité des phénomènes. Puisque la plupart des problèmes d'origine chimique touchant l'écosystème des Grands Lacs ont été observés, étudiés et maîtrisés, on peut s'inspirer de cette expérience et appliquer ses résultats à des écosystèmes marins et estuariens, à l'intérieur d'une aire relativement restreinte. De plus, les gradients nord-sud de température, de profondeur et de productivité, ainsi que les gradients et le transport ouest-est des concentrations d'éléments chimiques, permettent des recherches sur les facteurs qui influencent la contamination et ses effets, tant à l'intérieur du golfe que dans des écosystèmes marins similaires tels que celui de l'Arctique.

Un programme de recherche sur les substances chimiques contaminantes doit comporter deux volets importants. Puisque la toxicité de ces substances et ses effets sont indissociables d'un contact avec les substances en question, il faudrait tout d'abord déterminer les teneurs et la distribution des produits chimiques à l'intérieur du golfe puis étudier leurs transformations et leur aboutissement. Dans ce dernier cas, il faudrait se pencher plus particulièrement sur les mécanismes de précipitation et de distribution associés au mélange de l'eau douce et de l'eau salée. Le fleuve Saint-Laurent fonctionne effectivement comme une décharge vers un écosystème marin où les produits chimiques dissous et en particules vont précipiter dans la zone de turbidité et seront distribués selon les principes d'hydraulique associés aux marées et aux phénomènes de stratification et de mélange. Ce qui importe le plus dans ces études, c'est de bien reconnaître les processus et les facteurs qui contribuent à la contamination des espèces commerciales, des espèces qui sont particulièrement sensibles à la contamination et de découvrir les produits chimiques qui auront le plus tendance à se concentrer, soit par enrichissement des sédiments ou par bio-accumulation dans la chaîne alimentaire.

Le deuxième volet consisterait à identifier les effets et leur importance dans le contexte de la productivité des pêches. Les effets comprendraient la toxicité directe pour les poissons, toxicité qui pourrait entraîner une réduction du recrutement ou de la croissance, la toxicité pour les composantes du réseau trophique, qui pourrait réduire

gram of monitoring the genetic variability of some commercially important species (preferably a developing fishery in order to assess the possible impacts of exploitation and environmental change on genetic diversity). Such a program could also evaluate temporal variability in population integrity.

Chemical Contaminants in Fish Populations

The Gulf of St. Lawrence offers important opportunities for research on chemical cycling and effects in estuarine and marine ecosystems. In size, complexity, relevance, scale, and degree of contamination, the Gulf is intermediate between the Great Lakes and the Atlantic Ocean. Since most significant chemical problems have been observed, studied, and managed in the Great Lakes ecosystem, there are opportunities to build on this experience and extend it to marine and estuarine ecosystems within a relatively confined area. Furthermore, the north-south gradients of temperature, depth and productivity, and the west to east flows and gradients of chemical concentrations, allows research on factors controlling contamination and effects, both within the Gulf and in related areas, such as Arctic marine ecosystems.

There are two important components to a chemical program. Since chemical toxicity and effects cannot occur without chemical exposure, the first would be descriptive studies of the levels and distribution of chemicals within the Gulf and process studies of their cycling and fate. The latter would focus particularly on the precipitation and distribution mechanisms associated with the mixing of fresh and salt water. The St. Lawrence River effectively acts as a discharge to a marine ecosystem, and dissolved and particulate chemicals will be precipitated within the turbidity zone and distributed according to the hydraulics associated with tides, stratification and mixing. The most important aspect of these studies would be the identification of processes and factors that contribute to contamination of commercial species, of species that are particularly vulnerable to contamination, and of chemicals that are most likely to be concentrated, either through sediment enrichment or food-chain biomagnification.

The second component would be the identification of effects and their significance to fisheries productivity. Effects would include direct toxicity to fish causing impairment of recruitment or growth, toxicity to components of the food web that would reduce productivity at higher trophic levels, and contamination of fisheries la productivité aux niveaux trophiques plus élevés, et une contamination si importante des produits pêchés qu'ils sont inutilisables, ce qui provoque une diminution du rendement. Ces études devraient viser les parties estuariennes du golfe où l'eau douce rencontre l'eau salée, ainsi que les endroits où il existe des sources ponctuelles. Si les effets indirects ne sont pas évidents, il est peu probable que l'on puisse les observer au large, dans le golfe. Les exceptions à cette règle générale seront les effets d'un enrichissement des sédiments en produits chimiques en zone calme, de la bio-accumulation dans la chaîne alimentaire et d'événements catastrophiques tels que les naufrages. Les deux premiers peuvent être reconnus par une description détaillée de la distribution des produits chimiques à l'intérieur du golfe, mais, dans le dernier cas, toute recherche planifiée est difficile.

Biogéographie et réchauffement du climat à l'échelle du globe

Comme on le mentionne dans l'introduction, le golfe du Saint-Laurent est une région géographique unique pour étudier les effets du réchauffement climatique dans les zones limites de distribution des espèces de poissons. Les populations sont observées aux limites méridionales de distribution naturelle pour les espèces vivant en eaux froides (comme le flétan du Groenland, le capelan et le crabe des neiges). De plus, on trouve des populations appartenant à des espèces qui vivent en eaux tempérées, comme le maquereau, à l'intérieur du golfe, aux limites nord de leur distribution naturelle. Comme tel, le golfe est un laboratoire naturel dans lequel on étudie les modifications de la distribution comme une fonction des tendances au réchauffement de la Terre. Le groupe de travail recommande de considérer comme prioritaires les projets ou les orientations de recherche suivants :

1. observations supplémentaires portant sur la distribution des populations de géniteurs appartenant à des espèces commerciales et non commerciales de poissons et d'invertébrés dans le golfe du Saint-Laurent;
2. identification des lacunes dans l'échantillonnage actuel des espèces de poissons (notamment des espèces non commerciales qui sont rares);
3. évaluation d'un programme de surveillance et de prélèvement rentable;
4. études centrées sur les populations de poissons et d'invertébrés vivant respectivement aux limites nord et sud de leurs aires de distribution et dont l'objectif serait de déterminer les causes de la diminution de ces populations vivant aux limites physiologiques, génétiques et écologiques particulières à chacune;
5. incorporation d'un programme de surveillance et de suivi de la biogéographie des poissons à un programme portant sur le changement du climat océanique et touchant toutes les régions du golfe.

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products to the extent that they are unusable, thereby reducing yield. These studies should be focused on the estuarine portion of the Gulf where freshwater meets salt, and in other areas where point sources exist. If indirect effects are not evident, it is unlikely they will be observed in the open Gulf. Exceptions to this general rule will be effects arising from chemical enrichment of sediments in settling zones, from food-chain biomagnification, and from catastrophic events such as shipwrecks. The former two could be identified by a thorough description of chemical distribution within the Gulf, but research on the latter cannot be easily planned.

Biogeography and Global Warming

As stated in the introduction section, the Gulf of St. Lawrence is a unique geographic area to study the impacts of global warming on the limits of distribution of fish species. Populations are observed at the southern end of the range of cold water species, such as Greenland halibut, capelin and snow crab. In addition, temperate water species sustain populations within the southern Gulf of St. Lawrence at the northern limit of their distribution, such as mackerel. As such, the Gulf is a natural laboratory within which to study shifts in distribution as a function of trends in global warming. The working group recommends that the following projects or research orientations should have a high priority:

1. Consolidation of observations on the distribution of spawning populations of both commercial and non-commercial fish and invertebrate species in the Gulf of St. Lawrence;
2. Identification of gaps in present day sampling of fish species (particularly for rare non-commercial species);
3. Evaluation of cost-effective monitoring and collection program;
4. Focused studies on populations of fish and invertebrate species at respectively the southern and northern limits of their distributional limits to address the question of the causes of diminution of populations at the limits of the distribution of species (at the boundary of physiology, genetics, ecology);
5. Incorporation of fish biogeography monitoring program within overall Gulf program on ocean climate change.

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Rapport de l'atelier de travail sur les invertébrés[1]

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Introduction

La présentation de Y. de Lafontaine *et al.* (1991) à ce colloque fait ressortir certaines caractéristiques particulières au golfe du Saint-Laurent en regard des autres régions côtières; on y observe, par exemple, un système à trois couches d'eau, des concentrations élevées d'éléments nutritifs dans la couche inférieure, la présence de glace, un apport important d'eau douce, trois régions ayant des régimes de production primaire différents. Il peut donc s'avérer impossible d'appliquer adéquatement les connaissances acquises lors de l'étude de ce système pour modéliser d'autres écosystèmes côtiers. Pour cette raison, les membres du groupe de travail sur les invertébrés, commentant les objectifs de leur atelier, ont souligné que l'approfondissement des connaissances relatives au golfe du Saint-Laurent et à ses composantes est un objectif important en soi et que l'applicabilité des résultats à d'autres systèmes ne devrait pas, de prime abord, être un objet de préoccupation.

Les membres du groupe de travail sont d'avis que le réchauffement climatique à l'échelle mondiale aura très probablement un impact important sur les invertébrés. Ces changements climatiques pourraient avoir des effets sur l'abondance et la distribution des invertébrés adultes ainsi que sur quelques-uns de leurs caractères biologiques. En raison de l'importance des stades larvaires pélagiques chez les invertébrés, en particulier chez ceux qui présentent une valeur commerciale, on croit que les processus de recrutement pourraient être plus gravement touchés par les changements climatiques qui comprennent non seulement la hausse des températures mais également les changements qui touchent d'autres phénomènes physiques comme le vent, les modèles de circulation, le moment du réchauffement annuel, la formation des glaces, les précipitations et le niveau de l'eau.

Report of the Workshop on Invertebrates[1]

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Introduction

De Lafontaine et al. (1991), in their review, pointed out that many features of the Gulf of St. Lawrence are distinctive relative to other coastal areas: e.g., three water-layer system, high nutrient concentrations in the bottom layer, ice, high freshwater input, three regions with different primary production regimes. It may prove to be impossible to properly use knowledge acquired from this system to model other coastal ecosystems. Therefore, as a general comment to the Workshop mandate, the Invertebrate Workshop participants emphasized that understanding more about the Gulf of St. Lawrence and its components is an important goal in itself and that the applicability of results to other systems should not be an a priori preoccupation.

Workshop participants agreed that global climatic warming was very likely to exert significant impact on invertebrate species. The abundance and distribution of adult invertebrates as well as some of their biological characteristics could be affected by climatic changes. Moreover, because of the prevalence of pelagic larval stages among invertebrates, particularly those of commercial value, it was thought that recruitment processes could be even more strongly affected by climatic changes, including not only an increase in temperature but also changes in other physical features such as wind, circulation patterns, timing of seasonal warming, ice formation, rainfall, and water level.

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[1] Ce rapport fait partie des Compte rendus d'un atelier/symposium tenu à l'Institut Maurice-Lamontagne, Mont-Joli (Québec) du 14 au 17 Mars 1989.

[1] This report forms part of the Proceedings of a Workshop/Symposium held at the Maurice Lamontagne Institute, Mont-Joli, Quebec, 14–17 March 1989.

Cependant, étant donné que la nature, l'amplitude et la direction des effets secondaires du réchauffement à l'échelle mondiale ne sont pas encore prévisibles, et que nous connaissons encore mal, dans le contexte actuel, l'influence des variables physiques, notamment sur les processus de recrutement, les participants ont soutenu que toute tentative de prévision des effets qu'un nouvel ensemble de conditions environnementales aurait sur le recrutement aurait un caractère hautement spéculatif. De plus, étant donné la grande variété de cycles de vie des différentes espèces en présence, les effets du réchauffement de la planète chez les invertébrés ne devraient pas être généralisés. Par conséquent, les participants ont mis l'accent sur les objectifs de ce groupe de travail qui portent sur les solutions aux problèmes majeurs de conservation des ressources. Pour les fins de notre travail, nous définissons le terme conservation comme la gestion des ressources dans le but de maximiser le rendement des pêches à long terme ou encore de permettre un rendement durable.

Les membres du groupe de travail se sont surtout penchés sur des projets spécifiques dans des secteurs pour lesquels des données essentielles font présentement défaut. Bien que certaines expériences à grande échelle n'aient pas été exclues, on a cru préférable, en raison du grand nombre d'espèces en présence et de la diversité de leurs cycles de vie, de procéder à un certain nombre d'expériences à petite échelle ayant pour but de vérifier des hypothèses précises, adaptées à chaque région et à chaque espèce. Dans le but d'établir des comparaisons entre les conditions passées, présentes et futures, on a sélectionné des secteurs pour lesquels nous possédons déjà des données sur les espèces qui nous intéressent. Ces bases de données devraient nous permettre d'établir des cartes illustrant la distribution récente des communautés et des espèces, ce qui représenterait une contribution importante aux recherches sur les changements à long terme.

Étant donné qu'un rendement soutenu des pêches dépend de la production annuelle d'un stock, nous considérons que l'insuffisance de nos connaissances et de notre compréhension des conditions (tant biologiques qu'environnementales) permettant de maximiser cette production, ainsi que l'absence de moyens permettant de la prévoir, sont les principaux obstacles à l'acquisition d'une base scientifique solide pour la conservation des ressources halieutiques en ce qui concerne les invertébrés du golfe du Saint-Laurent.

Dans nombre de cas, les stades de développement des invertébrés s'observent dans des habitats différents et les invertébrés sont soumis à des contraintes extrêmement diverses tout au long de leur cycle de vie. En conséquence, les projets recommandés ont été classés selon les différents aspects suivants de la production annuelle d'un stock :

1. les relations entre le stock et le recrutement;
2. les mécanismes de recrutement;
3. la croissance et la survie : a) des stades larvaires, b) des juvéniles, c) des prérecrues et d) des recrues;
4. la dynamique écosystème-communauté.

However, given that the exact nature, amplitude, and direction of the physical side effects of global warming are not yet predictable, and given that the effects of physical variables, particularly on recruitment processes, are not well known under the present conditions, it was agreed by Workshop participants that any attempt to predict what effects a new set of environmental conditions would have on recruitment would be highly speculative. Furthermore, given the large number of life-history patterns involved, spanning several phyla, the effects of global warming on invertebrates as a group could not be generalized. The Workshop, therefore, focused on that part of the general mandate dealing with the solution of major long-term problems of resource conservation. For our purposes, we considered conservation to mean resource management aimed at maximizing fishery yields on a long-term or sustainable basis.

The Workshop concentrated on specific projects in areas where key information is currently lacking. Due to the large number of species involved and the diversity of their life-history patterns, it was thought preferable to carry out a number of small-scale experiments to test particular hypotheses adapted to each area and species, although certain large-scale experiments were not excluded. A selection of working areas was also made for which historical databases are available for the species of concern, which would serve to establish comparisons between historical, present, and future conditions. These databases should allow the preparation of base maps of the recent distribution of communities and species which could have considerable value in documenting long-term changes.

Given that the basis for a sustainable-yield fishery is annual production within the stock, we identify the general lack of knowledge and understanding of conditions (both biological and environmental) that maximize annual production and the absence of a capability to predict annual production as the major constraints to providing a sound, scientific basis for conservation of invertebrate fishery resources in the Gulf of St. Lawrence.

The different life stages of invertebrates are often found in different habitats and subjected to vastly different constraints throughout their life history. The recommended projects were, therefore, divided according to the various components of annual production in a stock as follows:

1. Stock-recruitment relationships;
2. Recruitment mechanisms;
3. Growth and survival of (a) larval stages, (b) juveniles, (c) prerecruits and (d) recruits;
4. Ecosystem/Community dynamics.

Relations entre le stock et le recrutement

Durant les stades larvaires planctoniques de nombreux invertébrés d'importance commerciale, on observe une dispersion à grande échelle des individus qui entraîne un mélange des populations. Pendant le stade benthique suivant, la mobilité est beaucoup plus restreinte. Les populations exploitées, distinctes du point de vue géographique, mais pas nécessairement du point de vue génétique, sont considérées, pour fins de gestion, comme des «stocks» individuels.

La relation entre le stock et le recrutement n'a été établie pour aucune des principales espèces d'invertébrés du golfe du Saint-Laurent, encore que certaines données sur les homards du détroit de Northumberland indiquent que la relation est asymptotique. Il s'avère important de déterminer la forme générale des diverses relations entre le stock et le recrutement ainsi que la position actuelle des stocks sur les courbes. Pour le moment, il est impossible de déterminer avec certitude l'importance du recrutement moyen de quelque espèce que ce soit, même si on connaît la biomasse de frai. Les bases de données connues devraient être examinées afin de déterminer s'il existe quelque possibilité d'acquérir des indications quant à la forme générale des relations entre le stock et le recrutement. Les séries temporelles des estimations ou des indices de la biomasse de frai, de la population de la phase de recrutement, de l'abondance des prérecrues ainsi que du recrutement à la phase exploitable devraient être développées. À longue échéance, ces données serviraient de base à une étude détaillée des relations entre le stock et le recrutement. À brève échéance, elles permettraient de répondre aux demandes constantes d'avis scientifiques de la part des gestionnaires.

Pour déterminer le genre de relations existant entre le stock et le recrutement, il serait important d'entreprendre des études spécifiques, à petite échelle; en voici quelques exemples :

1. l'étude de la population restreinte et isolée de crabes des neiges de Bonne Bay;
2. l'étude des populations de buccins, dont la phase larvaire est benthique;
3. l'étude des populations de pétoncles géants (Placopecten), dans les baies isolées de la basse Côte Nord du Québec.

Mécanismes de recrutement

On connaît très peu les processus et les mécanismes qui déterminent à quel endroit les larves produites dans une aire donnée vont éventuellement se fixer ou s'ajouter à une population. Il n'existe aucune population pour laquelle nous ayons une indication de l'importance de la contribution du frai local au recrutement local ou encore de la variabilité de cette contribution d'une année à l'autre.

Cette question est celle qui se prête le mieux à des études multidisciplinaires à grande échelle puisque plusieurs espèces d'invertébrés, importantes sur le plan commercial, libèrent leurs larves planctoniques durant les mois d'été, les soumettant de ce fait à l'influence des mouvements des masses d'eau qui entraînent leurs dispersion.

Stock-Recruitment Relationships

During the planktonic larval stages of many invertebrate species of commercial importance, large-scale dispersal and population mixing takes place. This is followed by a much less mobile benthic stage. Exploited populations which are geographically, but not necessarily genetically, discrete are treated as individual "stocks" for management purposes.

For none of the major invertebrate species in the Gulf has a stock-recruitment relationship been determined, although data for Northumberland Strait lobsters indicates the relationship is asymptotic. It is important to determine the general shape of stock-recruitment relationships and where present stock sizes lie on the curves. In no species, at this time, is it possible to indicate with any confidence whether average recruitment will be high or low at any given level of spawning biomass. Existing databases should be examined to see if there are any possibilities of getting indications of the general shape of stock-recruitment relationships. Time series of estimates or indices of spawning biomass, population recruitment, prerecruit abundance, and recruitment to standing stocks should be developed. Over the long term, these would provide the basis for examining stock-recruitment relationships in some detail; and over the short term, they would have important application to ongoing requirements for provision of scientific advice to managers.

Specific studies should be undertaken to determine the type of relationships between stock and recruitment. Possibilities for small-scale studies include:

1. The small and isolated population of snow crab in Bonne Bay;
2. Whelk populations, for which the larval phase is benthic;
3. Giant scallop (*Placopecten*) populations in isolated bays along the lower Quebec North Shore.

Recruitment Mechanisms

Processes and mechanisms which determine where the larvae produced in a given area eventually settle or recruit to a population are largely unknown. For no population is there an indication of the extent to which local spawning contributes to local recruitment or whether it is highly variable from year to year.

This topic is the one offering the greatest potential for large-scale, multi-disciplinary studies, since several species of commercially important invertebrates release planktonic larvae during the summer months thereby subjecting them to dispersal through water mass movements. Although large-scale studies are essential to under-

Bien que les études à grande échelle soient essentielles à la compréhension des mécanismes du recrutement, l'utilisation de simples collecteurs pour la surveillance du recrutement post-larvaire des différentes espèces fournirait un outil de prévision à long terme du recrutement à la phase exploitable. Différentes études ont été proposées. En voici quelques-unes :

1. L'hypothèse selon laquelle les populations de homards de la côte ouest de Terre-Neuve sont «ensemencées» par la dérive des larves provenant de la côte nord québécoise et de l'île d'Anticosti (Hudon *et al.*, 1991) devrait être vérifiée par l'étude de la dérive larvaire dans cette région. Cette étude pourrait également s'intéresser à la dérive larvaire de plusieurs autres espèces de crustacés (crabe des neiges, crevettes, crabe commun) et de poissons (hareng), se produisant dans la couche de surface pendant l'été. Une telle étude serait aussi l'occasion de vérifier l'hypothèse selon laquelle la partie nord du golfe du Saint-Laurent constitue une «unité de recrutement» qu'on pourrait soumettre à des mesures de gestion générales. De plus, pour les larves d'autres espèces d'invertébrés, on sait généralement peu de chose de la répartition horizontale et verticale, des mouvements verticaux, de la synchronisation et de la durée des stades larvaires. Des efforts devraient également être faits pour éclaircir certains autres aspects de l'écologie des larves d'invertébrés dans le cadre de l'étude entreprise pour mieux comprendre les mécanismes de dispersion.
2. À partir de l'examen des données biologiques et physiques disponibles, il faudrait formuler des hypothèses à propos de l'existence possible d'autres «unités de recrutement» dans la partie sud du golfe du Saint-Laurent.
3. Il faudrait concevoir et standardiser des collecteurs pouvant mesurer la colonisation des naissains chez les bivalves, des traîneaux ou chaluts de fond servant à recueillir des juvéniles précoces de crabes des neiges et des crevettes d'un an, ainsi que des supports de colonisation pour les juvéniles de homards. Un suivi annuel de la descente post-larvaire devrait permettre la mise au point d'indices de recrutement pour chacune des espèces dans certaines régions clés et d'établir ainsi une relation entre le recrutement et les prises subséquentes.

Développement et survie

Stades larvaires. Le homard est la seule espèce ayant fait l'objet d'une description minutieuse de cette phase de la dynamique du recrutement. La variabilité observée est très grande et elle diffère d'une région à l'autre ainsi que d'une année à l'autre. De toute évidence, la température joue un rôle de premier plan, mais des recherches doivent être effectuées afin de déterminer si d'autres facteurs, tels la disponibilité de la nourriture ou la densité larvaire, contribuent à cette variabilité. Plusieurs projets de recherche ont été proposés :

1. Une corrélation positive a été établie entre l'apport en eau douce dans le golfe et les prises de homards subséquentes. La relation entre ces deux phénomènes n'est

standing the mechanisms of recruitment, the use of simple collectors for monitoring post-larval recruitment of the different species could provide a tool for long-term prediction of recruitment to standing stocks. The following possibilities are identified:

1. The hypothesis that lobster populations off the west coast of Newfoundland are "seeded" by larvae drifting from the Quebec North Shore and Anticosti Island (Hudon et al. 1991) should be tested by studying larval drift in that area. The drift of several other species of crustacean (snow crab, shrimp, rock crab) and fish (herring) larvae occurring in the surface layer during the summer could also be included in this study. Such a study would also provide an opportunity to test the hypothesis that the northern Gulf is a "recruitment unit" to which it might be possible to apply general management measures. Also, for other invertebrate larvae, generally, horizontal and vertical distribution, vertical movements, timing, and duration of larval stages are poorly known. An attempt should be made to elucidate these and other factors of invertebrate larval ecology as part of the foregoing study aimed at understanding dispersal mechanisms.
2. Available biological and physical data should be examined to develop hypotheses regarding the possible existence of other "recruitment units" in the southern part of the Gulf.
3. Collectors should be designed and standardized to measure spat settlement in bivalves, benthic sleds or trawls to collect early juvenile snow crab, and age-1 shrimp and settlement trays for juvenile lobsters. Yearly monitoring of post-larval deposition should allow the elaboration of recruitment indices for each species in key areas and to relate it to subsequent landings.

Growth and Survival

Larval Stages. Only for lobsters has any serious attempt been made to describe this phase of recruitment dynamics. There appears to be substantial variability between areas and between years. Temperature is obviously very important; but research is required to determine if other factors such as food availability, larval densities, etc., contribute to variability. The following suggestions for further study are offered:

1. A positive correlation between freshwater run-off and subsequent lobster landings in the Gulf has been demonstrated. The link is unknown but an hypothesis

pas encore connue, mais une étude sur le terrain permettrait de vérifier l'hypothèse selon laquelle une stratification plus marquée, attribuable à un plus grand apport d'eau douce, entraîne une augmentation de la température de la couche supérieure, contribuant ainsi à augmenter le taux de survie des larves de homards.

2. L'étendue des effets de facteurs biologiques tels que la famine et la prédation sur la survie des larves de crustacés devrait faire l'objet de recherches dans des secteurs de forte rétention de larves comme la baie de Plaisance (Îles de la Madeleine) ou la baie Bonne.
3. Afin de faciliter les études de terrain sur des larves de mollusques, il est nécessaire de mettre au point une méthode de description et d'identification rapide ainsi qu'un dispositif d'échantillonnage automatisé.
4. L'utilisation de marqueurs génétiques et phénotypiques doit être envisagée pour différencier les différents stocks d'invertébrés et déterminer ainsi l'étendue du mélange larvaire entre les populations.
5. Des études expérimentales portant sur la croissance et la survie des larves dans différentes conditions doivent être entreprises pour la plupart des espèces, à l'exception du homard.

Juvéniles. Peu de recherches sur le terrain ont été effectuées sur ce stade du cycle de vie des principales espèces d'invertébrés. Les descriptions élémentaires de même que les indications précises sur les facteurs en cause font défaut. Il semble que les variations interannuelles touchant la croissance et la survie des juvéniles contribuent largement au recrutement à la phase exploitable et, de ce fait, à la production annuelle.

En plus de ces questions de portée générale, mentionnons quelques sujets de recherche particuliers :

1. Les études de terrain sur les juvéniles de crevettes, de crabes des neiges et de homards nécessitent la mise au point de méthodes d'échantillonnage quantitatif.
2. Les principales «pouponnières» de plusieurs espèces d'invertébrés doivent être trouvées et caractérisées.

Prérecrues. Il existe des descriptions élémentaires du développement des prérecrues pour les principales espèces, mais il n'y en a pas pour le crabe des neiges. Les descriptions de la variation entre les secteurs font défaut, en particulier pour le homard et le crabe des neiges. Cependant, les taux de survie jusqu'au recrutement sont inconnus, tout comme les facteurs qui peuvent causer la variation interannuelle de la croissance et de la survie. Tout progrès dans les connaissances scientifiques fondamentales en matière de gestion des pêches d'invertébrés dépend de façon cruciale des connaissances sur la variabilité de la croissance et de la survie des prérecrues, aussi bien que d'un indice ou d'une estimation de l'abondance des prérecrues. Ce sont les deux facteurs-clés permettant de prévoir le recrutement à la phase exploitable qui, en règle générale pour les stocks d'invertébrés, représente la majeure partie de la production annuelle.

Outre les sujets de recherche qui précèdent et sur lesquels on s'entend généralement, on a proposé l'étude des questions suivantes :

that should be tested in a field study is that greater stratification in years of high run-off leads to higher temperature in the upper layer which in turn leads to better survival of lobster larvae.

2. The extent to which biological factors, such as starvation and predation, affect survival of larval crustaceans should be investigated in areas of high larval retention such as Baie de Plaisance (Îles de la Madeleine) or Bonne Bay.
3. To facilitate field studies on molluscan larvae, a method for ready characterization and identification and an automated sampling device need to be developed.
4. The possibility of using genetic/phenotypic markers for invertebrate stock separation and determining the extent of larval mixing between populations should be investigated.
5. Experimental studies of larval growth and survival under different conditions are required for most species except lobster.

Juveniles. There has been little field research focused on this life cycle phase of any of the main invertebrate species. Basic descriptions are lacking as well as clear indications of the factors involved. It is likely that year-to-year variation in growth and survival of juveniles is a major contributor to variability in recruitment to standing stocks and, hence, annual production.

In addition to the foregoing, which applies generally, the following are particular items requiring research attention:

1. Field work on juvenile shrimp, snow crab, and lobsters requires development of quantitative sampling methodologies.
2. Important "nursery areas" for various invertebrate species should be identified and characterized.

Prerecruits. Basic descriptions of growth of prerecruits are available for the main species, but it needs improvement for snow crab. Particularly for lobsters and snow crabs, descriptions of variation between areas are lacking. However, rates of survival to recruitment are unknown as are factors which may cause year-to-year variation in either growth or survival. Any improvement in the scientific basis for invertebrate fishery management is critically dependent on knowledge of variability in growth and survival of prerecruits along with an index or estimate of prerecruit abundance. These are the keys to predicting recruitment to the standing stock which, for invertebrate stocks generally, is the major part of annual production.

Other than a general need for the kind of research described above, the following particular item is identified:

1. La répartition verticale et les mouvements des crevettes, des prérecrues notamment, devraient être étudiés. De plus, on devrait chercher à déterminer l'influence de la direction et du déplacement des différentes masses d'eau sur la distribution horizontale et la stabilité des patrons de distribution pour chacun des stades du cycle de vie.

Recrues. L'état des connaissances sur la croissance est aussi peu avancé pour les recrues que pour les prérecrues. Il y a place à amélioration, particulièrement en ce qui a trait au homard et au crabe des neiges. Pour toutes les espèces, les estimations du taux d'exploitation devraient être révisées. Nous ne possédons pas de données sur la variation interannuelle de la croissance et de la survie des recrues pendant ou après les saisons de pêche subséquentes et nous ne savons pas dans quelle mesure ces variations contribuent ont un effet sur la production annuelle.

En plus de ce qui précède, une attention particulière doit être portée à ce qui suit :

1. Il serait nécessaire d'effectuer des travaux sur le terrain afin de déterminer si l'abondance des recrues a une incidence sur la croissance et la survie des juvéniles et des prérecrues. Le moment est propice à une telle entreprise, particulièrement dans la partie sud du golfe, puisque les prises de homard ont augmenté considérablement durant les années 1980, après une longue période pendant laquelle elles avaient diminué de façon importante. Nous possédons, pour fins de comparaison, des données historiques sur la croissance, mais les recherches devraient être poursuivies lorsque l'abondance de recrutement diminue à la suite de fortes prises.

Dynamique écosystème-communauté

Les populations d'invertébrés d'importance commerciale constituent une fraction importante des communautés ou des écosystèmes dont elles font partie. Il est toutefois admis que les interactions dynamiques entre toutes les composantes d'une communauté ou d'un écosystème auront des répercussions sur la production annuelle d'une population donnée. En plus des études détaillées sur la dynamique des populations des espèces d'importance commerciale, il est nécessaire d'effectuer des études sur la communauté afin de comprendre, entre autres, la dynamique des réseaux alimentaires, le transfert d'énergie, la prédation, la compétition, etc. Quelques-unes des petites baies du golfe sont, au moins jusqu'à un certain point, des systèmes mi-clos offrant d'excellentes conditions pour résoudre les problèmes les plus complexes que posent la dynamique des populations d'espèces bien précises ainsi que la dynamique écosystème-communauté. Parmi les endroits répondant à cette description, mentionnons la baie Bonne, la baie St. George, la baie des Chaleurs, Mingan et les Îles de la Madeleine.

Nous avons accès à des vastes collections de données sur les communautés benthiques de différentes parties du golfe. Un examen attentif de ces collections devrait nous aider à identifier des communautés qui pourraient s'avérer intéressantes pour des études détaillés.

1. The vertical distribution and movements of shrimp, particularly prerecruits, and the extent to which different water masses moving in different directions at different depths are involved in horizontal distribution and in maintaining different distribution patterns for different life-history stages should be investigated.

Recruits. The status of basic descriptions of growth of recruits is similar to that for prerecruits. For lobsters and snow crab particularly, there is much room for improvement. For all species, estimates of exploitation rates need refinement. Year-to-year variation in growth and survival of recruits during or following fishing seasons and the extent to which these contribute to annual production are unknown.

In addition to the foregoing, the following is identified for particular attention:

1. Field studies aimed primarily at determining whether growth and survival of juvenile and prerecruit lobsters are affected by recruit abundance should be undertaken. In the southern Gulf particularly, the timing is opportune since lobster landings have increased substantially during the 1980's following a lengthy period of decline to a low level. Some historical growth data are available for comparison, but the study should be continued as recruit abundance declines following peak landings.

Ecosystem/Community Dynamics

The commercially important invertebrate populations are major components of the communities or ecosystems to which they belong. However, it is recognized that dynamic interactions between all components of a community or ecosystem will affect annual production within a given population. In addition to detailed studies of the population dynamics of commercially important species, comprehensive studies at the community level, which would include food-web dynamics, energy transfer, predation, competition, etc., are required. Some of the small bays within the Gulf are, to some extent at least, semi-closed systems within which it might be possible to tackle some of the more intractable aspects of population dynamics of particular species as well as ecosystem/community dynamics with good chances of success. Areas that were identified for special consideration are Bonne Bay, St. Georges Bay, Baie des Chaleurs, Mingan, and Îles de la Madeleine.

Extensive collections from benthic communities in different Gulf areas are available. Detailed examination of these could help to identify particular communities that might be especially attractive for detailed study.

Les participants ont insisté sur l'importance d'une approche multidisciplinaire dans l'étude de ces communautés et dans toute autre recherche visant à résoudre plusieurs des problèmes reliés à la compréhension des processus et des mécanismes qui interviennent de façon déterminante dans la production annuelle de certaines populations d'invertébrés. Si l'on veut vraiment progresser dans ce domaine, un effort de concertation sera nécessaire pour mettre sur pied des équipes multidisciplinaires réunissant des spécialistes des sciences de la mer et pour s'engager dans des projets spécifiques. Les problèmes sont tellement complexes que seule cette approche présente des chances de succès.

Nous soumettons les propositions de recherche suivantes :

1. Procéder à des observations à long terme sur des communautés représentatives (comprenant des populations d'une ou plusieurs grandes espèces d'invertébrés) sélectionnées dans les régions côtières, dans les eaux peu profondes du plateau ainsi que dans les parties profondes du chenal, tant dans les eaux plus froides de la partie nord du golfe que dans les eaux plus chaudes de la partie sud.
2. Rechercher les causes de la présence de fortes concentrations de crevettes à l'entrée des chenaux et le long des bordures du plateau.
3. Chercher à expliquer la contradiction entre la faible productivité primaire et la grande abondance de crevettes et de crabes des neiges dans la partie nord-est du golfe.
4. Étudier les collections existantes d'assemblages suprabenthiques de larves et de juvéniles provenant des habitats de crevettes et de crabes des neiges de la partie ouest du golfe et de l'estuaire.

Qualité de l'environnement

Le groupe de travail sur les invertébrés devrait, en second lieu, se pencher sur les solutions aux principaux problèmes qui, à long terme, touchent la qualité de l'environnement; il s'est, en règle générale, limité aux conséquences qu'entraînent les variations de conditions et de facteurs clés sur les diverses composantes de la production annuelle d'une population. Toutefois, les participants se sont intéressés brièvement aux aspects de la qualité de l'environnement reliés aux changements climatiques à l'échelle du globe.

Outre la hausse de température prévue à l'échelle mondiale, il est difficile d'imaginer l'évolution et l'ampleur des changements en ce qui a trait à d'autres variables du climat telles que le vent, les modèles de circulation etc. La démarche que nous préconisons consiste d'abord à dégager les processus biologiques qui risquent d'être sensibles aux changements «climatiques», en analysant les données que nous possédons sur les rapports entre les variables climatiques et la dynamique des communautés d'invertébrés.

La mesure et l'évaluation des effets des changements climatiques sur les invertébrés vont nécessiter une approche multidisciplinaire et une étude exhaustive. À l'instar des travaux entrepris par P.-L. Ardisson et E. Bourget (Université Laval, données inédites), nous

The workshop stresses the importance of a multidisciplinary approach to community studies and to others aimed at resolving many of the problems associated with understanding the underlying processes and mechanisms that determine annual production in particular invertebrate populations. If any real progress is to be made, a concerted effort will be required to put together teams which include expertise from the various marine-science disciplines to focus on particular projects. The problems are too complex for anything less to be very successful.

Particular suggestions for research include:

1. Representative communities, which include populations of one or more of the main invertebrate species, should be selected from coastal, shallow shelf, and deep channel areas, preferably for each of the southern, warm-water and northern, cold-water portions of the Gulf, and monitored over the long term.
2. Investigation of the causes of high shrimp concentrations at the heads of channels and along shelf edges.
3. Investigation of the paradox between low primary productivity and high abundance of shrimp and snow crab in the northeastern portion of the Gulf.
4. Existing collections of suprabenthic assemblages from larval and juvenile shrimp and snow crab habitat in the western Gulf and estuary should be examined.

Environmental Quality

Consideration by the Invertebrates Workshop of the second part of the general mandate dealing with the solution of major long-term problems of the quality of the environment was generally limited to the impact of variability in key factors, conditions, etc., on the various components of annual production in a population. However, the global climatic change aspect of environmental quality was briefly addressed.

Aside from the predicted global temperature rise, it is difficult to predict trends and magnitudes of changes in other variables such as wind, circulation patterns, etc. A suggested approach is to first identify the critical biological processes likely to be sensitive to "climatic" change by reviewing present knowledge of invertebrate dynamics in relation to climatic variables.

Assessing and evaluating the impact of climatic change on invertebrates will require a comprehensive, multidisciplinary approach. It is recommended that representative cold-water and warmwater communities be selected for monitoring of changes both in the communities and recommandons la sélection de communautés représentatives des eaux chaudes et des eaux froides, dans le but d'observer à long terme les changements qui se produisent tant dans les communautés que dans leur environnement.

Les participants ont souligné le fait qu'il existe des différences dans la composition des communautés d'invertébrés de certains habitats du golfe, en particulier ceux des eaux froides de la partie nord et ceux des eaux plus chaudes de la partie sud. Certaines espèces ou certains stades de cycle de vie pourraient sans doute être très utiles pour un dépistage précoce des effets des changements climatiques. Il faudrait procéder à de telles observations pour déceler toute modification significative de la distribution et de l'évolution de l'abondance des espèces sensibles à ces changements. Nous suggérons, entre autres, de surveiller, en divers endroits du golfe, la fixation annuelle du naissain sur des collecteurs artificiels afin d'évaluer la variabilité du recrutement des pétoncles d'Islande (*Chlamys*), au nord, et des pétoncles géants (*Placopecten*), au sud. Toute modification de l'abondance relative de ces deux espèces pourrait être un indice de changement climatique.

Les participants ont également remarqué qu'il existe d'importantes collections d'invertébrés benthiques provenant de diverses régions du golfe. Ces collections ont été réunies à l'occasion de recherches sur l'écologie benthique menées par le département de biologie de l'Université de Montréal depuis les années 1950. Des cartes illustrant la distribution des communautés et des espèces dominantes pourraient être dressées à partir de données tirées de ces collections et de la littérature. Ces cartes seraient d'un grand intérêt et permettraient de suivre les changements à long terme.

Références

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in their environments as undertaken by P.-L. Ardisson and E. Bourget, Laval University (unpublished data).

It is noted there are differences in composition of invertebrate communities in particular habitats in the northern, cold-water and the southern, warmwater portions of the Gulf. Certain species or particular life-history stages would likely provide good opportunities for early detection of the impact of climatic change. Monitoring should be conducted to detect significant shifts in distribution and trends in abundance of sensitive species. One particular suggestion is to monitor annual spatfall on artificial collectors for variability in recruitment success of the northern Iceland scallop (*Chlamys*) and the southern sea scallop (*Placopecten*) at several sites in the Gulf. A shift in the balance between the two species might provide an indication of climatic change.

The availability of extensive collections of benthic invertebrates from various areas in the Gulf is noted. These were obtained as part of benthic ecology research projects conducted by the Department of Biology, University of Montreal, since the 1950's. Preparation of base maps of the recent geographic distribution of communities and dominant species from these collections as well as the literature would have considerable value in terms of documenting long-term changes.

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CHAPITRE III.
REVUES SUR INVITATION

CHAPTER III.
INVITED PAPERS

The Physical Oceanography of the Gulf of St. Lawrence: A Review with Emphasis on the Synoptic Variability of the Motion[1,2]

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KOUTITONSKY, V. G., AND G. L. BUGDEN. 1991. The physical oceanography of the Gulf of St. Lawrence: a review with emphasis on the synoptic variability of the motion, p. 57–90. *In* J.-C. Therriault [ed.] The Gulf of St. Lawrence: small ocean or big estuary? Can. Spec. Publ. Fish. Aquat. Sci. 113.

The Gulf of St. Lawrence (GSL) is a highly-stratified semi-enclosed sea connected to the North Atlantic Ocean through Cabot Strait to the southeast, and through the Strait of Belle-Isle, a smaller strait to the northeast. It is forced at various temporal and spatial scales by: (1) tides from the Atlantic ocean, (2) local and large-scale meteorological seasonal and transient events, (3) freshwater runoff and heat flux, and (4) perturbations at the edge of the continental shelf. Indications are that the GSL responds as an integrated physical oceanographic system, although little evidence is available to support this hypothesis.

Recent hydrodynamical studies are reviewed, with a particular emphasis on the synoptic variability of the motion and water mass properties. Except for tidal processes which are deterministic in nature, the response of the GSL system to the integration of the other forces, mostly stochastic in nature, has yet to be fully understood. This will require long-term simultaneous measurements at several strategic locations in the system, as well as multi-institution concerted actions. In the meantime, a numerical GSL laboratory, consisting of three-dimensional circulation and water quality numerical models, may be used to study Gulf-wide processes and the interaction between its various regions.

Le Golfe du Saint-Laurent (GSL) est une mer semi-renfermée et hautement stratifiée qui communique avec l'océan Atlantique par le détroit de Cabot au sud-est, et par le détroit de Belle-Isle, un plus petit détroit au nord-est. Le golfe est forçé à diverses échelles spatiales et temporelles par : (1) les marées océaniques, (2) les événements météorologiques transitoires à l'échelle locale et à grande échelle, (3) les débits d'eau douce et les flux de chaleur, et (4) les perturbations océaniques en bordure du plateau continental. La réponse du GSL à ces forces semble être celle d'un système hydrodynamique intégré, mais les informations disponibles ne sont pas suffisantes pour supporter cette hypothèse.

Les récentes études hydrodynamiques sont revues, avec une emphase particulière sur la variabilité synoptique du mouvement et des propriétés des masses d'eau. A l'exception des processus marégraphiques qui sont de nature déterministe, la réponse du GSL à l'ensemble des autres forces, plutôt de nature stochastique, est loin d'être bien comprise. Ceci nécessitera des mesures simultanées à long terme et à divers endroits stratégiques, ainsi qu'une action concertée de la part de plusieurs institutions océanographiques. Entre temps, un laboratoire numérique du GSL comprenant un ensemble de modèles numériques tri-dimensionnels de circulation et de transport d'éléments dissouts pourrait être utilisé pour étudier les processus hydrodynamiques à l'échelle du golfe et les interactions entre ses diverses régions.

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[1] A contribution to the Centre Océanographique de Rimouski and to the Bedford Institute of Oceanography.

[2] This paper forms part of the Proceedings of a Workshop/Symposium held at the Maurice Lamontagne Institute, Mont-Joli, Québec, 14–17 March 1989.

1. Introduction

The Gulf of St. Lawrence is a highly stratified semi-enclosed sea (Fig. 1), with an approximate surface area of 226 000 km^2 and a volume of 34 500 km^3 (Forrester 1964; Forrester and Vandall 1968). It exchanges salt with the North Atlantic Ocean and receive considerable freshwater from surrounding rivers. As a consequence, it responds as large estuaries where Coriolis effects are important and baroclinic processes such as frontogenesis, eddy formation and current instabilities are to be expected. Biological oceanographic studies (eg. Legendre and Demers 1984; Legendre et al. 1986; Sinclair et al. 1986, 1987) suggest that such processes will influence biological production, the early life stages and retention of larvae, and possibly fish migration. On the other hand, since the inflowing rivers drain large watersheds where highly industrialized developments are located (eg. Great Lakes, Fig.1), this semi-enclosed sea constitutes a potential sink for industrial pollutants advected seaward over the years. Therefore, careful management and conservation of the living resources in the GSL system requires a thorough understanding of its hydrodynamics. However, a review of the literature indicates that practically nothing is known about the hydrodynamics of this system, as compared to other semi-enclosed seas such as the Baltic Sea (e.g. Voipio 1981; Nihoul 1982). To say the least, this is matter of serious concern if one considers that the GSL yields about 25% of Canadian total commercial fish catch by weight (Dickie and Trites 1983), and that more than 5 million metric tons of crude oil are being transported through the Gulf each year (R. Archambeault, ULTRAMAR, Québec, personal communication), implying a chronic or sudden threat to the ecosystem.

Attempts to study the hydrodynamics of the GSL system date back to the pioneering work of Dawson (1897, 1913), Sandstrom (1919) and others. Previous GSL reviews (Trites 1968a; Hassan 1970; Trites 1972; Trites and Walton 1975; El-Sabh 1973; Bugden et al. 1982; Dunbar et al. 1980; Dickie and Trites 1983) strongly support the idea that the GSL forms an integral physical oceanographic unit. However, given the large dimensions of the system, and the lack of resources to measure simultaneously the variability in all parts, most studies were limited to the description of "monthly-averaged" parameter distributions, estimated from samples collected at different times and places, without reference to the variability in the system.

Oceanic variability results from a combination of processes, each acting at different time scales. Table 1 presents a classification of the various temporal scales of variability normally encountered in the oceans, together with some processes occurring in each class (Monin et al. 1977; Nihoul and Djenidi 1987). With the advent of satellite remote sensing and long-term recording current meters, recent studies in some regions of the GSL (section 4.2) revealed the existence of large subtidal fluctuations in the fields of motion and related oceanographical variables. The time scales involved were from days to months, which according to Table 1, corresponds to *oceanic synoptic variability*. Its principal manifestation on continental shelves (e.g. Mooers 1986; Nihoul and Jamart 1989) is aperiodic formation of eddies with spatial scales ranging between 10 to 100 km. In the GSL, these fluctuations were attributed to local buoyancy and meteorological forcing, instability of the motion, but also to some "non-local" or large-scale forcing. Realizing the need to understand the large-scale hydrodynamics of the

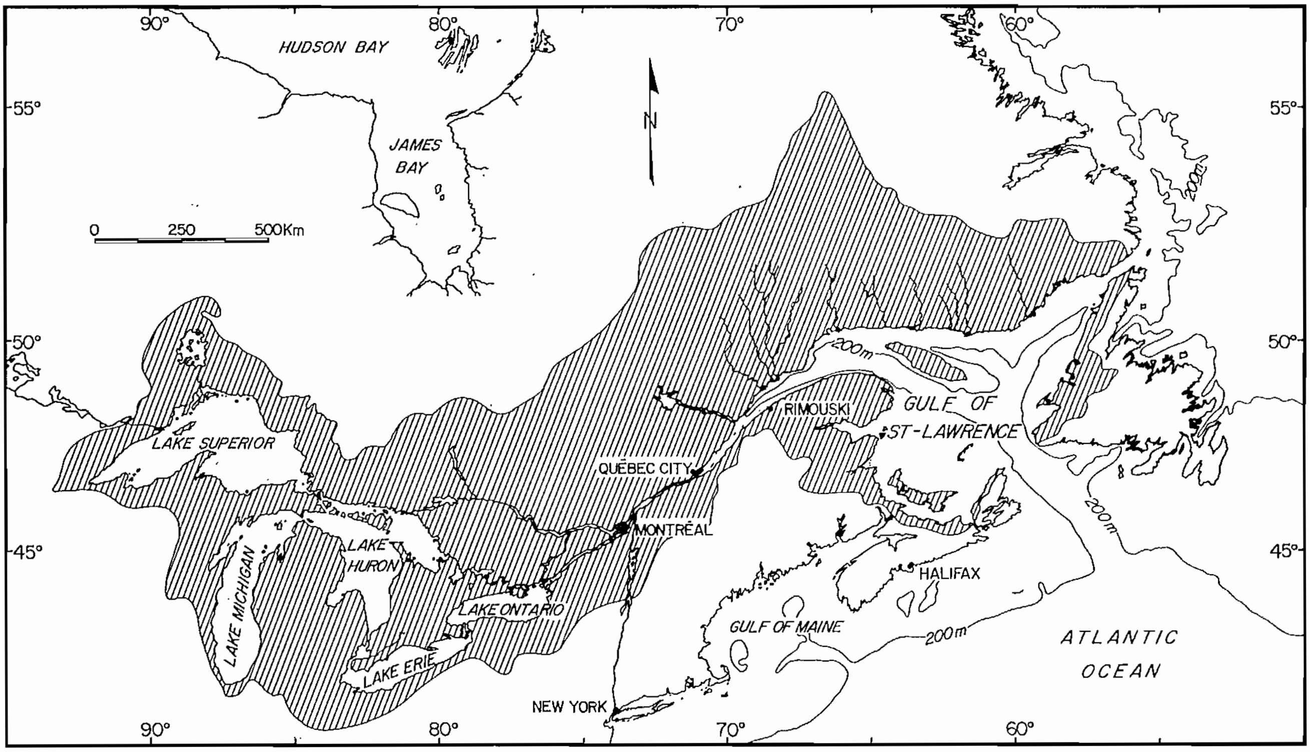

FIG. 1. The Gulf of St. Lawrence watershed.

TABLE 1. Classification of oceanic variability.

Variability	Time scales	Processes
Small-scale	Fraction of a second to tens of minutes	Turbulence, wind waves, internal waves, evolution of vertical micro-structure.
Mesoscale	Hours to one day	Tidal motion, inertial motion, storm surges, diurnal winds.
Synoptic	Days to months	Eddy-motion, geostrophic frontal currents, Rossby turbulence.
Seasonal	One year period	Seasonal thermocline, ice cover, Indian Monsoon.
Year-to-year	Years	Gulf-stream northern branch, El-Ninio.
Secular	Tens of years	Global warming.
Century-to-century	Hundreds of years	Ice ages, sea-level rise, Paleo-warming.

system, a 2 yr Gulf-wide measurement program was designed in 1973 (Environment Canada 1973). Due to costly logistics, the project was never funded and the system's overall hydrodynamics remain to be understood.

The objective of this review is to describe some aspects of the physical oceanography of the Gulf of St. Lawrence, with particular emphasis on the forcing functions and the resulting variability of the motion and water masses at synoptic and other time scales. The GSL is considered as a multiple input / single output system, acted upon by a combination of forces, or inputs. The output consists of the fields of motion and state variables responding to the forcing functions. The system is described in section 2. The inputs are examined in section 3, and the output is discussed in section 4 at various scales of variability. Suggestions for future research directions are made in section 5.

2. The Gulf of St. Lawrence System

The GSL (Fig. 2) has two connections with the North Atlantic Ocean: Cabot Strait to the southeast where the maximum depth is 480 m, the width is 104 km and the cross-sectional area is 35 km^2, and a much smaller one to the northeast, the Strait of Belle-Isle, where depths are less than 60 m, the width is about 15 km and the cross-sectional area is 1 km^2 (Trites 1972). A major topographic feature of the system is the Laurentian Channel, a 300–400 m deep trough extending over some 1000 km from the North Atlantic continental slope, through Cabot Strait, up to the head of the Lower St. Lawrence Estuary at Tadoussac. The abrupt shoaling of the topography at Tadoussac provides for a natural subdivision of the St. Lawrence Estuary into an Upper Estuary starting at Québec city, and a Lower Estuary ending at Pointe-des-Monts where the width suddenly diverges. Two other deep channels branch off from the Laurentian Channel

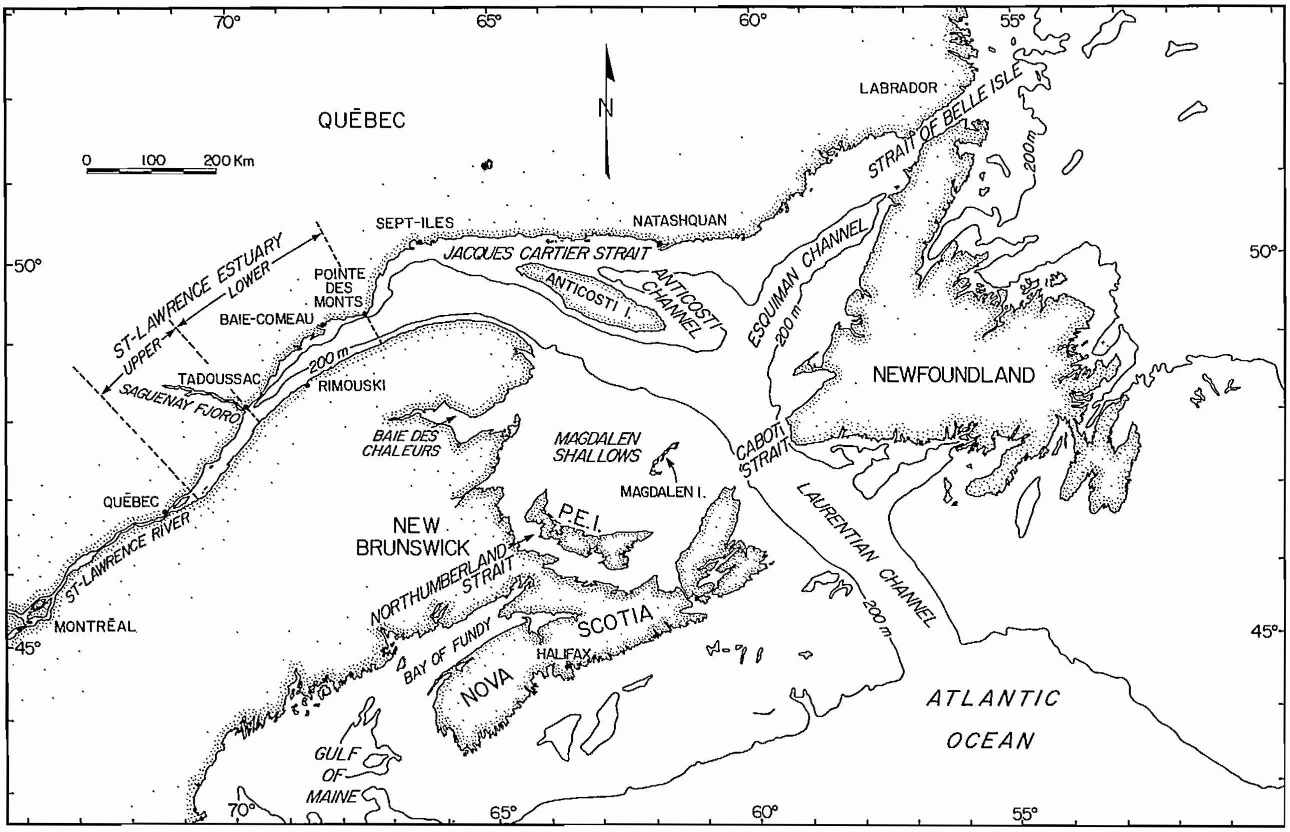

FIG. 2. The Gulf of St. Lawrence system.

between Newfoundland and Anticosti islands: the Esquiman Channel extending towards the Strait of Belle-Isle, and the Anticosti Channel extending into Jacques Cartier Strait, north of Anticosti Island. The deep channels occupy about half the surface area of the Gulf, and constitute the network through which incoming intermediate Atlantic waters slowly flush the GSL system. By contrast, the southern portion of the Gulf is a wide and shallow plateau, called the Magdalen Shallows, where depths seldom exceed 80 m. Seven islands with a peculiar lagoon network, called the Magdalen Islands, are located on this plateau to the west of Cabot Strait. Further to the southwest, Prince Edward Island is separated from the province of Nova Scotia by an approximately 200 km long, 20 km wide and 20 m deep strait, called Northumberland Strait.

3. The System Inputs: The Forcing Functions

At least four inputs are known to affect the GSL system: (1) tidal forcing from the Atlantic ocean, (2) buoyancy forcing from freshwater runoff and heat fluxes, (3) local and large-scale meteorological forcing over the Gulf, and (4) other oceanic forcing from the Atlantic, each acting at their own spatial and temporal scales. The system's response being governed by the equations of conservation of momentum, mass and energy in stratified fluids (e.g. LeBlond and Mysak 1978), some terms in these equations may integrate the effects of more than one input. Therefore, it is important to examine first the nature and time scales of each of the inputs.

3.1 Buoyancy Forcing

It is now generally admitted that the continuous supply of freshwater from the St. Lawrence River and other tributaries in the GSL watershed (Fig. 1) maintains a basic state of motion in the Gulf which, when averaged laterally, resembles an estuarine density-driven circulation. Previous estimates of freshwater runoff to the GSL (Trites 1972; Jordan 1973; El-Sabh 1977a; Dickie and Trites 1983) have singled out two regions from which most of the freshwater is supplied to the GSL system: the St. Lawrence Estuary (SLE) and the northern shore of the Gulf. The relative mean contributions of these buoyancy inputs are re-examined here, from data obtained for the period of 1950–84 (Environment Canada 1988; Environnement Québec 1988). The sum of freshwater runoff into the SLE, at the mouth of the Estuary, was computed following Carrier (1976) and by allowing for appropriate advection lags estimated from Tee and Lim (1987). This sum will be referred to as RIVSUM. Table 2 presents the monthly and annual mean runoff contributions from the following three regions: (a) the St. Lawrence Estuary up to Pointe-des-Monts, (b) the north shore of the Gulf from Pointe-des-Monts to Blanc Sablon, and (c) the remaining Gulf perimeter. Freshwater fluxes through the surface (Bugden 1981) are also included. Results indicate that the annual runoff to the GSL is close to 600 km^3, with a maximum rate of 32 370 m^3/s in May and a minimum of 14 196 m^3/s in February. The percentage contributions from each region are: 83.8% from RIVSUM, 13.5% from the north shore rivers, and 2.7% from all other rivers. Estimates of annual freshwater fluxes through the surface amount to some 120 km^3/yr, or about 24% of RIVSUM. Therefore, RIVSUM has to be considered as the main driving force for the estuarine-like circulation of the GSL. Standard deviations in Table 2 show that significant runoff fluctuations do occur about the long-term monthly means. These fluctuations result from the combined effects of RIVSUM hydroelectric regulations (Neu 1975) and the natural variability of the system (Bugden et al. 1982). In view of its influence on the hydrodynamics and the fisheries of the GSL, several authors have examined the RIVSUM variability (Trites 1972; Jordan 1973; Sutcliffe et al. 1976; Koutitonsky 1979; El-Sabh 1979; Bugden 1981; Bugden et al. 1982; Therriault and Levasseur 1985; El-Sabh 1988). This variability is now updated and briefly discussed at various time scales, using the 1950–84 data base.

TABLE 2. Mean monthly freshwater runoff (1950–84) into the Gulf of St. Lawrence from the St. Lawrence Estuary, the north-shore rivers, and all other rivers, with their standard deviations, in m^3/s. Estimates of precipitation (*P*) minus evaporation (*E*) minus ice formation (*I*) from Bugden (1981) are also included.

Month	St. Lawrence Estuary	North shore	Others	Total runoff	P–E–I
January	13878 ± 1859	856 ± 52	210 ± 11	14944 ± 1860	-500
February	13282 ± 1377	724 ± 46	190 ± 11	14196 ± 1378	100
March	13550 ± 2337	641 ± 44	229 ± 18	14420 ± 2338	6800
April	15876 ± 3112	1169 ± 96	772 ± 62	17817 ± 3114	7900
May	23641 ± 3812	6822 ± 422	1907 ± 136	32370 ± 3838	6300
June	22163 ± 4010	7039 ± 489	761 ± 44	29963 ± 4040	5500
July	16766 ± 2511	2804 ± 183	308 ± 20	19878 ± 2518	5700
August	14658 ± 1825	2206 ± 141	271 ± 18	17135 ± 1830	4300
September	13990 ± 1428	2320 ± 160	255 ± 18	16565 ± 1437	3000
October	14068 ± 1591	2738 ± 174	394 ± 28	17200 ± 1601	2300
November	14404 ± 2006	2113 ± 134	412 ± 24	16929 ± 2010	3800
December	14426 ± 1885	1451 ± 89	367 ± 21	16244 ± 1887	900
Mean	15892 ± 4114	2574 ± 2181	506 ± 485	18972 ± 6421	3840

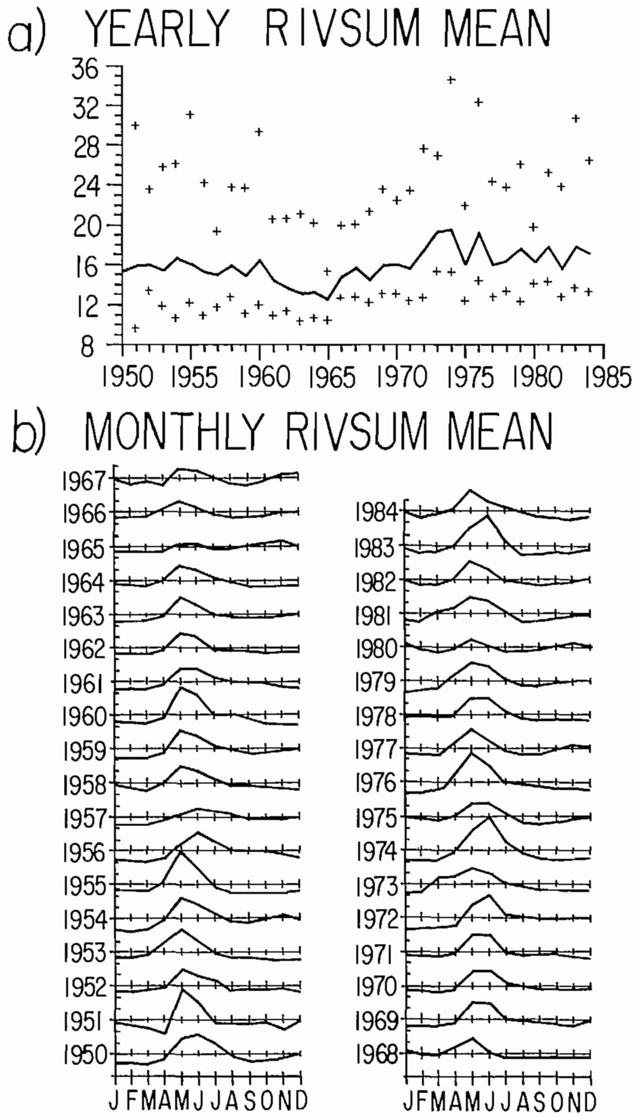

FIG. 3. (a) Yearly RIVSUM mean (1950–84), with year low and high shown in crosses, (b) Monthly RIVSUM fluctuations about the yearly mean. Y-axis intervals are 5000 $m^3 \bullet ^{-1}$.

The annual RIVSUM means (Fig. 3a) reveals considerable year-to-year and secular variability, with a minimum of 12 570 m^3/s in 1965, a maximum of 19 588 m^3/s in 1974. Extremes during each year (crosses in Fig. 3a) indicate that a minimum discharge of 9 744 m^3/s occurred during April 1951, while a maximum discharge of 34 600 m^3/s occurred during June 1974. Note that no significant 11 years periodicity is evident, as was previously reported by Neu (1975) and El-Sabh (1977a). The RIVSUM monthly fluctuations about their annual mean from 1950 to 1984 (Fig. 3b) show large runoff pulses occurring during May–June, but occasionally during June–July. A second pulse of nearly the same magnitude as the spring pulse occasionally occurs in autumn (eg. 1965, 1967, 1980). Note that during most years, the April RIVSUM is almost equal to the corresponding annual RIVSUM mean. Finally, the RIVSUM synoptic variability can be assessed from the runoff time series presented in Fig. 4. The series are daily and trend fluctuations about the mean, for the period of April to September 1979 for RIVSUM, for the St. Lawrence River runoff, for the Saguenay Fjord runoff, and for individual runoff from the three rivers on the northshore of the Lower Estuary. Pulses of considerable magnitude (order of 1 000 $m^3 \bullet s^{-1}$) are seen to issue from the Saguenay Fjord and from the three north shore rivers, and become superimposed onto the Québec pulse in RIVSUM. These are presumably caused by runoff hydroelectric regulations at the Maligne dam in the Saguenay Fjord, and at the Manicouagan complex dams in the three northshore rivers (Neu 1975). Having time scales of the order of one month, it will be shown (section 4.2.1) that these pulses are largely responsible for the synoptic variability of the motion in the Lower Estuary and in the Gaspé region. Finally, one should be aware that the regulation of the northshore rivers in the GSL is a project now under consideration by the Québec government. At this time, Table 2 indicates that on the average, the highest runoff from these rivers lags that of RIVSUM by about 1 month, presumably because of the relatively colder air temperatures in the northern latitudes.

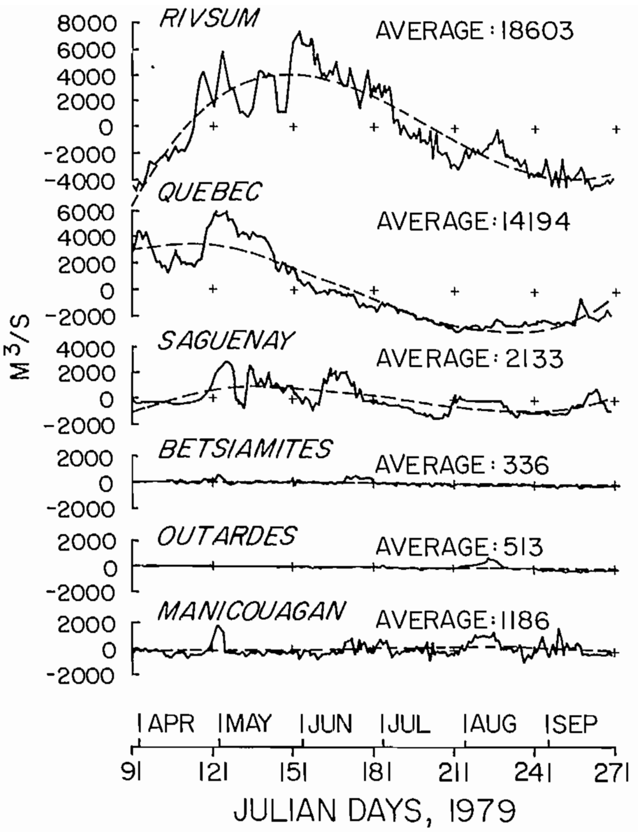

FIG. 4. Daily RIVSUM fluctuations about the average from April to September, with individual contributions from the St. Lawrence River, the Saguenay Fjord, and the three northshore rivers (Betsiamites, Outardes, and Manicougan).

Surface heat fluxes also contribute to buoyancy forcing through the formation of a seasonal thermocline in summer, vertical mixing of the water column during autumn, and ice formation during winter. Mean monthly air-temperature distributions over the GSL (eg. Vigeant 1984) indicate that above freezing temperatures generally appear over the Upper Estuary and the southwestern region of the Gulf by the end of March, and extend over the Gulf by April. Isotherms then adopt a zonal distribution in summer, reaching their maximum in August (18°C over Northumberland Strait and 12°C over Belle Isle Strait). Below freezing temperatures appear over the northern shores of the Gulf and the Estuary by November, and extend to Cabot Strait by December. The monthly-averaged interannual variability is of the order of 1 to 5°C, and may be useful in the interpretation of annual differences in processes such as ice formation, or abnormal timing in the onset of fish migration into the Gulf (Loucks and Trites 1981; Koutitonsky et al. 1986).

Heat budget estimates for the GSL (Lauzier and Graham 1958; Coombs 1962; Matheson 1967; Boudreault 1969) show that radiation terms constitute the major source of heat during spring and summer, while evaporation and conduction account for autumn and winter heat losses. Surface heat fluxes throughout the GSL (Bugden 1981) become positive during the first week of March on average and increase considerably during April. At that time, the ratio between the buoyancy supplied by surface heat flux and that supplied by freshwater discharge becomes 0.9 (Bugden et al. 1982). Maximum heat flux values are reached in June (180 W • m^{-2} in the northeastern Gulf and 256 W • m^{-2} in the St. Lawrence Estuary). Heat fluxes then decrease to 0 W • m^{-2} in the Magdalen Shallows by September, then progressively throughout the Gulf, and finally in the Lower Estuary by October. By December, heat fluxes in all areas reach minimum values of -250 W • m^{-2}, and ice starts to form.

3.2 Meteorological Forcing

Wind-stress forcing is a major source of kinetic energy for the GSL, but has not been well documented. Monthly-averaged wind stresses distributions have been estimated from mean sea-level pressures, interpolated over the Gulf from shore-based meteorological stations, using numerical models based on the geostrophic method (Murty and Taylor 1970; Vandall 1973; Koutitonsky et al. 1986). These studies revealed that strong winds blow from the north over the Gulf from December to April, in equilibrium with a low pressure centre lying to the east in the Atlantic ocean. From June to October, weaker winds blow from the northeast in the Estuary and the

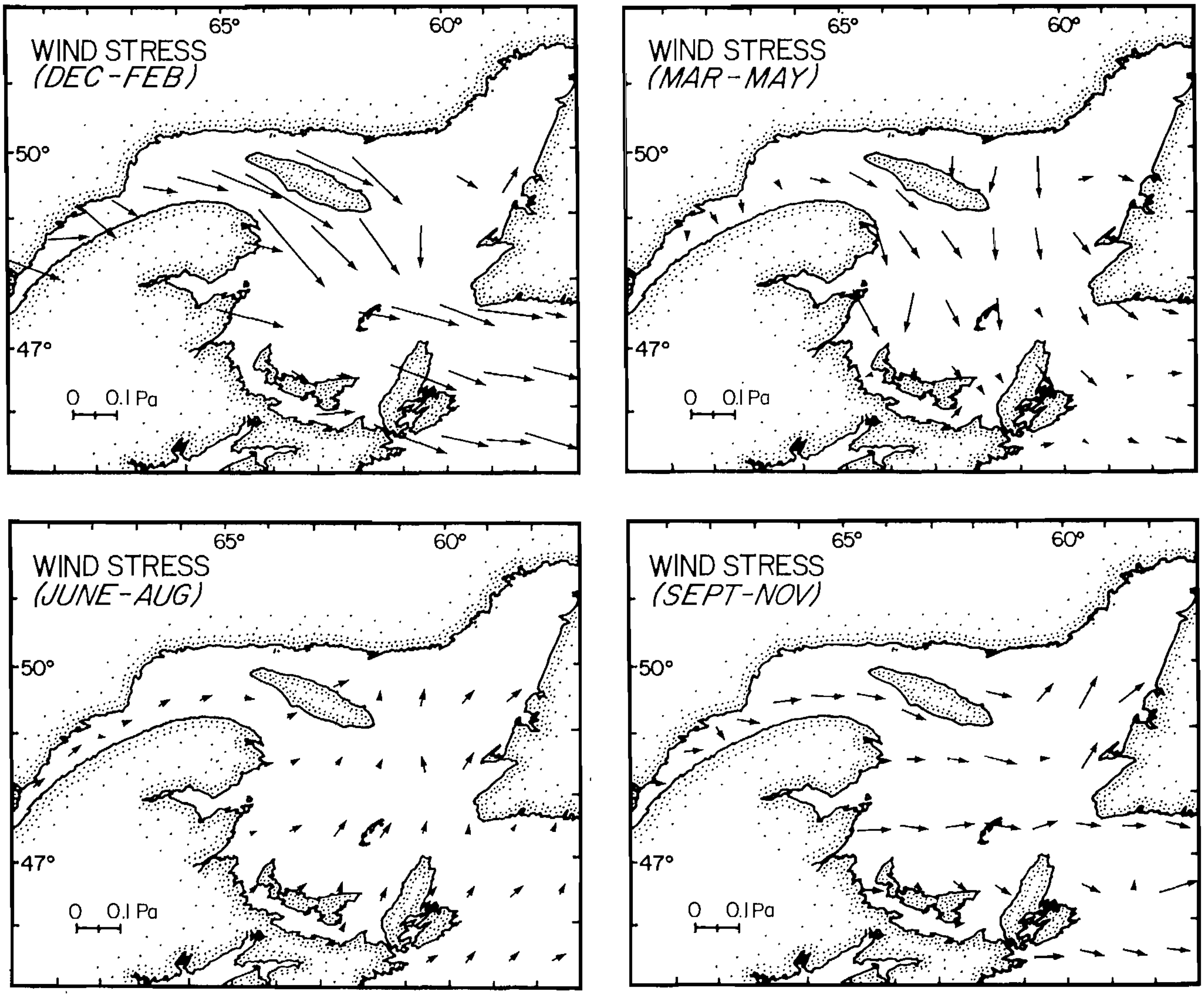

FIG. 5. Mean seasonal wind stress (1941–72) over the Gulf of St. Lawrence, averaged from ship observations (from Saunders 1977).

Northwestern (Anticosti) region, but from the southwest over the Magdalen Shallows and the Newfoundland region, implying a cyclonic curl of the wind stress over the GSL. Wind stress magnitudes were found to be of the order of 0.1 Pa during winter and 0.01 Pa during summer. However, when we compared numerical model results (e.g. Koutitonsky et al. 1986) to wind stress measurements averaged over the same interval of time, considerable differences in amplitude and direction were noted for most shore stations. Orographic steering tends to influence the wind field in most coastal areas of the GSL. Herfst (1984) documented this effect for the St. Lawrence Estuary, where surface winds are steered along its axis by the mountains located on both shores. It is also suspected that the Gaspé Péninsula mountains will deflect the predominantly northwesterly winds to a direction parallel to the shoreline. This may have interesting implications for the dynamics of the Gaspé Current. Therefore, wind computations from geostrophic pressure maps should not be used close to shore unless some parametrization of coastal boundary effects are included. High spatial variability in the wind stress field over the GSL was also noted by Saunders (1977). He estimated mean seasonal wind stresses over the North Atlantic continental shelf, using winds reported by ships over 32 yr (1941-72). His results, isolated for the GSL in Fig. 5, indicate a predominantly westerly direction for wind stresses during all seasons, with marked northerly components in spring and southerly components in summer. Again, magnitudes reach 0.1-0.15 Pa during winter, but decrease to about 0.03 Pa in summer.

Whereas the above wind stresses represent conditions averaged over many events, it is instructive to examine the spatial and temporal scales of variability involved in a single wind-forcing event. Archibald (1945) reports that the low pressure centres of intense storms propagate over the GSL along preferred tracks. Their average location are shown for each season in the upper four panels of Fig. 6 (adapted from Murty 1984). One can distinguish two spatially-varying forcing patterns: (a) *northern storms*, propagating from the west to the northeast with their centre lying to the north of the Gulf, and (b) *southern storms*, propagating from the south to the northeast with their centre lying over water near the eastern boundary of the Gulf. The spatial extent and associated geostrophic wind directions for the July-September period are sketched in the lower two panels of Fig. 6, as the northern (left) and southern (right) intense storms propagate along their preferred tracks. These findings are of utmost importance. They reveal that, in

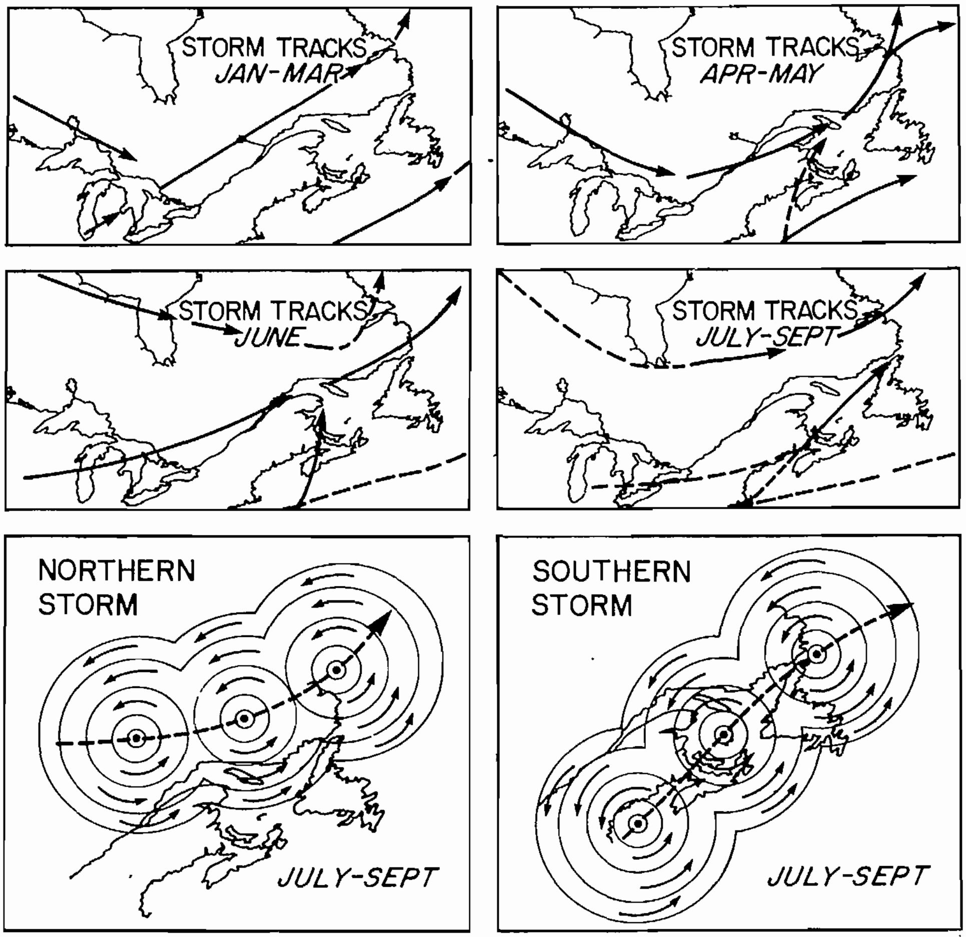

FIG. 6. Mean seasonal tracks of intense storms (solid lines) and secondary storms (dashed-lines) over the Gulf of St. Lawrence (upper four panels, from Murty 1984), and sketches of northern (bottom left) and southern (bottom right) storms progressing along their July-September tracks, with corresponding geostrophic wind-stress directions.

view of their large dimensions, storms affect the whole Gulf and coherent Gulf-wide motion can be expected. Furthermore, offshore Ekman transport in the surface layer will differ regionally, depending on which storm is progressing over the Gulf.

The temporal variability of wind forcing can be appreciated by looking at a sequence of daily weather maps (AES, Environment Canada) highlighted on Fig. 7a to 7h, which consist of mean-sea-level isobar distributions (anomalies from 1000 mb), recorded at 0:00 hours GMT from July 2 to 8, 1979. This sequence features the propagation of a northern storm over the Gulf (2-5 July, left column), immediately followed by that of a southern storm (5-7 July, right column). The arrows shown represent geostrophic wind directions, speed being proportional to the isobar spacing. Three points are worth noting from Fig. 7. First, the time scales involved in meteorological forcing are of the order of days, implying synoptic time scales. Secondly, forcing from the southern storm (Fig. 7e to 7h) is relatively more energetic since the low-pressure track lies above the water. Thirdly, the southern storm moves relatively faster over the GSL, implying wind forcing of shorter duration. These findings can be verified from spectral analysis of long-term series of wind measurements. For instance, we performed a frequency-domain empirical orthogonal function analysis (Wallace and Dickinson 1972) of hourly zonal (U) and meridional (V) wind component time series, recorded from April to September 1979 at five stations in the northwest Gulf and the Estuary. Results in Fig. 8 show the total variance of the series Tr (trace of

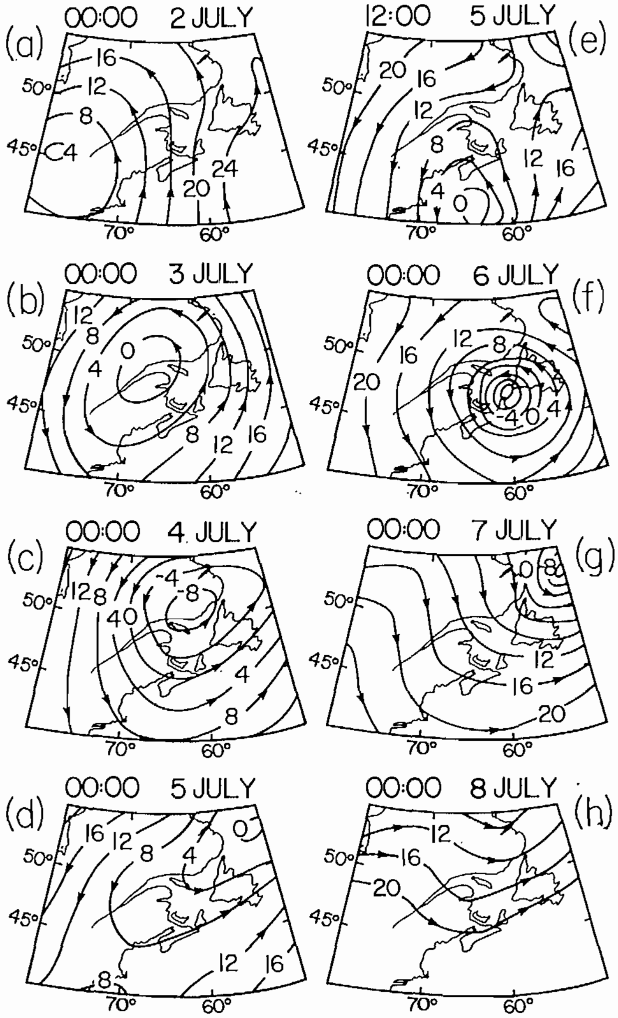

FIG. 7. Mean-sea-level pressure maps at 00:00 hours GMT from (a) July 2 to (h) July 8, 1979. Arrows indicate geostrophic wind directions.

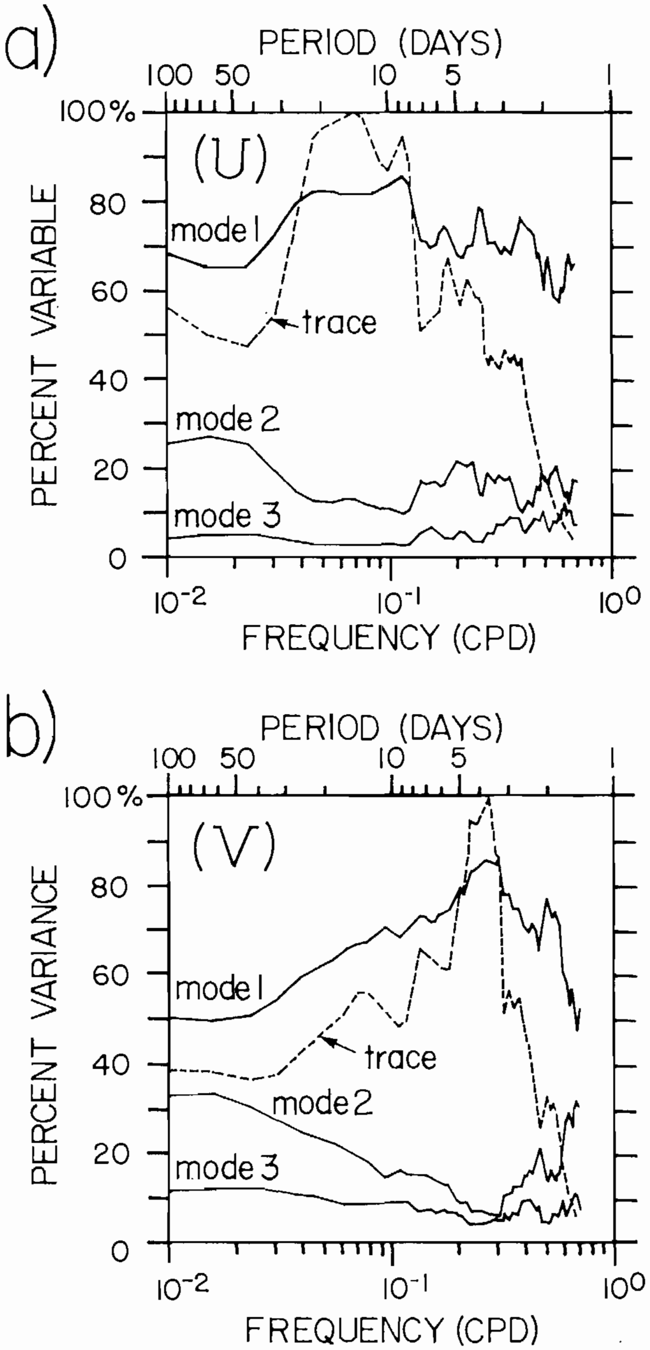

FIG. 8. Frequency-domain empirical orthogonal function analysis of (a) zonal winds U, and (b) meridional winds V at Mont-Joli, Baie-Comeau, Rivière-du-Loup, Sept-Îles, and Rivière-au-Renard from May to September 1979. Dotted lines represent trace (Tr) of the cross-spectral density matrix (in % of maximum Tr or 100%), and solid lines are spectral densities of modes 1 and 2 (in % of Tr), as a function of frequency.

the cross-spectral density matrix, given in percentage of maximum trace, dotted line), and the percentage of Tr explained by the first three empirical modes, as a function of frequency. Synoptic wind forcing is found to be highly coherent over that area (about 80% of Tr explained by first mode), in two frequency bands. The zonal wind fluctuations (Fig. 8a) are coherent and most energetic at periods of 8–15 d, whereas the meridional fluctuations (Fig. 8b) are most energetic at periods of 3–5 d. This suggests that northern storms which produce zonal wind fluctuations over the Gulf (Fig. 6) are of longer duration, while southern storms produce shorter period meridional fluctuations. This implies that wind-driven motion in the Gulf is more effectively generated by northern storms which have longer forcing time scales relative to the spin-up time of the Gulf. Similar frequencies of oscillation were obtained for winds in the Estuary (El-Sabh et al. 1982; Mertz et al. 1988a; Tee 1989), in the Gaspé Current (Benoit et al. 1985), in the Strait of Belle-Isle (Garrett and Toulany 1981), and in the northeastern Gulf (Rose and Leggett 1988a).

3.3 Tidal Forcing

Tides and tidal streams in the GSL are maintained by non-local tidal forcing from the Atlantic Ocean, acting at Cabot Strait and to a lesser extent at the Strait of Belle-Isle, and by local tide-generating forces. Tidal characteristics in the GSL are determined by the ratio between its dimensions and each tidal harmonic wavelength, and by the amplitudes and phases of these constituents in the North Atlantic Ocean (see Farquharson 1970 for details). Semidiurnal M2 tides (Fig. 9 top) along the oceanic shores of Newfoundland propagate in an anticlockwise sense around an amphidromic point located in the middle of the Atlantic Ocean (not shown), with phases of about 180° at Belle-Isle Strait and 240° at Cabot Strait. The K1 diurnal constituent (Fig. 9 bottom) features large phase differences across Cabot Strait, due to the proximity its amphidromic point on the Scotian Shelf. Local tidal-generating forces can usually be neglected in semi-enclosed seas, when compared to the non-local component. This holds for the GSL (Farquharson, 1970; Godin, 1979), although Pingree and Griffiths (1980) verified that neglecting the local body force introduces a 5° bias in M2 tidal phases.

3.4 Oceanic Forcing

Lauzier and Trites (1958) believed the deeper waters of the GSL to be composed of Labrador and Slope Waters mixing in relatively constant proportions and supplied continuously to the Laurentian Channel. They noted variations in the characteristics of the deeper waters on decadal time scales which they attributed to changes in the temperature of the Labrador water. Subsequent work has disputed the existence of Slope Water with a constant T–S correlation (Gatien 1976). Rather, in the region east of the Scotian Shelf, appreciable variations in T–S properties occur, generally related to location. The waters found in the Slope Water region appear to be formed of a mixture of Labrador and Atlantic Waters in varying proportions, the proportion of Labrador Water generally decreasing with alongshore distance from the Grand Banks as well as offshore distance from the Scotian Shelf (Lee 1970). More recently, Bugden (1991) documented changes of up to 2°C in the deep waters of the GSL subsequent to the study of Lauzier and Trites (1958). He suggested that the deep waters in the Laurentian Channel are made up of a mixture of Labrador and North Atlantic waters in varying proportions. The proportions vary on time scales of several years and may be monitored by remote sensing through the position of the Shelf–Slope water boundary. He also suggested that shear dispersion results in the applicability of a simple advection–diffusion equation to the up-channel propagation of the parameter anomalies thus providing some forecasting ability as the disturbances move slowly inward at the mean advection velocity. The results of his analysis indicate that the primary factor determining the characteristics of the deep waters of the GSL is changes in the properties of the oceanic waters at the edge of the continental shelf. These properties change on time scales of months to decades but strong cross-channel mixing allows only the lower frequency events to propagate up the Laurentian Channel.

4. The System Output: The Response

As stated earlier, the simultaneous response of all regions of the GSL system to the above forcing functions is not well understood, except perhaps for barotropic coastal tides, a deterministic process monitored by tide gauges around the Gulf for many years. In this section, we present what is considered to be a long-term basic state for the GSL. We then review the Gulf-wide responses to tidal forcing, and to climatic forcing in terms of "monthly-averaged" properties. Finally, we review from more recent studies in restricted regions of the Gulf the variability of the motion at mesoscale, synoptic, and longer time scales.

4.1 Gulf-Wide Studies

4.1.1 The Basic State

Without loss of generality, the basic state of motion for the GSL system consists of a density-driven circulation maintained by forces of climatic origin (sections 3.1, 3.2), modified by the Coriolis force, and interacting with the system's topography. A sketch of its main features along the Laurentian Channel during summer is presented in Fig. 10a. The water column is vertically stratified, and the motion is estuarine-like, with a thin upper layer (10–30 m) of low salinity (27–32‰) waters moving towards the Atlantic ocean. Typical vertical T–S profiles (Fig. 10b) show an upper layer separated by a sharp seasonal thermocline from an intermediate cold (-1°C–2°C) and saltier (31.5–33‰) layer which extends down to about 125 m. During winter, the surface layer disappears and the cold layer extends to the surface, as inferred the T–S diagram in Fig. 10c. The cold layer is largely the product of *in situ* winter cooling, although a fraction of its volume comes from Labrador shelf waters entering the Gulf through the Strait of Belle-Isle. Whereas

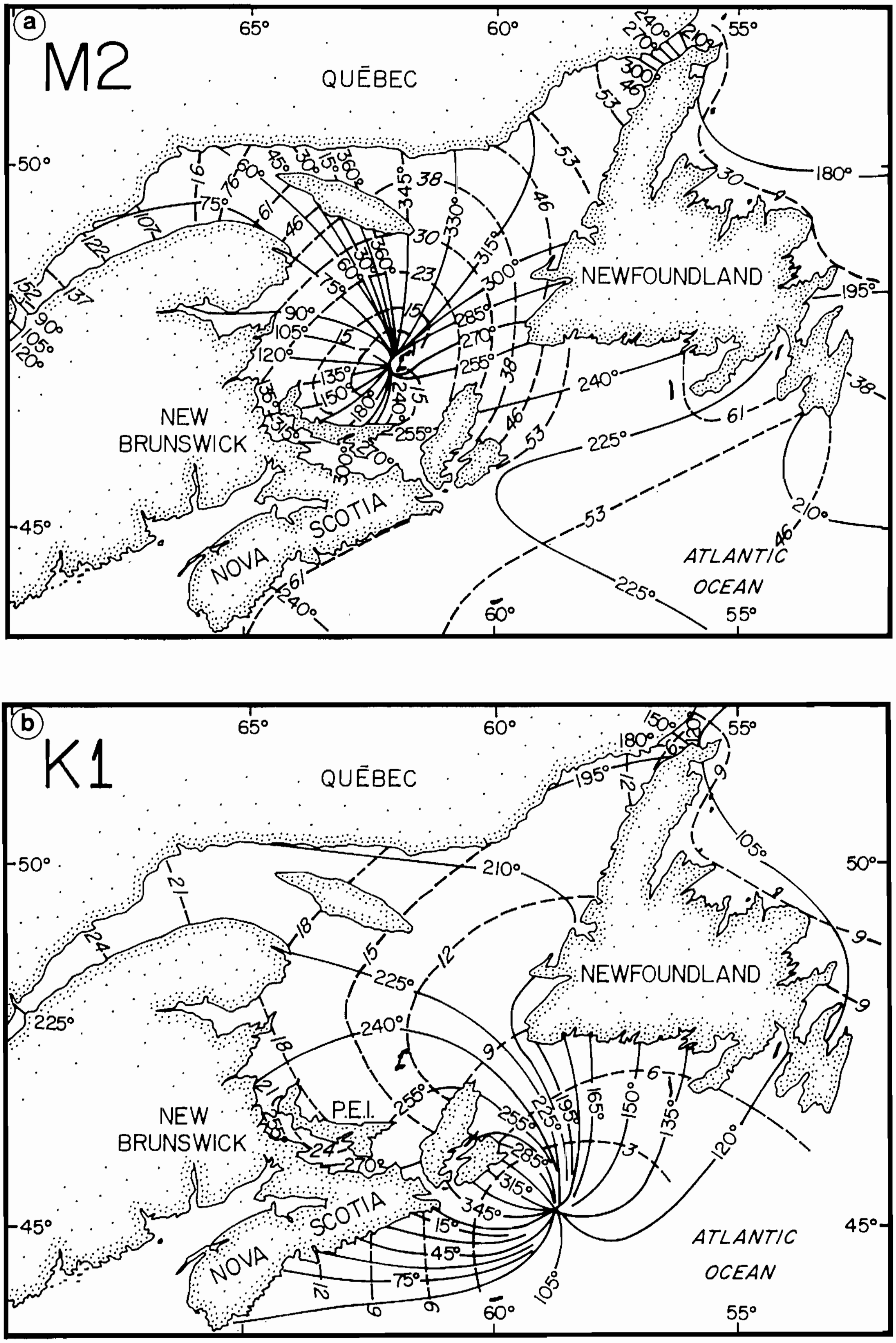

FIG. 9. Co-amplitude (dashed) and co-phase (solid) lines for the M2 (top) and K1 (bottom) tides in the Gulf of St. Lawrence, (from Farquharson 1970). Amplitudes are in cm, and phases are relative to GMT zone.

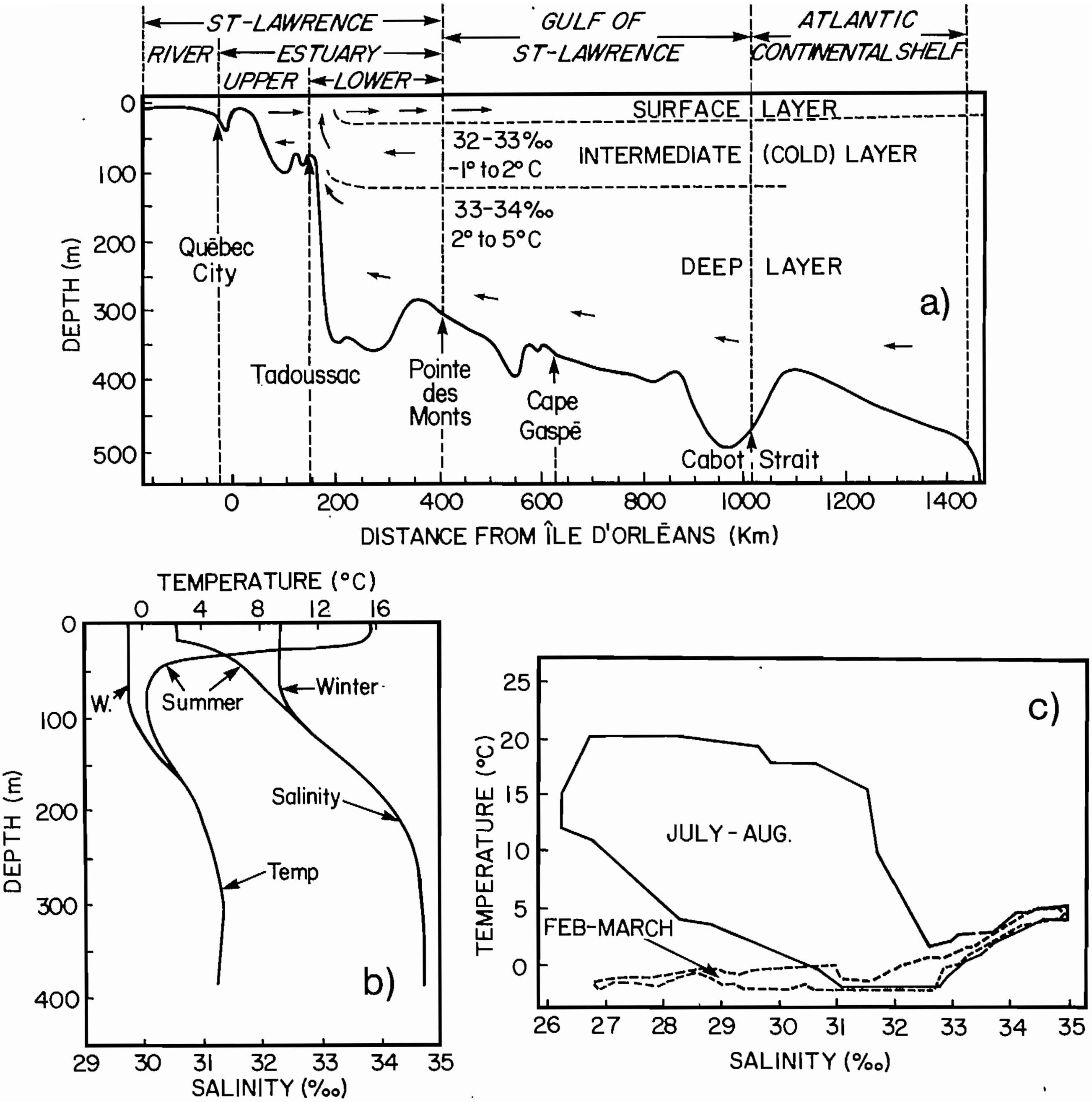

FIG. 10. (a) Sketch of the basic state of motion along the Laurentian Channel during summer (from Dickie and Trites 1983), (b) typical temperature and salinity profiles (from Trites 1972), and (c) T-S diagram (from Forrester 1964) for the Gulf of St. Lawrence.

Banks (1966) estimated this fraction to be 14%, it was recently updated by Petrie et al. (1988) to about 35%. Little is known about the circulation in the cold intermediate layer, except in the Lower St. Lawrence Estuary where cold waters from the GSL were shown to be advected towards the head at a mean speed of about 6 cm • s^{-1} over 75 d (Ingram 1979). Salinities in the deepest layer are close to 34.6‰, and temperatures vary between 4°C and 6°C, typical of Atlantic waters at the edge of the Scotian Shelf (Lauzier and Bailey 1957). These waters enter the Gulf at Cabot Strait and fill all deep channels, accounting for about 45% of the volume of the Gulf (Trites 1972).

4.1.2 Response to Tidal Forcing

The response of the GSL to tidal forcing has been estimated from harmonic analysis of shore based sea-level measurements around the Gulf, and subsequent interpolation over the Gulf (Farquharson 1970; Godin 1979). Tidal elevations are dominated by the M2 constituent in the semidiurnal band (Fig. 9 top) and by the K1 constituent in the diurnal band (Fig. 9 bottom). Godin (1979) has classified tidal elevations to be predominantly semidiurnal in the Estuary, in the northwest and in the northeast of the GSL, mixed in the north and centre of the Gulf, and predominantly diurnal near the two M2 amphidromic points located in the southern Gulf. A major amphidromic point is located to the west of the Magdalen Islands, while the other lies near the western end of Northumberland strait. Tidal amplitudes vary between 0.2 and 0.5 m in the Gulf, but increase considerably in the Estuary due to topographic convergence. Amplitudes in excess of 2 m are recorded at the head of the Estuary near Québec city (Godin 1979).

Semidiurnal tides exhibit neap-spring fortnightly modulations about mean sea level. In deep waters, the Msf and the longer Mm tidal constituents have negligible amplitudes (Godin 1979). However, in shallow water, tidal waves are significantly affected by friction, and the modulation of the semi-diurnal constituents produces a fortnightly fluctuation of the daily mean sea level. This occurs at Québec city, for example (Godin 1979). Such fortnightly waves are generated by the modulation of the frictional forces due to the fortnightly variations in tidal velocities (LeBlond 1979). This process may have considerable implications on the synoptic variability in the Estuary. For instance, the fortnightly rise and fall of mean sea-level at Québec will respectively retain or release the freshwater runoff from the St. Lawrence River.

Tidal currents seldom exceed 30 cm • s^{-1} in the GSL, except in confined areas such as the Upper Estuary and other coastal regions where values in excess of 100 cm • s^{-1} have been recorded (Farquharson 1970). Depth-averaged phases and amplitudes of K1 and M2 tidal currents at various locations in the Gulf are shown in Fig. 11. These values may not be accurate because they were averaged from measurements at only two depths (13 and 80 m), and over a short period of time (15 or 29 d). Furthermore, they may have been contaminated by baroclinic currents due to internal waves of tidal periodicities (Farquharson 1970; Forrester 1970, 1974; Gagnon and El-Sabh 1980). In the Estuary for example, the interaction of the incoming surface or barotropic tide with the shoaling topography of the Laurentian channel near Tadoussac produces internal tides which propagate back towards the Gulf. The M2 internal waves are of the Poincaré type with a wavelength of about 60 km, while the K1 waves are Kelvin waves (see also Forrester 1974; De Borne de Grandpré et al. 1981). As noted by Trites and Walton (1975), internal tides may exist elsewhere in the Gulf, and could produce regions of relatively strong convergence and divergence.

Two-dimensional numerical models (e.g. Pingree and Griffith 1980) have been used to compute tidal elevations and barotropic currents for the M2 semi-diurnal constituent, and the corresponding stratification index (Simpson and Hunter 1974) for the GSL. Areas of intense tidal mixing were identified in the Strait of Belle-Isle, around the Magdalen Islands, the western part of Jacques Cartier Strait, Northumberland Strait and at the head of the Lower St. Lawrence Estuary. Intermediate cold waters were often detected at the surface from satellite images of these areas (e.g. Lacroix 1987; Gratton et al. 1988; Fig. 24), implying vertical tidal-mixing. Long-term current profiles and bottom pressure recordings are needed to describe tidal features in the GSL with more accuracy.

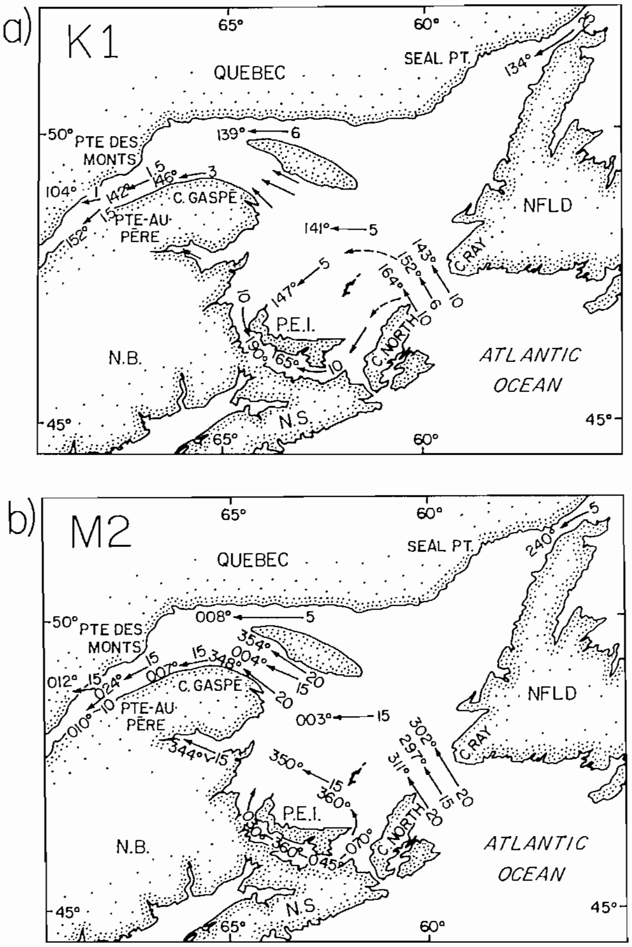

FIG. 11. Phases (relative to GMT) and amplitudes (cm • s^{-1}) of the K1 (top) and M2 (bottom) vertically-averaged tidal currents at various locations in the Gulf of St. Lawrence (from Farquharson 1970).

4.1.3 Response to Seasonal Climatic Forcing

Climatic forcing has been subdivided in section 3 into meteorological and buoyancy forcing. However, it is difficult to separate the response of the GSL to each of these forces, unless the coupling between river discharge and atmospheric conditions is first identified (e.g. Koslow et al. 1986). Therefore, the seasonal circulation and water mass variability will be examined in this section in response to "climatic forcing".

4.1.3.1 Water Mass Variability

The seasonal response of the surface layer to heat flux, mixing and advection by mean currents can be described in terms of monthly sea-surface temperature (SST) distributions. Weiler and Keeley (1980) analyzed SST data from 21 000 bathythermograph casts obtained in the GSL from 1944 to 1979. The year-to-year SST variability for each month was found to exceed the variability within each month. Vigeant (1987) used objective mapping techniques to display monthly SST distributions from 230 000 measurements reported by ships over 136 yr (1860–1980).

His results (Fig. 12) have higher SST resolutions, particularly in the St. Lawrence Estuary and the Magdalen Shallows. Cold waters at the surface near the mouth of the Saguenay Fjord, and high temperature gradient in the upper Estuary were identified during summer. The overall surface layer warming in the GSL progress from the southwest shallow regions to the northeast as the summer season evolves, generally in accordance with surface heat fluxes (section 3.1). The resulting Gulfwide pressure gradient will contribute to an overall eastward motion in the surface layer.

Bugden et al. (1982) divided all salinity measurements available for the GSL up to 1982 at the Marine Environmental Data Service, Ottawa, on the basis of the freshwater runoff from Lake Ontario since 1900. Monthly salinities in the surface layer were then separated according to high-runoff and low-runoff years (Fig. 13). Several points are worth noting here. First, irrespective of runoff, lower salinity waters are seen to be confined closer to the Gaspé Peninsula shores once they leave the Estuary. They adopt a cyclonic distribution in the Magdalen Shallows, and exit the GSL near the southern boundary of Cabot Strait, as expected from geostrophy in the northern hemisphere. In this respect, the GSL behaves as a large estuary. During high discharge years, horizontal salinity gradients are increased, lower salinities are observed close to shore and extending further offshore, and the 29‰ isohaline reaches Cabot Strait around August (El-Sabh 1976). During low discharge years, it remains confined to the southwestern Gulf. As a result, a year-to-year variability in the vertical stratification of the water column can be expected, particularly in the Magdalen Shallows. This will affect primary production and fish migration in the GSL (e.g. Sutcliffe 1972, 1973; Bugden et al. 1982; Therriault and Levasseur 1985; Koutitonsky et al. 1986; Sinclair et al. 1986). Effects of this year-to-year runoff

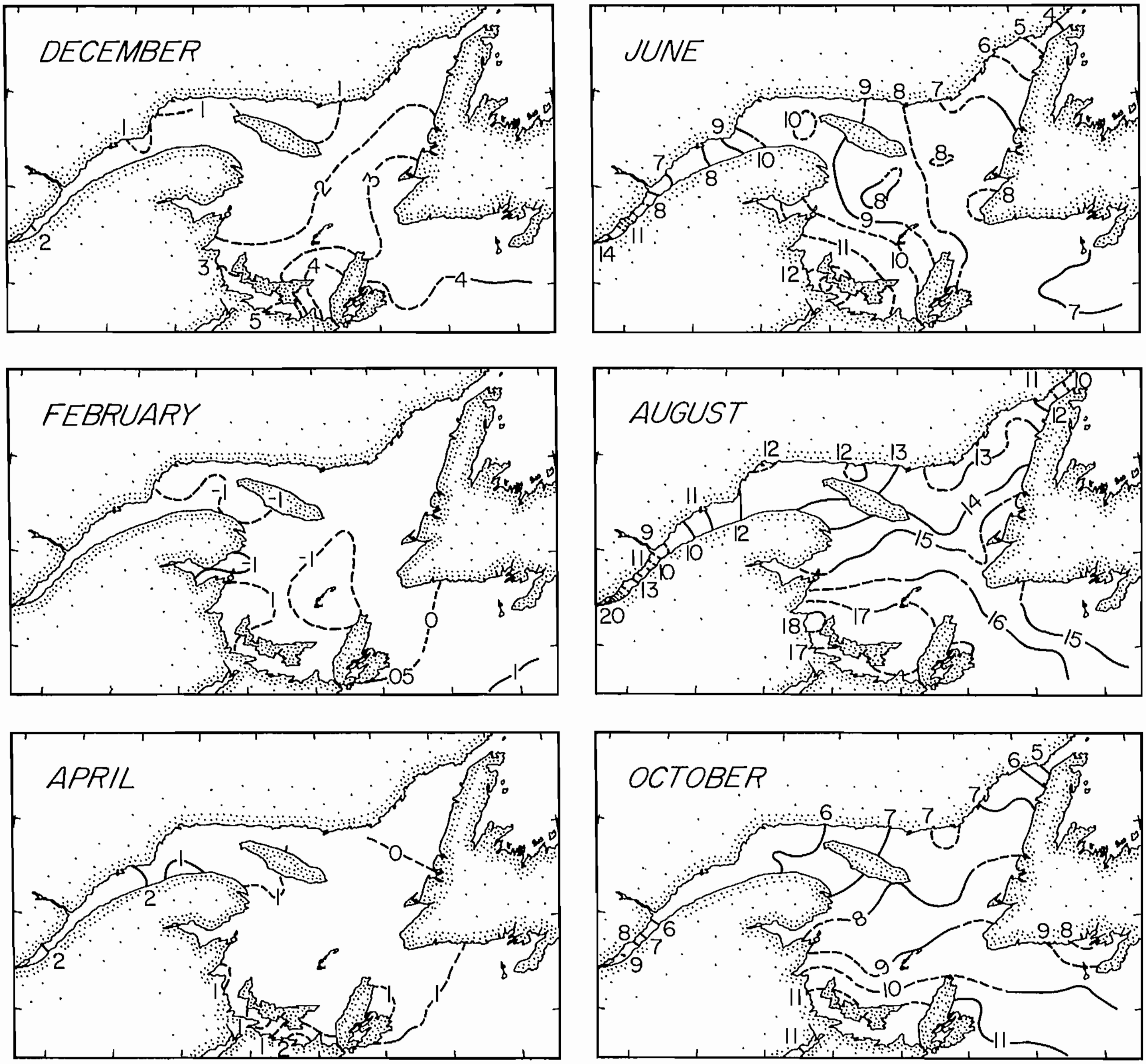

FIG. 12. Mean-monthly SST distributions (1860–1980) from ship measurements in the Gulf of St. Lawrence (from Vigeant 1987).

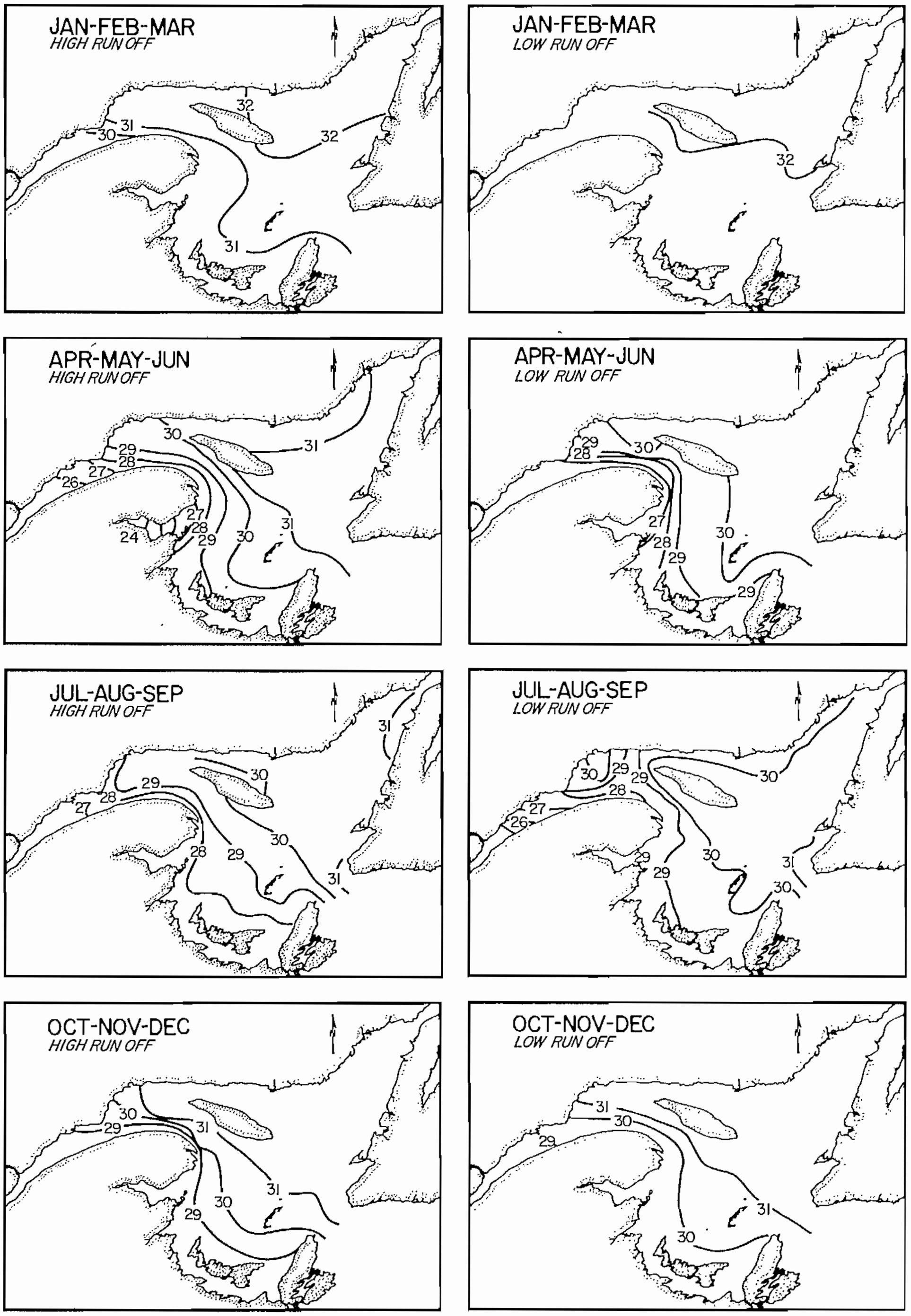

FIG. 13. Surface-layer salinities in the Gulf of St. Lawrence, averaged over years of high and low runoff (from Bugden et al. 1982).

variability can also be felt along the Scotian Shelf (Sutcliffe et al. 1976; Drinkwater et al. 1979; Smith 1983), and in the Gulf of Maine (e.g Sutcliffe et al. 1977), although effects in the Gulf of Maine have been disputed by Koslow et al. (1986), when they included direct meteorological forcing in their study.

4.1.3.2 Circulation Variability

As stated earlier, gulf-wide simultaneous current measurements have yet to be made. Nonetheless, a typical summer circulation pattern for the upper layer was sketched by Trites (1972), using all Lagrangian (Bumpus and Lauzier 1965; Lauzier 1967; Blackford 1965, 1967; Trites 1968b) and Eulerian current measurements (Farquharson 1963, 1966; Farquharson and Bailey 1966; Forrester 1970). The main features (Fig. 14) are a strong coastal current — the Gaspé Current — developing in the Estuary, reinforced by a southward current at the mouth of the Estuary and intensifying around the Gaspé Peninsula. Estuarine-like two-way exchanges at both Cabot Strait and the Strait of Belle Isle are also observed. The overall circulation appears to be cyclonic around the Gulf. Trites (1972) estimated the mean flushing time of freshwater in the GSL to be in the neighbourhood of 6–8 mo. Also, if a particle released near Tadoussac in the Estuary was advected by the mean currents, it would reach Cabot Strait in under 3 mo. This brings up the question of whether all the surface water exits at Cabot Strait, or whether a fraction of it recirculates in the Gulf along the cyclonic path (see Fig. 14). Surface drifter studies made during the summer period (Boudreault et Heritier 1971; Messieh 1974) suggest that some waters recirculates around the Gulf.

The similarity between the cyclonic circulation pattern and the surface salinity distributions in the Gaspé and Magdalen Shallows regions implies that surface currents are in geostrophic balance with the horizontal pressure gradient field. This principle was used by El-Sabh (1976) to estimate geostrophic currents from "monthly-averaged" density fields, estimated from temperature and salinity data collected in the GSL at various times (June to August, November, February and March) between 1950 and 1969. The surface geostrophic currents during summer (e.g. August, Fig. 15) are similar to Trites (1972) results, except that the spatial structure now features several gyres of 20–100 km in diameter. During winter, El-Sabh (1976) estimates indicate weaker geostrophic currents (2–10cm • s^{-1}) and less spatial structure. It is not clear however if these gyres are permanent features of the GSL circulation. Their existence was never verified from long-term current measurements. Some of them may well be the result of using the "monthly-averaged" data, constructed from observations obtained during different years, then averaged at each location over different number of years. This approach may be used in deep oceanic waters where steady-state equilibrium can be justified over a month. This is not the case for the GSL where considerable synoptic variability in state variables has recently been reported (see section 4.2). In fact, the only gyres ever observed in the Gulf were reported to last only a period of a few days (Blackford 1967; Trites 1968b; Keyte and Trites 1971; Sevigny et al. 1979; Benoit et al. 1985). Therefore, eddy motions are synoptic features of the GSL circulation and not permanent monthly features as suggested by El-Sabh's results.

Bugden (1981) also used all temperature and salinity measurements made between 1947 and 1974 to estimate monthly-averaged volume, salt, and heat fluxes between four regions of the Gulf (Fig. 16), for the months of March through December. The horizontal transports shown for the upper 50 m agree with previous geostrophic transport estimates in the Gaspé current (Benoit et al. 1985) and through Cabot Strait (El-Sabh 1976). Bugden showed that nearly 80% of the water transported in upper 50 m of the Gaspé current is upwelled from the 50–100 m layer, 71% of which originates in the northwestern Gulf and 9% in the Lower Estuary. The remaining transport is due to surface recirculation from adjacent regions (17%) and to freshwater discharged from the Estuary (3%). However, the increase of freshwater discharge and surface heat fluxes throughout the summer leads to vertical stratification, and increases the upper 20 m layer transport relative to that in 20–50 m layer (Bugden 1981). Entrainment towards the surface becomes more pronounced in regions of high shears like the

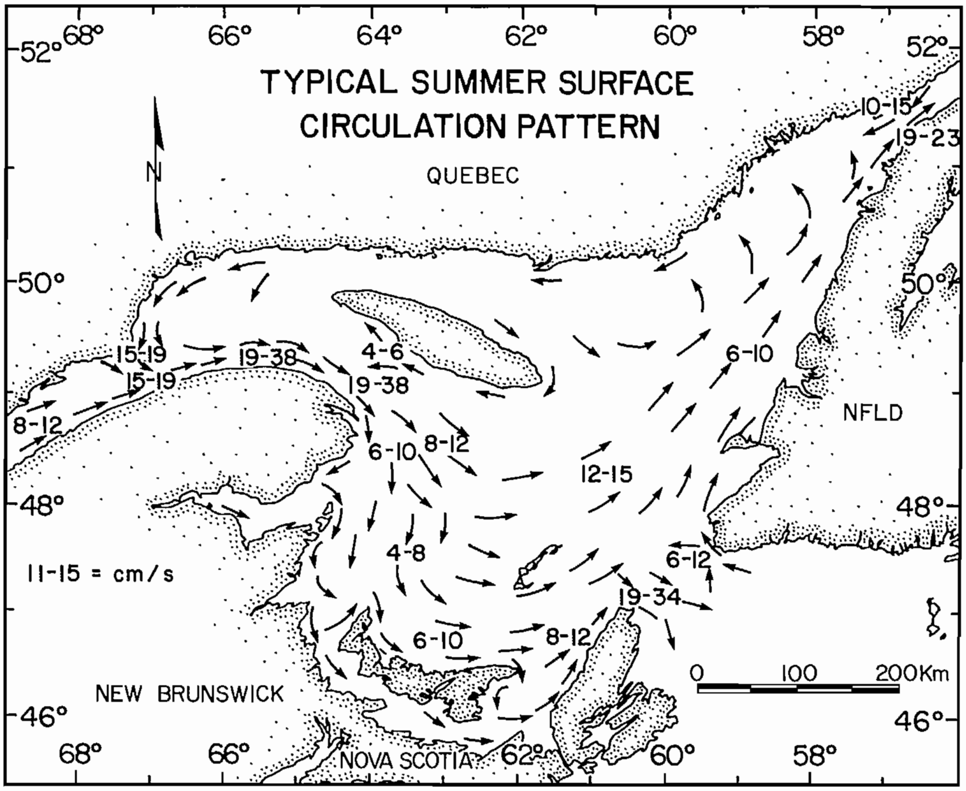

FIG. 14. Summer surface circulation pattern for the Gulf of St. Lawrence (from Trites 1972). Current speed ranges are given in cm • s^{-1}.

Estuary–Gaspé region and the Magdalen Shallows. Finally, Bugden's transport estimates showed no significant recirculation from the Magdalen Shallows to the Northeastern Gulf.

The subsurface circulation in the GSL is less documented. Recent current measurements close to the bottom in the Laurentian Channel (Bugden, unpublished data) revealed strong events of up to 20 cm • s^{-1} on time scales of

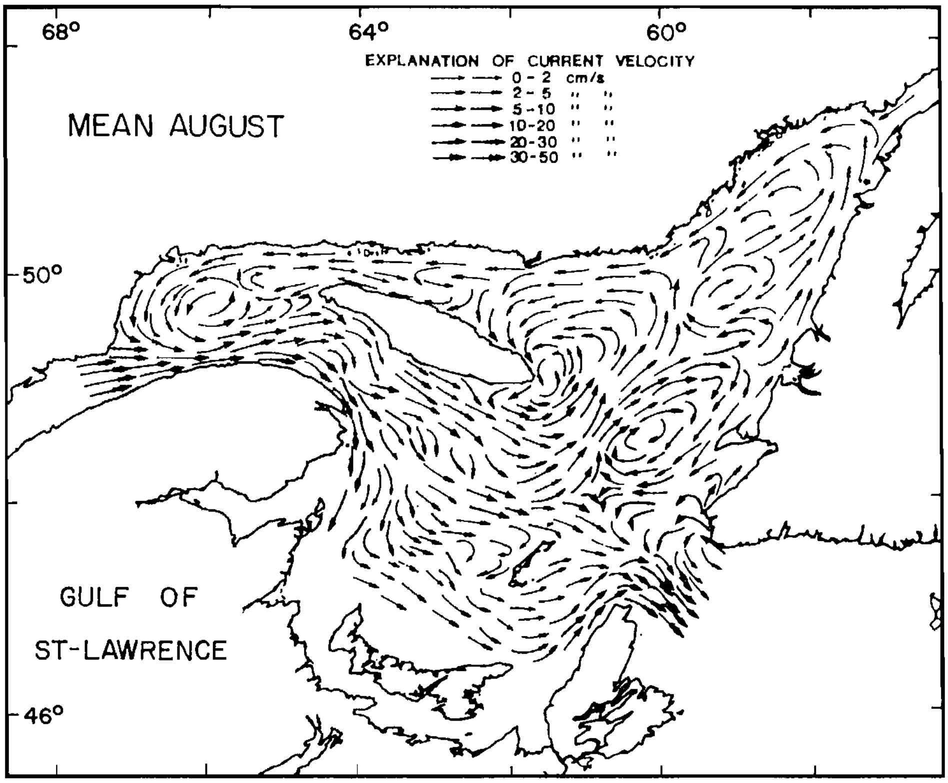

FIG. 15. Mean surface geostrophic currents during August in the Gulf of St. Lawrence (from El-Sabh 1976).

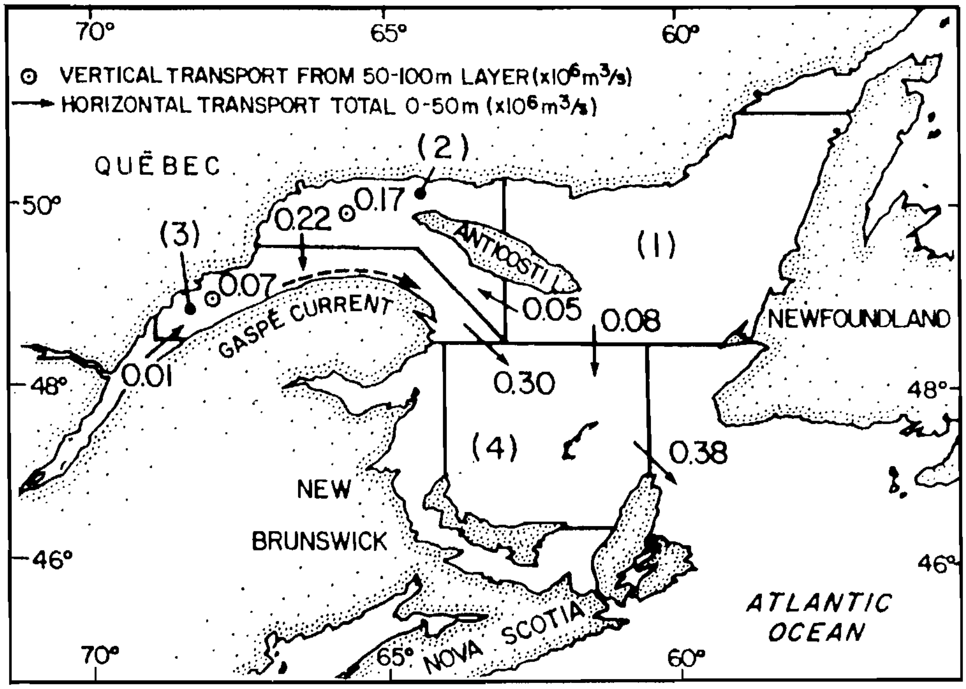

FIG. 16. Water transport and upwelling in four regions of the GSL (from Bugden 1981).

10-20 d driven by meteorological forcing. On average, the currents in the channel are dominated by strong cross-channel shear with inflow on the northeastern side of the channel and outflow on the southwestern side. Average current speeds near the channel edges approach 5 cm • s^{-1}. The cross-channel averaged current is about 0.5 cm • s^{-1} upstream. Similar results were found for currents in the deeper parts of the Lower St. Lawrence Estuary (Ingram 1979; Koutitonsky and El-Sabh 1985). This little information confirms at least that the GSL behaves like an estuary, with a return flow near the bottom. Bottom drifter trajectories reported by Messieh (1974) indicate a convergence on the Magdalen Shallows towards the Magdalen Islands. Assuming a cyclonic circulation around these islands (e.g. Fig. 14), this may be explained by simple Ekman spiral arguments, whereby waters near the shoaling bottom are deflected to the left of their course towards the islands.

Murty and Taylor (1970) attempted to isolate the barotropic response of the Gulf to monthly-averaged wind stress, using a vertically-integrated, linear, steady-state and homogeneous numerical model of the Gulf. The authors claim that most of the circulation features in the Gulf, except for the Gaspé Current, were reproduced by this simple model. These include (a) a general cyclonic circulation in the central Gulf, (b) outflow on the Cape Breton side of Cabot Strait, (c) inflow on the Newfoundland side, (d) an anticyclonic cell in the Northwestern Gulf, and (e) a cyclonic cell in the Estuary. The overall cyclonic motion in the central part (result a) is realistic in view of the cyclonic nature of the mean wind field over the GSL (section 3.3). Ekman transport sets up the water level to the right of the (cyclonic) wind and a geostrophic response occurs in the wind direction. However, results (b) to (e) appear to be artifacts of the model's grid-size and boundary conditions. For instance, the grid size being close to 19 km, the model resolution is too coarse to resolve eddy motion in the Estuary (width 20-45 km). Also, it is not clear how wind-driven exchanges or "leak currents" can be reported at Cabot Strait when the simulations showed these currents to be negligible, which ultimately led the authors to close that boundary. Clearly, more appropriate numerical models are needed to examine the wind-driven response of the GSL. These should be time-dependent, and three-dimensional in space to resolve the transient nature of wind forcing and the vertical dependence of the response in a stratified water column.

One such model is being developed for the GSL (Koutitonsky et al. 1987). This model integrates the time-dependent and fully non-linear equations of conservation of momentum, continuity and mass (e.g. Simons 1980). The model has a free surface, a leap-frog scheme in time, an Arakawa C-grid in horizontal space, and constant levels in the vertical separating a variable number of layers. Vertical motion is allowed through the intermediate levels. Preliminary generic simulations (time step 20 s) were performed over two inertial cycles (32 h) to examine the adjustment of the GSL to constant wind stress (0.1 Pa) from the north and from the southeast. The actual topography was used with a grid-size of 5 km, and three layers were imposed in the vertical separated by levels at 20 and 100 m below the surface. The same water density was assigned to all layers, implying a homogeneous GSL. Open boundary conditions of the radiation type (Orlanski 1976) were imposed at Cabot Strait, at the Strait of Belle-Isle and at Tadoussac in the Estuary. Horizontal layer velocities were vertically averaged and are shown after 32 h in Fig. 17a for northerly (top) and southwesterly winds (bottom), with corresponding sea level elevations in Fig. 17b. Again, these results are preliminary in the sense that they are not calibrated or validated, baroclinic effects are not considered, and wind forcing is uniform. Nevertheless, relative features can be detected in each case, including sea-level setup, weak vertically-averaged currents offshore (1-5 cm • s^{-1}), stronger coastal currents (10-20 cm • s^{-1}) in the direction of the wind component parallel to shore, non-local forcing in the Estuary and Baie des Chaleurs from pressure gradients in the Gulf, as well as some eddy motion in the Magdalen Shallows, in the Anticosti region, and in the Northwestern Gulf. Work is now in progress to include vertical stratification in the model in order to examine the combined influence of synoptic wind and buoyancy forcing on the circulation variability in the GSL system.

4.1.3.3 Ice Variability

Ice behaviour in the GSL has received considerable attention over the years because of its adverse effect on shipping during winter. A common finding is the high year-to-year variability of ice formation, ice cover, ice drift, and ice melting (eg. Forward 1954; Brochu 1960; Matheson 1967; Black 1972). This is not surprising considering that these processes are strongly dependent on air temperatures, wind stresses, surface layer convection, and surface currents, all highly variable factors in view of their stochastic nature (Ingram et al. 1969; Farmer et al. 1970; Pounder et al. 1973). The ice cover variability in the GSL can be assessed from Table 3, where various probabilities of occurrence for ice formation and melt are presented for four main regions of the Gulf (Ice Forecasting Central, Environment Canada, Ottawa). For example, the yearly variability is such that over a period of 3 consecutive years (1958, 1959, 1960), the Gulf was respectively almost ice-free, ice-covered, and again ice-free. In this case, the variability appeared to be related to mean winter air-temperatures at the Magdalen Islands (Markham 1973). Mean dates of ice formation and melt in the GSL are given in Fig. 18, but one has to agree with Black's (1972) conclusion: "it is difficult to speak of average ice conditions in the Gulf, because wide climatic variations in the winter months have powerful effects on ice formation throughout the region."

4.2 Regional Studies

In this section we report on the variability of the motion in several regions of the GSL system. These regions are examined in a cyclonic sense around the Gulf, following the overall surface circulation. Processes occurring in the Lower St. Lawrence Estuary (LSLE) are reviewed in some details as they may influence the composition of water masses and the dynamics of the motion in the GSL (Dickie and Trites 1983).

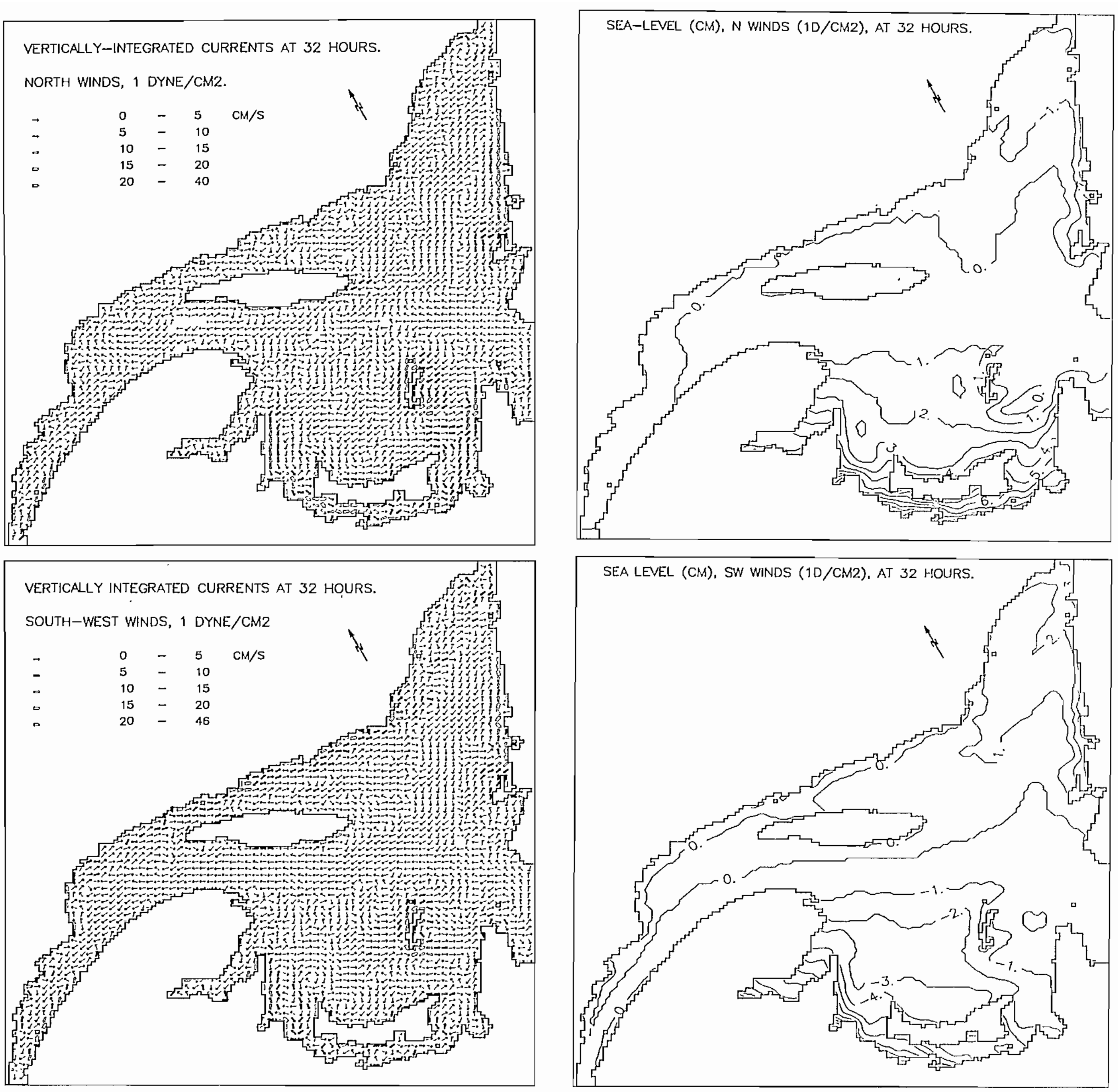

FIG. 17. (a) Vertically-averaged currents, and (b) corresponding sea-levels after 32 h of constant 0.1 Pa wind stress forcing, from preliminary application of a three-dimensional, vertically homogeneous model of the GSL with three-layers in the vertical (0–20, 20–100, 100 m-bottom).

TABLE 3. Mean dates of ice formation and melt in four regions of the Gulf of St. Lawrence, in terms of their probability of occurrence.

Probability of occurrence	Date of ice formation			Date of ice melting		
	10%	50%	90%	10%	50%	90%
Regions						
Lower Estuary	18/12	26/12	08/01	15/03	01/04	15/04
Southwestern Gulf	01/01	10/01	22/01	26/03	16/04	14/05
Central Gulf	08/01	22/01	05/02	05/03	05/04	30/04
Northern Gulf	01/01	10/01	22/01	26/03	15/04	21/05

4.2.1 The Lower St. Lawrence Estuary

We begin by providing a brief dynamical framework for discussing the synoptic variability of the motion in stratified rotating channels. This should be useful in interpreting synoptic observations made in the LSLE and elsewhere in the GSL. A fundamental length scale for the motion in stratified seas is the baroclinic (or internal) Rossby radius of deformation $R_i = c \cdot f^{1}$ where c, the long internal wave phase speed, is a function of the Brunt-Väisälä frequency, and f is the Coriolis parameter (LeBlond and Mysak 1978). It is the horizontal length scale over which baroclinic motions along a coast or away from a buoyancy perturbation adjust to geostrophy. Assuming a typical two-layer density profile for the LSLE,

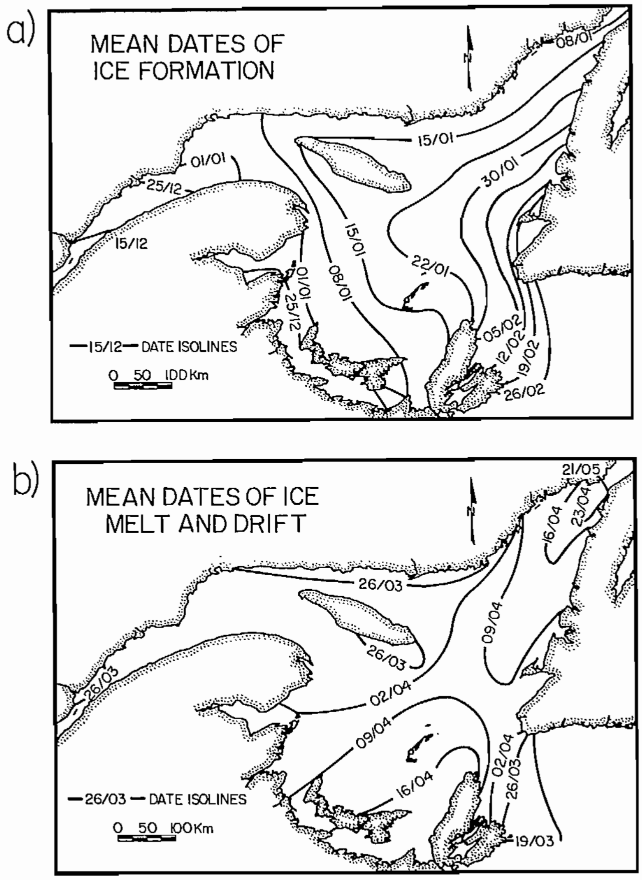

FIG. 18. Mean dates of ice formation and melt in the GSL (from Ice Central, Ottawa).

Mertz et al. (1988b) estimate $R_i \simeq 10$ km. Now, since the width L of the LSLE is greater than R_i, the Kelvin number $K = L/R_i$ is greater than 1, and Coriolis effects become important. This makes the LSLE one of the most laterally stratified estuaries in the world (Larouche et al. 1987). In such channels, a baroclinic coastal current may separate from one shore to flow along a density front to the other shore (Hsieh and Gill 1984). In other instances, a local buoyancy flux at the coast will produce an anticyclonic eddy of length scale $O(R_i)$ (e.g. Ikeda 1984; James 1987). During the adjustment process, Kelvin and Poincaré waves propagate away from the domain (Gill 1982). The runoff from the three north shore rivers constitutes such a flux. In each case, the motion will adjust to geostrophy within a time scale $T = O(R_i/c = f^{-1})$ provided the Froude number $F = U/c$ is small, U being a typical velocity scale. On the other hand, when a coastal current U is accelerated along one shore of the channel (or along a density front), shear instabilities may develop in the current field (e.g. Mysak and Schott 1977). In this case, the time scale for baroclinic adjustment is $T = O\ (R_i/U)$. Assuming a coastal perturbation of length scale $O(R_i)$, the current instability may grow into wave-like disturbances of length scale $2\ \pi\ R_i$. Mertz et al. (1988b) noted that these disturbances are large enough to occupy the width of the LSLE. In summary, eddy synoptic motion may occur in the LSLE (and elsewhere in the GSL where $K > 1$) due to geostrophic adjustment of the motion, due to barotropic–baroclinic instabilities in the current field, or due to a sequence of these processes.

With this in mind, we proceed to document some aspects of the synoptic variability of the motion in the LSLE. Our focus will be on the occurrence, or absence of (a) the mixing processes at the head of the LSLE, (b) the density fronts in the Rimouski region and the mouth of the LSLE, and (c) the anticyclonic eddy motion near the mouth. These features may influence the biological production zonation in the LSLE (Therriault and Levasseur 1985), as well as the dynamics of the motion further downstream in the GSL. Complementary physical oceanography aspects were reviewed by El-Sabh (1979, 1988).

(a) *Mixing near the head of the LSLE*: The runoff of the St. Lawrence River mixes in large proportions with salt water in the Upper Estuary, where it also drives an estuarine coastal current close to the south shore (Neu 1970; Meric 1975). This current is reinforced at the head of the LSLE by the brackish outflow of the Saguenay fjord, and proceeds seaward close to the south shore. Ingram (1979) documented the residual circulation near the head of the Laurentian Channel to be upstream in the intermediate layer near the north shore, toward the south at the topographic rise (100 m), and downstream near the south shore (Fig. 19). One notes that topographic-induced convergence of residual currents at depth is favourable to upwelling and surface divergence of cold intermediate waters. Ingram (1979) also shows that the intensity of upstream currents in the intermediate layer was proportional to fresh water runoff. On the other hand, intense tidal mixing occurs at the head of the LSLE, between water masses from the Upper Estuary, from the Saguenay fjord, and from the cold intermediate layer in the Laurentian channel. Temperature and salinity measurements made at the head of the channel (Ingram 1975; Therriault and Lacroix 1976; Greisman and Ingram 1977) indicate that isopycnals are periodically advected towards the surface by incoming tides (vertical excursion ≃ 50–120 m). Flood tides literally lift the water column along the abrupt rise in the Laurentian channel topography, such that intermediate cold waters are spilled at high tides over the shallow mid-channel area (Reid 1977). In the process, internal tides are generated at the pycnocline which propagate downstream in the LSLE (section 4.1.2), and tidally-induced frontogenesis occurs near high tide in the mid-channel shallows (Ingram 1976). During ebb tides, the upwelled cold waters are mixed and flushed downstream close to the south shore by the combined action of strong tidal currents, fresh water runoff from the Saguenay and outflow from the Upper Estuary. As a result, relatively dense (and cold) waters are found at the surface near the head of the LSLE on a quasi-permanent basis. Satellite thermal images of the region (e.g. Lacroix et al. 1985; Gratton et al. 1988) confirm these findings. However, mixing at the head of the LSLE may be suppressed by vertical stability in the water column during high runoff events (Reid 1977). We showed that these events occur at synoptic time scales (e.g. Fig. 4), implying that the mixing intensity will also vary accordingly. The mixing intensity may further be modified by neap-spring tidal current fluctuations and synoptic winds. In fact, from a sequence of satellite images, Gratton et al. (1988) find that cold waters at the surface are not only confined to the head of the LSLE, but often extend 100 km downstream until Rimouski. They call this extension the "cold anomaly", and conclude that other mixing mechanisms must be at work as this anomaly extends downstream, such as enhanced mixing by wind and tidal current due to a reduced vertical stability near the surface. Clearly, mixing processes in the upper half of the LSLE must be examined more thoroughly.

(b) *The density fronts*: The occasional extent of the dense anomaly until Rimouski may contribute to the formation of a density front across the LSLE in that region. This front would separate the anomaly from lighter surface waters supplied further downstream by the three north shore rivers, and by the buoyant outflow from the Upper Estuary which remains confined to the south shore until Rimouski. As discussed earlier, this front may provide a discontinuity along which the buoyant coastal current would separate from the south shore and veer towards the north shore. The presence of Bic island (Fig. 20) may promote this separation. Indeed, currents measured across the Estuary near Rimouski (Forrester, 1970) revealed northward residual currents with speeds of 7 cm • s^{-1} at 10m below the surface, and 1 cm • s^{-1} at depth. Further evidence of northward residual currents near Rimouski was reported by Murty and El-Sabh (1977). A drifter released near Rimouski was recovered 1.5 d later close to the north shore (Fig. 20a). The dynamics suggested was geostrophic adjustment of the flow after the passage of a storm. Another possibility is that the storm extended the cold anomaly to Rimouski, thus creating the density front along which the coastal current veered towards the northshore after the storm. Water mass analyses in the LSLE (e.g. El-Sabh 1977b; Therriault and Levasseur 1985) show isopycnals crossing the Estuary towards the north-shore near Rimouski, confirming the occasional presence of a density front in the region (Fig. 20b,c). Similar dynamics seem to govern the motion at the mouth of the estuary, where another density front separates lighter surface waters in the LSLE from more saline waters in the GSL (Tang 1980a; 1983). Currents measured across the mouth (Farquharson 1966) showed a persistent cross-channel flow setting towards the south shore near the surface, with speeds ranging between 10 and 40 cm • s^{-1}, and a similar but weaker flow at depth (75 m). From Lagrangian measurements during five days (Fig. 21a), Farquharson (1966) reported some anticyclonic eddy motion in the LSLE, whose "intensity is closely associated with the magnitude of the transverse current [at the mouth]". According to Farquharson, the transverse currents and the eddy would intensify at a fortnightly frequency, presumably as a response to the Msf variability of tidally-induced residual currents in the Estuary. However, realizing that wind fluctuations have periodicities close to the Msf tidal constituent (10–15 d versus 14.77 d), Mertz et al. (1988a) showed that wind stress, and not Msf tidal forcing, was the dominant source of synoptic variability at the mouth.

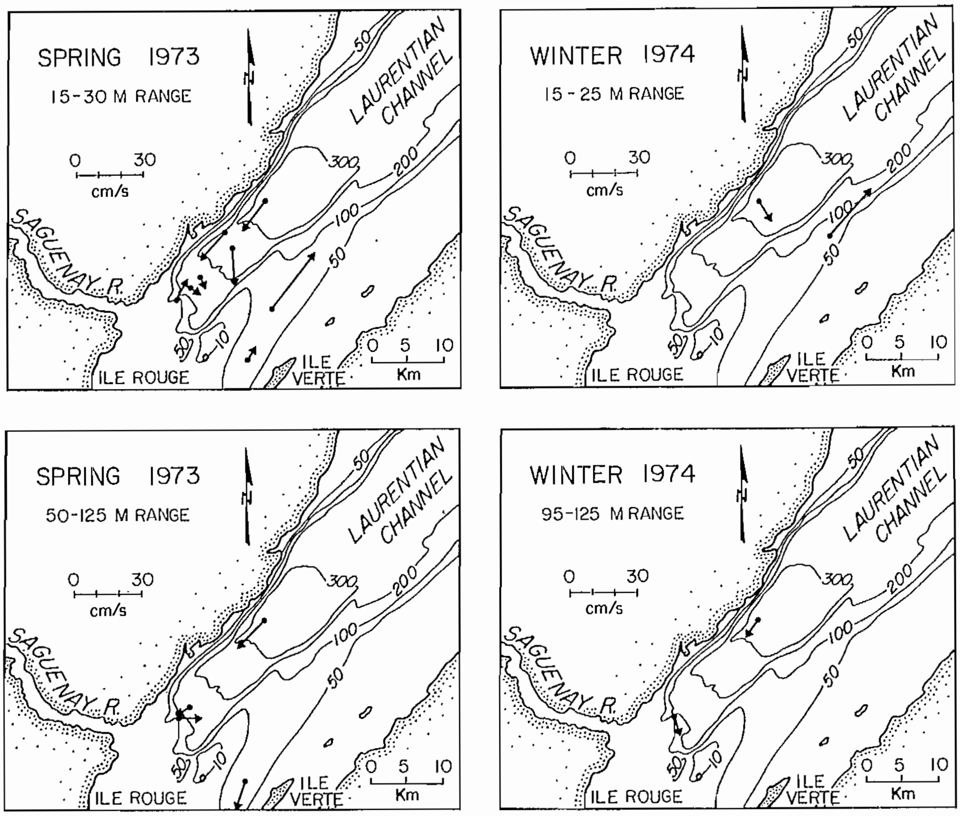

FIG. 19. Residual circulation in the upper (top) and intermediate (bottom) layers near the head of the LSLE, during spring (left) and winter (right), from Ingram (1979).

(c) *Anticyclonic eddy motion near the mouth*: Dynamic height computations near the mouth (Fig. 21b,c) point to the presence of anticyclonic eddy motion in the LSLE, coupled to the southward currents at the mouth. Using a two-dimensional numerical model, Murty and El-Sabh (1980) reported some anticyclonic motion in the LSLE due to tidally-induced residual circulations. The reported speeds however are too small (1–5 cm • s^{-1}) in comparison to the current observations (10–50 cm • s^{-1}) discussed later, and therefore tides must be excluded as a major forcing agency for eddy motion. A large-scale circulation experiment, conducted from May to September 1979 near the mouth (Koutitonsky et al. 1980) provided further evidence of eddy motion in the LSLE. First, the mean currents are shown in Fig. 22, together with Farquharson's (1966) mean currents at the mouth. It is clear that LSLE does not behave as a classical estuary. Instead, the mean circulation features two coastal currents flowing seaward near both shores at speeds of 20 cm • s^{-1}, an equally strong southward current at the mouth, and a 2 cm • s^{-1} upstream bottom current in the Laurentian Channel. This mean circulation is misleading however as it filters out important synoptic events. The low-frequency velocity component fluctuations about the mean value (Fig. 23) reveal two distinct synoptic scales of variability: (a) fluctuations with periods ranging from 2 to 15 d, and (b) slowly varying trends with time scales of the order of the record length (80–120 d). The two processes appear to

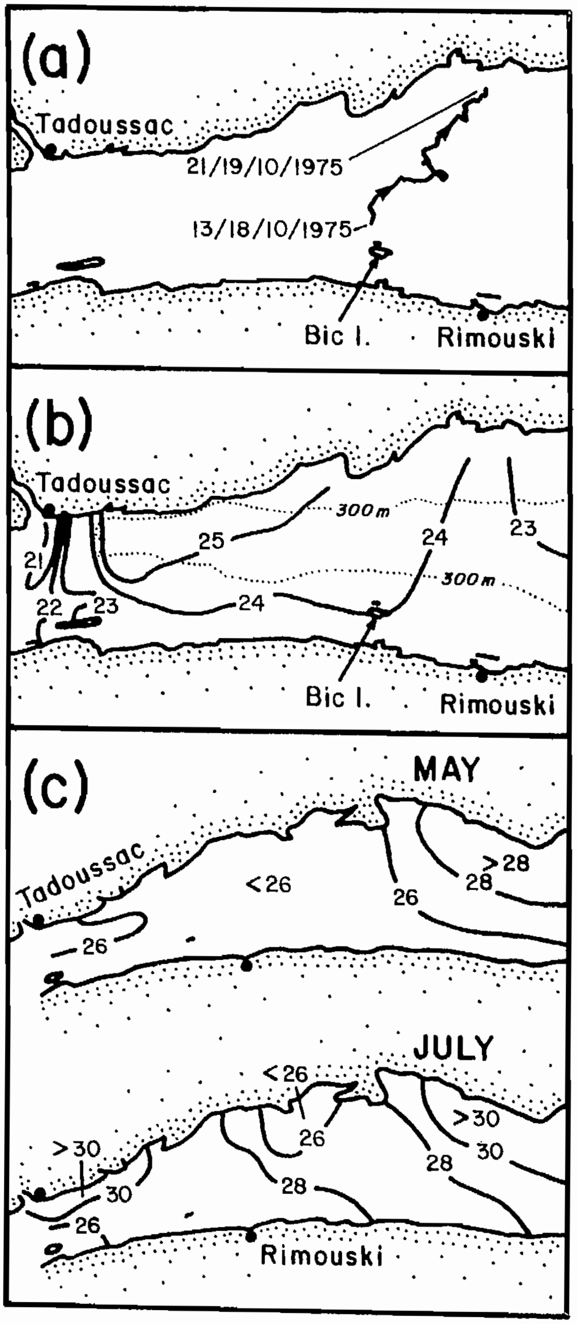

FIG. 20. (a) Parachute drogue trajectory (10 m depth) in the LSLE (from Murty and El-Sabh 1977), (b) isopycnals in the LSLE, 28–29 September 1973 (from El-Sabh 1977b), (c) surface isohalines in the LSLE in 1978 (from Therriault and Levasseur 1985).

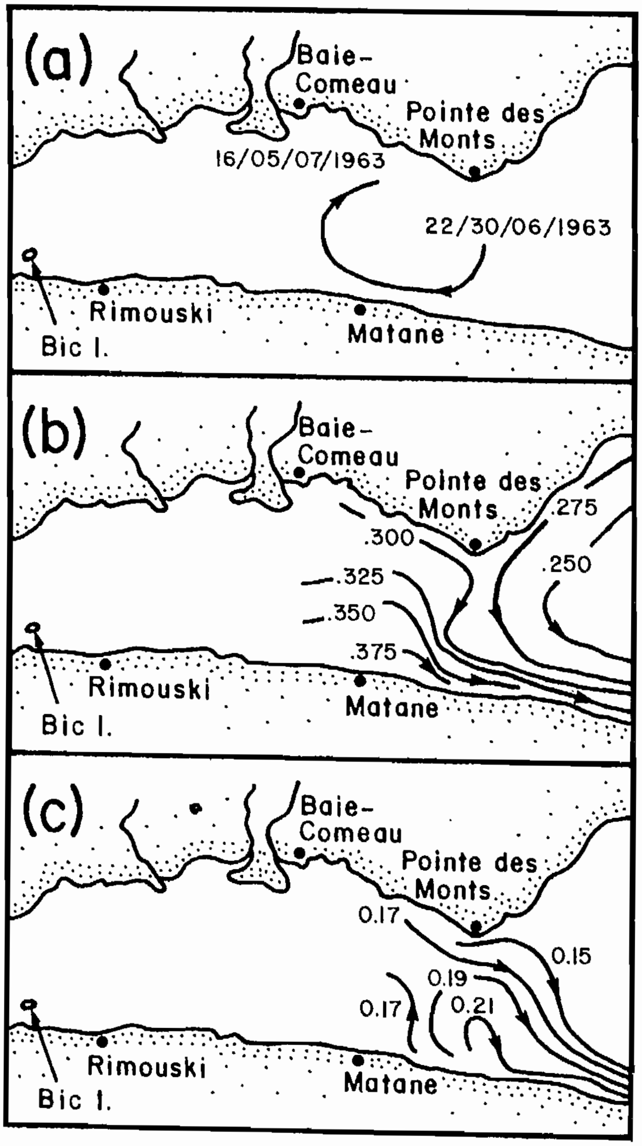

FIG. 21. (a) Parachute drogue trajectory (75 m depth) in the LSLE (from Farquharson 1966), (b) dynamic height topography relative to 100 m, 26 June–7 July, 1963 (from Farquharson 1966), and (c) dynamic height topography relative to 40 m, 23–29 September, 1978 (from Tang 1980a).

be statistically independent. Spectral and frequency domain EOF analysis of the shorter period fluctuations (Koutitonsky 1985) showed that currents were coherent over at least 50 km, and that highest variance levels occurred at periods of 3–5 and 8–15 d. Near the surface, these levels exceeded the variance due to tidal currents. It is interesting to note that these periods are similar to the ones obtained for winds over the northwestern GSL (Fig. 8). The shorter current fluctuations were indeed coherent with winds at these frequencies, and part of the variance in the current field at 3.5 and 8 d period could be explained by the free propagation of coastally-trapped waves along the south shore of the LSLE (Koutitonsky 1985). From data collected in 1982, Tee (1990) also reports that meteorological forcing generates, in the current and salinity fields, oscillations of periodicities of 10–15 and 40–50 d. Long trends with time scales of 130 d were also reported.

The 1979 longer current fluctuations, obtained through a 15 d running average, were described by El-Sabh et al. (1982). They featured two coupled and time-dependent eddies: the first located between cross-sections at Rimouski and Baie Comeau, and the second located between cross-sections at Baie-Comeau and the mouth, each eddy rotating 180 degrees out-of-phase with the other. This motion corresponds to the trends shown in Fig. 23 (dashed lines). During June and part of July 1979, the rotation near the mouth was anticyclonic, while in August it was cyclonic. Meteorological forcing was suggested as a possible generating mechanism, but the dynamics involved were not explained. Lie and El-Sabh (1983) proposed that the temporal evolution of this eddy field resulted from the superposition of two 80 d period baroclinic coastally-trapped waves, each propagating freely along one shore of the LSLE with that shore to the right, with their phases locked in time. For such free waves originating from a different source to remain phase-locked during exactly 80 d is highly unprobable. Mertz et al. (1989) re-examined the 15-d averaged data set and proposed instead that the current field in the LSLE exhibits two quasi-steady states: the first characterized by strong outflow along the north shore of the

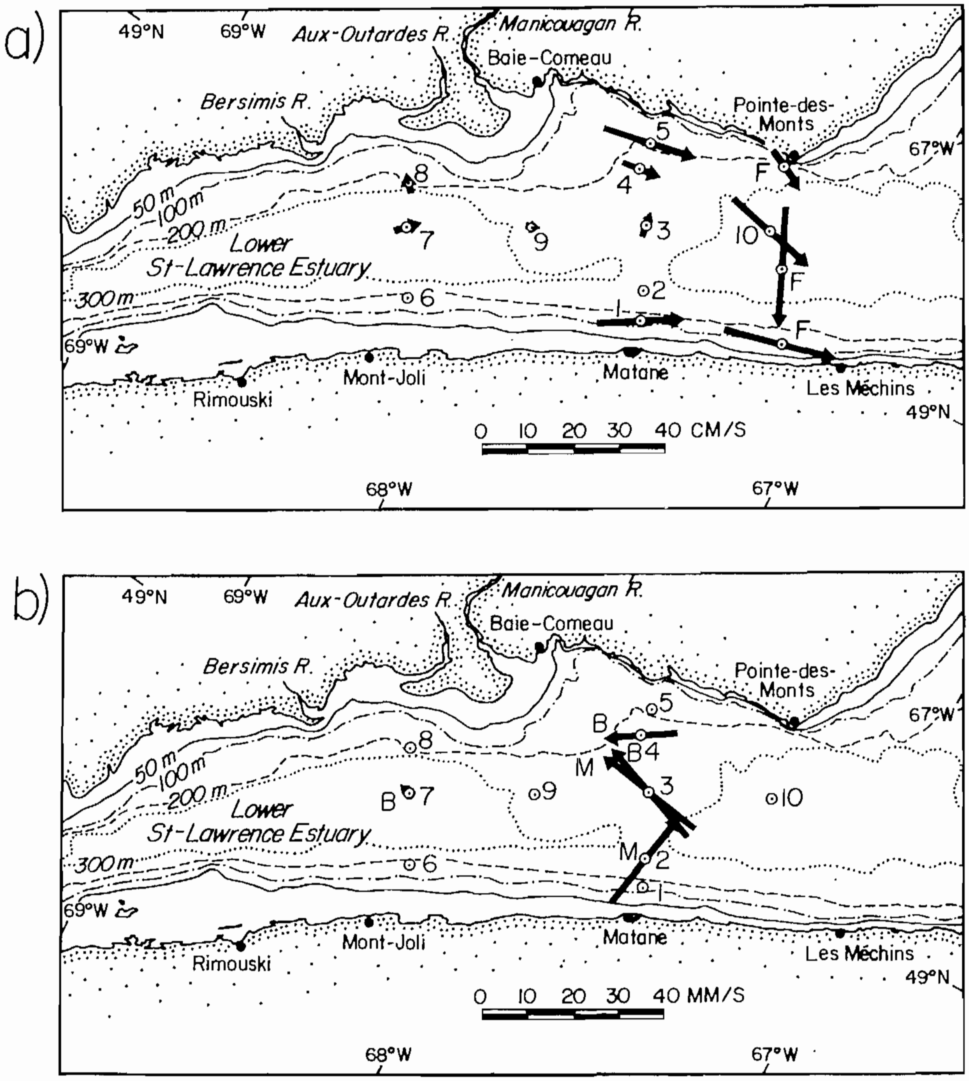

FIG. 22. Mean currents at 10 stations in the LSLE, from May to September 1979 (a) in the upper 30 m layer, and (b) in deeper layers (from Koutitonsky and El-Sabh 1985). Note change of velocity scale. Farquharson's (1966) mean currents at the mouth (labelled F) are included.

Estuary, with a transverse front at the mouth, and the other with inflow along the north shore and outflow along the south shore, more like a classical estuary. Transition between these two configurations was attributed by the authors to instability in the current field at the mouth and near Rimouski (see also Mertz et al. 1988b). An objective analysis of the 1979 trends (dashed lines in Fig. 23, Koutitonsky et al. 1990) further suggests that two quasi-steady states are geostrophically adjusted states of the LSLE to freshwater runoff pulses from the Saguenay and northshore rivers. Anticyclonic eddy motion was observed in June and part of July when large pulses were released from the Saguenay into the LSLE, and disappeared in August when RIVSUM values dropped below average (see Fig. 4 and trends in Fig. 23). Eddy motion resumed near the mouth in September when local pulses were released from the northshore rivers and the Saguenay fjord. A reduced-gravity numerical model (Koutitonsky et al. 1990) was used to show that lighter surface waters between the fronts at the mouth and near Rimouski will adjust geostrophically into anticyclonic eddy motion because $K > 1$. Furthermore, numerical estimates of local internal radii R_i from buoyancy frequency profiles measured in the LSLE showed that R_i will vary between 15 and 30 km depending the local Brunt-Väisälä frequency and depth (Koutitonsky and Wilson 1988). Since the width L of the LSLE increases from 20 km at Tadoussac to about 45-50 km at the mouth, the condition $K = L/R_i \simeq 1$ (in this case L delimited by the 50 m isobath) may only be achieved somewhere near Rimouski. The reduced-gravity model did show that the LSLE will only accommodate anticyclonic motion from Rimouski to the mouth. The fronts at the mouth and further upstream, and the eddy motion in between (warmer surface waters), can be seen on two NOAA-9 satellite images of the LSLE taken on July 12, 1986 at 03:18 EST (Fig. 24 top) and 14:48 EST (Fig. 24 bottom). Considerable diurnal (mesoscale) variability in surface temperatures is also observed between both image, implying that the interpretation of low frequency dynamics from satellite images may be misleading. Images of the LSLE in June 1979 showed the presence of similar anticyclonic motion, which was verified from *in situ* measurements (Koutitonsky et al. 1990). Finally, current data collected in 1982 (Tee 1989) confirmed the presence of estuary-wide eddies near the mouth, with time scales of about 80 d, forced by freshwater runoff from the St. Lawrence River.

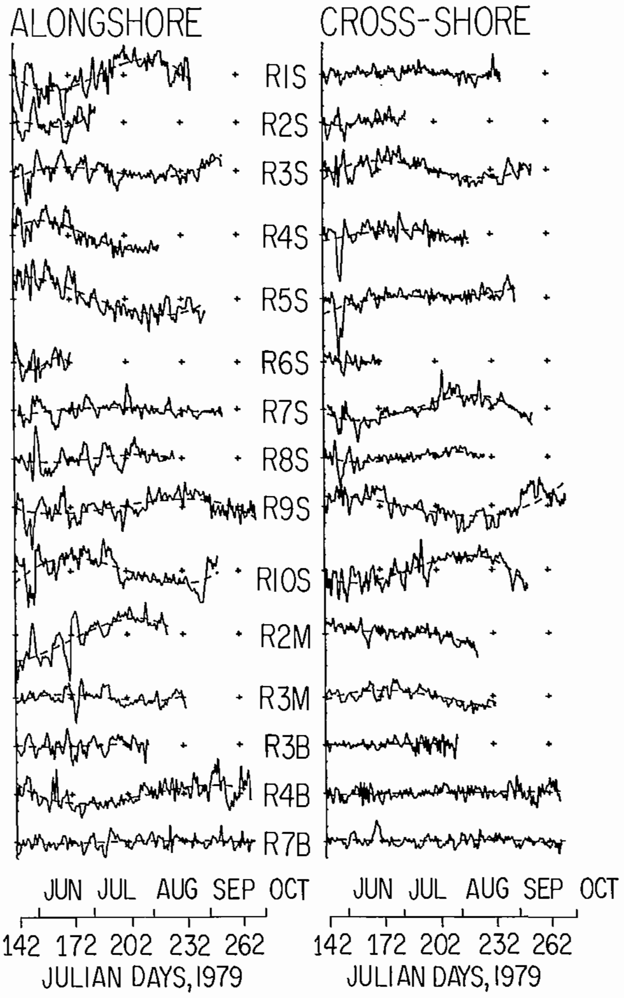

FIG. 23. Low frequency current fluctuations about the mean (Fig. 22) in the LSLE. Alongshore (U) and cross-shore (V) components are positive downstream (24°) and towards the north-shore, respectively (top of figure). Speed intervals are 25 cm • s^{-1} for surface (S) series, 10 cm • s^{-1} for mid-depth (M) series, and 2.5 cm • s^{-1} for near-bottom (B) series.

In summary, both geostrophic adjustment and instabilities in the current field may be at work in the LSLE depending on local Froude and Kelvin numbers, under the combined influence of synoptic freshwater and winds fluctuations. Non-local forcing from the GSL is expected (e.g. Fig. 17b). Three-dimensional eddy resolving models should be used to understand these complex interactions. The significance of these findings is that oceanographical processes previously investigated in terms of monthly averaged RIVSUM (e.g. Sutcliffe 1973) should now be examined in terms of the synoptic circulation in the LSLE. This can only be achieved through long-term monitoring (years) of the circulation at key locations such as the mouth of the LSLE.

4.2.2 The Gaspé Current

Perhaps the most persistent feature of the circulation in the GSL system is the Gaspé Current. First discovered in 1895 by Dawson (1913), its main features have since been documented from geostrophic calculations and direct current measurements (Farquharson 1963, 1966; El-Sabh 1976; Tang 1980b; Benoit et al. 1985). It is a baroclinic coastal jet driven by the runoff from the St. Lawrence Estuary into the GSL. It starts organizing along the southshore of the Estuary, and in the presence of anticyclonic motion near the mouth, it is reinforced by the transverse currents setting towards the south shore at the mouth (e.g. Fig. 24). The Gaspé Current achieves its highest intensity (100 cm • s^{-1}) around the Gaspé Peninsula, where its width is about 15-20 km in the top 40-50 m of the water column (Tang and Bennet 1981). However, as noted in The St. Lawrence Pilot, 1894 Edition, "the rate of this current has been noted off different parts of the coast in the months of June, July, August and September, in different years, and scarcely

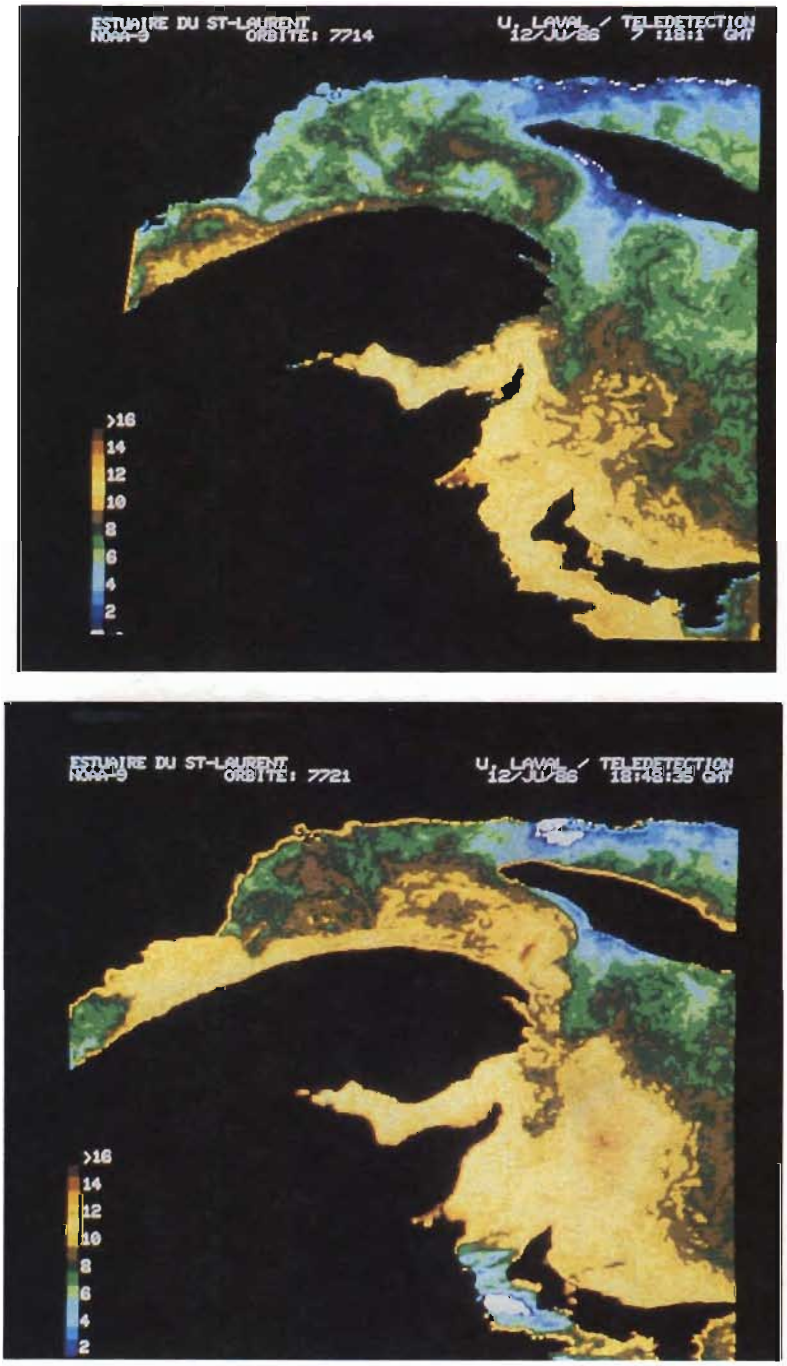

FIG. 24. NOAA-9 thermal satellite images of the LSLE and western Gulf on 12 July 1986 at 03:18 EST (orbit 7714, top), and at 14:48 EST (orbit 7721, bottom), with temperature scale (from A. Condal, Laval University, Québec).

ever found the same." (Farquharson 1966). About hundred years later, the advent of thermal satellite images provided several investigators the opportunity to examine the nature and causes of such synoptic variability. For instance, Tang (1980b) documented a 10 d summer event during which the Gaspé Current axis moved offshore for several days, and deeper currents reversed their normal seaward direction. When the current returned close to shore, a 60 km long wave-like feature began to form, continued to develop and eventually broke. A finding of fundamental importance is that the instability events documented by Tang occurred in response to a change of RIVSUM in the LSLE at synoptic time scales. Tang modelled the event in terms of barotropic instability of a coastal jet, triggered by its offshore excursion from the stabilizing effect of the coast. His model predicted an e-folding time of 1 d, a wavelength of 50 km, and a period of 4 d, which compared favourably with satellite observations. Mertz et al. (1988b) extended Tang's work to show from a sequence of satellite images (Fig. 25) that baroclinic instability is also an important source of synoptic variability during the summer period. Some of these disturbances were apparently triggered by an eastward wind pulse. In fact, current instability in the Gaspé

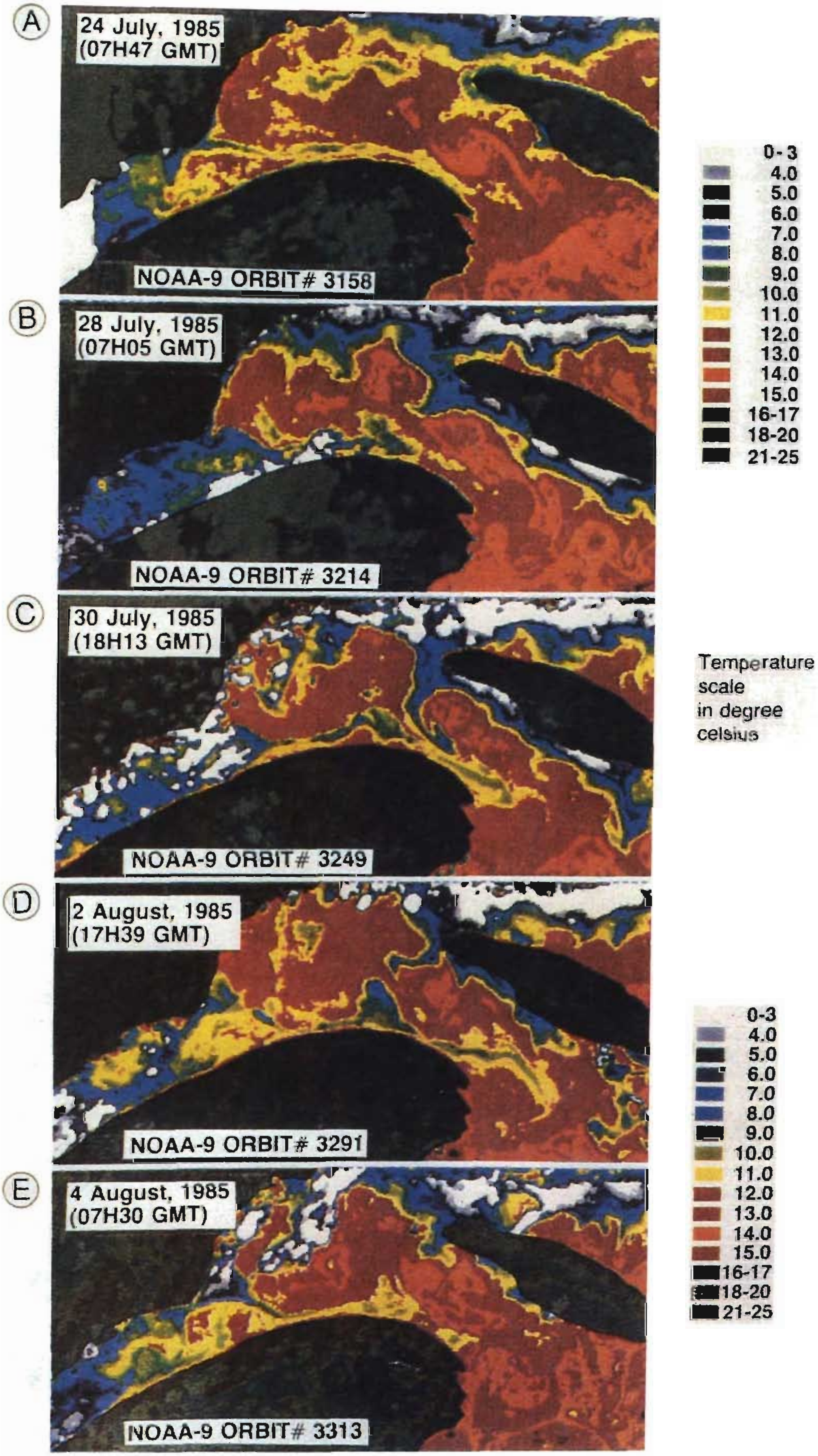

FIG. 25. Sequence of thermal satellite images in the Lower St. Lawrence Estuary and the Gaspé Current region, during July and August 1985 (from Mertz et al. 1988b).

Current may even occur during autumn, a period of the year when runoff from the Estuary is low (Mertz and El-Sabh 1989). Again, wind forcing was suggested as a triggering mechanism. Reduced stratification during autumn will enhance the frictionally-induced upwelling at the edge of the Current (Tang 1983), thus bringing larger volumes of cold water near the surface. On some occasions (see Fig. 24, 25), these cold waters are advected onto the Magdalen Shallows, essentially following the deepest isobaths close to Baie des Chaleurs.

4.2.3 The Magdalen Shallows

Part of the water advected by the Gaspé Current flushes the Magdalen Shallows before it exits to the Atlantic ocean through Cabot Strait. Isohalines on Fig. 13 indicate that the flushing process is strongly influenced by the yearly St. Lawrence Estuary runoff variability, with important consequences for the biological production of the Shallows (e.g. Sutcliffe 1973). On the other hand, the synoptic perturbations occurring in the St. Lawrence Estuary and in the Gaspé Current will also be advected, in some distorted form, onto the Magdalen Shallows (e.g. Fig. 24). So, are biological processes responding to "monthly-averaged" RIVSUM, or to synoptic perturbations reaching the Magdalen Shallows? Furthermore, this region being relatively shallow, wind and bottom stresses become relatively important mixing agents for the water column, and large scale features in the motion are likely to be broken down into higher wavenumber features. The expected outcome would be a highly variable environment, characterized by moving eddies, internal waves and transient frontogenesis. This variability can be inferred from the geopotential anomaly distributions, and the subsurface (10 m) parachute drogue trajectories reported by Keyte and Trites (1971) for two consecutive periods: June 18–22, 1968 (Fig. 26 top) and June 22–27, 1968 (Fig. 26 bottom). These results indicate the presence of eddies of varying dimensions and of opposite rotations. The largest eddy, to the southeast of the Gaspé Peninsula, had low salinities at its centre, and its translation speed, estimated by dividing the distance its centre has moved between the consecutive experiments, was in the range of 5–10 cm • s^{-1}. An important finding by Keyte and Trites is the good agreement between the drifter trajectories and the geopotential anomalies (Fig. 26), suggesting that these eddies are in quasi-geostrophic balance. However, as noted by the authors, geostrophic equilibrium only lasts for time scales of 2–4 d. Messieh and El-Sabh (1979) compiled over 120 surface and bottom isotherm contour maps for the Magdalen Shallows, from measurements available during April to November over 10 yr (1965–75). Again, several eddies were reported mostly during the months of May to July, in the area to the west of the Magdalen Islands where the Gaspé Current is thought to intrude onto the Shallows. As a consequence, strong density fronts and internal waves can be expected close to the western shores. One such front was documented by Côté et al. (1986), following the St. Lawrence Estuary spring discharge intrusion during July 1985 (Fig. 27).

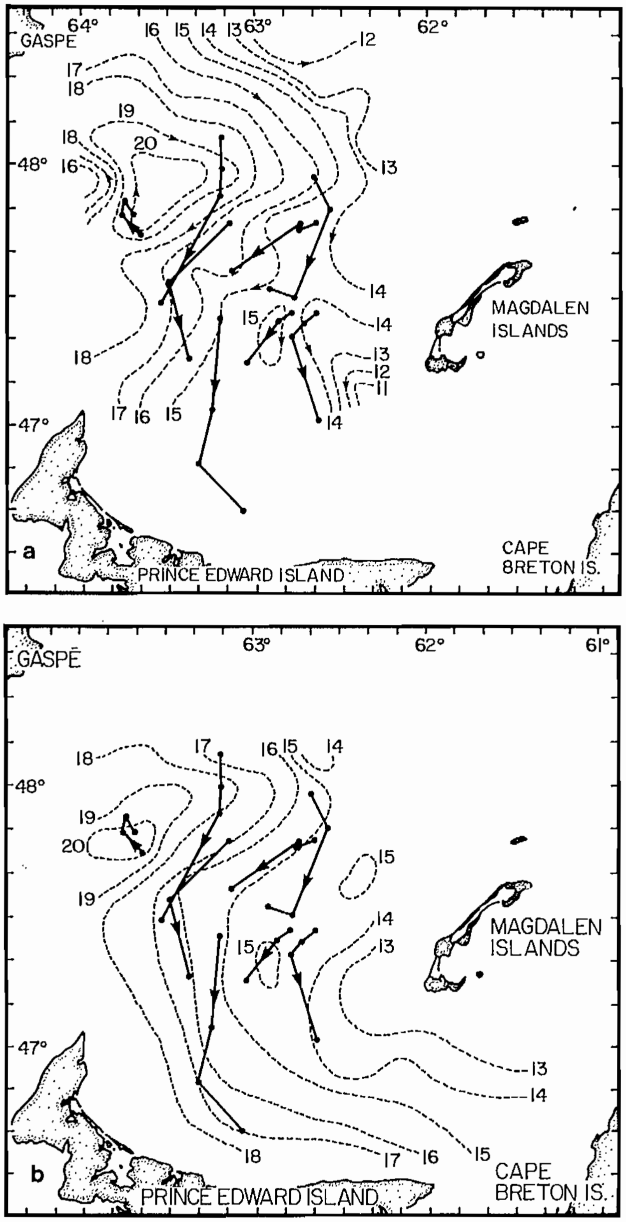

FIG. 26. Dynamic height topography relative to 40 db in the Magdalen Shallows, for 18–22 June 1968 (top), and 23–27 June, 1968 (bottom), with subsurface drifter trajectories followed from 18–27 June, 1968 (from Keyte and Trites 1971).

Current measurements on the Magdalen Shallows (Blackford 1978; Tang 1979) also revealed strong oscillations in the inertial frequency band (around 16 h), occurring in bursts of 2–3 d in the wake of wind stress transients. Time-series analysis of current records (El-Sabh et al., unpublished results), obtained from May to September 1984 off the Miramichi Estuary (Fig. 27), showed that these oscillations constitute about 20% of the total kinetic energy found in currents. Most energetic fluctuations however occurred at low frequencies (2–20 d) in the Gaspé current (M10) and in the Miscou-Shediac valley (M5) off the Miramichi Estuary. Finally, the preliminary numerical results presented in Fig. 17 indicate that predominant winds from the southwest may generate anticyclonic eddy motion in this valley, a rotation sense that is favourable to the retention of fish larvae in the area. Results also indicate that most coastal regions in the Magdalen Shallows (e.g., Baie des Chaleurs) will respond to pressure gradients set up by large scale winds, in addition to local winds.

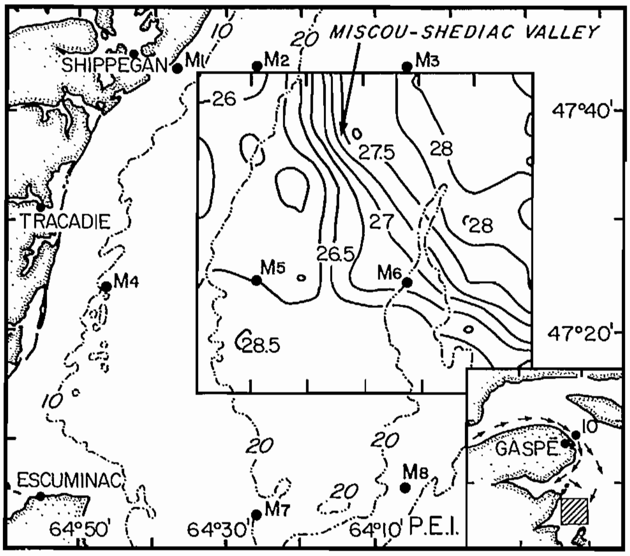

FIG. 27. Salinity front (middle inset) in the western Magdalen Shallows, and position of current meter mooring stations (M) (from Coté et al. 1986).

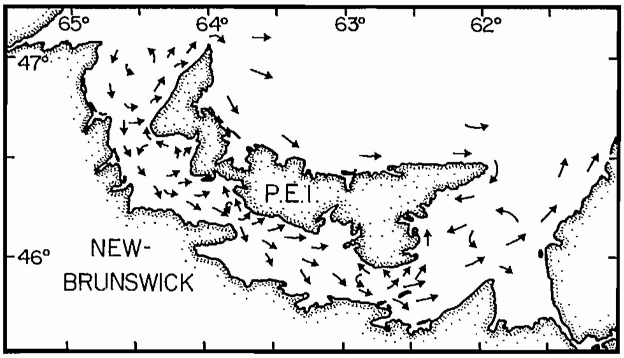

FIG. 28. Residual circulation inferred from drift bottle trajectories in Northumberland Strait (from Lauzier 1965).

4.2.4 Northumberland Strait

The circulation in the Strait has been described by Lauzier (1965). There seems to be a non-tidal drift from the northwest to the southeast at various points along the strait, with speeds varying seasonally in certain parts of the Strait. Drift bottle trajectories (Fig. 28, Lauzier 1965) indicate a southerly movement along the New Brunswick shores and the northerly drift along the Prince Edward Island, in accord with the large scale cyclonic motion in the Magdalen Shallows. The cyclonic eddy motion seen at both entrances to the Strait is more likely to be transient synoptic manifestations of wind-induced motion, or internal wave activity. Tidal currents are complex in this region (G. Seibert and B. Eid, personal communication) due to the presence of the M2 amphidromic point somewhere near the western end of the strait, and tidally-induced residuals can be expected around the several capes. Finally, in addition to local wind forcing, the strait will probably respond to non-local forcing from the Gulf, such as wind setup and relaxation during large scale cyclonic wind events (e.g. Fig. 17).

4.2.5 Cabot Strait

Cabot Strait constitutes the major avenue for water exchange between the GSL system and the Atlantic ocean (Fig. 1). To say the least, it is surprising to find that no study of the strait dynamics exists to date, as compared for example to the Strait of Belle-Isle (section 4.2.6). The only information available consists of water exchange estimates from short current measurements (Dawson 1913; Lawrence 1968) and from indirect geostrophic methods (MacGregor 1956; El-Sabh 1977a). The main features (e.g. Fig. 29) are a two-layer structure, with an outflow of lighter surface waters, more pronounced near Cape Breton, and an inflow of saltier waters at depth, reaching the surface close to the Newfoundland side. Water properties in the surface layer show considerable seasonal variability, in response to freshwater runoff to the Gulf. For instance, monthly-mean surface temperature and salinity, averaged over several years (Fig. 30),

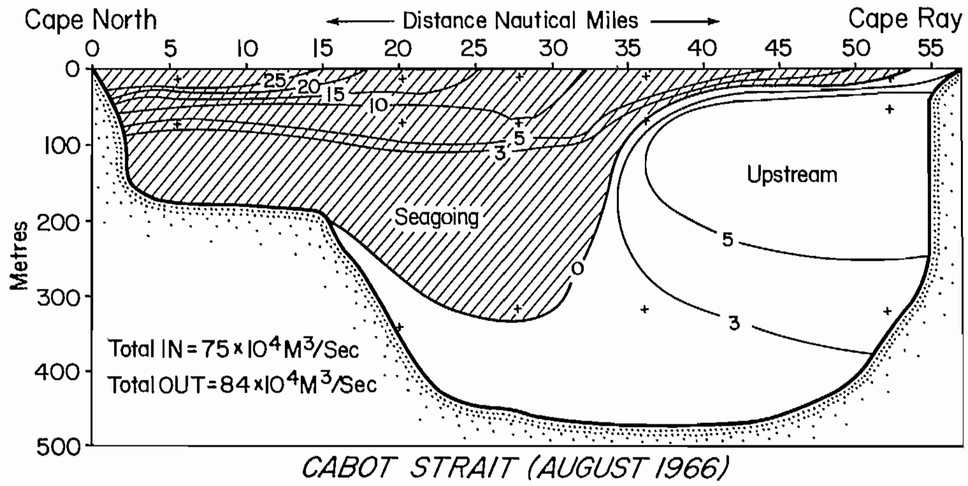

FIG. 29. Isotachs (cm • s^{-1}) and water exchange at Cabot Strait during August 1966 (from Trites 1972).

indicate that most of the freshwater runoff into the Gulf reaches the Strait by August, with lower salinities close to Cape Breton. The maximum net water transport through the section also occurs during August, at a rate of 25 × 10^3 $m^3 \cdot s^{-1}$, while the minimum transport occurs during February at a rate of 0.1 × 10^3 $m^3 \cdot s^{-1}$, both directed towards the ocean (El-Sabh 1977a). These net transport estimates, computed for the period of 1950 to 1974, are not equivalent to the total freshwater runoff into the Gulf (Table 2, 1950–84). Factors that may contribute to this difference are the relative increase of the annual RIVSUM for the period between 1974 and 1984 (see Fig. 3a), the errors arising in geostrophic computations (small differences between large numbers), and the fact that geostrophic transports are not well estimated within one internal Rossby radius of the Cape Breton side. As shown for other regions of the GSL, considerable variability in the motion can be expected at Cabot Strait at synoptic frequencies (2–20 d), in response to buoyancy and large scale wind forcing perturbations. For instance, Lawrence (1969) notes that "changes of up to 50% in the surface layer flow can be correlated with the barometric pressure gradients in the Gulf". Long-term measurements of currents, temperature and salinities in the Cabot Strait region are urgently needed to study the response of the GSL to oceanic, buoyancy and meteorological forcing, and to calibrate numerical circulation models currently being developed for the Gulf.

4.2.6 The Strait of Belle-Isle

The Strait of Belle-Isle, to the northeast of the GSL (Fig.2) has received considerable attention from the hydrodynamical point of view. One of the questions often asked is: What would happen to the GSL system, particularly during winter, if this Strait were to be closed? According to Neu (1968):

> "this would stop the interchanging flow between the cold waters of the Labrador Stream and the generally warmer waters of the Gulf of St. Lawrence. The heat retained in the Gulf is thought to be about 5.7 × 10^{15} kcal. Another large quantity of heat would probably be recovered by preventing Labrador ice from entering the Gulf. The heat gained from these two sources would presumably be sufficient to increase the temperature of the waters in the Gulf by one-quarter to one-half of a degree. This increase could reduce ice formation in the central and eastern sections of the Gulf appreciably, or stop its formation altogether."

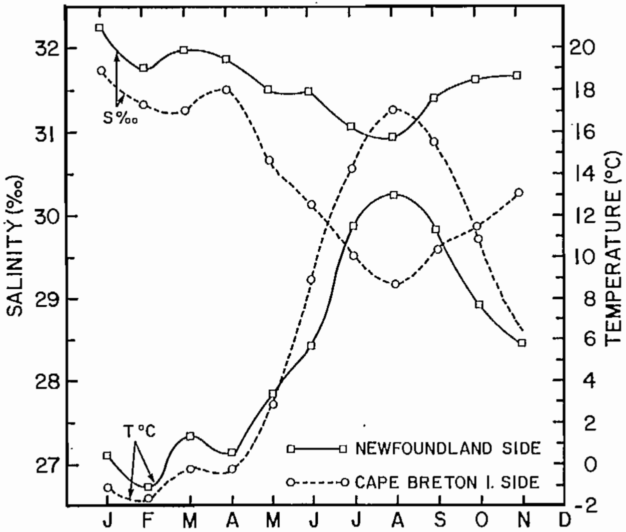

FIG. 30. Long-term salinity and temperature measurements near opposite shores of Cabot Strait (from El-Sabh 1977a).

Earlier circulation studies (Dawson 1907; Huntsman et al. 1954; Bailey 1958; Farquharson and Bailey 1966), together with more recent data, were examined by Garrett and Petrie (1981). They showed that the flow through the Strait is controlled by sea-level differences at opposite ends of the strait, produced by large scale meteorological forcing, and spins down in about 1.1 d. The incoming and outgoing current fluctuations seem to be confined to the south side of the channel, and the flow appears to be hydraulically controlled at times. According to Garrett and Toulany (1981), the flow was less coherent with wind stress than with the geostrophic wind itself. Highest coherence were obtained at periods between 2 and 30 d, for wind directions parallel to the west coast of Newfoundland. At lower frequencies, the variability of the flow was not directly associated with large scale meteorological forcing, and the authors suggest the estuarine circulation of the GSL as a probable cause of variability.

Recent findings by Petrie et al. (1988) reveal that the net transport through the Strait is usually towards the Gulf, with low rates during summer (0.13 × 10^6 $m^3 \cdot s^{-1}$, from July to October 1980), coupled to a net loss of heat to the Northeastern Gulf, and higher rates during winter (0.3 × 10^3 $m^3 \cdot s^{-1}$, from average sea-level and hydrographic conditions from January to May). As noted by the authors, this winter inflow will vary from year to year. During the January–May 1975 period, they estimated a net transport twice its average value, directed towards the Gulf. During average winter conditions, Petrie et al. (1988) estimate that the cold water transported through the Strait accounts for about 35% of the cold intermediate layer of the GSL.

4.2.7 Jacques Cartier Strait

The northern Gulf region receives the freshwater discharged from several rivers distributed almost equally from east to west (see Fig. 1, Table 2). Normally, such lateral runoff would induce an offshore pressure gradient, which in turn would support a mean coastal circulation towards the west, essentially closing the overall surface cyclonic circulation of the GSL (Fig. 14). The Jacques Cartier Strait, north of Anticosti Island (Fig. 2) is one of the least known areas of the GSL system. Its eastern boundary is about 110 km wide, with a maximum depth of about 250 m. The topography then converges towards the west to a narrow 30 km passage, where depths exceed 100 m only in the mid-channel area. In some respects, this strait bears some similarities with the Lower St. Lawrence Estuary. Recent satellite images (Lacroix 1987) revealed persistent upwelling of cold waters along the northern shores of the Gulf, presumably induced by winds from the NW. Strong mixing was also documented to occur in the western part of Jacques Cartier Strait, where strong tidal currents will mix cold intermediate waters with surface waters (Pingree and Griffiths 1980; Koutitonsky et al. 1987). Cold waters seen at the surface seen along the south shore of Anticosti (Fig. 24, 25) suggest that wind-driven upwelling or tidal mixing are also at work along this shore. As shown by Rose and Leggett (1988a,b), wind-induced coastal upwelling in the northern Gulf occurs at synoptic time scales, and will affect local biological processes and fish migration.

The prospect of future hydroelectric runoff regulations on the northshore, the lack of regional tidal information, and the need to examine the relationship between the hydrodynamics and fish stock recruitment in the area has prompted several institutions to join in a large scale multidisciplinary project. The COHJAC project (Circulation, Oceanography and Hydrography of the Jacques Cartier strait, project leader: D. Lefaivre, Fisheries and Oceans, Mont-Joli, Québec) involved seasonal larvae sampling, as well as long-term (1986–88) measurements of currents and bottom pressure at several locations (Fig. 31). The June–October 1986 alongshore and vertical variability of currents is presented in Fig. 32. This figure shows the mean currents, the principle axes of variability of the high- and low-passed currents (cutoff period 34 h), and the M2 tidal ellipses. Tidal and subtidal current fluctuations are seen to contribute almost equally to the total kinetic energy, whereas mean currents are weak, typically in the range of 1–5 cm • s^{-1}. Note that this mean westward circulation completes the overall cyclonic circulation in the GSL (Fig. 14). Spectral analysis of the 1986 data set indicates that low-frequency current fluctuations at both station were coherent in the alongshore direction, in the vertical, and with alongshore wind fluctuations, in both the 2–5 and 8–12 d frequency bands. Analysis of the complete COHJAC data set is currently underway.

4.2.8 The Northwestern Gulf

Previous hydrographic studies in this region (Trites 1972; El-Sabh 1976; Sevigny et al. 1979; Tang 1980a, 1983) have consistently revealed the presence of a quasi-permanent geostrophic cyclonic eddy to the west of Anticosti Island, whose vertical density structure forms an upward dome, with highest densities in the middle (Fig. 33). This feature links several dynamical processes, such as the outflow from the St. Lawrence Estuary along the south shore, the transverse motion at the mouth of the Estuary, the Gaspé current, its instabilities moving offshore and wind-induced coastal upwelling along the northshore, all of which were shown to exhibit considerable synoptic variability (e.g, Fig. 24 and 25). It is not clear at the moment which combination of these processes maintains this cyclonic eddy in motion, or whether it is forced by the cyclonic wind stress distribution in the area (section 4.1). Bugden (1981) estimated that most of the water transported in the Gaspé current is upwelled in this region of the Gulf, and that this transport is at it's minimum in July. In this context, upwelling corresponds to the vertical mass transport from below 50 m as calculated by a Bugden's box model. Mertz et al. (1991) attempted to explain the July minimum transport in the Gaspé current, a time of the year when runoff from the St. Lawrence Estuary is relatively high, in terms of the summer weakening of wind stress over the northwestern Gulf. As a consequence, lesser quantities of water upwelled offshore will be transported southward to feed the Gaspé Current. All these arguments suggest that the cyclonic eddy in the northwestern Gulf may be partially wind forced.

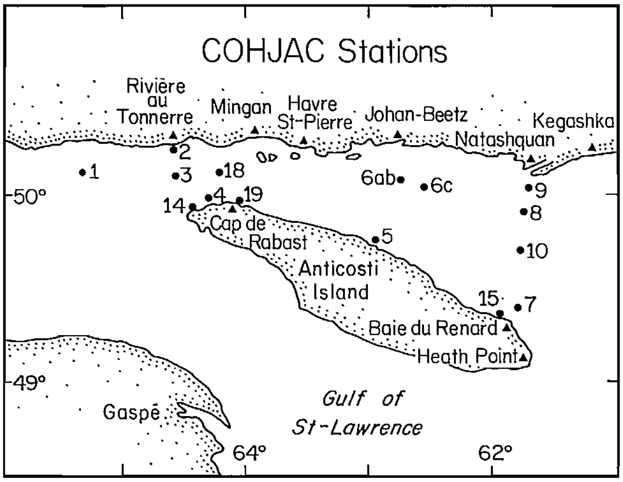

FIG. 31. Current mooring deployments (1986–88) in the Jacques Cartier Strait during the COHJAC experiment.

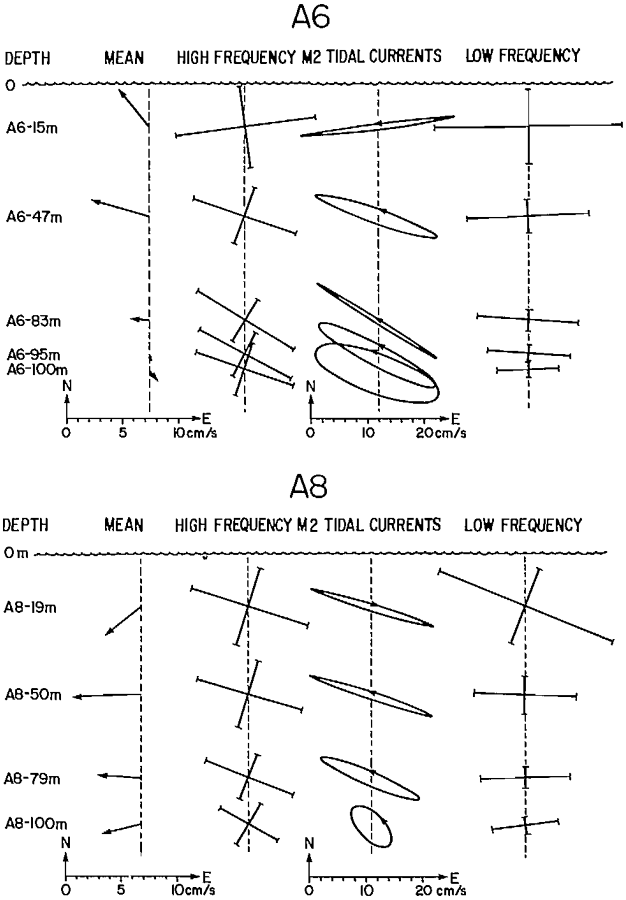

FIG. 32. Alongshore and vertical variability of currents at stations A6 and A8 (see Fig. 31), during the COHJAC phase A experiment — May to September 1986 (available from Koutitonsky et al. in preparation).

5. Summary and Recommendations

The Gulf of St. Lawrence is a highly stratified semi-enclosed sea, which forms an integral physical oceanographic unit. It is acted upon by the following inputs:

1) Buoyancy forces, resulting from freshwater runoff into the GSL from the surrounding rivers, from precipitation minus evaporation, and from heat fluxes through the surface. The annual freshwater runoff to the Gulf is about 600 km^3, with a contribution of 84% from the St. Lawrence Estuary, and 14% from the rivers along the northern shore of the Gulf. Precipitation minus evaporation, including ice formation and melt, amount to some 120 km^3/yr. Therefore, the freshwater discharge to the St. Lawrence Estuary (RIVSUM) is the major driving force for the observed density-driven circulation in the GSL, with lesser contributions from other sources. The RIVSUM variability at synoptic time scales was shown to be as important as the monthly-averaged RIVSUM differences. This is presumably due to the combined effects of climatic variability and runoff regulations for hydro-electricity. In April, RIVSUM is still low and buoyancy forcing from surface heat fluxes is almost equal to that due to freshwater flux. During winter, heat fluxes are negative and about 65% of water masses in the intermediate layer are cooled locally.

2) Local and large-scale meteorological forcing, resulting from the propagation of low pressure systems along preferred tracks, and generating coastal currents, upwelling of cold waters along the north shore, inertial motion and large scale sea-level setup. Seasonal wind forcing is cyclonic over the Gulf, and highest winds occur during the winter season. Synoptic wind forcing is predominant at two time scales: 2–5 d and 8–15 d. It is suggested that the shorter time scale corresponds to the rapid propagation of extra-tropical cyclones along the eastern boundary of the Gulf, while the longer time scale corresponds to the passage of pressure systems along the northern boundary.

3) Non-local tidal forcing from the Atlantic ocean, producing mixed surface tides, internal tides, tidal mixing fronts in coastal areas, and tidal residuals in shallow confined areas.

4) Non-local forcing by very low frequency perturbations at the edge of the Atlantic shelf.

The response of the system is estuarine-like at yearly time scales, with an outflow of lighter waters near the surface, and a penetration of Atlantic waters in deeper layers. Horizontally, offshore pressure gradients induced by runoff and cyclonic wind stress are in balance with Coriolis accelerations, and the resulting circulation is

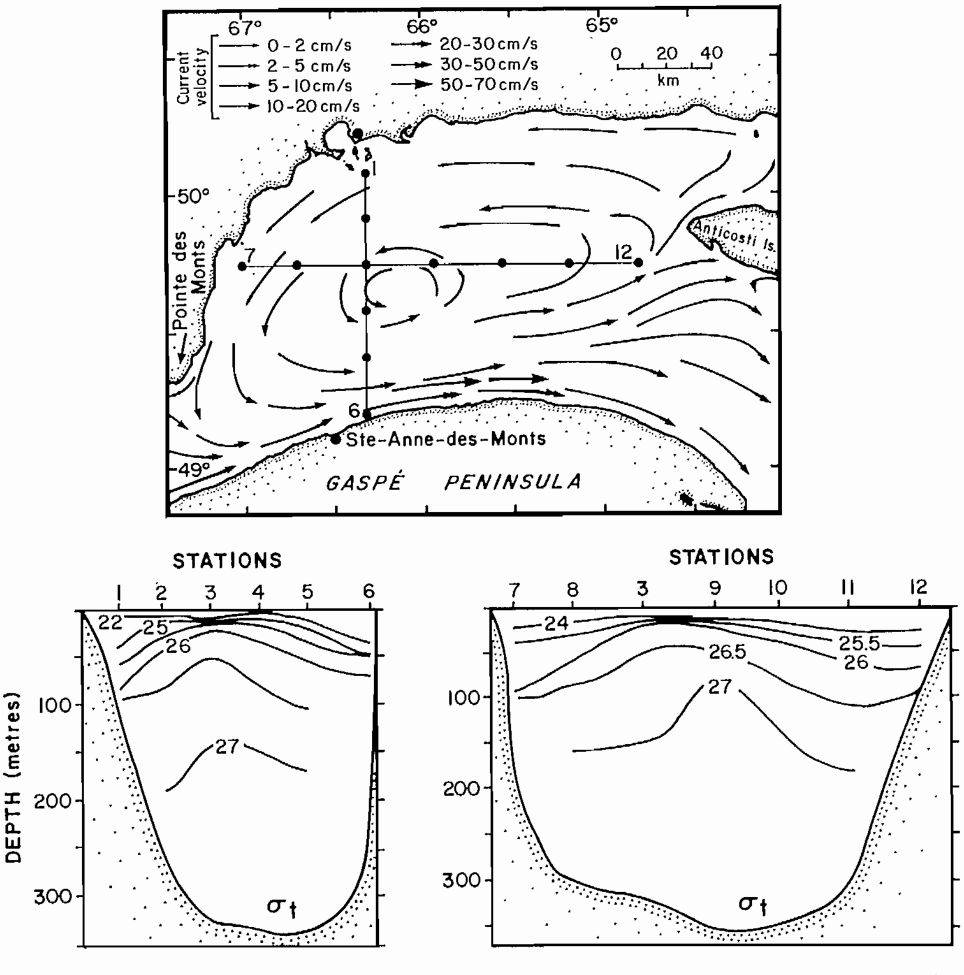

FIG. 33. Monthly-averaged surface geostrophic currents for July (El-Sabh 1976) and density sections (19–25 July, 1976) in the northwestern Gulf of St. Lawrence (from Sevigny et al. 1979).

cyclonic near the surface. Little is known about the circulation in deeper layers or during winter. Regional studies and satellite images revealed considerable variability about this mean circulation at synoptic time scales. Since the water is stratified, the dominant spatial scale is the internal radius of deformation. This allows for the formation of mesoscale and synoptic eddy motion of length scales between 10 and 50 km, frontogenesis, internal waves, and instability of the motion. These features were documented in details for the LSLE and the Gaspé current region. Anticipating that these processes may be advected in some distorted form to the Magdalen Shallows, it is suggested that dynamical and biological processes occurring there be also examined in relation to what has previously occurred in the LSLE and the Gaspé Current. Highest variance levels are found at mesoscale (inertial, tidal) and at synoptic frequencies. Fluctuations at periods of 2–15 d are predominantly produced by meteorological forcing, while fluctuations of 40–80 d periods are more likely produced by climatic (buoyancy and meteorological) forcing. Yearly and decadal fluctuations are also expected in response to climatic changes and non-local forcing from the Atlantic Ocean. In this respect, the GSL responds more like a small ocean. The dominant synoptic variability of the system will present considerable challenges to oceanographers, some of whom may want to describe the response of the system using the concept of "geostrophic turbulence" (e.g. Nihoul and Jamart 1989) instead of presenting "monthly-averaged" state variables. For instance, it is desirable that future circulation maps of the GSL include at least the principle axes of variability of the currents in the upper, intermediate and deep layers, at mesoscale, synoptic and yearly periodicities, in addition to averaged currents (e.g. Fig. 32). In the mean time, some recommendations are offered:

1) All institutions involved in sampling programs in the Gulf must act in a concerted manner, so that with the resources available simultaneous observations can be made in several regions of the Gulf. If possible, observations should be sufficiently long to resolve at least one synoptic event (e.g. 15 d).

2) Long term (years) monitoring of parameters such as currents, bottom pressure, temperature and salinity must start at key locations in most of the regions discussed. This will provide future scientists with series of significant length to enable them to resolve the longer time scales, and to study the interaction between all parts of the system.

3) A numerical laboratory for the GSL system, consisting of a three-dimensional eddy-resolving circulation model and related dispersion models, must be developed and shared by oceanographers to understand the response of the GSL system to various buoyancy and meteorological forcing conditions, and to estimate fluxes of dissolved and suspended matter in the system.

4) Remote sensing technology, non-existent today, should be developed to monitor the synoptic variability in both the horizontal and vertical dimensions, to calibrate numerical models and to interpret long-term monitoring observations.

Acknowledgements

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Brief Overview of the Chemical Oceanography of the Gulf of St. Lawrence[1]

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In this brief overview we examine the current knowledge of the chemical oceanography of the Gulf of St. Lawrence, identify some of the gaps in knowledge, and discuss how to go about the study of the Gulf in the future.

Nous résumons brièvement l'état des connaissances actuelles de l'océanographie chimique du Golfe Saint Laurent, identifions certaines des lacunes, et discutons la façon de procéder pour des recherches éventuelles dans le Golfe.

Introduction

In the science of oceanography, chemistry plays two important roles. It provides precise and accurate chemical measurements of great value to the study of the physical, biological, and geological nature of the ocean, and it provides information and knowledge about the chemical composition, properties, and reactions of sea water, sediments, and suspended particulate matter. An important aspect of marine chemistry is the distribution of chemical species in the marine environment and the processes that control this distribution. Paradoxically, chemical studies have been less successful in estuaries and coastal waters than in the open ocean. The difficulties encountered in estuarine studies can to some extent be tied to the progressively smaller scale of temporal and spatial variability and the larger degree of complexity as one moves landward from the open ocean through the coastal zone into the estuaries.

In many estuaries, the influence of chemical reactions on the composition of water and particulate matter is difficult to observe because of intense mixing and rapid flushing. This is the case for the upper St. Lawrence Estuary, which is the region between the head of the Laurentian Trough, near the entrance to the Saguenay Fjord, and the limit of salt-intrusion at Québec (Fig. 1). For example, the distribution of dissolved trace metals in this estuary is completely controlled by physical mixing, with the exception of iron and chromium (Yeats 1988a). To a large extent, physical mixing also controls the composition of the suspended particulate matter and the bottom sediments (Gobeil et al. 1981). In the deep, permanently stratified waters of the Gulf of St. Lawrence, however, chemical and physical processes are more balanced, and it is correspondingly less difficult to observe how chemical reactions affect the composition of water, particles, and sediment. The Gulf of St. Lawrence is also relatively accessible. It is therefore well suited for studies of estuarine and ocean chemistry.

In this brief overview we examine the present state of knowledge of the marine chemistry of the Gulf of St. Lawrence. We show that even though this knowledge has been significantly improved during the last 20 years, we are still far from having developed the understanding and insight that will be necessary to deal with the ever-growing pressures on the Gulf of St. Lawrence caused by human activities. Developing this knowledge will be a challenge for chemical oceanographers in the years to come.

An Examination of the Present State of Knowledge

Nearly 20 years ago, in 1970, a workshop was held at the Bedford Institute of Oceanography to review the state of research in the Gulf of St. Lawrence and to discuss the desirability of setting up a coordinated and concerted research program. The workshop identified several important questions that needed the attention of chemical oceanographers (Hassan 1971):

1. What are the concentrations of pollutants in the Gulf, and which are their pathways within the system?
2. What is the seasonal variation and speciation of classical nutrients in various regions?

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[1] This paper forms part of the Proceedings of a Workshop/Symposium held at the Maurice Lamontagne Institute, Mont-Joli, Quebec, 14–17 March 1989.

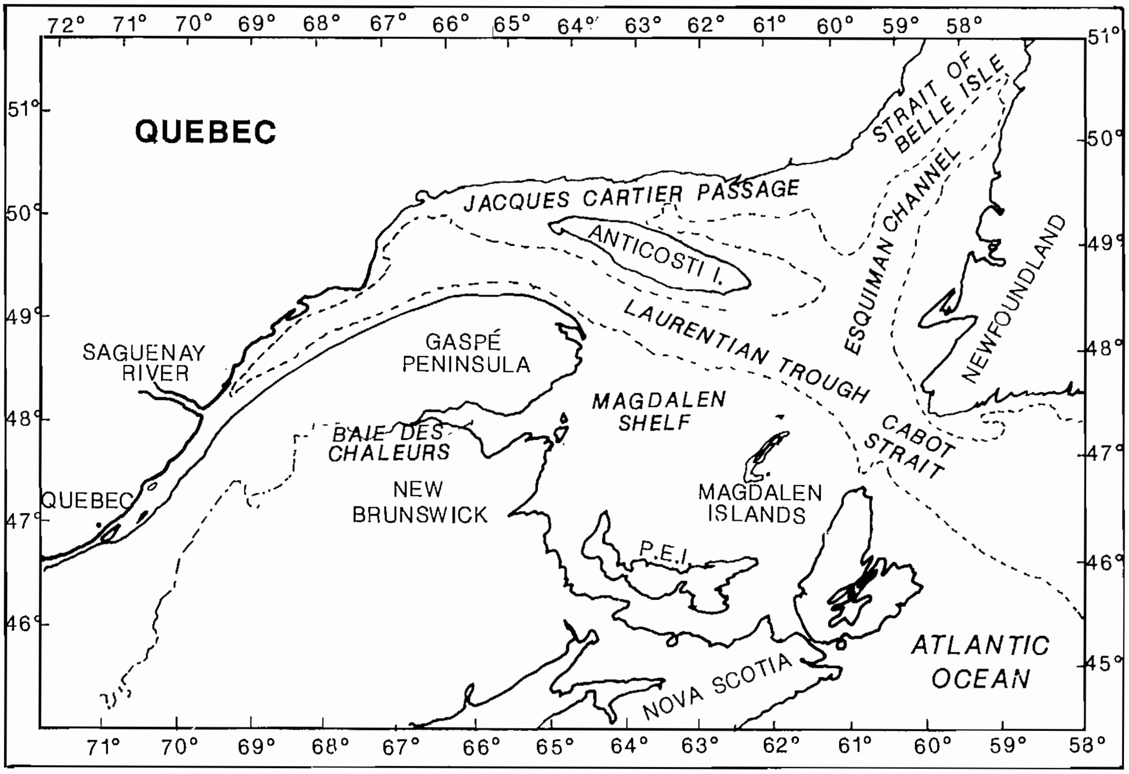

FIG. 1. The Gulf of St. Lawrence. Note the two principal physiographic features: the deep Laurentian Trough and the shallow Magdalen Shelf.

3. What is the nature, abundance, and distribution of the organic material in the water and the suspended matter of the Gulf?
4. What is the functional role of suspended matter in relation to the transport and deposition of the numerous chemical species?
5. In what way does the ice cover influence the exchange of important dissolved gases such as CO_2, N_2, and O_2 and what are the consequential effects on productivity?
6. To which extent are various chemical constituents mobile or fixed in sediments?

A substantial research program was proposed in order to examine these questions. Unfortunately, it was not funded. The knowledge of the chemistry of the Gulf of St. Lawrence was therefore not developed in the coordinated and concerted way that had been hoped for. Instead, it was developed somewhat haphazardly, and mostly as a result of the personal interest of individual researchers. In the early 1970's the exploration of the Gulf of St. Lawrence was spearheaded by chemical oceanographers from the Bedford Institute of Oceanography, who conducted an average of two major cruises per year to the Gulf between 1970 and 1976. Since then, their activity in the Gulf has greatly diminished, and only two cruises have been conducted since 1976. The work of this group has been summarized in Strain (1988). In the middle 1970's chemical oceanography began to expand in the Québec universities, particularly at the Université du Québec à Rimouski, where the emphasis was placed on sediment chemistry and benthic boundary layer processes (Silverberg and Sundby 1990). For logistical reasons, this group was not able to fill the void left by BIO in the Gulf proper, but concentrated its efforts in the Lower St. Lawrence Estuary.

Most of the early chemical work in the Gulf was aimed at describing the distribution of various elements and compounds in the water column and in the surficial sediments. As a result of these studies, we have a good first-order understanding of the concentration levels and distribution patterns of dissolved oxygen (d'Anglejan and Dunbar 1968), nutrients (Coote and Yeats 1979; Yeats 1988b), suspended particulate matter (Sundby 1974; Yeats 1988c), organic carbon (Pocklington 1988), trace metals (Yeats 1988a). The work on sediment chemistry was summarized by Loring and Nota (1973). The general distributions of oxygen and nutrients can be understood in terms of an overall two-layered estuarine circulation, superimposed upon which are phytoplankton production in the surface layer and degradation of organic matter and regeneration of nutrients at depth. There is a suggestion that the same processes control the distribution of some of the trace metals. Other processes that were identified in these studies were the resuspension of bottom sediment, which creates the bottom nepheloid layer, and diagenetic release of some metals from the bottom sediments.

As data on the distribution of the various chemical species became available, they were combined with data on water exchange to provide estimates of the fluxes of chemical species within the Gulf and between the Gulf and the Atlantic Ocean. Such calculations are fraught with uncertainty, of course, dependent as they are not only on representative chemical data but also on representative values for the inflow and outflow of water across the various boundaries. Crude though they may be, the purpose of these calculations is to identify gaps in knowledge. As such, they can often be helpful.

An example of such calculations are the attempts to construct a budget for sediment fluxes. The first such attempt led to the conclusion that the export of suspended particulate matter from the Gulf matched the suspended sediment transport by the St. Lawrence River (Sundby 1974) (Fig. 2a). This was interpreted to mean that there was extensive erosion of coastlines and shallow coastal areas supplying additional sediment to the deeper areas of the Gulf. Since then, more detailed estimates of the transport of water and the distribution and composition of suspended particulate matter have allowed a revised budget to be prepared, yielding quite different conclusions (Yeats 1988c) (Fig. 2b). According to this budget, the net export of suspended matter from the Gulf is an order of magnitude less than the river transport. Furthermore, the suspended matter leaving the Gulf bears little resemblance to the predominantly inorganic particulate matter carried by the rivers. Rather, it appears to be mostly biogenic material, produced within the Gulf. The revised budget indicates that virtually all the riverborne suspended material sediments inside the Gulf, and that mostly authigenic material is exported.

Budgets such as these will undergo many more revisions as new information comes to light. For example, although we know little about sedimentation rates in the Gulf of St. Lawrence, the few measurements we do have suggest that the the sedimentation rate estimates used in the suspended matter budgets are too low, and that internal sources of sediments are indeed needed to satisfy the accumulation rates in the Laurentian Trough (Silverberg et al. 1986). A great deal of uncertainty is also attached to the flux estimates for Cabot and Belle Isle Straits because of uncertainties in the data for water transport.

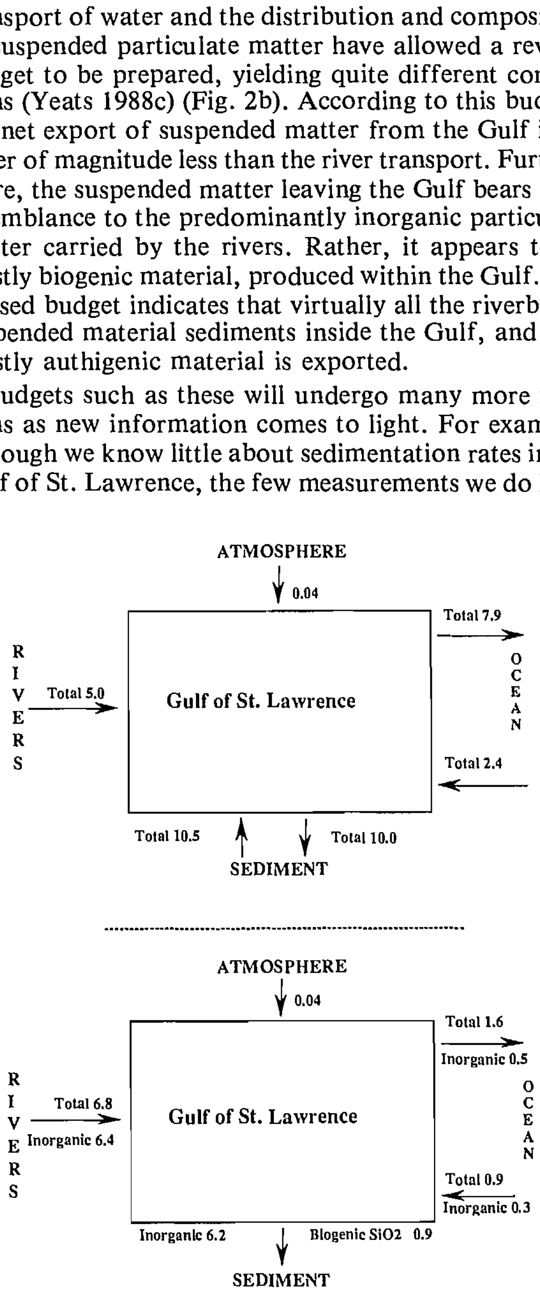

FIG. 2. Examples of suspended sediments budgets (in 10^6 tons yr^{-1}) for the Gulf of St. Lawrence. *Top:* from Sundby (1974); *Bottom:* from Yeats (1988c).

The flux of an element from the continents to the deep ocean is an important component of the global geochemical cycle. In order to construct such a cycle, one would like to know the amount of weathering products carried by rivers that is trapped in continental margin sediments, and the amount that actually escapes to the deep ocean. The earliest calculations of such fluxes considered that trace metals carried on suspended particles could be neglected in the budget. This appeared to be a reasonable assumption since the overwhelming proportion of sediment carried by rivers does not escape the continental margin. The calculations also considered that a certain proportion of metals carried in solution would be sequestered by particles in estuaries, further reducing the flux to the ocean. When a mass balance was constructed for the Gulf, using a box model, the conclusion was that as much as 50–75% of the freshwater input of Ni, Cu, Zn and Cd are exported to the ocean (Bewers and Yeats 1977). The budget also showed that the flux of dissolved manganese to the ocean was comparable to the flux to the Gulf via the rivers. These results have implications for the residence time of trace metals in the ocean and therefore provide information about their chemical reactivity.

Since the early budgets, evidence has come to light that the flux of continental weathering products to the ocean can be qualitatively and quantitatively modified in the coastal zone.The most complete evidence for this comes from studies of the element manganese. It was discovered that the particulate matter that is suspended in the bottom water of the Laurentian Trough is highly enriched in manganese. The manganese content of these particles is more than one order of magnitude higher than that of the suspended matter carried by the St. Lawrence River (Sundby 1977). This discovery, coupled with observations of very high concentrations of dissolved manganese in the bottom water of the Laurentian Trough, showed that the bottom sediments release dissolved manganese which subsequently precipitates in the water column (Yeats et al. 1979) (Fig. 3). The dissolution of manganese is brought about by the reducing conditions which exist in the sediment below a thin oxidizing surface layer. Subsequent precipitation in the water column creates micron-size particles, containing as much as 40% manganese (Sundby et al. 1981). It is believed that a large proportion of the manganese export from the Gulf is accomplished by these fine, slow-settling, metal-rich particles.

The sediments are an important component of the chemical factory that is the Gulf of St. Lawrence. They are the home of macro- and micro-organisms which make a living ingesting and degrading the organic matter that rains out from the water column. In so doing, these organisms change the chemical composition of the sedimentary environment and influence the transport of solutes and solids within the sediment and across the

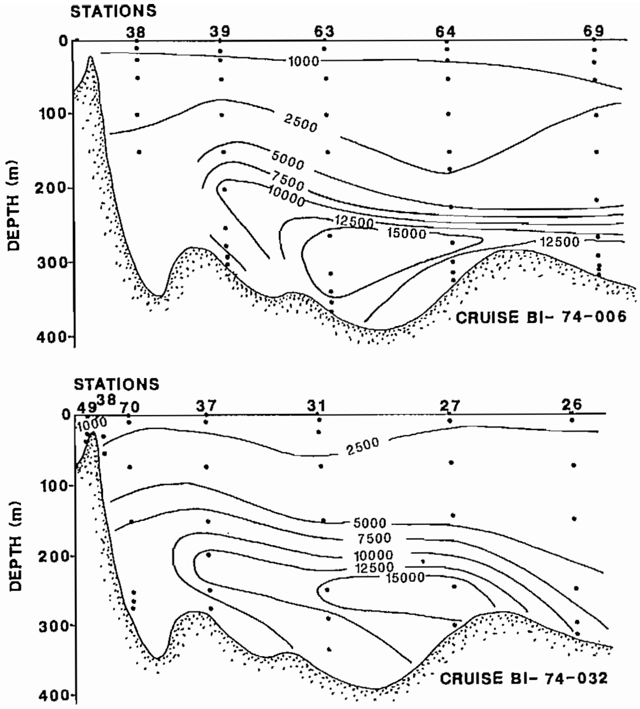

FIG. 3. The vertical distribution of dissolved manganese (top) and the manganese content of the suspended particulate matter (bottom) on a station in the Laurentian Trough. (From Yeats et al. 1979.)

sediment-water interface. Studies of the pore water composition of sediments from the Laurentian Trough by the Rimouski group have shown that dissolution and precipitation reactions affect trace metals and other compounds. For example, the pore water contains concentrations of iron, manganese, cadmium, mercury, and lead that are higher than in the overlying water column, in some cases by orders of magnitude. For some elements, notably cadmium, the highest concentrations are found just below the sediment-water interface (Gobeil et al. 1987) (Fig. 4), indicating that cadmium is solubilized from particulate matter by reactions associated with the aerobic degradation of organic matter. For other elements, notably manganese, the highest concentrations occur deeper in the sediment as a result of the transition from oxidizing to reducing conditions. In each case there are steep concentration gradients along which the metals migrate from one zone of the sediment to another and sometimes across the sediment-water interface. Thus, some elements will be recycled between the sediment and the water column many times before they are ultimately buried to depths where they are out of further contact with the sea. Using manganese as an example, the intensity of such recycling has been calculated (Sundby and Silverberg 1985). When the rates of cycling were compared to the reservoir of recyclable manganese in Laurentian Trough sediment, the striking conclusion that was reached is that all the manganese contained in the surface sediment goes through a cycle of burial, dissolution, migration, and precipitation several times per year. The main driving force of this cycle is benthic organisms which transport particles across the redox boundary in the sediment.

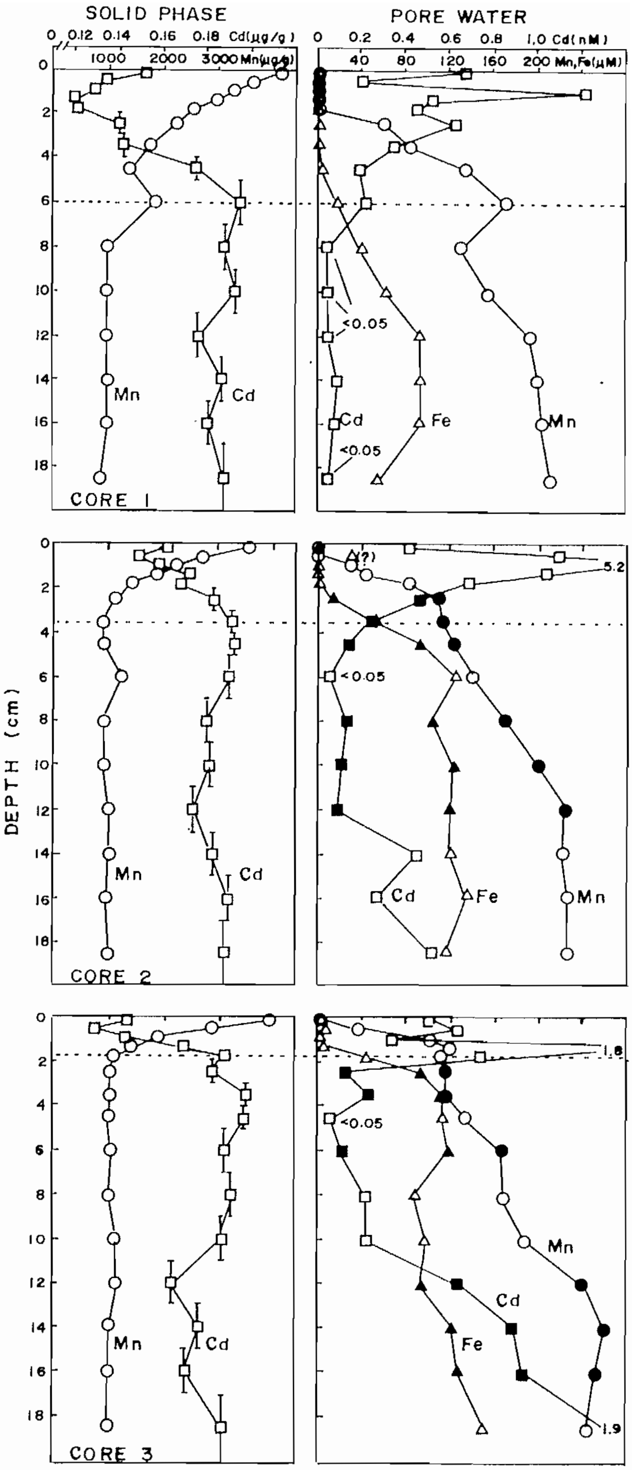

FIG. 4. The contrasting distributions of dissolved and solid-phase cadmium and manganese in a sediment core from the Laurentian Trough. (From Gobeil et al. 1987.)

Regions where sediments accumulate without being disturbed by bioturbation offer the opportunity to determine the history of chemical contamination. The sediments in the Saguenay Fjord have been studied for this purpose and have given valuable information on the trends of contamination by mercury, radionuclides, polycyclic aromatic hydrocarbons, and organochlorines in the Saguenay drainage basin (e.g. Fig. 5). These studies have

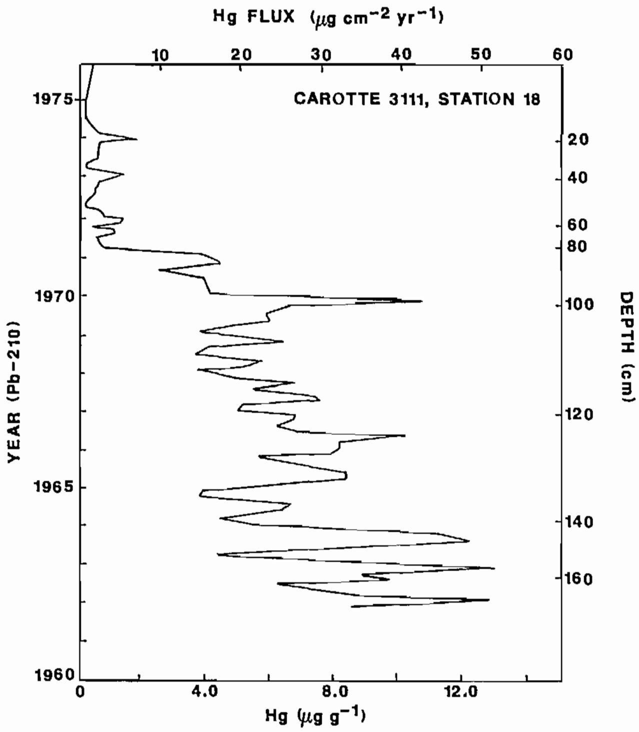

FIG. 5. Historical variations in mercury fluxes to the sediments in the Saguenay Fjord. (From Smith 1988.)

also allowed trends in sedimentation rates and historical episodic events to be identified (Smith 1988).

Some Gaps in Knowledge

The Workshop of 1970 identified a number of important questions about the Gulf, and it is useful to see what progress had been made in answering these questions. The comments below relate to work done specifically in the Gulf.

1) We have developed new knowledge of the concentration and distribution of pollutants. We know that the concentrations in the water column of most species considered to be pollutants are so low that their measurement is a challenge to the skills of the best analytical chemists (Yeats 1988a). In sediments and biological tissues the concentrations are higher and easier to measure. We know that the concentration of petroleum residues in the water column (Levy 1988) and the input of the toxic metals mercury (Smith 1988) and lead (Gobeil and Silverberg 1989) has been decreasing over the last several years, possibly as a result of regulations to control the use and disposal of such substances. We know less about organic than about inorganic contaminants, but the occurrence of high concentrations of chlorinated hydrocarbons in the fatty tissue of beluga whales, for example, has shown that man-made organic contaminants have entered the marine food chain (Martineau et al. 1987). It is nevertheless fair to say that we know little about the processes that control the distribution of such contaminants.

2) Nutrients have been studied extensively in relation to primary productivity. It has been established that the nutrient supply, which is dominated by the upwelling of intermediate depth water, rarely limits the productivity in the Lower Estuary. The productivity is more dependent on conditions of light and stratification (Therriault and Levasseur 1985). Internal tides create important variations in the nutrient distribution field in the lower estuary, and one can observe vertical excursion of as much as 100 m in the concentration isopleths (Therriault and Lacroix 1976).

3) We still know very little about the organic material in solution and in suspension in the waters of the Gulf except the concentration of dissolved and particulate carbon, and the C:N ratio of this material (Pocklington 1988).

4) We have a first order idea of the distribution of suspended particulate matter, and we know something about the functional role of suspended matter in relation to transport of chemical species (Yeats 1988c). We know that the vertical transport of particulate matter is accomplished by fairly large, fast-settling particles (Silverberg et al. 1985). We also know that the composition of these particles is quite different from the underlying sediment, and that extensive degradation and transformation of the settling material takes place at the sediment surface and in the sediment column (Gendron et al. 1986; Gobeil et al. 1987).

5) To our knowledge, no work has been done on gas exchange or on the effect of ice cover on gas exchange in the Gulf.

6) It has been established that many inorganic components of sediments, including the trace metals, are mobile (e.g. Sundby and Silverberg 1985; Gobeil et al. 1987; Belzile 1988; Gobeil and Silverberg 1989). We have little information on the mobility of organic compounds in sediments.

Where Do We Go From Here

It is certain that chemistry will continue to play an important role in providing the chemical measurements needed to advance the knowledge of the physical, biological and geological nature of the Gulf of St. Lawrence. It is also certain that chemistry will be at the heart of efforts to understand the effects of environmental stresses on the Gulf environment. Chemistry is also an important component of climate oriented studies.The more that is learned about the chemical nature of the Gulf system, the better the environmental questions can be addressed. The question is how to best go about the study of the chemical oceanography of the Gulf.

A useful way to think about the chemistry of a system such as the Gulf of St. Lawrence is to consider the pathways a chemical substance follows between its sources and the locations where it is finally removed from further interaction with the marine environment. The term "pathways" stands for the combination of physical transport and chemical reactions that a chemical species undergoes from source to final resting place. The pathways include transport in gas, solution and solid, and they include partitioning among these phases, incorporation into biological tissue, and transformation to other chemical species by a variety of reactions. A snapshot of these pathways would represent a concentration field. By the same analogy, the pathways themselves are like a movie, describing the movement of a chemical species within phases and across phase boundaries and the interactions that take place along the path of movement. Figure 6 is a qualitative description of the pathways of manganese in an estuary (Sundby et al. 1981). A quantitative description of some of the fluxes involved is given in Sundby and Silverberg (1985). The pathway concept is equally useful for describing the distribution and fate of a toxic chemical as it is for describing the marine cycle of carbon.

Focusing on pathways is an excellent strategy for understanding environmental problems. For example, part of the climate question is tied to the oceanic pathways of carbon. They include the supply of carbon to the continental shelf from land drainage and from the atmosphere, the exchange of carbon between shelf and deep sea, the fixation of carbon on shelves, and the burial of carbon in continental margin sediments. Closely associated with the carbon cycle is the supply and recycling of nutrients, especially nitrogen, which facilitate the fixation of carbon in organic matter. An important problem is to determine the rates of mineralisation of organic matter and the rates of withdrawal of organic carbon from the oceanic carbon cycle by burial in coastal sediments.

The ultimate description of pathways would be a mathematical model from which the concentration field and the fluxes of a chemical species within the concentration field could be derived quantitatively. Three kinds of information are required to construct such models for a system such as the St. Lawrence: (1) a function describing the input of a chemical species to the system, (2) the dynamics of the transport processes which disperse it throughout the system, and (3) the kinetics of the chemical reactions that act upon it.

Examples of input functions are the rate of atmospheric fallout of radionuclides as a consequence of nuclear weapons testing, and the rate with which a river delivers soluble and particulate major and minor elements to an estuary. In the St. Lawrence system, we have a fair idea of the river flux of some of the major and trace elements, but little or no such knowledge for organic and many inorganic chemical species that occur at trace levels in river water. Nor do we know much about the many trace constituents that are transported to the Gulf of St. Lawrence via the atmosphere.

A good basic understanding of circulation and mixing processes in the Gulf of St. Lawrence is indispensable for developing pathways models. Equally indispensable is an understanding of the physical transport across the air-water and the sediment-water interface, as well as transport within the the sediment column. Transport processes in the sediment are closely tied to the activity of living organisms which transport and transform sedimentary material as part of their normal activities. The importance of these processes is now well established, but quantitative information is still rare. The only data on bioturbation rates in the Gulf of St. Lawrence are found in Silverberg et al. (1986).

If there is one particular area of marine chemistry that needs to be developed more than any other, it is the identification of important chemical reactions and their kinetics. In the past, equilibrium concepts have been

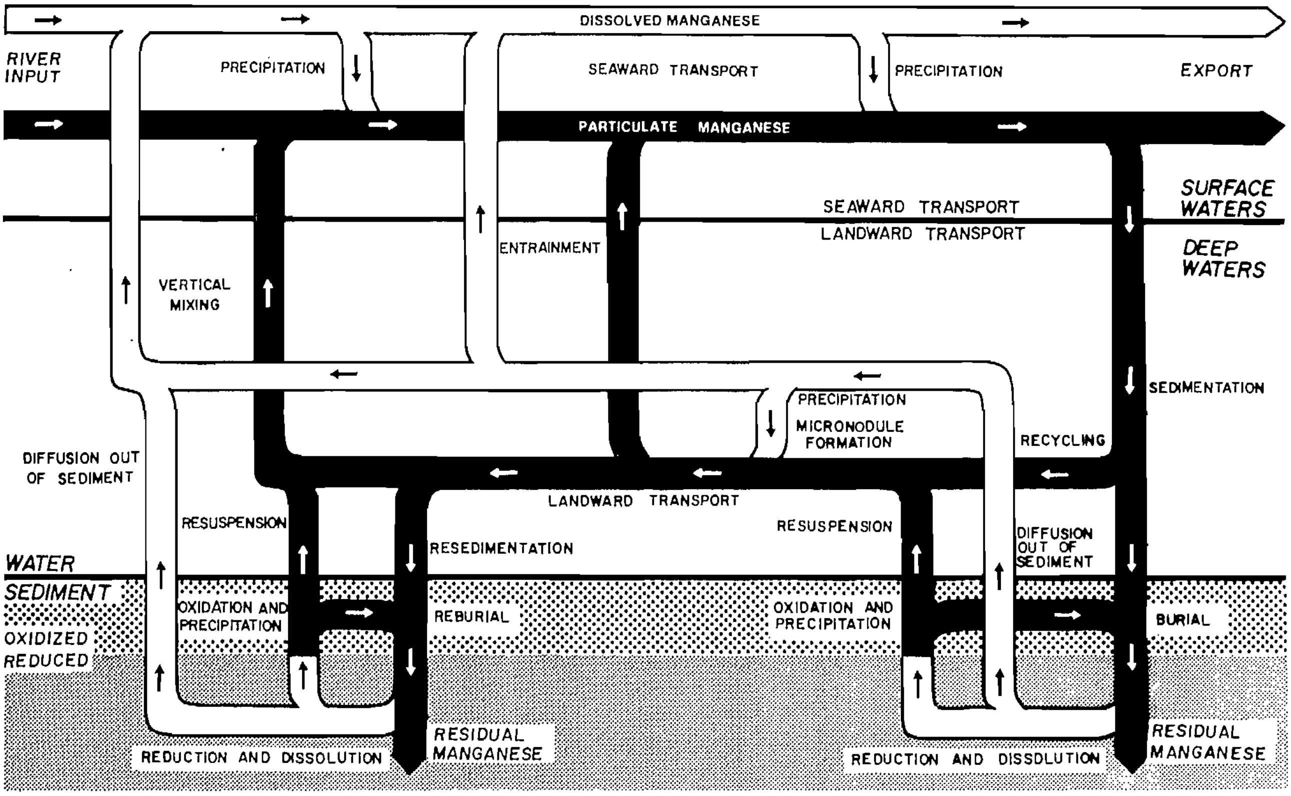

FIG. 6. Pathways of manganese in an estuary. (From Sundby et al. 1981.)

applied to describe the distribution of chemical species in sea water. Although equilibrium concepts have their use in marine chemistry, the systems that we study are rarely in a state of equilibrium, and are often better described with kinetics. Among the few examples of chemical rate measurements in the Gulf of St. Lawrence are studies of sulfate reduction rates (Edenborn et al. 1987) and manganese oxidation rates (Edenborn et al. 1985) in the Laurentian Trough sediments. An example of a model which incorporates reaction rates is given in Gratton et al. (1990).

A Research Program for the Chemical Oceanography of the Gulf of St. Lawrence

For the chemical oceanographer who has to develop his knowledge from the analyses of individual samples of water, sediment and suspended matter, collected from ships that move at speeds of only 10–15 knots between stations, the immense physical dimensions of the Gulf of St. Lawrence are daunting. Mapping the distribution of chemical species in the Gulf at any but the coarsest of spatial and temporal scales is prohibitively expensive. It is not surprising, therefore, that so little has been done in relation to questions asked at the first Gulf of St. Lawrence workshop such as for example: What is the nature, abundance and distribution of the organic material in the waters and suspended matter in the Gulf of St. Lawrence?

Even if it were economically feasible to carry out extensive mapping of the distribution of chemical species in the Gulf, mapping alone would not provide the knowledge we seek. In terms of the pathways analogy, mapping would give us snapshots but not the movie. A better approach is needed, such as trying to understand and quantify the processes that act upon a species along the path from source to ultimate sink, and use this knowledge in a pathways model to derive the distributions. The combination of a process-oriented approach with field measurements to provide inputs to the model and verify the results would be scientifically cost effective.

For the process-oriented approach to work, it will be necessary to verify that specific locations in the Gulf can be found that are representative of the Gulf as a whole. This will necessarily involve studies of the scales of spatial and temporal variability in order to be able to sample representatively and to understand some of the important processes. It is not easy to designate areas that are representative of the vast Gulf of St. Lawrence with its diversity of physical conditions. Fortunately, however, two principal physiographic features distinguish the Gulf: the deep trough system and the shallow Magdalen Shelf system (Fig. 1). The permanent stratification in the troughs and the seasonal stratification on the shelf provide different mechanism for bringing bottom water to the surface. The fine-grained sediments which accumulate in the troughs support completely different bottom communities and chemical reactions than do the coarse-grained, mostly relict sediments on the Magdalen Shelf. Concentrating the effort on representative parts of these two systems is likely to provide information applicable to the Gulf as a whole.

Until now, most of the research activities in chemical oceanography have concentrated on the trough system (Strain 1988) and mostly on the landward part of the Laurentian Trough, the Lower St. Lawrence estuary (El-Sabh and Silverberg 1990). The shallow southern Gulf has received little attention. It would seem that time has come to include the study of the Magdalen Shelf in chemical oceanography programs along with continued studies of the trough system.

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Pelagic Food Web Interactions and Productivity in the Gulf of St. Lawrence: A Perspective[1]

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DE LAFONTAINE, Y., S. DEMERS, AND J. RUNGE. 1991. Pelagic food wed interactions and productivity in the Gulf of St. Lawrence: a perspective, p. 99–123. *In* J.-C. Therriault [ed.] The Gulf of St. Lawrence: small ocean or big estuary? Can. Spec. Publ. Fish. Aquat. Sci. 113.

Based on a literature review, information on phytoplankton, zooplankton and ichthyoplankton of the Gulf of St. Lawrence is synthesized (1) to give a preliminary description of the nature and dynamics of the planktonic communities and (2) to evaluate the actual gaps of our knowledge and understanding of the dynamics and trophic links among the constituents of these communities. Lines of evidence suggest that the Gulf of St. Lawrence has distinct hydrographic and oceanographic conditions relative to adjacent Atlantic waters. Data on abundance and dynamics of nutrients and various plankton components suggest that the Gulf can be divided into four different subregions and therefore it should not be considered as an homogeneous biological ecosystem. The seasonal cycle of phytoplankton abundance varies among regions and is apparently linked to the physical characteristics and the availability and dynamics of the nutrient supply. The species composition and the size structure of phytoplankton, zooplankton and ichthyoplankton are also different among the four regions. Despite the seasonal variability in plankton communities and size structure observed within a particular region, the large-scale spatial differences are evident at different times of the year. It is suggested that these regions represent different planktonic food webs which are maintained due to hydrodynamic, topographic and climatic variability. A conceptual framework of the structure and dynamics of the Gulf of St. Lawrence food webs is presented in the context of fisheries oceanography where recruitment variability of some fish stocks in the Gulf appears to depend on the nature of the food webs with which these populations are associated.

Une synthèse réalisée à partir de données de la littérature sur le phytoplancton, le zooplancton et l'ichtyoplancton du Golfe du Saint-Laurent est présentée afin (1) de décrire la nature et la dynamique des communautés planctoniques du Golfe du Saint-Laurent et (2) d'évaluer les lacunes actuelles de notre connaissance et compréhension de la dynamique et des relations trophiques entre les différentes composantes de ces communautés. Le Golfe du Saint-Laurent possède des conditions hydrographiques et océanographiques distinctes de celles des eaux adjacentes de l'Atlantique Nord. Les données sur l'abondance et la dynamique des sels nutritifs et différentes composantes du plancton suggèrent que le Golfe peut être divisé en quatre sous-régions. Le Golfe ne peut donc pas être considéré comme un écosystème biologique homogène. Le cycle saisonnier du phytoplancton varie selon les régions et est apparemment lié aux caractéristiques physiques et à la disponibilité et la dynamique des sources de sels nutritifs. La composition spécifique et la structure de taille du phytoplancton, zooplancton et ichtyoplancton varient aussi entre les régions. Malgré la variabilité saisonnière des communautés planctoniques à l'intérieur d'une région, les différences spatiales à grande échelle demeurent évidentes à différentes périodes de l'année. Il est suggéré que ces sous-régions représentent des chaînes trophiques différentes dont l'existence est maintenue par les variations dans les conditions hydrographiques, topographiques et climatiques. Un modèle conceptuel de la structure et de la dynamique des chaînes trophiques du Golfe du Saint-Laurent est élaboré dans le contexte d'océanographie des pêches où la variabilité du recrutement de certaines populations de poissons du Golfe semble dépendre de la nature de la chaîne alimentaire à laquelle ces populations sont associées.

Introduction

Traditionally, the Gulf of St. Lawrence (Fig. 1) has been a highly productive fishing zone which contributed initially to the "discovery" of Canada by the European fishermen during the sixteenth century and subsequently to the development of the economical and social life of Eastern Canada. During the last 40 yr the Gulf has sustained a high level of exploitation for several commercially important species of fish and crustaceans yielding between 300 000 and 400 000 t • yr^{-1}. Since the establishment of the 200-mile limit zone in 1976, the relative importance of the Gulf in terms of total fish landings in Eastern Canada has however slightly declined from 40%

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[1] This paper forms part of the Proceedings of a Workshop/Symposium held at the Maurice Lamontagne Institute, Mont-Joli, Quebec, 14–17 March 1989.

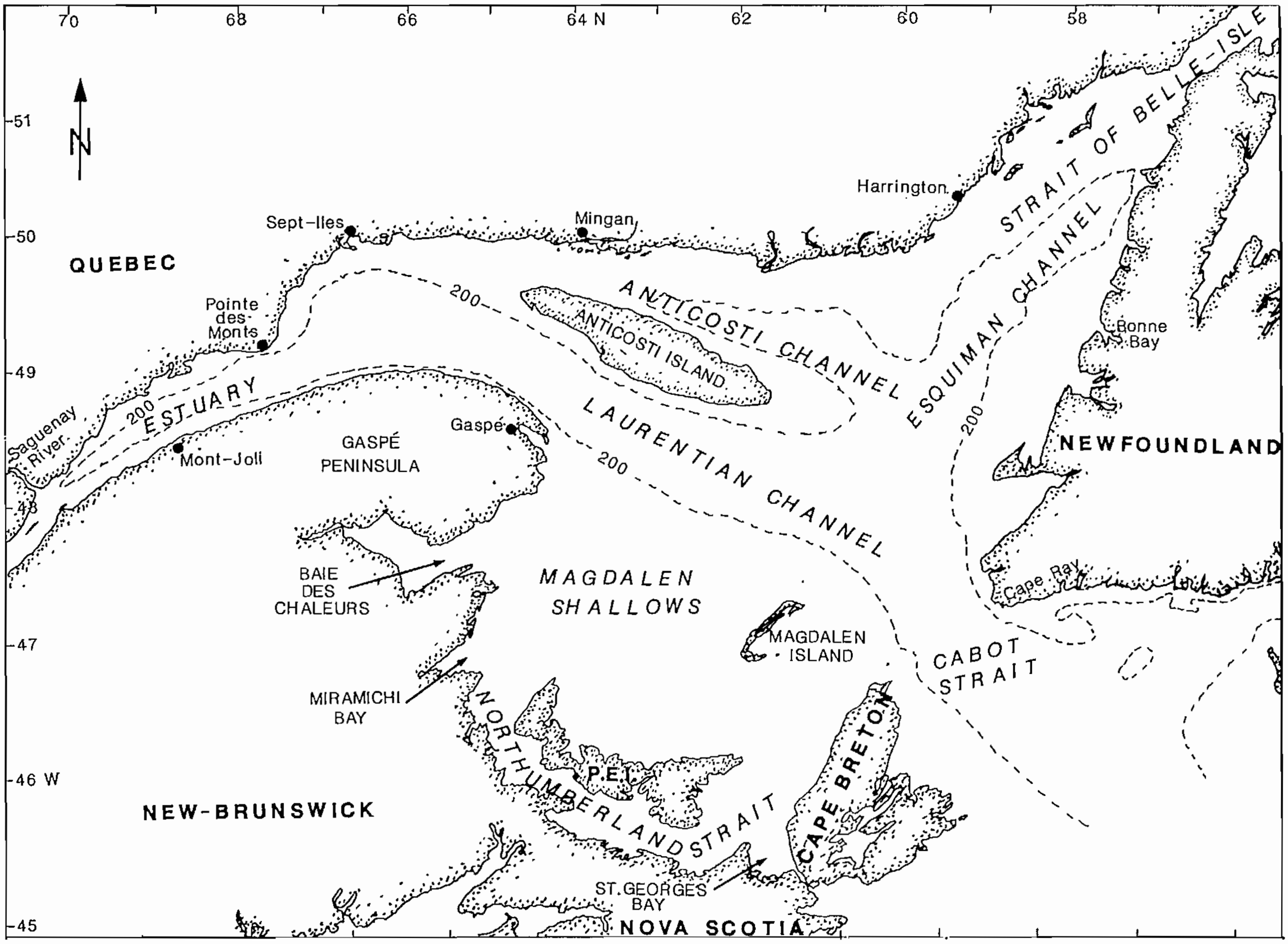

FIG. 1. The Gulf of St. Lawrence, with reference to locations mentioned in the text.

in early 70's (Dunbar 1977; Dickie and Trites 1983) to about 20% in recent years (Chadwick and Sinclair, 1991). The high level of fish exploitation in the Gulf of St. Lawrence has often been assumed to reflect the high productivity of Gulf waters at all trophic levels. This implicit assumption is central to the history and development of biological research realized in the area to date.

The first biological investigation in the Gulf of St. Lawrence was the Canadian Fisheries Expedition (1914–1915) which, under the direction of the Norwegian scientist Johan Hjort, proposed to "collect a quantity of material which would serve to elucidate both the conditions with regard to marine currents and the character of the fauna in the Gulf of St. Lawrence" (Hjort 1919, p. xvii). The most important contribution of this expedition, which surveyed 23 stations in the Gulf on two occasions during summer 1915, was the recognition that the Gulf of St. Lawrence has distinct hydrographic and biological features relative to the adjacent Atlantic waters (Hjort 1919). Given the objectives and the questions addressed at that time and the rapidity with which data were treated and published, the Canadian Fisheries Expedition provided highly valuable information on hydrography, plankton and fisheries and can be considered as a "scientific success", despite the limited temporal and spatial coverage achieved. Unfortunately, and despite Hjort's hope that "*the work would pave the way for further research*" (p. xxi), research activity in the Gulf was somewhat neglected in the following years and really began only after the Second World War (Fig. 2). As discussed later in this review, several subsequent research programs conducted in the Gulf have collected a large amount of material which, for various reasons, has not

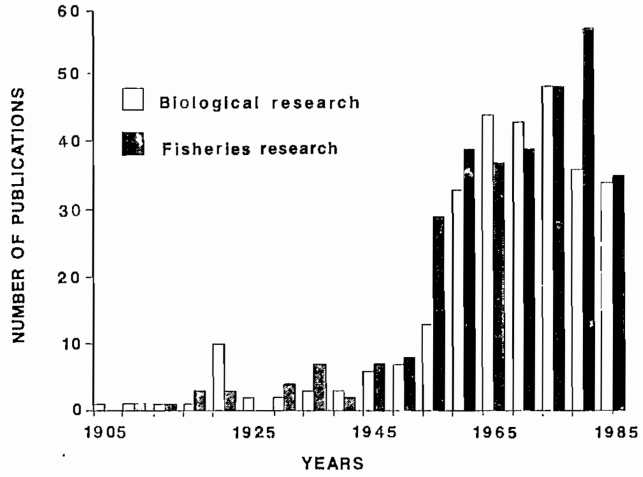

FIG. 2. Number of publications in biological oceanography and in fisheries research conducted in the Gulf of St. Lawrence to date.

been fully analyzed nor yielded scientific information as exhaustive as expected.

Research in the Gulf was stimulated by the development of programs sponsored by the Fisheries Research Board of Canada from the St. Andrews Biological Station and by the creation of the Bedford Institute of Oceanography (BIO) in Halifax in 1962. Research activities conducted primarily in Baie-des-Chaleurs during the mid-60's by scientists from Laval University and the large-scale International Biological Program (IBP) in 1969–72 under the supervision of Dr. D.M. Steven from McGill University have largely contributed to the peak in scientific literature on the biological oceanography in the Gulf between 1970 and 1980 (Fig. 2). The decline since 1980 reflects a regional shift of research activities by scientific staff from the BIO and St. Andrews laboratories to new programs within the Canadian offshore waters extending to the 200-mile limit zone.

For the Gulf of St. Lawrence, the significant positive correlations observed between freshwater runoff and fisheries landings (Sutcliffe 1972, 1973) have been interpreted as evidence for the "linear food chain hypothesis" where increased organic production at lower trophic levels may enhance productivity at higher levels. However, even if the Gulf appears to be very productive at lower trophic levels (Steven 1974, 1975; Dunbar 1977, 1980; Dickie and Trites 1983), the biomass and production of higher trophic levels (fish and crustaceans) in the Gulf are not significantly higher than contiguous shelf waters (Sinclair et al. 1984, 1986). It has been therefore postulated that the interannual variability in fisheries production for the Gulf *may not be* related to trophic dynamics (Sinclair et al. 1986). These two contrasting views of the potential link in production and energy transfer among trophic levels highlight the necessity to better understand the structure and the dynamics of the constituents of biological communities in the area, and not simply restrict the analysis to "state variables" (e.g. biomass, production) of the ecosystem.

Understanding the biological productivity of marine systems is fundamental to biological oceanographic research on the transfer of carbon through the food web. The flux of carbon in the upper oceans is mainly controlled by the physical, chemical and biological processes and it is recognized that the size structure of biological community and the coupling efficiency between the different trophic levels may play an important role in regulating production of various size groups of organisms. This is particularly relevant given that the classical concept of a phytoplankton-macrozooplankton-fish linear food chain with 10% biomass conversion efficiency at each step (Ryther 1969; Steele 1974) is now considered to be inadequate to explain the dynamics of energy and nutrient flow in the ocean (Goldman and Caron 1985; Jones and Henderson 1987). The new concept of "microbial loop" which postulates that a fraction of the carbon fixed by primary producers is taken by bacteria and heterotrophic flagellates before returning to the main food chain (Fenchel 1982; Azam et al. 1983), may contribute substantially to the carbon cycling (Nielsen and Richardson 1989).

We believe that the food web structure and the existing trophic interactions must be properly defined in order to elucidate potential links between organic production at the *ecosystem level* and recruitment variability at the *population level.* This complex problem represents a major issue for biological oceanographic research in general and for the Gulf of St. Lawrence in particular.

In this paper, we first synthesize, based on data available in literature, the present knowledge on the biological oceanography of the Gulf of St. Lawrence to tentatively describe the nature and dynamics of the planktonic communities. The gaps in actual information are pointed out. We then suggest new research lines to increase our understanding of the trophic dynamics and their effects on the renewable resources in the area. Although we recognize that a benthos-plankton coupling probably exists in the Gulf (Hargrave and Phillips 1986), our analysis is restricted to the pelagic ecosystem and the ecology of benthic communities is not reviewed. A more complete list of references concerning the biological oceanography and fisheries in the Gulf is presented elsewhere (St-Pierre and de Lafontaine 1991).

The lower St. Lawrence Estuary, which can be considered as part of the Gulf, will not be included in the present review because several aspects of its biological oceanography have been recently reviewed (Therriault et al. 1990; Runge and Simard 1990; de Lafontaine 1990).

The Gulf of St. Lawrence

The Gulf of St. Lawrence is a triangular-shaped semi-enclosed sea of about 200 000 km^2 (Fig. 1). Two connections with the external Atlantic Ocean exist: the Cabot Strait, 104 km wide and 480 m deep and the Strait of Belle-Isle, 16 km wide and 60 m deep. The Strait of Belle-Isle, despite its restricted water exchange, is an important migration route for salmon, seals and whales (Dunbar et al. 1980). The topography of the Gulf is characterized by two deep channels (Laurentian and Esquiman) with an average depth of 420 m, corresponding to nearly 50% of the total surface area. In the southwestern part, the Magdalen Shallows, a large and shallow (average depth 50 m) area, have always been a traditional fishing ground which yielded about 50% of the total fish landings in the Gulf (Dickie and Trites 1983).

The water column in the Gulf is characterized, during the summer, by a three-layer system which is atypical for north temperate areas (Bjerkan 1919; Tremblay and Lauzier 1940; Lauzier and Trites 1958). The *Surface Layer* of relatively low salinity (25–32 ‰) and warm temperature (reaching 20°C in the Magdalen Shallows) varies between 10 and 20 m in thickness. The *Intermediate Layer* centered at approximately 80 m and extending to as deep as 150 m, consists of very cold (-0.5 to $+1$°C) and moderately saline (31.5–33 ‰) waters and is formed *in situ* by winter cooling processes (Forrester 1964). The *Deep Layer* fills the deeper parts of the Laurentian and Esquiman channels and is characterized by higher temperatures (up to 6°C) and salinities (around 34.6 ‰). During the winter, the surface and intermediate layers mix and form a single layer extending down to 150 m with temperature as low as -1.7°C. Summer-winter differences are insignificant for the deep waters, which comprise about 45% of the total water volume of the Gulf (Lauzier and Bailey 1957; Trites 1971). The Gulf of St.

Lawrence represents the most southerly region in the northern hemisphere where sea ice occurs. Ice covers nearly 100% of the area in February (Dunbar 1977). The ice-free period extends from mid-April to early-December.

The Gulf is subjected to a large annual freshwater input of about 424 km^3 (Sutcliffe et al. 1976; Bugden et al. 1982), most of which (75%) originates from the St. Lawrence River system. The residence time of water is between 200 and 500 d and most of the water exchange is through Cabot Strait (El-Sabh 1977; Bugden et al. 1982). The oxygen saturation levels at a depth of 150 m decrease from 60% near Cabot strait to 40% and less at the mouth of the St. Lawrence Estuary (Dunbar 1977; Pocklington 1986). The deep layer is therefore oxygen poor and this depletion resulting from local oxidative processes (including respiration and detritus breakdown) is related to the low (25%) export rate of organic matter from the Gulf (Pocklington 1986).

Bugden et al. (1982) concluded that, from a physical oceanographic point of view, the Gulf of St. Lawrence can be considered as a different ecosystem within which the dynamics may be controlled, to a large extent, internally rather than by influences of large-scale oceanic processes. The internal physical conditions of the Gulf may govern the size structure of plankton communities and affect the links among the food web and the population dynamics of exploitable resources. The significant correlation between St. Lawrence river runoff and American lobster (*Homarus americanus*) landings with an appropriate lag (Sutcliffe 1972, 1973; Drinkwater and Myers 1987) contributed to support the hypothesis that recruitment variability in Gulf populations may be strongly regulated by local environmental variability transmitted throughout the food chain. The variability in recruitment and year-class strengths of Gulf cod stocks which are not synchronous with fluctuations of other cod stocks along the western Atlantic coast (Martin and Kohler 1965; Koslow 1984; Koslow et al. 1987) also suggests that Gulf fish stocks are regulated by "internal" factors (Bugden et al. 1982).

The distinct character of the Gulf does not imply that it is an homogeneous system and it has long been recognized that this inland sea represents a composite of different "regions". Natural divisions within the Gulf were first established in 1953 by the International Commission for Northwest Atlantic Fisheries (ICNAF/NAFO) which defined three fishing zones (subareas 4T, 4R & 4S, Fig. 3a) in relation to the distribution and migration patterns of gadoids (in particular cod) stocks apparently different on both sides of the Laurentian Channel (R. Halliday, Fisheries and Oceans Canada, B.I.O., Halifax, pers. comm.). Based on IBP results, Steven (1971, 1974) divided the Gulf of St. Lawrence into four zones characterized by different levels of production and dynamics (Fig. 3b). More recently, Dunbar et al. (1980) have described 11 biogeographic subregions representing natural ecological patterns in the distribution of organisms at various levels of the food web (Fig. 3c). However, the degree of similarity among the regions could not be quantified and the trophic relationships of the food webs were not resolved.

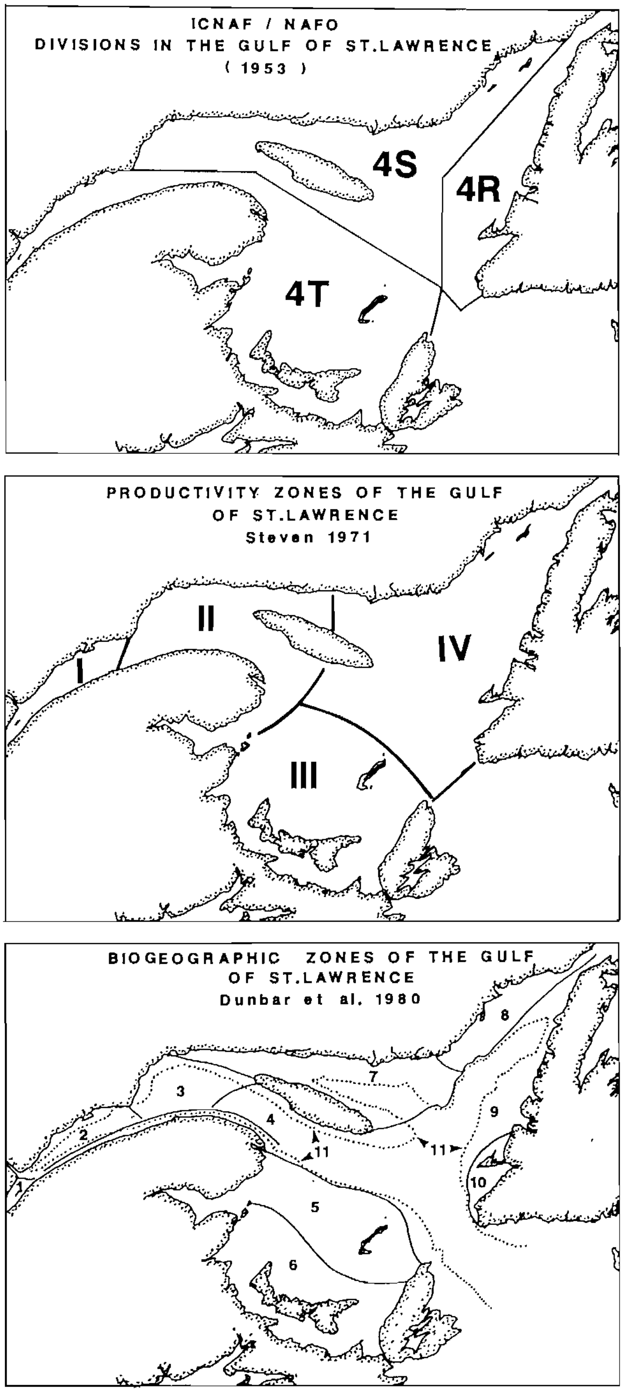

FIG. 3. Subdivisions in the Gulf of St. Lawrence: (a) ICNAF/NAFO fishing zones defined in 1953, (b) biological production zones defined by Steven (1971), (c) biogeographic zones defined by Dunbar et al. (1980).

The exact nature, the role and the dynamics of these geographic regions on the reproduction, recruitment and maintenance of exploitable resources in the Gulf remain however speculative. Do these regions or zones represent different community structures and different food webs? Do these communities interact, and if so, how and to what extent? What are the trophic links between the various components within the different communities? How may these trophic links lead to variable recruitment patterns and mechanisms?

In an attempt to answer some of these questions, we divided the Gulf into four "regions" (Fig. 4) based on the general topography and the physical oceanographic regimes of the Gulf. The first region (I) is the northwestern part characterized by a permanent cyclonic gyre (El-Sabh 1976). The Gaspé Current flowing along the north shore of Gaspé peninsula determines region II which is separated from region I by a frontal system (Tang 1980; Mertz et al. 1988). The boundary between the Magdalen Shallows (region III) and the offshore deep waters of the northeastern Gulf (region IV) was established along the 200 m isobath. While such a partitioning may be simplistic and somewhat arbitrary, it does, however, share some common features with the various schemes presented in Fig. 3. Our main objective was to use this partitioning as a geographical framework to evaluate the general hypothesis that the Gulf of St. Lawrence is not an homogeneous biological ecosystem and that amalgations of results from various parts of the Gulf may lead to erroneous interpretation of the community structure and the biological dynamics of the pelagic food webs (Paine 1988).

Nutrients, Phytoplankton, and Primary Production

Few studies of nutrients and phytoplankton dynamics have been undertaken in the Gulf of St. Lawrence and these components of the food web are poorly described. Gran (1919) presented the first descriptive investigation of the phytoplankton species composition in the Gulf. The first estimates of primary production were obtained by Legendre and Watt (1970) in Baie-des-Chaleurs using data collected in 1956. Between 1969 and 1972, the Canadian Contribution to the International Biological Program (IBP) covered more than 600 sampling stations in the Gulf of St. Lawrence (Steven 1974) and accumulated an important data set on the physical characteristics, nutrient concentrations, phytoplankton biomass and productivity, and zooplankton displacement volume and dry weight estimates. Recent research programs on the pelagic and benthic food webs in St. Georges Bay, in the southwestern Gulf, were summarized in Hargrave et al. (1985) and Hargrave and Phillips (1986).

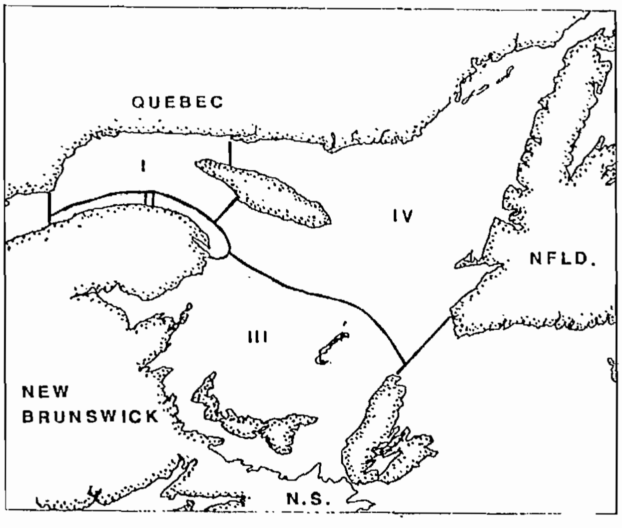

FIG. 4. Divisions in the Gulf of St. Lawrence used in the present paper (see text for criteria).

Nutrients

Nutrient concentrations in the deep layer of the Gulf are approximately three times higher than those at similar depths in the North Atlantic outside the Gulf (Coote and Yeats 1979). The observation that the concentrations of nutrients at depth (below the surface layer) increase from Cabot Strait toward the head of the two main channels in the Gulf led Coote and Yeats (1979) to suggest that the Gulf acts as a trap for nutrients. The combination of water circulation and nutrient regeneration processes would result in the cycling of nutrients between the intermediate layer and the surface layer (Bugden et al. 1982). However, the potential link between this large pool of nutrients at depth and the high biological productivity of Gulf waters remains speculative.

Studies of the processes of nutrient supply within the surface layer in the Gulf have led to contradictory interpretations. Steven (1974) first proposed the concept of a "nutrient pump" at the head of the Laurentian Channel, where nutrients from the intermediate layer are upwelled to the surface and advected downstream along the Estuary to stimulate production within the Gulf. Therriault and Lacroix (1976) further demonstrated that nutrient enrichment of the estuarine surface layer ("nutrient pump") is linked to intense vertical mixing driven by high amplitude internal waves. This nutrient source by upwelling would represent more than 75% of the total nutrient supply to the euphotic zone in the estuary, the remainder (<25%) being of freshwater origin (Greisman and Ingram 1977). In a subsequent paper, Sinclair et al. (1976) argued that estuarine nutrient transport could not account for the high levels of primary production in the Gulf as reported by Steven (1974). Apart from the fact that Steven's (1974) production rates were apparently overestimated (Sinclair et al. 1976; Sévigny et al. 1979), Sinclair et al. (1976) concluded that the magnitude of the nutrient pump and the estuarine nutrient transport have an impact on a much smaller geographical area (possibly only the Gaspé current area) than originally assumed by Steven (1974) and that additional sources of nutrients should be considered. Besides, Levasseur and Therriault (1987) have shown that simultaneous exhaustion of nitrate ans silicate can occur within the St. Lawrence Estuary following a bloom event.

Vertical transport at the centre of the relatively permanent cyclonic gyre west of Anticosti Island was suggested to be a local source of nutrients for primary production in the area (El-Sabh 1976). This hypothesis was dismissed by Sévigny et al. (1979) who indicated that, at least during the summertime, the gyre surface layer is nutrient poor due to the presence of a strong and shallow stratification preventing nutrient enrichment from the deep layer. However, local nutrient supply may contribute to high production and biomass of phytoplankton observed within the gyre during the spring when stratification is weak (de Lafontaine 1979).

Nutrient dynamics over the Magdalen Shallows and other coastal zones in the Gulf are also unresolved. Nutrients are rapidly depleted following the spring bloom and nitrogen appears to be the limiting factor for phytoplankton growth in the southern Gulf (Hargrave et al. 1985). Vertical diffusion of nutrients cannot contribute a significant portion of the nutrient required for primary production and *in situ* nutrient regeneration by microplankton and bacteria must occur (Hargrave et al. 1985). Rapid depletion of nutrients after the spring bloom has been also observed within Baie-des-Chaleurs (Lambert 1982) where the surface cyclonic circulation could induce local nutrient upwelling by the compensating intrusion, at depth and along the north shore, of colder and more saline waters (Legendre 1987). Benthic nutrient regeneration may also be an additional supply of nutrients to waters over the Magdalen Shallows when stratification is weak (Hargrave and Phillips 1986) and possibly in other well-mixed areas. These hypothetical sources of nutrients must be adequately investigated in the future.

Phytoplankton Composition and Dynamics

Gran (1919) observed that 57 of the 96 species of phytoplankton collected in the Gulf of St. Lawrence were diatoms and all the species of common occurrence were well known from the North European waters. However, the low number of samples was insufficient to describe the phytoplankton dynamics in the Gulf. In 1954–55, Brunel (1962) described the taxonomy of phytoplankton in Baie-des-Chaleurs and presented distribution maps for the main species. Very little information concerning the phytoplankton species composition has been extracted from the IBP program and the general species description still remains poorly documented for the Gulf of St. Lawrence.

Sévigny et al. (1979) showed that, during the summertime, the species composition and the cell size distribution is heterogeneous within the northwestern part of the Gulf. Flagellates and dinoflagellates dominate in the gyre area (region I) with more than 80% of the total biomass, whereas diatoms account for 70% in the Gaspé current system (region II) (Fig. 5a,b). This results in significant differences in the cell size distribution (Fig. 5c). Stations

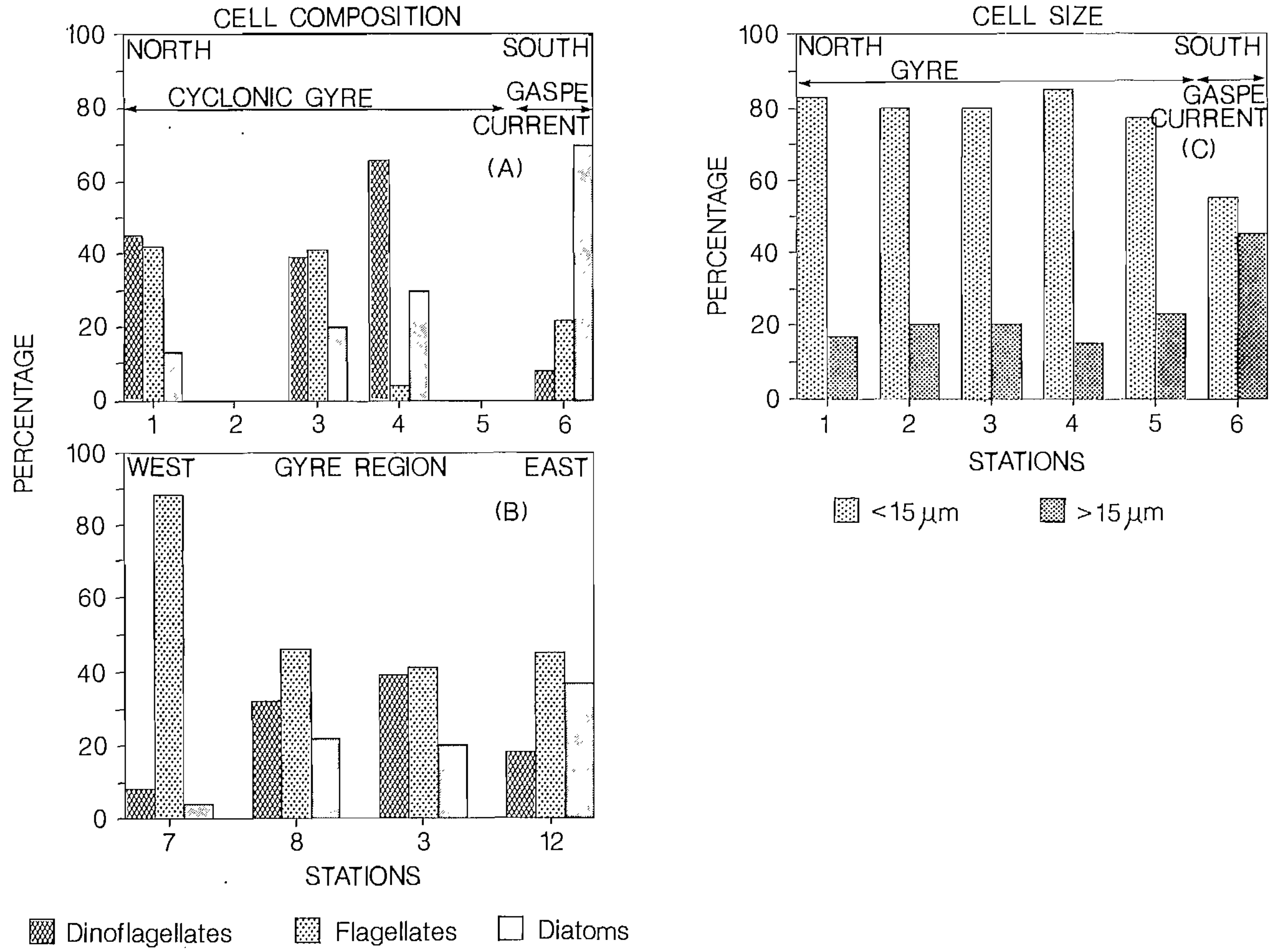

FIG. 5. Phytoplankton composition along a north–south transect (A) and a west–east transect (B) and cell size distribution along the north–south transect (C) in the northwestern Gulf of St. Lawrence during July 1976. Stations 1 to 5 are located in the cyclonic gyre system and station 6 is representative of the Gaspé Current system. Data from Sévigny et al. (1979).

located in the gyre contain a large proportion (80%) of particles less than 15 μm, whereas phytoplankton in the Gaspé Current consists of an equal proportion of particles bigger and smaller than 15 μm. Chlorophyll maxima occur near the surface at all stations.

Sévigny et al. (1979) concluded that the Gaspé Current and the Anticosti gyre represent two identifiable pelagic ecosystems: (a) the Anticosti gyre (region I) characterized by nutrient-limited phytoplankton growth, small flagellates, large copepod species, euphausiids and decapod larvae; (b) the Gaspé Current (region II) characterized by large-celled diatoms contributing to a large phytoplankton biomass, continuous high summer production and high growth rates suggesting locally active nutrient sources through entrainment and/or horizontal advection, small copepods and fish larvae. The gyre forms a relatively stable environment characterized by a considerable uniformity in plankton species composition and trophic level biomass. The relatively more dynamic nature of the Gaspé Current is probably responsible for the high and continuous levels of primary production within this region from April to October (Steven 1974). Subsequent sampling in the same area at different times of the year revealed that these two systems can be still distinguished, although phytoplankton biomass is much higher in the gyre than in the Gaspé Current during the spring period (de Lafontaine et al. 1981, 1984). The noticeable difference in cell size and herbivore size would imply that the phytoplankton–zooplankton link is quite different between the Gaspé Current and the northwest cyclonic gyre.

The community structure of phytoplankton in Baie-des-Chaleurs appears to be under the control of environmental factors such as nutrients, light and temperature (Legendre 1973). Due to local nutrient upwelling, daily rates of primary production and mean concentrations of chlorophyll *a* measured in the central part of the bay are relatively higher than those measured nearshore or over the Magdalen Shallows in the Gulf (Legendre and Watt 1970; Legendre 1971; Lambert 1982). Phytoplankton production is inversely related to the degree of thermal stratification in the bay and therefore declines throughout the summer (Legendre 1971). Following the spring bloom in early-May, chlorophyll *a* concentrations in Baie-des-Chaleurs decrease and are minimal in June, but increase from mid-July to September (Lambert 1982; de Lafontaine et al. 1984). Similarly, high levels of primary production and biomass are observed during the spring (April) in St. Georges Bay, southern Gulf (Hargrave et al. 1985). Both production and biomass in St. Georges Bay decrease to low levels in June, but gradually increase again between June and October due to local sources of nutrients (Hargrave et al. 1985). Import of nutrients is unlikely because high biological consumption in the spring results in low nutrient concentrations outside the bay.

During the summer, chlorophyll maxima are usually observed below the surface at or near the pycnocline within Baie-des-Chaleurs (Lambert 1982), St. Georges Bay (Hargrave et al. 1985) and over the Magdalen Shallows (Vandevelde et al. 1987). Using high frequency sampling during a 3-day period in August, Vandevelde et al. (1987) showed that the subsurface chlorophyll maximum consists mainly of small naked flagellates and is continuously observed in the lower part of the photic layer, at a depth just above the nutricline, corresponding to the maximum vertical stability of the water column. Their results demonstrated that temperature and *in vivo* fluorescence vary with a frequency of 16 h in association with internal waves. They concluded that the subsurface chlorophyll maximum results not only from environmental conditions favouring phytoplankton accumulation but also from active photosynthetic responses of phytoplankton. However, this work, conducted at a single station near the Magdalen Islands, did not resolve the spatial distribution of the phytoplankton composition and production.

Primary Production and Annual Cycle

As indicated by a comparison of daily production rates measured by various workers (Table 1), there is some uncertainty about estimates of primary production in the Gulf of St. Lawrence. Production rates measured over the entire Gulf (IBP results) were found to be highest in the northwest part and in the Gaspé current (Steven 1974, 1975; Dunbar 1977). However, Sinclair et al. (1976) and Sévigny et al. (1979) reported primary production values an order of magnitude lower than the values measured by IBP in the same area (Steven 1974). The reason for this discrepancy is unknown. Primary production in St.

TABLE 1. Comparison of daily production rates (mg C • m^{-2} • d^{-1}) measured in various studies in different regions of the Gulf.

Area	Apr.	May	June	July	Aug.	Sept.	Oct.	Source
Main Gulf	1600	790	870	930	850	500	330	Steven (1975)
Gaspé Current	2940	1640	2880	1020	1760	380	280	Steven (1975)
Anticosti gyre				75				Sévigny et al. (1979)
Gaspé Current				500				" "
Baie-des-Chaleurs (mouth)		1400	850	350	700			Legendre (1971)
Baie-des-Chaleurs (inside)		1320	940	650	700			Legendre (1971)
St. Georges Bay	371	153	223	290	490	517	403	Hargrave et al. (1985)

Georges Bay during the summer (Hargrave et al. 1985) also appeared to be lower than those observed in other areas in the Gulf (IBP results), although this may be partially related to the smaller depth of integration (15 and 30 m for St. Georges Bay and 50 m for the IBP stations). Although midsummer data from Baie-des-Chaleurs are relatively high, they are lower than those reported by Steven (1975) for the main Gulf area. Due to the complete lack of winter data, total annual phytoplankton production cannot be estimated. Moreover, it is premature, based on actual estimates, to conclude that the Gulf waters are more productive than adjacent oceanic systems.

Except for the temporal series in coastal waters (Bonne Bay: Spence and Steven 1974; Baie-des-Chaleurs: Lambert 1982; St. Georges Bay: Hargrave et al. 1985), there is no report on the seasonal distribution and variability in phytoplankton for the open Gulf of St. Lawrence. Using the results of the IBP program (Steven et al. 1973a,b,c), we therefore attempted to describe the seasonal evolution of water stratification (delta sigma-*t* between 0 and 75 m), nitrate concentrations (average over 50 m), phytoplankton biomass (chlorophyll *a* integrated over 50 m) and zooplankton biomass (dry weight integrated over the entire water column) at various stations distributed in five regions of the Gulf: the northeastern Esquiman Channel, the Jacques Cartier Passage, the northwest cyclonic gyre, the Gaspé Current and the Magdalen Shallows in southern Gulf (Fig. 6 and 7). Calculations were made by averaging data gathered over different years at seven stations selected within each region. Despite this bias, it is interesting to note that variability between years and among stations within specific region is quite small. This is true for all regions over the entire Gulf.

Stratification (delta sigma-*t*) shows similar pattern in all regions (Fig. 6). In early April, the stratification is generally low, but increases gradually as a result of solar heating and freshwater runoff to reach a maximum in June and July followed by a decline at the end of August and early fall. Most stratified waters are usually found at stations within the Gaspé Current which receives large freshwater input from the estuary.

Nutrients in the upper water column are generally low throughout most of the year indicating a rapid depletion in early spring, except for the Gaspé Current area where high concentrations are reported until mid-May (Fig. 6). The seasonal evolution of nutrients varies among the different areas in relation to the spring bloom of phytoplankton (Fig. 6, 7). The onset of the spring bloom clearly exhibits a temporal gradient among the various parts of the Gulf (Fig. 7). The northeastern Gulf shows a very low phytoplankton biomass at all sampling times with no apparent bloom. However, the decreasing values in early April suggests that the phytoplankton bloom has probably been missed and should occur earlier at the end of March or beginning of April immediately after the ice melts. In the Jacques Cartier Passage, the end of the spring bloom is noted in early-April followed by low phytoplankton biomass during the summer months. The gyre area supports an active bloom in mid-April whereas, in the southern part of the Gulf, the bloom is delayed until the end of April. It should be remembered that the southern Gulf is covered with ice until mid-April. In each region, the phytoplankton biomass stays relatively low during the summer and there is no evidence of a definite autumn bloom. The Gaspé current differs significantly from the other areas. The bloom starts at the end of May and persists till the end of June and a second peak is noted at the end of August. The phytoplankton biomass in the Gaspé Current remains relatively high during all summer months.

We conclude from these results that the timing of the phytoplankton bloom is not synchronous over the entire Gulf of St. Lawrence. Although the paucity of observations during winter precludes any firm conclusion, the regional difference in phytoplankton dynamics is probably related to the establishment of stratification following the ice break-up and the timing of freshwater runoff. The low concentrations of nutrients measured in each region (except the Gaspé Current) suggest that the spring bloom was probably very active before sampling began (Day 100 : April 10). As suggested by Steven (1974, 1975), the bloom within the Gaspé Current may be retarded by runoff related advection.

Zooplankton and Secondary Production

The first studies of zooplankton in the Gulf were undertaken by Willey (1919) and Huntsman (1919, 1921a,b), who analyzed samples collected during the Canadian Fisheries Expedition. In 1923, Huntsman and coworkers examined zooplankton composition in late summer in the Strait of Belle-Isle as part of a study of the circulation patterns in this region (Pinhey 1926, 1927; Huntsman et al. 1954). Between 1931 and 1935, samples collected in the Strait of Belle-Isle and the eastern Gulf were analyzed for interannual differences in displacement volumes and in composition and abundance of pelagic tunicates as indicators of variability in the influx of the Labrador Current (Frost et al. 1933, 1934; Thompson and Frost 1935, 1936; Frost 1937). Between 1940 and 1960, the Station de Biologie Marine de Grande-Rivière focused on describing distribution and abundance of zooplankton in Baie-des-Chaleurs and adjacent fishing banks area (e.g. Lacroix and Filteau 1969, 1970, 1971). In the 1970's, the IBP surveys provided measures of zooplankton displacement volume and dry weight (Steven 1974), while productivity, biomass, and composition of zooplankton were also investigated in St. Georges Bay, southern Gulf (e.g. Lambert 1980; Hargrave et al. 1985). Recently, research on zooplankton distribution and productivity in the Estuary and northwest Gulf has been initiated by researchers at the Maurice Lamontagne Institute, Mont-Joli.

While gaps in our knowledge of zooplankton in the Gulf are large, the above data nevertheless allow some inferences to be drawn about the composition of zooplankton communities in different regions of the Gulf and their population dynamics and potential interactions with higher trophic levels.

Zooplankton Composition

As typically observed in north temperate oceans, copepods usually constitute more than 75% of the total number of animals in plankton net catches from the Gulf

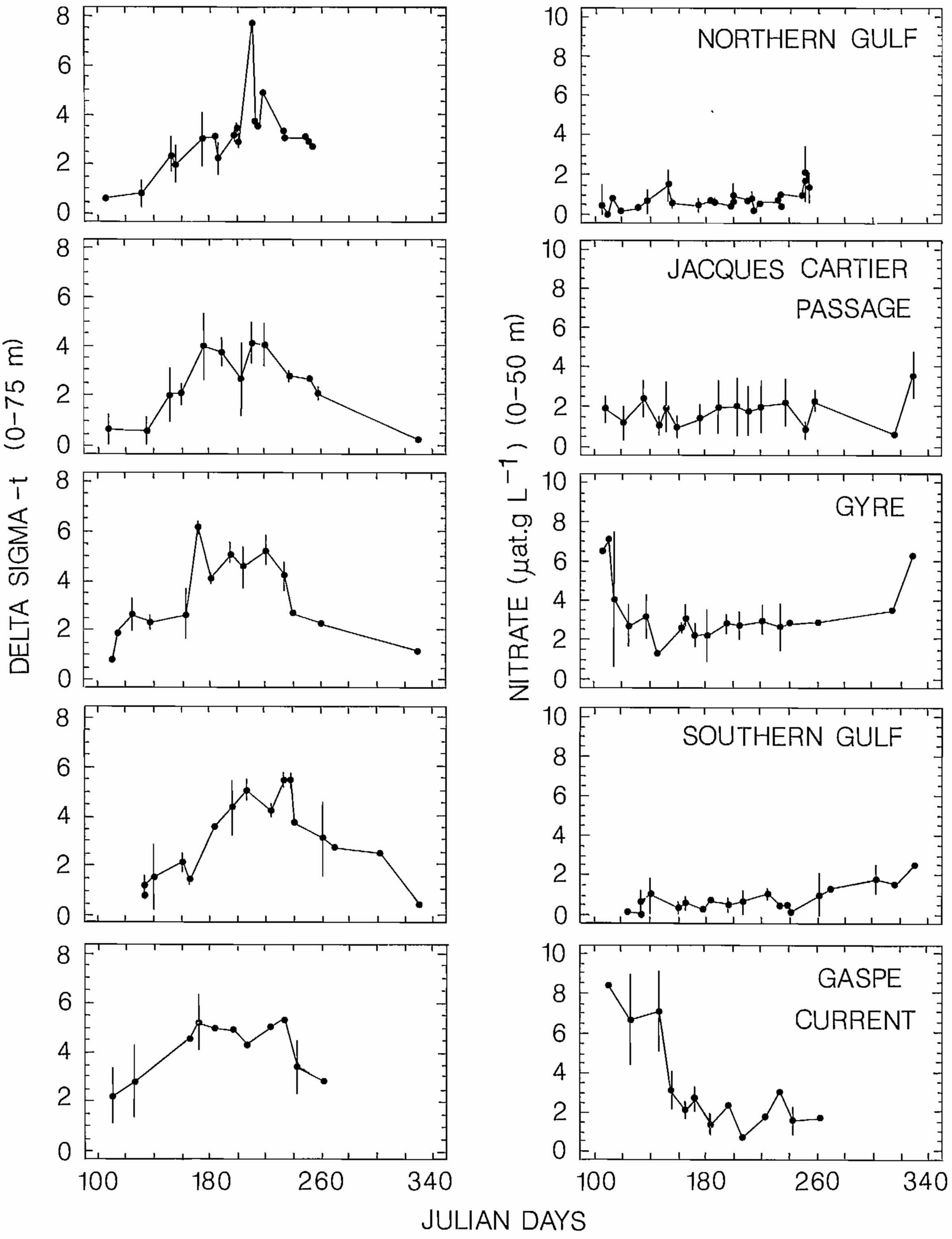

FIG. 6. Temporal variation in water stratification (delta sigma-*t* between 0 and 75 m) and nitrate concentrations (averaged between 0 and 50 m) in five regions of the Gulf of St. Lawrence. Data obtained from IBP results (Steven et al. 1973a,b,c).

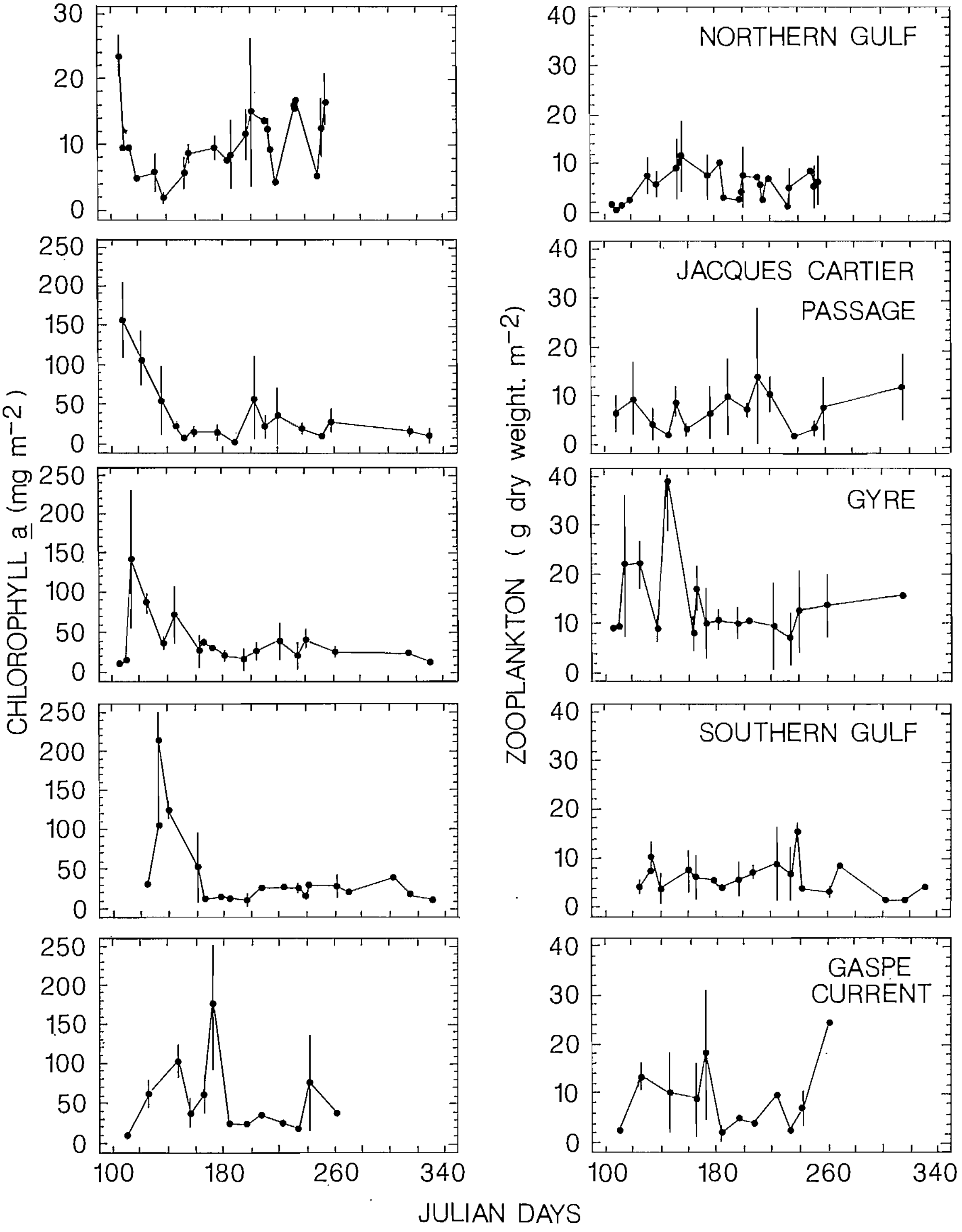

FIG. 7. Temporal variation in phytoplankton biomass (mg chlorophyll *a* m^{-2}) and zooplankton biomass (g dry weight • m^{-2}) in five regions of the Gulf of St. Lawrence. Data obtained from IBP results (Steven et al. 1973a,b,c).

(Table 2). Larvaceans, cladocera, and euphausiids make up most of the remaining number, along with fish eggs and meroplankton which are seasonally abundant in Baie-des-Chaleurs and St. Georges Bay, respectively. Although less important numerically, amphipods, chaetognaths, pteropods, and jellyfish are regularly present and may occasionally contribute a large fraction of the zooplankton biomass.

While the numerical predominance of the copepoda is undeniable, the nets used in most of the studies (usually 50 cm diameter with a mesh size >300 μm) capture inefficiently or not at all the microzooplankton, such as ciliated protozoans and planktonic larvae, and the macrozooplankton, like euphausiids, jellyfish, and ichthyoplankton. In the northern Gulf, euphausiids (*Meganyctiphanes norvegica, Thysanoessa raschii,* and *T. inermis*) form dense aggregations with mean densities of 0.5–2.4 g dry weight m^{-3} and values up to 7 g dry weight m^{-3} and 53 g dry weight m^{-2}, especially along the 100 m isobath of the northwest Laurentian Channel and in the Jacques Cartier Passage (Sameoto 1976, 1983; Berkes 1976, 1977; Simard et al. 1986). These euphausiid aggregations are probably important nutritional sources for adult fish and baleen whales in the Gulf, particularly the blue whale, for which euphausiids are the principal prey (Mitchell 1975). In the southern Gulf, Harding et al. (MEL 1980) noted that tintinnids and bivalve larvae were abundant in 66–125 μm and 125–250 μm size-fractionated zooplankton samples taken with a fine mesh net (57 μm). Cladocerans, cyprid and bivalve larvae were present in the 250–509 μm size class. Steven (1974) noted that larval echinoderms, bivalves, and gastropods were abundant in the summer catch with a 230 μm mesh net in the Magdalen Shallows. Thus meroplankton, which predominates in May–June (due mainly to the presence of cyprid larvae), may be more prominent than represented in Table 2 during the summer on the Magdalen Shallows. In addition, Medusae were presorted from the catch and therefore are not accurately represented in the data from St. Georges Bay (T. Lambert, BIO, Halifax, pers. comm.). Jellyfish swarms are probably a very important component of the summer community in the Magdalen Shallows and southern Gulf area. Thus, there is not enough known about the ecology of jellyfish and the smaller zooplankton in the Gulf to make specific statement about the relative role of these groups in the food web interactions in the different regions of the Gulf.

TABLE 2. Relative composition by number (percent; x denotes presence) of major zooplankton taxa found in net tows in the Baie-des-Chaleurs/Fishing Banks (333 μm Hensen net towed vertically from the bottom to the surface: Brunel 1959) and in St. Georges Bay (405 μm mesh 0.5 m ring net towed horizontally at 10 m; Lambert 1980).

	May–June	July	Sept.
	Baie-des-Chaleurs/Fishing Banks		
Copepoda	75	86	90
Large eggs	13	4	x
Larvaceans	3	1	6
Cladocera	x	6	x
Euphausiids	1	2	2
Meroplankton	x	x	x
Coelenterates	x	x	x
Chaetognaths	x	x	x
Polychaetes	1	x	0
Other	6	x	x
	St. Georges Bay		
Copepoda	42	88	73
Large Eggs	2	0	0
Larvaceans	0	0	0
Cladocera	0	8	22
Euphausiids	6	2	1
Meroplankton	50	1	3
Coelenterates	0	1	1
Chaetognaths	0	0	0
Polychaetes	0	0	0

Studies of zooplankton in the Gulf have concentrated on copepoda and involved considerable sampling effort. The data from this research are sufficient to show differences in the composition of copepods species among regions. Data in Willey (1919) clearly indicated a pronounced shift in species composition of copepods between waters overlying the Laurentian Channel in the north and the Magdalen Shallows in the south (Fig. 8a). In the deep Laurentian Channel, species of *Calanus* (probably a mixture of *C. finmarchicus* and *C. glacialis*) overwhelmingly dominated the catch of copepods in the upper 130 m or so of the water column. In other deeper tows in the same area, the much larger *C. hyperboreus*, which is usually considered to be of Arctic origin (Conover 1988), frequently constituted more than 50% of the total number of copepods captured. At a much shallower (32 m) station near the mouth of Miramichi Bay in the southern Gulf, *Calanus* formed a low proportion (20%) of the community, which was dominated instead by small species of the genus *Temora* and *Tortanus*.

However, the very large mesh size (650 μm) used during the Canadian Fisheries Expedition may have allowed small zooplankton species to escape. Data collected by Filteau (1951) and Filteau and Tremblay (1953) using a 203 μm mesh net at a single station located between the Laurentian Channel and the mouth of Baie-des-Chaleurs (Fig. 9a) indicate that *Oithona* (nominally *O. similis*), a small cyclopoid species with a body size two orders of magnitude less than *Calanus, Pseudocalanus* and *Temora longicornis* are relatively more numerous than in the earlier study, but are still less than the proportion of the *Calanus* species. The relative proportion of the different copepod species varies seasonally, shifting towards smaller species in late-summer. These results confirm that *Calanus* is the dominant constituent, certainly in terms of biomass and even numerically at certain times of year, of the copepod community in the Laurentian Channel region.

The copepod composition in St. Georges Bay, southern Gulf, is dominated by small species during the summertime (Fig. 9b: MEL 1980; Lambert 1980). There is also a seasonal succession from a spring community comprising principally *Temora longicornis* and a small

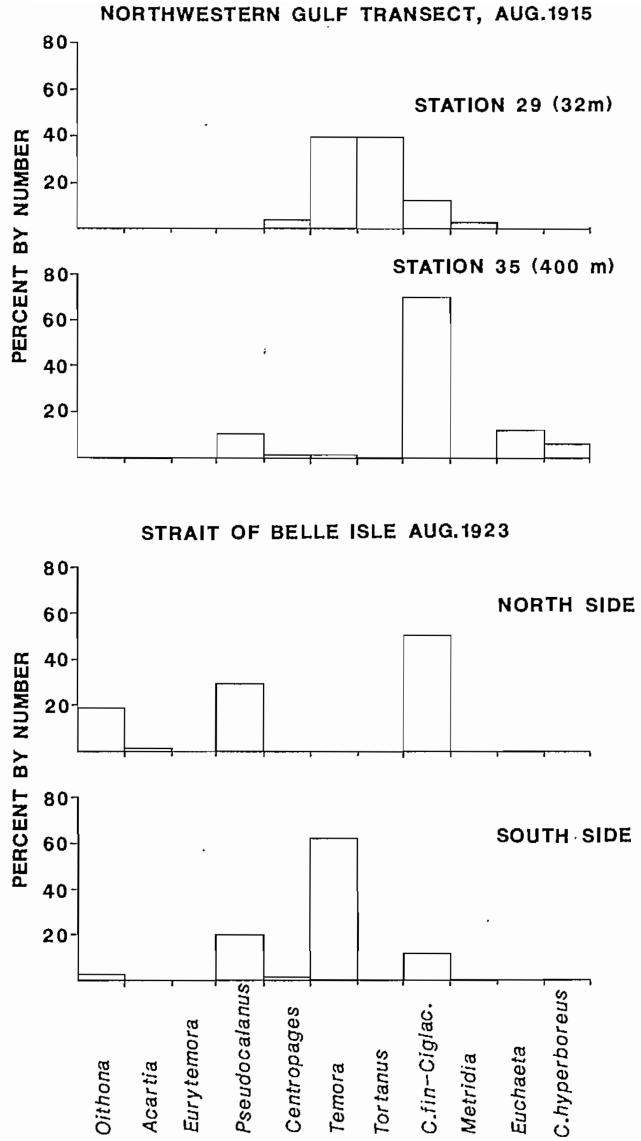

FIG. 8. Relative composition by number of copepod species at two stations along a transect in the northwestern Gulf (St. 29: near Miramichi bay; St. 35: over Laurentian Channel) in August, 1915 (650 μm mesh vertical net, Willey 1919) and in the Strait of Belle-Isle in August, 1923 (282 μm mesh net, Hunstman et al. 1954).

TABLE 3. Average body sizes of adult females of copepod species listed in Fig. 8–10.

Species	Prosome Length (mm)
Oithona similis	0.8
Acartia clausi	1.0
A. hudsonica	1.0
A. longiremis	1.1
Eurytemora affinis	1.1
Pseudocalanus sp.	1.2
Centropages hamatus	1.3
Temora longicornis	1.5
Tortanus discaudatus	2.1
Calanus finmarchicus	3.2
C. glacialis	3.6
Metridia longa	4.1
Euchaeta norvegica	7.0
Calanus hyperboreus	7.0

proportion of *Calanus* and *Pseudocalanus* species to a late summer community composed of species of *Centropages, Tortanus,* and *Acartia. Pseudocalanus* may be abundant in some years (MEL 1980) but *Calanus* is always rare during the summer months. The large mesh size (405–460 μm) used in these studies is likely to under-represent species on the smaller end of the spectrum, which would reinforce differences with the northern Gulf and other deep areas.

The copepod community structure can also vary within regions of the Gulf. In Baie-des-Chaleurs, for example, the local species assemblage in August changes from the mouth to the head of the bay (Fig. 10). Over the fishing banks area just outside the bay, the copepod community, as previously shown, is dominated by *Calanus, Pseudocalanus,* and *Oithona.* In the central section of the bay, *Calanus* is still present but the dominance shifts to *Temora. Oithona* and *Pseudocalanus* would have been undersampled because of the larger mesh (366 μm) used; however, the relative scarcity of *Pseudocalanus* cannot be attributed solely to this factor. In the shallow, estuarine portion of the bay at the mouth of the Restigouche River (Lacroix and Legendre 1964), *Acartia clausi* and *Temora longicornis* were very abundant and overwhelmingly dominant.

The reasons for shifts in zooplankton community structure within and among various regions in the Gulf are not precisely understood. In part, the relative composition of each area reflects the particular environmental conditions and the species-specific population growth rates in response to these conditions. Depth may be the most important environmental factor. Mortality rates of *Calanus* populations in the southern Gulf, for example, may be exceptionally high because the shallow depth prevents daytime vertical migration to a light level low enough to avoid visual predators (Frost 1988). The life history of some copepod species (e.g. *Centropages, Acartia,* and *Tortanus:* Uye 1985) includes a resting egg period during which eggs lay dormant on the sea floor, a strategy which may only be successful in the shallow southern Gulf. The Magdalen Shallows also supports a considerable benthic community (Hargrave et al. 1985) and consequently planktonic larval forms that are much less abundant in the deeper waters to the north.

The influence of temperature on zooplankton community structure must be also considered. For its latitude, the Magdalen Shallows in summer is unusually warm while the intermediate layer in the Laurentian Channel is unusually cold. Although the vertical distribution of *Calanus* in the Laurentian Channel is apparently not affected by the temperature in the intermediate layer (Willey 1919; Lacroix and Filteau 1970), the cold water may interfere with population growth rates of other species like *Temora* and *Centropages* that may be expected

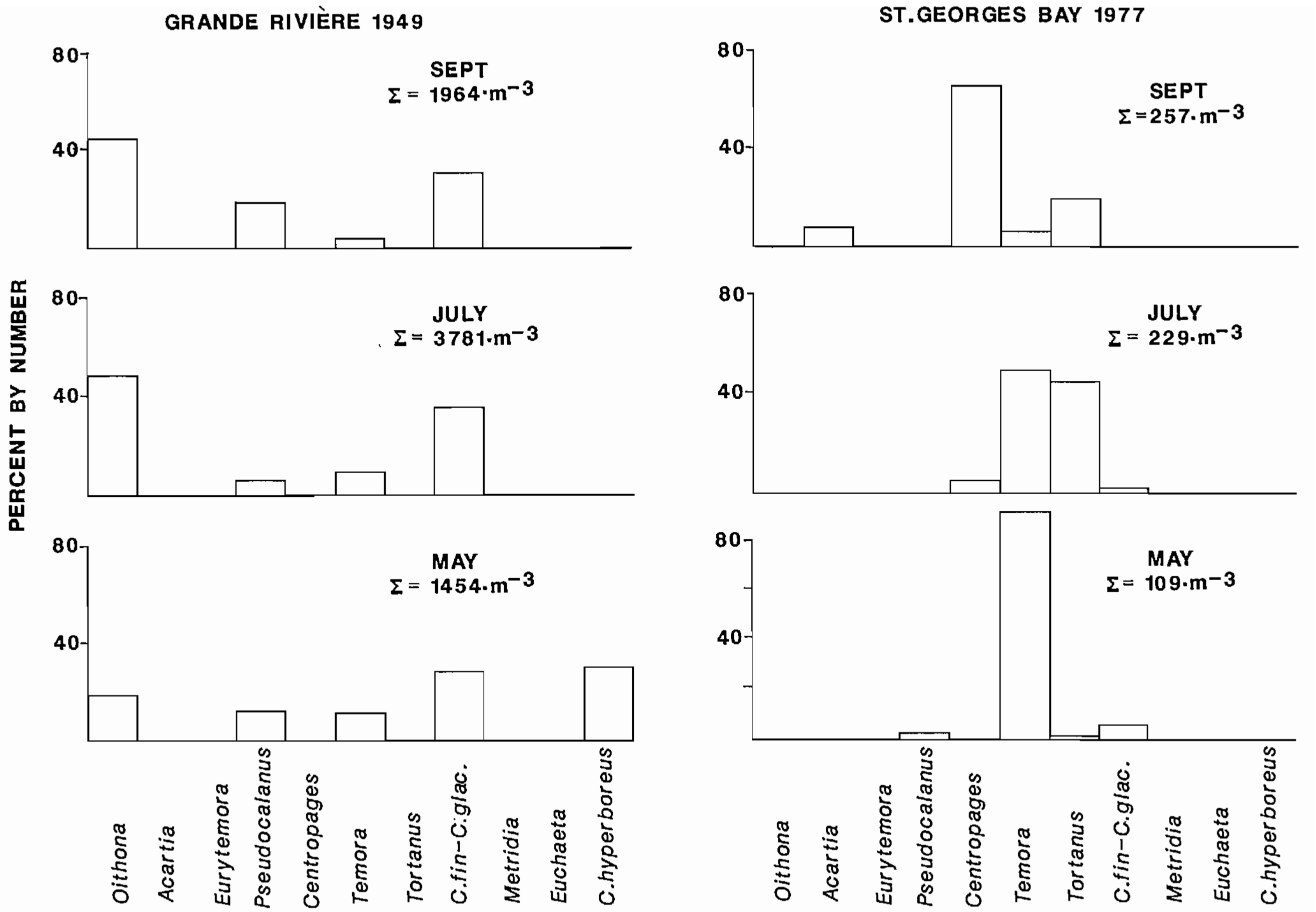

FIG. 9. Relative composition by number of copepod species at the Grande-Rivière station (Filteau 1951) and in St. Georges Bay (MEL 1980). Samples from Grande-Rivière were taken with a 203 μm mesh ring net towed vertically from near bottom (station depth: 76 m) to the surface. Copepod concentrations calculated by dividing number in sample (provided in original document) by 5.6 m^3 (volume filtered by a net of 12" diameter towed vertically through 75 m of water: G. Filteau, pers. comm.). Samples from St. Georges Bay were collected with a 1 – m, 460 μm conical net towed obliquely from the bottom (about 34 m) to the surface.

to be relatively more abundant based on their distribution in coastal waters of the northwest Atlantic (Paranjape and Conover 1973). Physical factors influencing nutrient dynamics and water column stability will also affect zooplankton community structure, as species have different population growth responses to the size structure and seasonal cycle of primary production (Runge 1988).

In some cases, small-scale differences in zooplankton composition in the Gulf may also be due to advection of water masses of different origin. Huntsman et al. (1954) described distinct differences in community structure at stations approximately 30 km apart on the north and south sides of the Strait of Belle-Isle (Fig. 8b). The north shore community was dominated by species of *Calanus, Pseudocalanus,* and *Oithona,* whereas *Temora longicornis* prevailed along the southern side. This was attributed to the residual circulation pattern in the Strait, where the cold water of the Labrador current containing the characteristic cold-water community moves inward on the north side while there is an outward movement on the southern side of warmer water containing *Calanus* and relatively high concentrations of *Temora* and *Centropages* produced locally. In addition to changes in copepod composition, Huntsman et al. (1954) noted that the Arctic origin of water along the north side of the Strait is indicated by the presence of other Arctic zooplankton species, in particular the ctenophore, *Mertensia ovum,* and two amphipods species, *Themisto libellula* and *Pseudolibrotus glacialis.*

In summary, the studies on species composition to date indicate that there are, potentially, multiple pelagic food webs in the Gulf. The major distinction is between the deep, cold northern Gulf, where large species of the genus *Calanus* predominate, and the shallow, warm Magdalen Shallows, where smaller species, especially *Temora, Centropages,* and *Tortanus* are dominant. Adequate information on zooplankton composition and size distribution in the Gaspé Current area is however still lacking. Within each region there are likely to be smaller areas with different species composition or mix of the predominant species. Seasonal variability in species composition is also noticeable within regions; generally there is a shift in abundance from larger to smaller species by the end of summer.

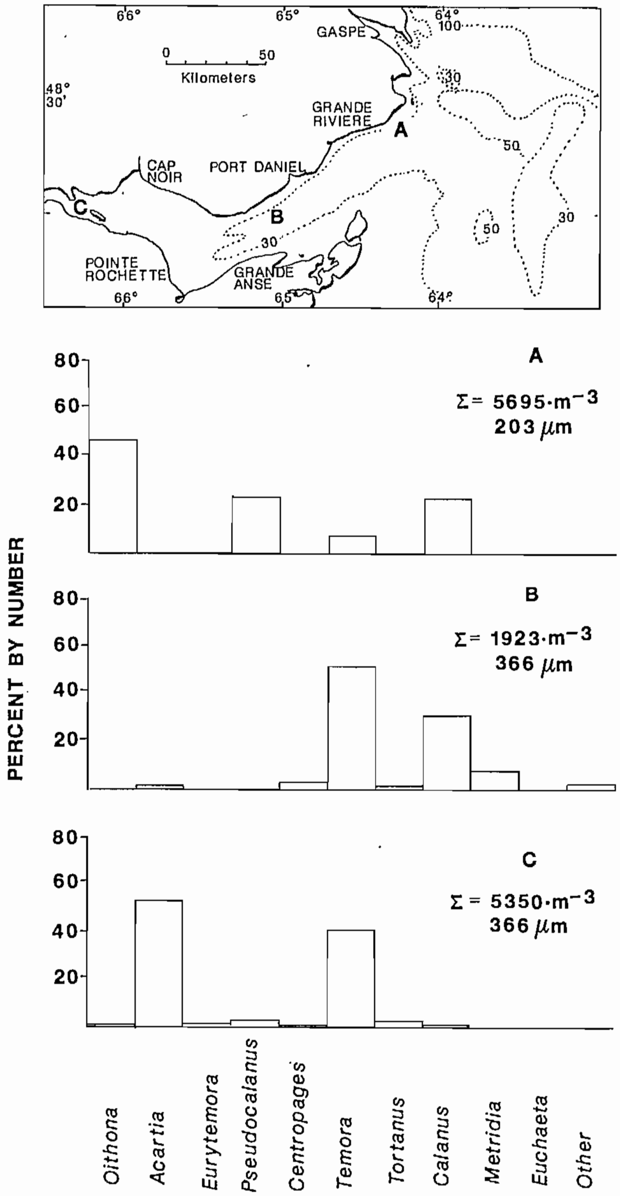

FIG. 10. Relative composition by number of copepod species at three locations in August in Baie-des-Chaleurs. Site A from Filteau (1951; Fig. 9, this paper) sampled in 1949 (mesh size: 203 μm); Site B from Lacroix and Filteau (1970) sampled in 1964 (mesh size: 366 μm); Site C from Lacroix and Legendre (1964) sampled in 1962 (mesh size: 366 μm).

Productivity and Population Dynamics

The only published estimates of zooplankton productivity in Gulf waters were provided in the study of the dynamics of the pelagic food web in St. Georges Bay by Hargrave et al. (1985). Based on successive biomass peaks in size fractions representing different copepod life history stages, they identified three major copepod cohorts between April and November, each corresponding roughly with algal blooms. Using literature-derived development times for the dominant copepod in each cohort, secondary production of copepod-sized organisms was calculated to be about 1 g C • m^{-2} • mo^{-1}, or approximately 3 mg dry weight • m^{-3} • d^{-1} during the summer months. Given a median copepod biomass of about 40 mg dry weight • m^{-3} during the summer (MEL 1980), this corresponds very roughly to a weight specific growth rate of about 7% • d^{-1} and a yield of 7–13% of the phytoplankton production. Microplankton production could not be estimated. Zooplankton biomass during the study period decreases during the summer months despite relatively constant level of secondary productivity. Hargrave et al. (1985) attributed this decline to heavy predation by planktivorous fish such as mackerel, herring, gaspareau and smelt.

Zooplankton biomass estimates from the composite IBP data (Fig. 7) do not show any clear seasonal relationship with chlorophyll concentrations in any of the five regions. Biomass for all regions are very high (averaging 10 g dry weight • m^{-2}) relative to other coastal areas for which data are available; for example, Davis (1987) reported zooplankton biomass on Georges Bank ranging from about 3 g dry weight • m^{-2} in May to 12 g dry weight • m^{-2} in July (using a carbon/dry weight ratio of 0.4). Mean values for the southern Gulf (5 g dry weight • m^{-2}) are approximately 2–3 times higher than those reported for St. Georges Bay (1.5–3 g dry weight • m^{-2} for water column depth of about 30 m — Fig. 14a). The high biomass from IBP results may represent the presence of very large, long-lived zooplankton such as *Calanus hyperboreus* and euphausiids, especially in the deep regions in the northern Gulf, including the gyre, the Gaspé Current, and the Jacques Cartier Passage.

Knowledge of the differences in copepod community structure discussed in the previous section is important for understanding population dynamics in the different Gulf regions. Individual species have different life history characteristics that cannot be scaled simply according to body size (e.g. Frost 1980); consequently the dynamics of each species and therefore each community in the Gulf may respond differently to environmental change. Supporting data for this statement are found in two multi-year plankton studies (Filteau 1951; Lacroix and Filteau 1970, 1971) in Baie-des-Chaleurs (Fig. 11). Both studies show interannual fluctuations by a factor of 3–7 in abundance of each of the three most common species. These fluctuations may represent variability in recruitment from the spring generation or variability in advective processes at the sampling site. In any case, interannual variation is not always correlated among species. For example, 1948 was a "good" year for *Calanus* but a "poor" year for *Temora.*

These data may provide some indication of the effects of climate change on plankton populations in the Gulf. The above two studies by Filteau (1951) and Lacroix and Filteau (1970, 1971) note that years of relative scarcity (1947, 1961) were correlated with severe winters, which resulted in delays in surface water warming as indicated by the sea surface temperature at the end of May (bottom panel in Fig. 11). Years with advanced spring warming (1948, 1949, 1962) were generally correlated with higher zooplankton standing stock. The authors proposed that warm water enhances local production and development of the temperate-boreal (*Calanus, Temora*) species. Much more remain to be done on the possible causes of the annual variations in the abundance and relative composition of zooplankton in the Gulf of St. Lawrence.

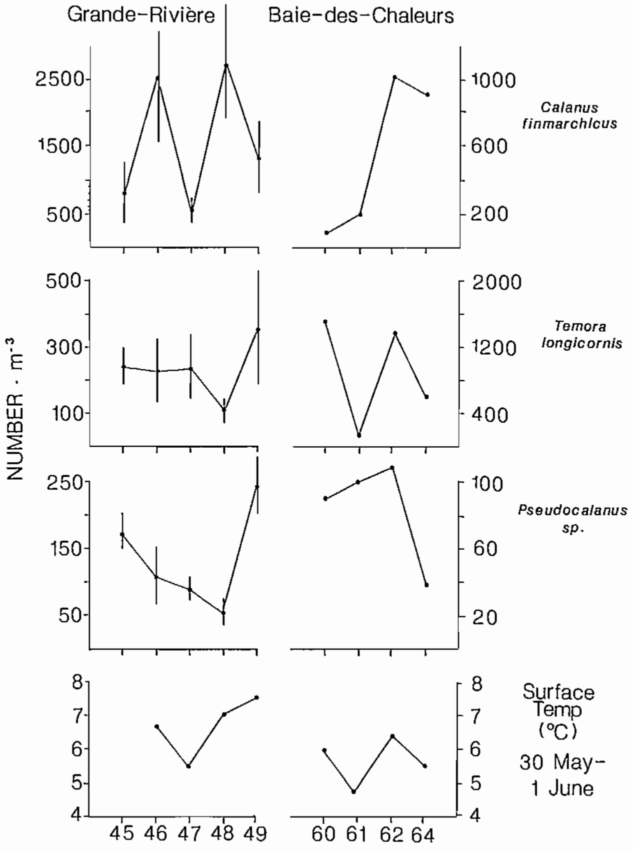

FIG. 11. Interannual variability of three of the common copepod species found in Baie-des-Chaleurs in July. Data for Grande-Rivière (Filteau 1951) are the means (and standard errors) of counts from net tows taken at various dates in July ($n = 2$-5) for each year. Copepod concentrations calculated as in Fig. 9. Data for Baie-des-Chaleurs (Lacroix and Filteau 1970, 1971) are mean abundance based on samples taken on 1-2 dates in July at 3-8 stations ($n = 6$-16: standard deviation not provided in original). Surface water temperature on 30 May-1 June is provided in the bottom panel (1945 temp. missing; 1947 temp. determined from linear interpolation of data from 23 May and 3 June).

Ichthyoplankton

Considerable effort has been allocated to ichthyoplankton research in the Gulf of St. Lawrence. The Canadian Fisheries Expedition in 1915 provided the first description of the ichthyoplankton in the Gulf including most of the species known to spawn in the area today, and identified the regional difference in fish communities between the Magdalen Shallows and the offshore deep (>200 m) waters overlying the Laurentian Channel (Dannevig 1919). Fifty years later, the St. Andrews fisheries laboratory initiated a ten-year sampling program (1965-75) to "provide basic information about the distribution and abundance of eggs, larvae and juveniles of teleost fish in the southern Gulf of St. Lawrence" (Kohler et al. 1977). Since 1977, an annual mackerel egg survey provides estimates of the annual spawning biomass of mackerel over the Magdalen Shallows (Ouellet 1987a). More recently, a shrimp larval survey program (Ouellet 1987b) has collected plankton from the northern Gulf. Ichthyoplankton studies have been (and still are) also carried out by various workers in different areas of the Gulf (northwestern Gulf and Gaspé Current: Able 1978; Jacquaz et al. 1977; de Lafontaine et al. 1981, 1984; west coast of Newfoundland: Frost 1938; Baie-desChaleurs and Magdalen Shallows: Bergeron and Lacroix 1963; Lacroix and Bergeron 1964; Lambert 1982; de Lafontaine et al. 1984; de Lafontaine and Gascon 1990; Northumberland strait: Faber 1976; Johnston and Morse 1988; St. Georges Bay: Lambert 1984; Lambert and Ware 1984; Ware and Lambert 1985; Hargrave et al. 1985).

More than 5 000 stations have been visited and over 15 000 ichthyoplankton samples have been collected in the Gulf to date. Sampling effort was however not evenly distributed in time and space (Table 4). A wide variety of sampling gears and protocols have been used and there has been a higher proportion of surface and horizontal tows (68.1%) relative to oblique tows (31.9%). Overall, the proportion of "quantitative" samples (i.e. samples for which volume of strained water is available) represents only 44.4% of all samples. Unfortunately, despite the large amount of samples (Table 4), no complete analysis or synthesis of these data has been achieved and the large-scale distribution of most ichthyoplankton species still remains poorly described. In fact, most of the published information comes from independent studies which were relatively restricted in their temporal and spatial coverage.

To date, the composition of ichthyoplankton in the Gulf includes 50 different species (a complete list is given in Kohler et al. 1977), which represent about 2/3 of the total number of adult fish species (teleost only) known to occur in the area (Table 5). Their occurrence among the four regions of the Gulf would indicate a higher species diversity (number of species) in the southern Gulf, but such a conclusion may be premature due to bias in both spatial and temporal sampling coverage (Table 4). The grouping of adult fish species into 3 biogeographic units (as in Dunbar et al. 1980) reveals that the spawning and larval occurrence of species having a wide range distribution is proportionally higher than that of cold water (boreal/arctic) or warm water (southern) species (Table 5).

The ichthyoplankton fauna of the Gulf is dominated by benthic spawning species (Table 5). The majority of species laying pelagic eggs (mackerel, cod, plaice, fourbeard rockling, hake, cunner, yellowtail), some of which are indeed considered to be warm water species (Dunbar et al. 1980), are primarily found in the southern Gulf area. Most cold-water species (capelin, seasnails, shanny, sculpins) are benthic spawners and are commonly reported in the northern part of the Gulf. Similarly lobster (*Homarus americanus*) larvae (warm water species) are most abundant in the Magdalen shallows (Scarratt 1963, 1968, 1973) while boreal shrimp (*Pandalus borealis*) larvae are mainly concentrated in the deep waters of the northern Gulf (P. Ouellet, DFO, Mont-Joli, pers. comm.). As discussed by de Lafontaine (1990), ichthyoplankton communities dominated by larvae from benthic eggs are characteristic of boreal-arctic waters and do not necessarily reflect spawning adaptations to hydrodynamic features or circulation patterns of a specific area.

It is beyond the scope of this paper to present the spatial distribution and abundance of the various species of

TABLE 4. Numbers of stations visited and numbers of samples (values in parentheses) taken during ichthyoplankton surveys in the different regions (see Fig. 4) of the Gulf of St. Lawrence to date.

		Régions			
		I	II	III	IV
APR.	15–30	24 (32)	9 (17)		3 (3)
MAY	1–15	27 (27)	2 (2)	147 (371)	74 (167)
MAY	15–31	74 (114)	3 (3)	611 (1797)	245 (630)
JUNE	1–15	38 (38)	3 (3)	364 (804)	106 (123)
JUNE	15–30	11 (33)	37 (74)	1511 (4244)	37 (126)
JULY	1–15			608 (1559)	
JULY	15–31	16 (16)	5 (5)	329 (889)	21 (59)
AUG.	1–15			189 (545)	23 (48)
AUG.	15–31			744 (2055)	110 (393)
SEPT.	1–15			134 (241)	1 (2)
SEPT.	15–30			233 (441)	4 (11)
OCT.	1–15			42 (153)	
OCT.	15–31	40 (40)		32 (32)	
NOV.	1–15				
NOV.	15–30			16 (68)	
DEC.	1–15				
DEC.	15–30			13 (61)	
Total Number of Stations:		5 873			
Total Number of Samples:		15 226			

TABLE 5. Number of adult species, percentage of pelagic spawners and percentage of larval occurrence for marine fish (teleost only excluding sharks, rays and anadromous fish) grouped by biogeographic units in the Gulf of St. Lawrence.

Biogeographic groups[a]	Adults[a]	Pelagic spawners		Larval occurrence	
	n	*n*	%	*n*	%
Boreal/Arctic	22	1	4.5	10	45.5
Wide Range	34	8	23.5	29	85.3
Southern	19	12	63.2	11	57.9
Total	75	21	28.0	50	66.7

[a]From Dunbar et al. (1980).

eggs and larvae and more detailed distribution maps can be found elsewhere (Hodder and Winters 1972; Messieh and Kohler 1972; Able 1978; de Lafontaine et al. 1981, 1984; Ouellet 1987a,b). Information compiled from quantitative results published by Lacroix and Bergeron (1964) and de Lafontaine et al. (1981, 1984) revealed striking differences in the spatial distribution of larval fish communities, both for pelagic and groundfish species (Fig. 12). In the spring, the northwestern Gulf and the Gaspé Current area (regions I & II) are virtually dominated by sand lance (*Ammodytes* sp.) larvae, while both sand lance and shanny (*Lumpenus* sp.) larvae dominate the southern Gulf area (region III). During the summer, Atlantic mackerel (*Scomber scombrus*) is numerically the dominant pelagic fish spawning in the southern Magdalen Shallows (region III), while capelin (*Mallotus villosus*) dominates in the northwestern Gulf and along the Gaspé coast (regions I and II). Capelin is also known to spawn all along the Québec north shore up to the Strait of Belle-Isle (Parent and Brunel 1977) where, presumably, it should dominate the ichthyoplankton community in the summertime. The regional shift between capelin and mackerel may be attributed to water temperature. Mackerel spawn when water temperature exceeds 11°C (Ware 1977; Ware and Lambert 1985) and may therefore be restricted to the warm waters of the southern Gulf. Although capelin spawning is generally associated with colder waters (6–10°C, Parent and Brunel 1977), the low abundance of this species in southern Gulf (southern limit is Baie-des-Chaleurs) is difficult to explain, since spawning could occur earlier when temperature would be appropriate.

Besides temperature, bathymetric characteristics are also important for the spatial distribution of spawning locations and the resulting ichthyoplankton assemblages. For example, larvae of redfish (*Sebastes* sp.), which spawn in offshore deep (>200 m) waters, are virtually absent from region III and occur primarily over the deep waters in regions I and IV (Fig. 12). Although larvae of

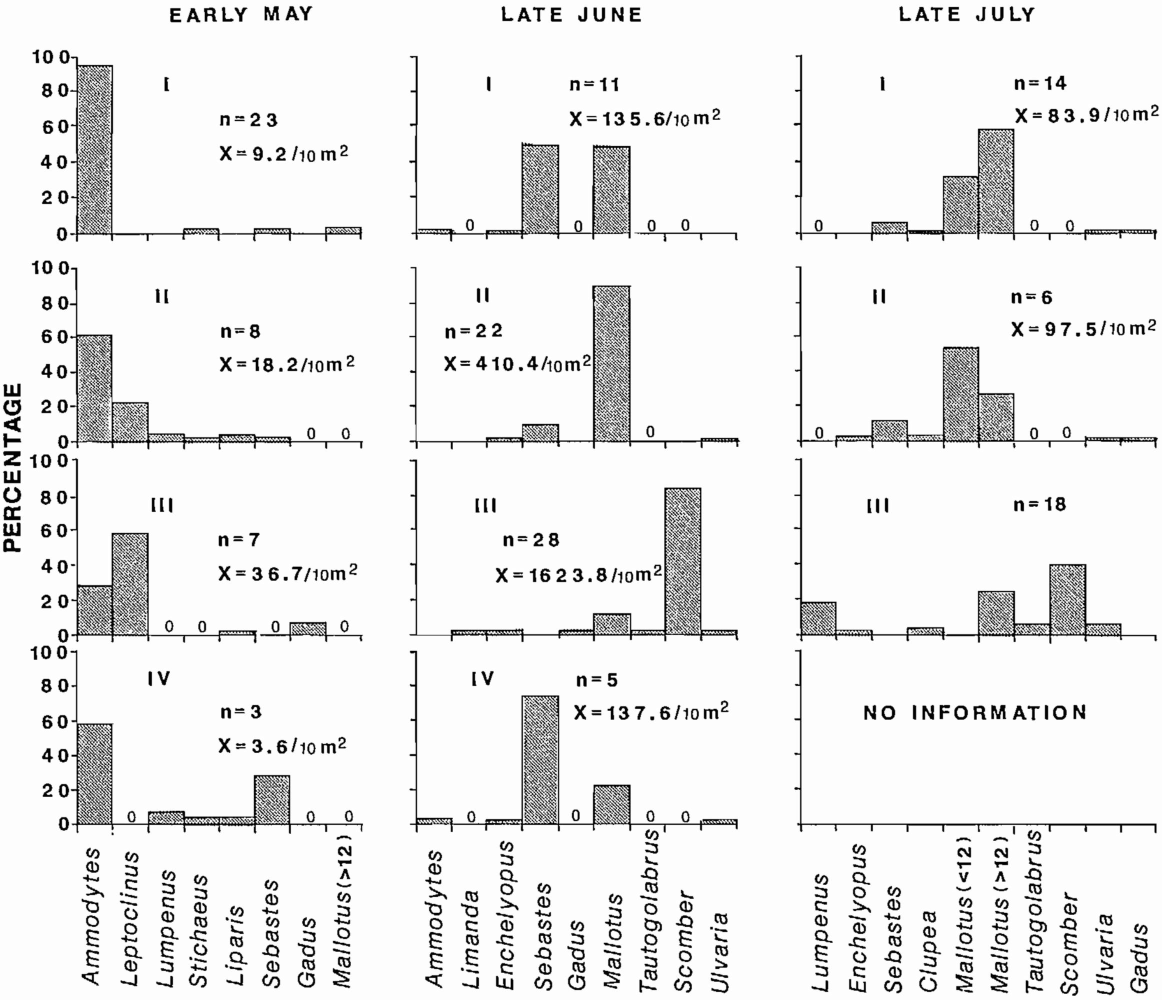

FIG. 12. Relative composition and abundance of ichthyoplankton for different regions of the Gulf of St. Lawrence at three times of the year. Data extracted from de Lafontaine et al. (1981,1984) and Lacroix and Bergeron (1964).

important commercial species such as cod (*Gadus morhua*), herring (*Clupea harengus*) and plaice (*Hippoglossoides platessoides*) are proportionally less abundant, they are mainly encountered in regions II and III and in coastal waters within region IV (Frost 1938; de Lafontaine et al. 1981, 1984; Ouellet 1987b and pers. comm.; de Lafontaine 1990). These species and many other benthic species (*Lumpenus, Stichaeus, Liparis, Enchelyopus* and *Ammodytes*) usually spawn in shallow waters (< 100 m) (Scott and Scott 1988). In the nearshore waters and shallow coastal embayments of the southern Gulf, cunner (*Tautogolabrus adspersus*), radiated shanny (*Ulvaria subbifurcata*) and winter flounder (*Pseudopleuronectes americanus*) larvae may contribute, at different times of the year, to a large fraction of the ichthyoplankton community (Northumberland strait, Faber 1976; St. Georges Bay N.S., Hargrave et al. 1985; Hillsborough Bay P.E.I., Johnston and Morse 1988). In summary, we can conclude that the Gulf of St. Lawrence supports different ichthyoplankton communities spatially segregated and that the total number of larval species and the overall abundance of ichthyoplankton are generally higher in regions II and III than in regions I and IV (Fig. 12).

The existence of different ichthyoplankton assemblages in the Gulf implies the presence of mechanisms ensuring the integrity and maintenance of these communities within the regions. However, very little is known about the eggs and larval distribution patterns in the Gulf of St. Lawrence. de Lafontaine et al. (1984) showed that the distribution of pelagic eggs parallel that of larvae except for the Gaspé Current area where ichthyoplankton appears to be rapidly exported seaward toward the southern Gulf. It was also demonstrated that the cyclonic gyre in the northwestern Gulf is not a major spawning ground and does not contribute to aggregate newly hatched larvae. However, the area is considered to be a nursery for capelin post-larvae and juveniles as a result of larval drift from the St. Lawrence estuary and the Québec north shore (Jacquaz et al. 1977; Bailey et al. 1977; de Lafontaine et al. 1981; Ouellet 1987b). Post-larval and juvenile capelin also aggregate near Baie-des-Chaleurs (Lacroix and Bergeron 1964) and in Gaspé fishing banks area (Hodder and Winters 1972).

Messieh and Kohler (1972) argued that herring larvae hatching from nearshore spawning grounds in region III slowly drift over the Magdalen shallows where the general circulation characterized by large-scale eddies may favour the retention of these larvae in this area. However, Hodder and Winters (1972) were unable to locate high concentrations of herring post-larvae and juveniles over the Magdalen Shallows in the fall. The size distribution of fish larvae in Baie-des-Chaleurs suggests that the area represents an important nursery (and retention) zone where larvae can grow (Lacroix and Bergeron 1964; de Lafontaine et al. 1984), but the lack of adequate description on the physical circulation and dynamics of the bay (as previously discussed in the phytoplankton section) precludes any firm conclusion. The apparent retention of ichthyoplankton produced in St. Georges Bay is supported by the calculated residence time of waters in the area (Petrie and Drinkwater 1978; Ware and Lambert 1985; Hargrave et al. 1985). We believe that complete analysis of existing data would be extremely useful by providing a better description of the distribution patterns of ichthyoplankton in the Gulf of St. Lawrence prior to development of new research programs.

Little attention has been devoted to the vertical distribution of ichthyoplankton in the Gulf of St. Lawrence to date. Lacroix and Bergeron (1964) made preliminary observations of the vertical distribution of different larval species captured during a single cruise in mid-July in Baie-des-Chaleurs. The ontogenetic variation in the vertical distribution of mackerel eggs and larvae has been recently described by de Lafontaine and Gascon (1990) who also showed that fish larvae were more vertically aggregated than their microzooplankton prey items. Further investigations on eggs and larval vertical distribution are absolutely necessary to adequately describe the larval distribution patterns and to rigorously evaluate the general hypotheses linking larval and zooplankton distribution.

Temporal distribution studies of ichthyoplankton in the Gulf are rare except for a weekly sampling program realized in Baie-des-Chaleurs by Lambert (1982) (Fig. 13). The number of larval species present at one time appears relatively constant during the summer, but the relative abundance of each species varies largely through time. Larval abundance is maximal in June and July and is mostly due to mackerel (*Scomber scombrus*), capelin (*Mallotus villosus*), Atlantic cod (*Gadus morhua*) and radiated shanny (*Ulvaria subbifurcata*). de Lafontaine et

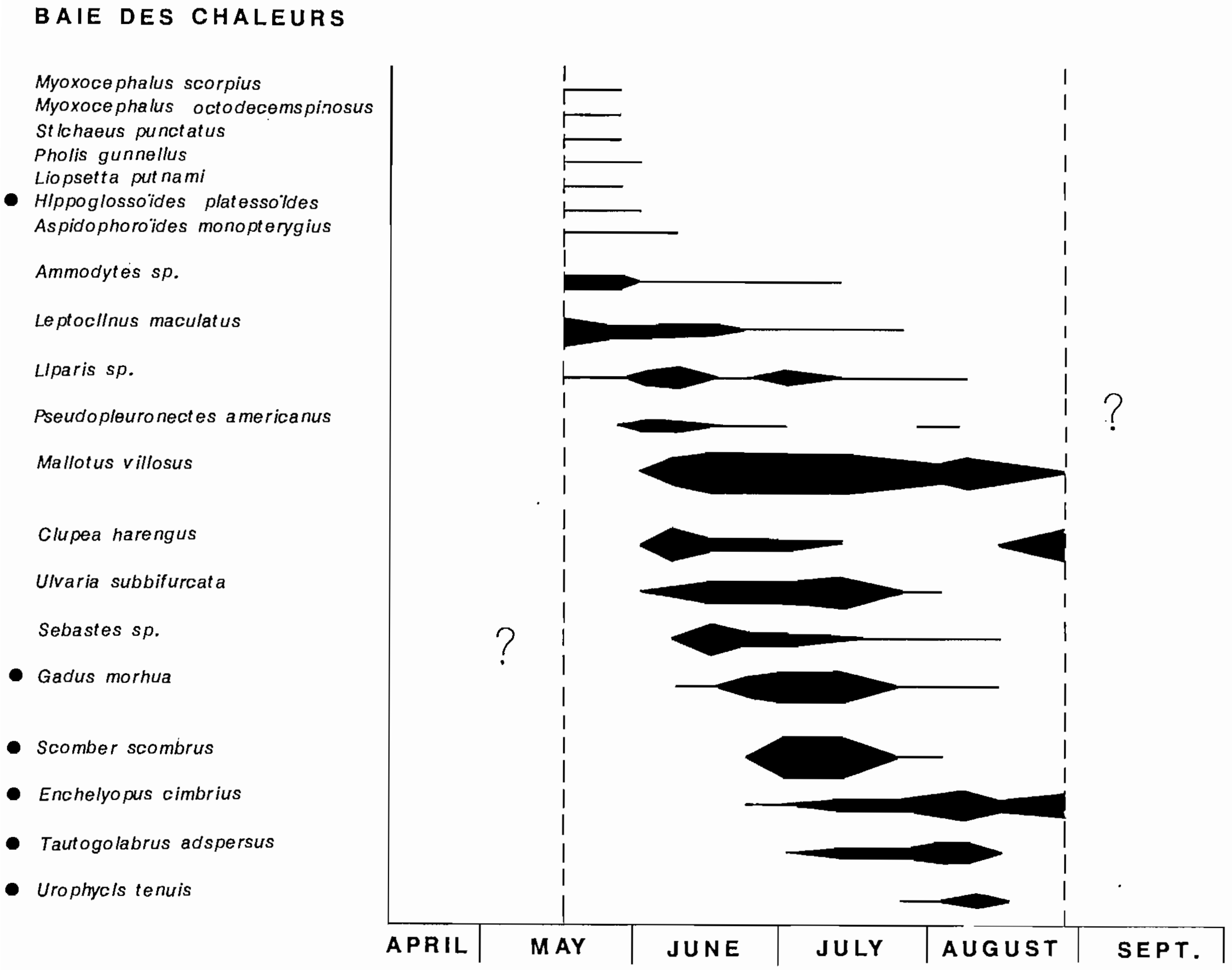

FIG. 13. Temporal occurrence of ichthyoplankton in Baie-des-Chaleurs, Gulf of St. Lawrence (redrawn from Lambert 1982 and de Lafontaine et al. 1984). Dots indicate species hatching from pelagic eggs.

al. (1984) showed that larval fish abundance was positively correlated to zooplankton biomass (>202 µm) in Baie-des-Chaleurs. Maximum zooplankton biomass during June was also observed in various parts of the Gulf (Fig. 8), including St. Georges Bay (Fig. 14). The temporal coincidence between larval and zooplankton abundance appears advantageous by ensuring an adequate food supply to larvae and also by reducing predation pressure due to large quantity of alternative prey available to larval fish predators (Frank and Leggett 1985; Pepin 1987; but see Pepin et al. 1987 and de Lafontaine and Leggett 1988 for opposing views). Since most fish species have a relatively fixed spawning period (Qazim 1956; Cushing 1970; Ware 1975), interannual variability in the timing of larval occurrence in the Gulf (Fig. 13) is expected to be minimal. It has been hypothesized that the succession of different larval cohorts may be linked to the size of planktonic food available for first feeding and would tend to reduce competition for resource allocation (Ware 1975; Lambert 1984; Lambert and Ware 1984). This hypothesis is supported by the general decline in the size of larvae at first-feeding from Baie-des-Chaleurs which parallels the reduction in the average size of plankton during the summer in the Gulf (St. Georges Bay) (Fig. 14). Both field and experimental evidence on the feeding diets of fish larvae and the predator-prey interactions between fish larvae and their potential predators are actually too scanty to test these hypotheses in the Gulf and should be highly emphasized in future work.

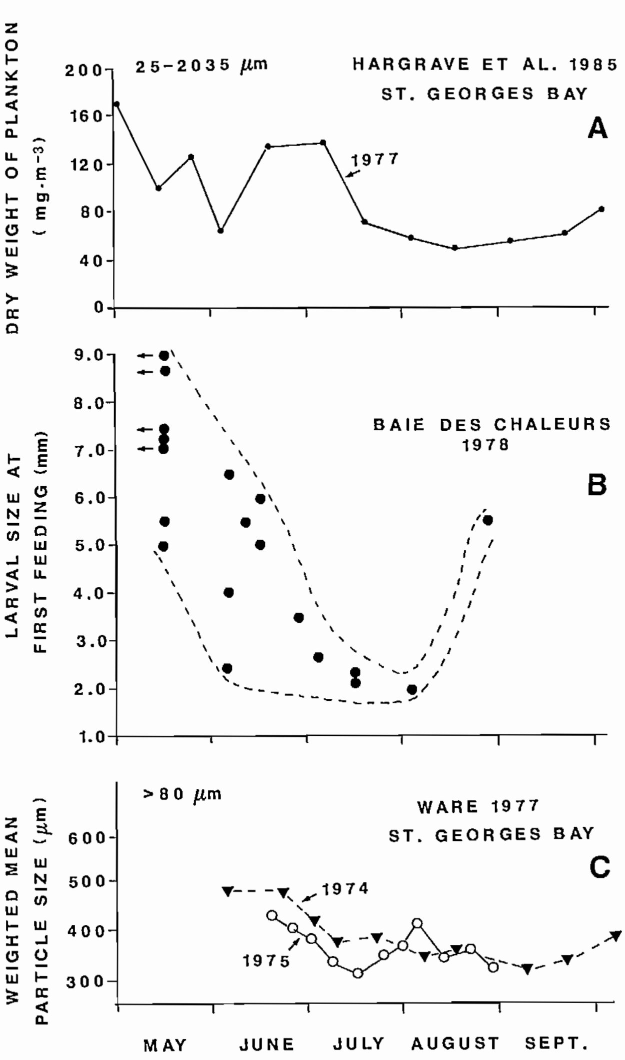

FIG. 14. Seasonal variation in (A) dry weight of plankton (mg dry weight m^{-3}) in the 25 µm - >2035 µm size fractions taken by nets of four different sizes in St. Georges Bay, 1977 (MEL 1980), (B) size of first-feeding larval fish in Baie-des-Chaleurs (data derived from Fig. 13) and (C) average size of particulate plankton (>64 µm) in St. Georges Bay (Ware 1977).

Food Webs and Recruitment

The above information on the species composition, distribution, and abundance of plankton at various trophic levels supports the hypothesis that the Gulf of St. Lawrence is not an homogeneous biological entity and may be subdivided into different regions each with a characteristic food web. Based on data discussed in the previous sections, we therefore propose a conceptual model to define these different food webs (Table 6) which appear to depend upon and reflect the topographic and physical characteristics used to divide the Gulf into natural regions (Fig. 4).

First, the northwestern gyre ecosystem (region I) is a physically stable zone supporting a distinct community characterized by phytoplankton consisting of large diatoms during the spring bloom and small flagellates in summer, low diversity of large zooplankton species (*Calanus,* euphausiids, chaetognaths and shrimps) and relatively low abundance of fish eggs and newly hatched larvae consisting almost exclusively of redfish, but high abundance of fish juveniles (primarily capelin). The dynamics of this ecosystem is more typical of oceanic regimes where the onset of phytoplankton bloom is linked to the physical stratification of the water column. Following winter mixing, high concentrations of nutrients from the deep water mix to the surface layer, and contribute to the high levels of phytoplankton biomass observed in the area in the spring. Depletion of nutrients in surface layer during the bloom period is accentuated by the strong seasonal thermocline resulting in low phytoplankton biomass during the summer.

The area under the influence of the Gaspé Current (region II) represents a second planktonic food web. Here the water column instability, due mainly to tidal processes and the input of freshwater runoff from the St. Lawrence estuary, results in high concentrations of nutrients supporting the development of large diatoms during most of the summer months. The phytoplankton bloom occurs later in spring than in other parts of the Gulf. The zooplankton community is poorly described but presumably comprises large numbers of a few large species (*Calanus,* euphausiids) which thrive on the phytoplankton production and contribute to a high biomass. Ichthyoplankton is more abundant than in the cyclonic gyre system, but mainly composed of small individuals (including fish eggs and recently hatched larvae) which are rapidly exported toward the southern Gulf. Presumably, the Gaspé Current system is strongly coupled with the dynamics of the lower St. Lawrence Estuary (Therriault et al. 1990).

The southern Gulf (region III) is undeniably a different ecosystem characterized by higher diversity of both zooplankton and ichthyoplankton. The composition of zooplankton favours smaller species and a temporal succession in the size structure of suspension-feeders is clearly observed. The structure of phytoplankton is poorly known but is expected to be highly diversified with a predominance of small cells. The onset of the phytoplankton bloom is later than that observed in the cyclonic gyre and the northern Gulf. This delay is probably associated with the presence of ice cover over the southern Gulf until the end of April. The Magdalen shallows and its embayments represent important spawning and feeding grounds for numerous fish species and larval fish abundance is higher than anywhere else in the Gulf.

The paucity of data for the northeastern part of the Gulf (region IV) does not allow adequate definition of the structure of the existing food webs in the area. One could tentatively speculate that, because of its great depth, this ecosystem is somewhat similar to the one described for the northwestern Gulf (region I). However, it is possible that different planktonic assemblages may be found in the coastal regions.

Finally and as a caveat, we acknowledge that the described regions and their associated food webs are interconnected to some degree and are not totally independent from each other. Some species may have populations which persist on the scale of the Gulf itself whereas others may have persisting populations on smaller spatial scales. The recognition that different planktonic communities coexist in the Gulf should however be appreciated and should lead to better understanding of plankton dynamics and interactions with other components of the ecosystem.

The differences in food webs observed in our conceptual model would influence the recruitment and population dynamics of exploitable resources. In our view, the transfer of the environmental signal throughout the food web will vary in relation to the different food web interactions (e.g. Runge 1988) and will not generate the same effect among the various food webs. To evaluate this hypothesis, we compiled information on the dominant year-classes strengths of various fish stocks in the Gulf of St. Lawrence (Table 7). Data revealed large differences in the generation of strong recruitment which is clearly not synchronous among the different fish populations. There is a strong correspondence between the year-class strength of mackerel and herring in the southern Gulf (area 4T) and in the coastal waters of western Newfoundland (area 4R). On the other hand, the year-class strengths of cod and particularly redfish (except for 1980) are somewhat out of phase relative to those of mackerel and herring. These results provide some support to our conceptual model which indicates that redfish larvae are associated with the offshore food web dominated by large copepods (*Calanus*) while mackerel and herring abundant in the southern Gulf would belong to a different food web (Table 6). This recruitment asynchrony is also supported by the analyses of Bugden et al. (1982) who found poor correlations in the lobster landings from various parts of the Gulf and very weak correlations between freshwater discharge and landings in most areas except for the Magdalen Islands stock as originally presented by Sutcliffe (1972, 1973). These results suggest species-specific and population-specific differences in the trophic response of larval fish to both prey and predator fields within a particular food web. It is also very interesting to note that the recruitment of both fall and spring herring populations occurs in adjacent years (Table 7), where

TABLE 6. Conceptual models of the food webs structure in various regions of the Gulf of St. Lawrence.

	Northwest gyre	Gaspé area	Southern Gulf	Northern Gulf
Stratification:	Strong but shallow (temperature)	Deep and variable (salinity)	Shallow but varies with water depth	Shallow (?)
Phytoplankton:				
— Bloom	Spring & short	Early summer & long	Spring & Short	Early spring & short
— Biomass	Very high	Very high	Lower	Low
— Variability	Low	High	Low	Low
— Species	Shift from large diatoms to small flagellates	Large diatoms	(Small ?)	?
Zooplankton:				
— Biomass	High	High	Lower	High
— Diversity	Low	Low	High	Low
— Size	Large copepods (*Calanus*) Euphausiids, Chaetognaths, shrimp	Large copepods (*Calanus*) Euphausiids	Small copepods (*Temora*) Meroplankton Jellyfish	Large copepods (*Calanus*) Shrimp?
Ichthyoplankton:				
— Spawning	Little	Moderate	Important	?
— Diversity	Low	Moderate	High	?
— Dominant species	Redfish & capelin juveniles	Redfish, small capelin	Mackerel, cod, herring shanny, cunner	Cod, herring, redfish (?)
— Abundance	Low	Moderate	High	?

TABLE 7. Dominant year-class strengths for some commercial fish stocks in the Gulf of St. Lawrence. Year-classes of fall (F) and spring (S) herring spawners are indicated.

Year	Mackerel	Herring				Cod		Redfish	Plaice
	4T	4T		4R		4T	4RS	4RST	4T
		F	S	F	S				
1950						50			
51									
52									
53									
54						54			
55									
56								56	
57						57			
58		58		58				58	
59	59		59						
1960									
61									
62									
63				63			?		?
64						64			
65									
66							—		—
67	67	67		67					
68			68		68		68		
69									
1970									
71							71	71	
72								72	72
73				73					
74	74		74		74				74
75						75			
76									
77							77		
78									
79		79		79				79	
1980			80		80	80	80	80	
81									
82	82		82		82	82(?)			
83									

a good fall year-class was often followed by a good spring year-class. No explanation can be provided at this stage, but such results would suggest that the phytoplankton production cycle *following* larval production may be more important than the one occurring before the larval release, as pointed out by Sinclair and Tremblay (1984). The link between the phytoplankton cycle, the zooplankton cycle and the fish spawning cycle does not appear to be straightforward as originally proposed by Cushing's (1975) match/mismatch model.

Conclusion

The information on pelagic populations gathered in the Gulf to date has essentially focused on quantitative estimations of "state" variables (e.g. biomass, production) with little distinction on the use of the term "plankton". For example, high and low levels of chlorophyll bear little meaning if the size structure of phytoplankton is not described. The problem related to toxic dinoflagellate blooms and their effect on other components of the food chain is undoubtedly masked when only "phytoplankton" biomass or production data are collected. It is now recognized that zooplankton feeding and probably reproduction is dependent on both the *quantity* and the *quality* of available phytoplankton (Huntley et al. 1987; Kiorboe et al. 1988). The species composition and the size structure of phytoplankton are poorly described in terms of abundance and distribution in the Gulf and therefore no prediction can be made concerning the dynamics of the food web components in response to the phytoplankton cycle. The dynamics of bacteria and microzooplankton in the Gulf are virtually unknown and the whole aspect of the "microbial loop" remains to be investigated. The role and dynamics of Coelenterates (jellyfish), which sporadically occur in large swarms in the southern Gulf, have never been studied. The availability of adequate (i.e. appropriate quality of prey) food for first feeding larvae is important for better growth and survival (Lasker 1975; Frank and Leggett 1986), but the feeding diet and predator-prey relationships of most larval fish in the Gulf are still undescribed. In our view, these aspects (Table 8)

TABLE 8. Suggestions for future research in biological oceanography in the Gulf of St. Lawrence.

1) Avoid generic use of the term "PLANKTON" and consider instead species- and size - structure identification (species-specific biomass and production versus size structure).
2) Obtain accurate estimates of phytoplankton production over the whole year and describe the dynamic of the onset of phytoplankton bloom in relation to ice and nutrients sources.
3) Emphasize studies on microbial loop, microzooplankton, jellyfish predators, and fish juveniles to properly identify their role in the food web structure.
4) Synthesize a description of large-scale distribution of ichthyoplankton based on analysis of existing data.
5) Study the feeding regime of fish larvae and the impact of predation on larval fish survival.
6) Describe the dynamics of the food webs components in response to variable signals at different frequencies (low frequency variability (i.e. runoff) versus high frequency variability (i.e. wind events)).
7) Study single species recruitment dynamics in the context of trophic interactions within the food web as opposed to a typical linear food chain approach.

may be recommended for further biological and fisheries research in the Gulf. As a corollary, the lack of definition concerning the structure and the interaction strength between the various components of the different pelagic communities do not allow us to make any quantitative prediction on the nature of the biological dynamics in the Gulf of St. Lawrence.

The identification of trophic links by which the pathways of energy and matter transfer within a community can be described requires that populations or species be segregated (Paine 1988). Because the number of trophic links is theoretically expected to be twice the number of species coexisting in a community (Paine 1988; Cohen and Newman 1988), it is important that the interaction strengths among species be quantified in order to identify the "key" players of a particular food web (Paine 1988). Much remains to be done before one can adequately resolve the existing trophic links in specific food webs for the Gulf of St. Lawrence.

The necessity of taking a food web approach appears essential to make predictions in regards to two general problems in biological oceanography: fisheries recruitment and expected global climatic changes (the CO_2 problem). These questions bring a new challenge to biological oceanographers and highlight, more than ever, the necessity of cohesive and collaborative research. In both cases, it is believed that changes in the physical characteristics of the water column and in circulation features can affect the chemical and biological responses of the ecosystems. It therefore requires an adequate quantification and understanding of the mechanisms of carbon transfer between the air–sea interface and *also through the food web* in studying the trophic interactions of the various components. The Gulf of St. Lawrence, being more or less an inland sea, is particularly vulnerable to changes from human activities and global climatic changes.

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Fisheries Production in the Gulf of St. Lawrence[1]

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An analysis of the marine resources in the Gulf of St. Lawrence indicated that about 80% of the commercial finfish and invertebrate biomass comprised three species, cod, herring and redfish. Total catch in the Gulf was comparable to other coastal areas of similar size in the northwest Atlantic (Labrador, Grand Banks, Scotian Shelf, and Georges Bank). While the annual catches in coastal areas were highly correlated, those from the Gulf of St. Lawrence generally were not, possibly indicating unique production characteristics of the Gulf. There was synchrony in production for stocks of the same species that resided in the Gulf, largely because of similar trends in recruitment, but there was no synchrony in production among species. Timing of catches, used as a proxy for migration timing, showed strong season and area effects, but small year effects, suggesting that there was little annual variation in the timing of fisheries. Each species had its unique migration route into and out of the Gulf, but unlike other species, herring and several anadromous species appeared to arrive in all areas of the Gulf at the same time. Finally, there was no single year that affected growth or migration timing of all species together, thus we concluded that studies on the influence of environmental factors on dynamics of fish populations would require careful understanding of the life history of each individual species.

Une analyse des ressources marines dans le Golfe du Saint-Laurent a indiqué qu'environ 80% de la biomasse commerciale de poissons et d'invertébrés comprenait trois espèces; la morue, le hareng et le sébaste. La totalité des captures dans le Golfe était comparable à celle des autres régions côtières d'étendue semblable dans le nord-ouest de l'Atlantique (Labrador, Grand Bancs, plateau Néo-écossais et Banc Georges). Alors que les captures annuelles dans les régions côtières étaient hautement corrélées, celles du Golfe Saint-Laurent ne l'étaient généralement pas, indiquant possiblement des caractéristiques de production unique au Golfe. Il y avait un synchronisme dans la production des stocks de la même espèce résidant dans le Golfe, causé surtout par des tendances de recrutement semblables, mais il n'y avait pas de synchronisme dans la production entre les espèces. La synchronisation des captures commerciales, utilisée comme mesure pour déterminer le temps de migration, a soulevé de sérieux effets sur la saison et la région, mais peu sur l'année, suggérant ainsi que la variation annuelle dans la synchronisation des pêches était minime. Chaque espèce avait sa propre voie de migration à l'intérieur et à l'extérieur du Golfe, mais contrairement à d'autres espèces, le hareng et plusieurs espèces anadromes semblaient arriver de toutes les régions du Golfe en même temps. Finalement, aucune année n'a influencé la croissance ou la période de migration de l'ensemble des espèces; alors, nous avons conclu que les études sur l'influence des facteurs environnementaux sur la dynamique des populations des poissons demanderaient une compréhension approfondie de l'historique individuelle de chaque espèce.

Introduction

There have been several reviews of fisheries production in the Gulf of St. Lawrence (Dunbar 1979; Dickie and Trites 1983). These papers have reviewed general biological attributes of the major fish species, including surveys for eggs, larvae and adult fish (Koeller and LeGresley 1981; Halliday and Pinhorn 1982), and they have discussed theories relating year-class strength of important Gulf species to oceanographic processes such as freshwater discharge (Sutcliffe 1973; Bugden et al. 1982), and to biological processes, such as predation (Lett et al. 1975; Winters 1976). Although these papers were provocative, they did not intend to present a quantitative comparison of production among the various fish stocks in the Gulf or among the other areas in the northwest Atlantic. The objective of this paper, therefore, is to undertake such an analysis.

We used commercial catch data and stock assessments based on these data to estimate production of important fish species in the Gulf, to compare the Gulf to other areas, and to detect annual synchrony in growth and

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production among the major fish stocks. Catch data were also used to examine availability and migration timing. Many finfish stocks that utilize the Gulf of St. Lawrence for spawning and feeding grounds undertake long annual migrations, probably in response to the extreme range of environmental conditions, such as warm water in summer and ice cover in winter. The fisheries in the Gulf depend on regular migrations and the relation between commercial catch rates and fish abundance is likewise influenced by variations in these migrations. Thus, we hoped to provide an overview of the spatial and temporal variation in commercial catches to find if there were patterns among species, which could be used to infer generalized migratory behaviour. In particular, we examined within and among stock variation in the timing of catches for the principal fish species in the Gulf.

Landings

Northwest Atlantic

We examined trends in fishing yield as a first approximation to production. Total catch and its trend over time in the Gulf was compared to other areas in the northwest Atlantic. Nominal catch data were available from the Northwest Atlantic Fisheries Organisation (NAFO). In order to record data on a geographic scale suited principally to cod and haddock stocks (R.G. Halliday, DFO, BIO, Dartmouth, N.S. personal communication), the NAFO convention area has been divided into Sub-Areas (eg. SA1), Divisions (eg. 4T), and Subdivisions (eg. 4Vn) (Fig. 1). Unfortunately, non-gadoid stocks may not be well represented by these boundaries. For example, boundaries of several Divisions that follow deep trenches between shallow banks, are in the middle of habitat occupied by deep water species like redfish. Other stocks, such as mackerel, range widely over several sub-areas; mackerel production that occurs in the Gulf (SA4) will contribute to catches in SA5 at some later time (Sette 1950). Consequently, we defined six areas to account for the production of at least the major fish species in the northwest Atlantic, namely cod, herring and redfish:

West Greenland	(SA1)
Labrador	(2+3K)
Grand Banks	(3LMNOPs)
Gulf	(3Pn 4RSTVn)
Scotian Shelf	(4VsWX)
Georges Bank	(SA5)

Nominal catch data were compiled from the statistical bulletins of ICNAF (1955–78) and NAFO (1979–85). In 1959, catches in Divisions 3P and 4V were split into northern (3Pn and 4Vn) and southern (3Ps and 4Vs) components. For the period prior to 1959 therefore, we put catches from Division 3P into the Grand Banks group and those from Division 4V into the Scotian Shelf group. This assumption did not greatly affect the time series of landings for the Gulf, because catches in the northern components were small in comparison to those in the south. Since 1959, landings from Subdivisions 3Pn and 4Vn have been combined with Gulf landings because they are more properly associated with Gulf stocks (see Templeman (1962, 1979) for cod stocks and Winters and Beckett (1978) for herring stocks).

The general pattern of landings for the coastal areas (i.e., Labrador, Grand Banks, Scotian Shelf, and Georges Bank) was for high catches in the 1960's to early 1970's followed by a decline, then relative stability in the 1980's at levels not unlike those of the 1950's (Fig. 2). For West Greenland a different pattern was observed: catches declined in the late 1960's to a level only half of the 1950's. By contrast, in the Gulf, there was a peak in catch around 1970 followed by an overall increasing trend since 1977. The net result was that total catch from the northwest Atlantic increased steadily from about 2.0×10^6 t in the late 1950's to between $3.2–3.9 \times 10^6$ t in the late 1960's. Catches dropped back to the 2.0×10^6 t range before the extension of jurisdiction in 1977, and they have been stable since.

The similarity in trends among the areas was further investigated with an analysis of correlations. To reduce the influence of low-frequency variation and extreme values giving spurious correlations, a rank correlation was used (Conover 1980). Catches in the coastal areas were all highly correlated (Table 1). There were also significant correlations between Labrador and West Greenland, and between the Gulf and the Scotian Shelf. Thus, there appeared to be some synchrony of production in coastal areas and possibly between the Gulf and the Scotian Shelf, perhaps because the latter two areas are linked by the Cabot Strait. Gulf catches were not correlated with those from Labrador or the Grand Banks, and they were negatively correlated to catches at West Greenland.

These trends in catches could not be directly interpreted as trends in production because fishing effort was a major factor influencing catch. The 1960's and early 1970's are remembered for the high effort by distant water fleets in the northwest Atlantic and for expansion of the Canadian offshore fleet. During this period, the fisheries were removing the accumulated biomass (see Sinclair and Annand 1986 for an example). Since the extension of fisheries jurisdiction in 1977, there has been a general reduction of fishing mortality on the major stocks within the Canadian 200 mile limit and a related increase in population biomass (CAFSAC 1988a, 1989 present examples for several cod stocks). The fishing grounds on the Atlantic coast were subject to more effort by foreign and Canadian offshore fleets than the Gulf, which was closed to foreign fishing, except for France, in 1972 (Anon. 1980) and fishing by Canadian vessels greater than 100' (offshore) based outside the Gulf has been restricted since 1980. Thus, the high correlations in catches among coastal areas could be due partly to similar trends in fishing effort.

Within the Gulf

Since 1960, cod, herring, and redfish comprised 75% of the total catch in the Gulf of St. Lawrence (Fig. 3). This proportion fell to about 65% in the 1980's due largely to an increase in the landings of invertebrates. Snow crab, lobster and shrimp were the dominant invertebrate species. Other important fish species were American

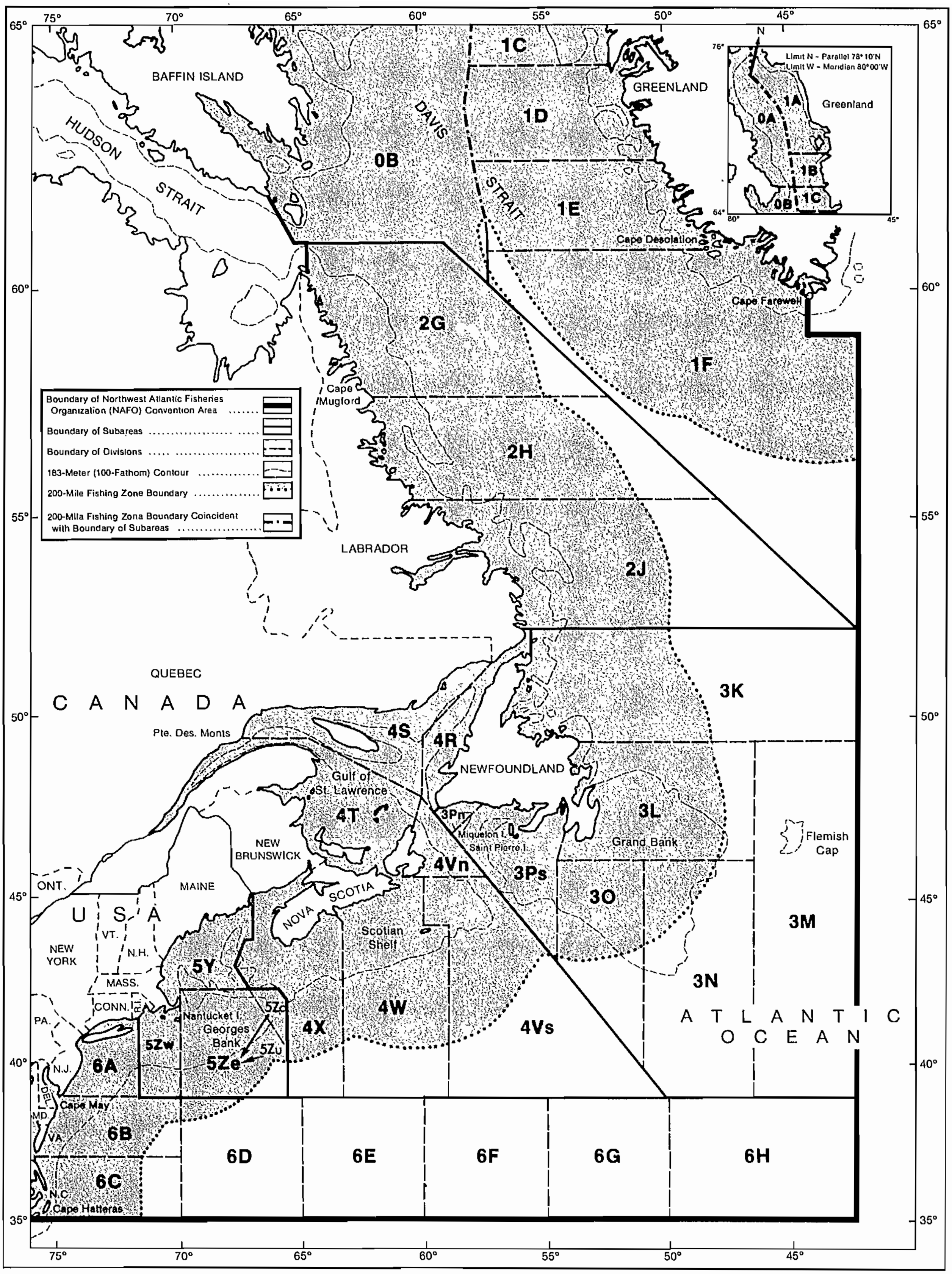

FIG. 1. NAFO Convention Area (taken from NAFO Statistical Bulletin).

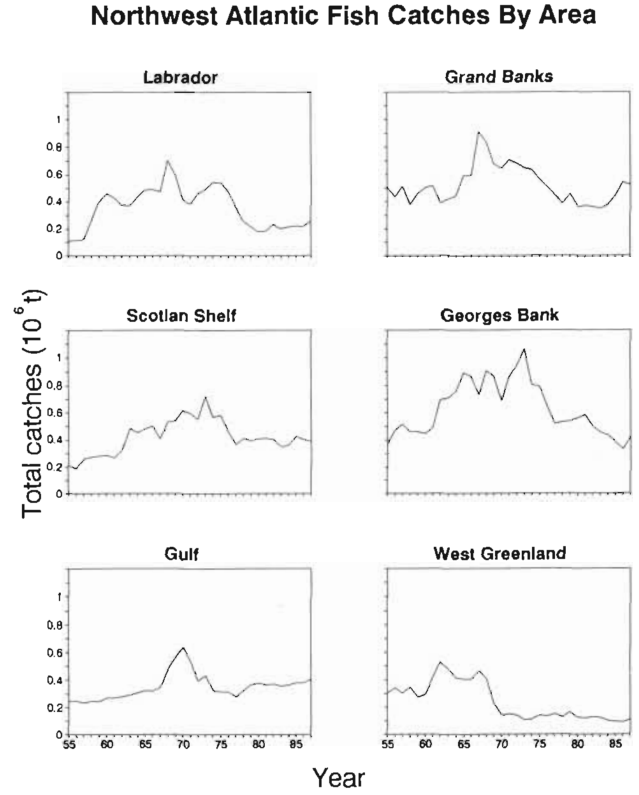

FIG. 2. Total catches of all species from selected areas of the northwest Atlantic.

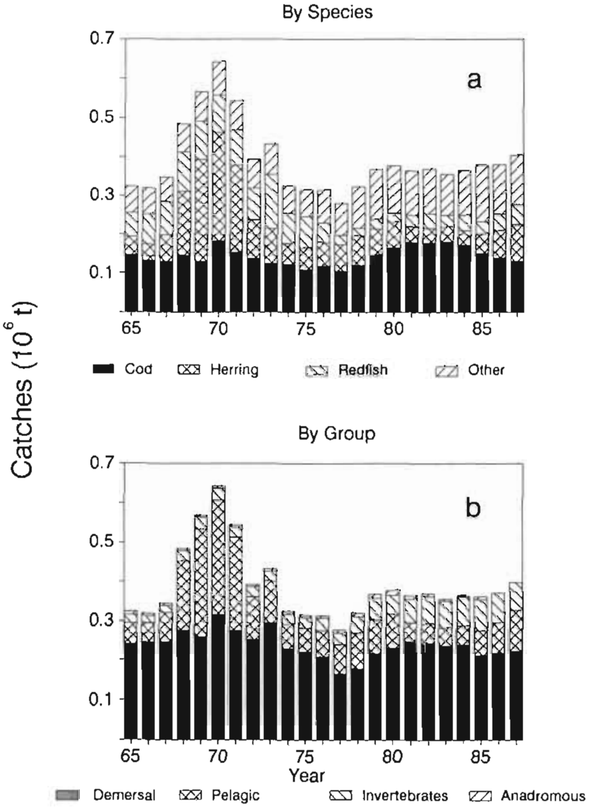

FIG. 3. Catches by (a) species and (b) ecological group in the Gulf of St. Lawrence.

plaice, mackerel and white hake. Together, these species comprised 90% of the catches since 1960.

The cod fishery in the Gulf has a long history dating back to the arrival of Europeans to the region, circa 1600. Inshore and offshore grounds have been exploited since at least the late 19th century. There are two major cod stocks in the Gulf, the northern stock inhabiting Divisions 3P, 4R and 4S, and the southern stock in Divisions 4T and 4Vn. Cod catches have been relatively stable in the past 20 yr, varying between 0.1-0.17 × 10^6 t.

The herring fishery yielded less than 0.05 × 10^6 t annually in the early 1960's and it was fished primarily with inshore gears. Landings rose sharply to a maximum of 0.28 × 10^6 t in 1970 with the heavy exploitation of the 1958-59 year-classes by a new purse seine fleet. Landings declined thereafter to about 0.04 × 10^6 t in 1981, remained stable to 1984 and have since increased to over 0.09 × 10^6 t. The purse seine fleet has been reduced in size and the majority of catch is again being taken by inshore gears. Herring spawn in the spring and fall, and for management purposes these components are considered separate stocks. Thus, there are four major stocks of herring in the Gulf comprising spring and fall spawners in Divisions 4T and 4R, respectively. Populations of unknown size also inhabit Division 4S.

The redfish fishery began in the late 1950's and expanded to a peak catch of 0.14 × 10^6 t in 1973. During the early 1970's exploitation of redfish increased due to the introduction of new vessels and midwater trawling. Following this expansionary period, landings declined to about 0.02 × 10^6 t by 1980. With the recruitment of new year-classes, landings increased to 0.05 × 10^6 t in

TABLE 1. Pearson ranked correlation coefficients of total catches from six regions in the northwest Atlantic. A single asterisk indicates significance at the $P < 0.05$ level while two asterisks indicate significance at the $P < 0.01$ level.

	West Greenland	Labrador	Grand Banks	Gulf	Scotian Shelf	Georges Bank
West Greenland		0.44*	0.22	−0.46*	−0.07	0.44*
Labrador			0.78**	−0.05	0.56**	0.71**
Grand Banks				0.36	0.57**	0.55**
Gulf					0.49**	0.13
Scotian Shelf						0.73**

1987. All catches of redfish in Divisions 4RST are considered as a single unit for management purposes. However, there is evidence for more than one species of redfish in the Gulf (Scott and Scott 1988).

The lobster, shrimp and crab fisheries in the Gulf expanded in the 1980's as indicated by an increase in both landings and fishing effort. The crab fishery has recently passed from an expansionary period to one of lower catches (CAFSAC 1988b), a transition typical of the exploitation of a virgin stock. Shrimp landings have stabilized at about 0.01×10^6 t, ten times higher than in the early 1970's. Lobster landings have increased in the last 5 yr to their highest levels in the century. Lobster fishing effort has been relatively stable and the rise in landings is indicative of an increase in biomass, and thus production, which has been a general trend for lobster in most of Atlantic Canada.

The biomass of important finfish and invertebrate species in the Gulf was derived by comparing exploitation rates to catches. For this purpose, exploitation rates referred to the fraction of the fishable population that was caught each year. Younger animals, due to their small size, are often not part of the fishable population. Exploitation rates were very different in finfish and invertebrate fisheries: they ranged from a low of 10% or less for redfish (Laberge 1988), to about 20% for cod (Chouinard and Sinclair 1988) and herring (Chadwick and Cairns 1988). For crab and lobster, the rates were in the 60–70% range (Mallet et al. 1988). The target exploitation rate for shrimp was 35% (CAFSAC 1987). Based on these rough approximations of exploitation rates (20% for finfish and 50% for invertebrates) and the breakdown of catches by species groups (Fig. 3), we concluded that the finfish species make up about 90% of the fishable population biomass in the Gulf.

Stock Production

We considered production (P) to be the biomass added to a population during a calendar year. Following the methods described by Rivard (1982):

$$P = R + G + D + Y$$

where R = recruitment biomass, the addition to beginning of the year biomass of the youngest year-class at the beginning of the year.

G = biomass increment of those fish that survive the year.

D = biomass increment of fish that die of natural causes throughout the year, and

Y = fishing yield during the year.

These various components of production were estimated for cod and herring using an age-structured, sequential population analysis (Pope 1972). This approach included only somatic growth because data were not available to include production of reproductive materials.

A general production analysis (Schaefer 1957) was used to estimate total annual production for redfish. The low exploitation rate for redfish and the large number of age classes precluded an age-structured analysis. The model produces annual estimates of stock biomass. The sum of recruitment (R) and growth (G) was obtained from the annual change in stock biomass ($B_{t+1} - B_t$), yield (Y), and the biomass of fish dying from natural causes (N).

$$R_t + G_t = (B_{t+1} - B_t) + Y_t + N_t$$

The N component was estimated as

$$N_t = B_t \exp(-Z_t)\, M/Z_t$$

where B_t = the biomass at the beginning of the year (time t)

Z_t = the instantaneous rate of total mortality

M_t = the instantaneous rate of natural mortality

Because there is no estimate of growth of fish that die through the year from natural causes, the D component would be underestimated. The value of M was assumed to be 0.1, which was consistent with the conclusions of Mayo (1980) for redfish in Gulf of Maine.

Age-structured estimates of production were calculated from the results of recent stock assessments for cod (Chouinard and Sinclair 1988, Fréchet 1988) and herring (Chadwick and Cairns 1988; McQuinn 1988). For redfish, annual estimates of biomass and catch from a general production analysis (Laberge 1988) were used to estimate production. It should be noted that in cohort analysis, population estimates for the last 4–5 yr are most dependent on input parameters, and therefore the least reliable.

Total production was significantly correlated ($P < 0.01$) for the two cod stocks in the Gulf (Fig. 4), mostly because of synchronous recruitment of relatively large year-classes in the late 1970's and early 1980's. Total cod production increased from 0.18×10^6 t in 1975, to a peak in the early 1980's of about 0.4×10^6 t (Fig. 5). In recent years, production has declined to less than 0.2×10^6 t in response to a decline in recruitment and also to a decline in weights at age (Chouinard and Sinclair 1988; Fréchet 1988). The northern stock (3Pn 4RS) was, on average, more productive.

Herring assessments have been conducted separately for spring and fall spawners. In 4T, 70% of the biomass was fall spawners, but in 4R 70% was spring spawners. Both the 4T fall and 4R spring herring stocks have experienced an increase in total production during the 1980's, largely because of increased recruitment. For the two smaller herring stocks (4T spring and 4R fall), total production was stable. Total production for all herring in the Gulf increased from 0.05×10^6 t annually in 1975, a period when the standing stock had been severely reduced, to 0.29×10^6 t in 1984 (Fig. 5). Since then production has fallen to about 0.16×10^6 t. Among the four herring stocks, total production was significantly correlated ($P < 0.01$) only for the 4T fall and 4R spring spawning components (Fig. 4). Given the spatial and temporal separation of these stocks, and the lack of other correlations it is difficult to attach any biological relevance to this observation.

There was little annual variation in total production of redfish. Good year-classes seemed to occur on a decadal time scale but their entry into the fishery was

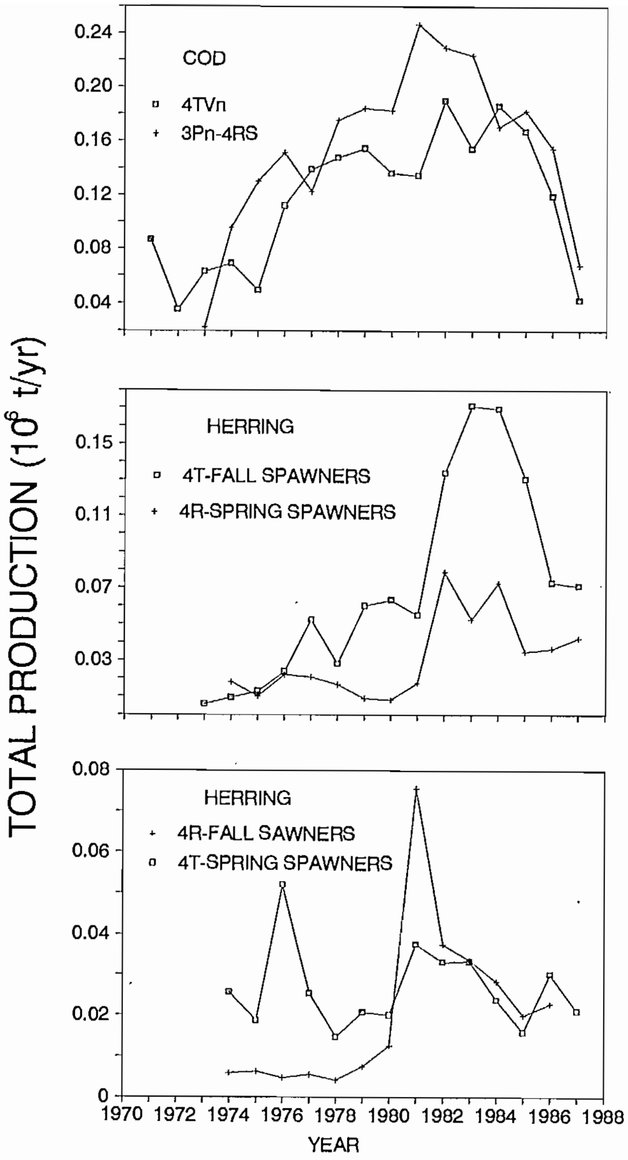

FIG. 4. Estimated total production for cod and herring stocks in the Gulf of St. Lawrence.

usually spread over 3–4 yr due to their slow growth. Since 1974, estimates of production varied between 0.14–0.21 × 10^6 t annually (Fig. 5).

The total biomass of cod, herring, and redfish has increased substantially over the past 12 yr, doubling from 1 × 10^6 t in 1974 to about 2.2 × 10^6 t in 1985–86 (Fig. 5). Total yearly production increased from 0.3 × 10^6 t to 0.8 × 10^6 t in 1982, and has declined to 0.5 × 10^6 t since. Assuming that these three species represent 80% of the commercial finfish biomass in the Gulf, then total finfish production in recent years has ranged between 0.6 to 1.0 × 10^6 t. Production of invertebrates has been in the range of 0.08 × 10^6 t in the 1980's, a value equal to total catch.

The use of age-structured data to estimate production, or the use of stock biomass estimates such as we have done for redfish, provide more accurate estimates of production than by simply adding up the catches. Over the period 1974–87, we estimated total production of cod, herring and redfish in the Gulf of St. Lawrence to be 7.4 × 10^6 t, while surplus production was 3.9 × 10^6 t. The difference between total and surplus production would be the production of those fish dying from non-fishing causes. Because total catch equalled 2.9 × 10^6 t, it underestimated total production by 60% and surplus production by 25%. This difference between surplus production and catch resulted in the doubling of biomass of these species over the 14 yr.

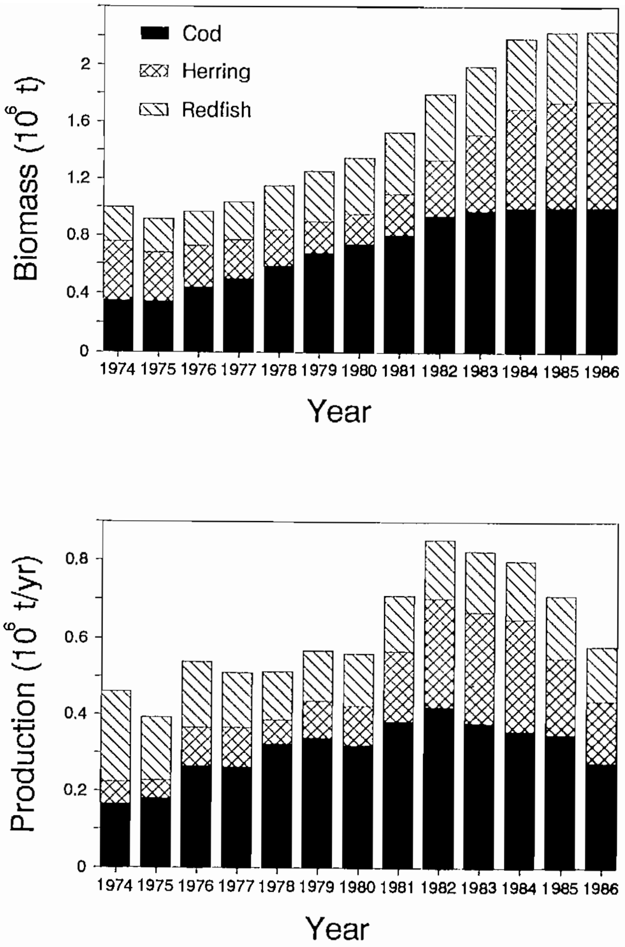

FIG. 5. Biomass and production of cod, herring and redfish in the Gulf of St. Lawrence.

Growth

The growth rates of individual cohorts of the cod and herring stocks were analyzed to determine if similar yearly patterns could be detected, which could possibly be related to important environmental events. Mean weight-at-age data from the respective assessment documents referred to above were used. The data originated from two sources, annual research vessel surveys and sampling of the commercial fisheries. The instantaneous growth rate of a cohort at a given age, calculated as the $\log_e$ ratio of weights at age in successive years, was modelled using dummy variables to represent age and year effects in a multiple regression (Draper and Smith 1966).

Data for the younger (ages 0–2 for cod and age 1 for herring) and older age-groups (age 10 and above) were not used because of low sample sizes and highly variable means. The range of years was dictated by the available data.

The age effect was important for each stock with growth rate decreasing with age. However, not all of the data sets had significant year effects (Table 2). Where year effects were significant, recent declines in growth rate were evident (Fig. 6). The interpretation of such trends in the commercial sampling data was complicated by possible shifts in the timing of the fisheries, rather than population changes. However, in the 4TVn (May–December) cod stock, the decline in growth rate was also apparent in data from research vessel surveys; these surveys were conducted at the same time each year, which indicated the decline was biological.

For stocks with significant annual variation in growth, no single year stood out as either high or low. Rather, the general trend for reduced growth rates in the recent past coincided with the doubling of biomass of these stocks. We cannot conclude that there were no significant environmental effects in this time period, but only that they did not show up as changes in growth.

Patterns in Availability

In this section, fish production is put into context with the pronounced seasonality of the Gulf by examining the spatial and temporal distribution of catches. In general, we believe that the distribution of catches could be used to infer some general aspects of the migratory behaviour of several fish species. Some of the questions that we addressed were as follows: when were fish resident in the Gulf? did they have different residence times and different migratory routes? were there patterns in the distribution of catches among different areas of the Gulf? what was the degree of annual variation in the distribution of catches? and finally, were there certain anomalous years where environmental conditions influenced migration timing and therefore timing of catches of all fish species?

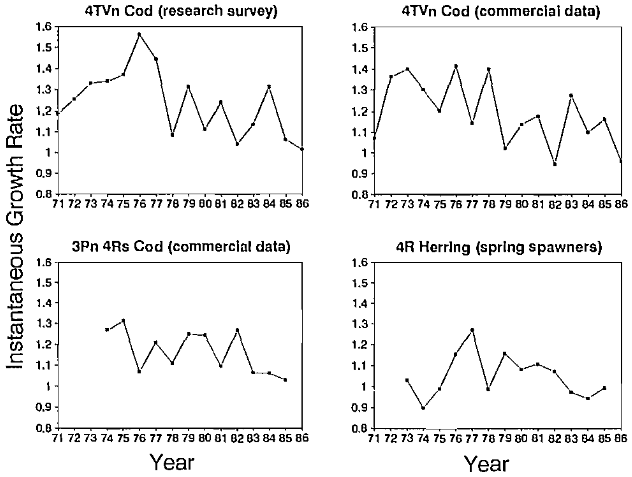

FIG. 6. Yearly growth rates for cod and herring in the Gulf of St. Lawrence standardized for age differences.

Migration timing of the major fish species was estimated from daily catches in commercial fisheries and tested for area, season and year effects. The major fish species were cod, herring, redfish, mackerel, white hake and plaice. When catches are sold, their weights are recorded in pounds on purchase slips. Purchase slips are completed separately for each fishing vessel and because a vessel normally makes no more than one trip per day, each slip is assumed to be one unit of fishing effort. Daily purchase slip data were available for 1978–87. Supplementary A and B slips were not included in the analysis.

Migration timing was described as the median catch date, or the day when 50% of the cumulative catch was taken during a particular season or year. A measure of the duration of the fishery was calculated as the number of days between the first and third quartiles. Although many different fishing gears are used in the Gulf, data were treated for all gear types combined. Similarly, no adjustments were made to account for any changes in fishery regulations.

TABLE 2. Summary of results of a multiple regression analysis of instantaneous growth rates of several Gulf of St. Lawrence fish stocks as a function of age and year. An 'S' denotes a significant effect.

Stock	Ages	Years	Effects		
			Age	Year	R^2
Cod 4TVn(M-D) RV	3-9	71-87	S	S	0.80
Comm	3-9	71-87	S	S	0.55
3Pn 4RS Comm	3-9	72-86	S	S	0.67
Herring 4T Spring Comm	2-9	74–76, 82–86	S		0.49
4T Fall Comm	2-9	74–76, 82–86	S		0.72
4R Spring Comm	2-9	73-86	S	S	0.74
4R Fall Comm	2-9	73-86	S		0.37

Twenty four NAFO statistical unit areas within the Gulf of St. Lawrence were delineated to examine area differences in fishery timing for each species (Fig. 7), and thus to infer migratory patterns.

Season effects were treated separately for each species. Seasonal peaks in catches were identified for each year and area from frequency distributions of daily catches. For all species, except herring and mackerel, a distinct peak in catches was seen during the winter months and therefore catches from January to March were treated separately from the other months. For the remaining part of the year, seasons were defined as follows: herring had two seasons, before and after July 1, which corresponded to the spring and fall spawning-group fisheries; cod had two seasons, in Cape Breton (4Tf and 4Tg) and Chaleur Bay (4Tl and 4Tm), before and after August 31; mackerel had two seasons, in Cape Breton (4Tf, 4Tg and 4Th) and Sydney Bight (4Vn), before and after August 31; and, redfish had two seasons that were separated in all areas by July 31. The seasonal peaks were less pronounced for redfish than the preceding three species and the analysis was also repeated by assuming that this species had only one seasonal peak in catch. The remaining two species, plaice and white hake had only one peak in their daily catch distributions.

Run timing of selected anadromous species was also calculated. Good measurements of run timing were available for anadromous species because they are counted in rivers at various locations in the Gulf (Chadwick et al. 1985). The following areas and species were considered: salmon in 4R(a,b,d) and 4T(g,l,m); smelt in 4Tg and 4Tl; and gaspereau in 4Tg and 4Tl.

Multiway ANOVA was used to test for significant differences in median dates in migration timing and duration for species, area, season and year effects. The analysis was done using PROC GLM procedure (SAS 1986).

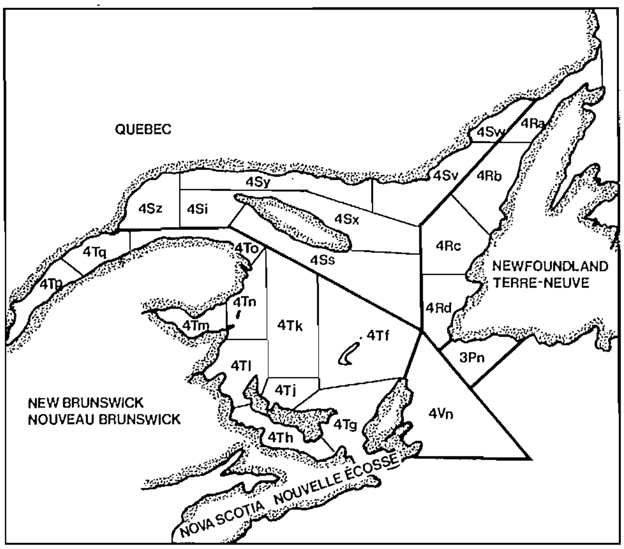

FIG. 7. NAFO unit areas in Gulf of St. Lawrence.

Seasonal Variation

Some marine species were resident year round in the Gulf but they had seasonal patterns in their abundance. Winter fisheries were present in all Divisions (Fig. 8), except the southern Gulf (4T). Divisions 4V, 4R and 3P had relatively important winter fisheries; the fisheries in 3P were later than the other Divisions. Three peaks in the summer-fall fisheries were most apparent in 4S and 4T, which suggested that seasonal patterns in abundance were most apparent in these Divisions. Variation in the timing of peaks was significant among areas and species, but not among years.

Spatial Variation

Winter fisheries, i.e. fisheries before day 100, were concentrated in only deeper waters of the Gulf. Thus catches were taken in only 8 of 24 possible unit areas, including 4Tf, 4Ss, 4Ra, 4Rb, 4Rc, 4Rd, and 4Vn. Finally, only 5 of 6 species were caught at this time; mackerel were absent and herring were caught only in 4Vn during January.

For summer-fall fisheries, migration times were different for each species (Fig. 9). Over 70% of herring fisheries had only 10-20 d between quartiles 1 and 3, which indicated that they were generally of short duration and that

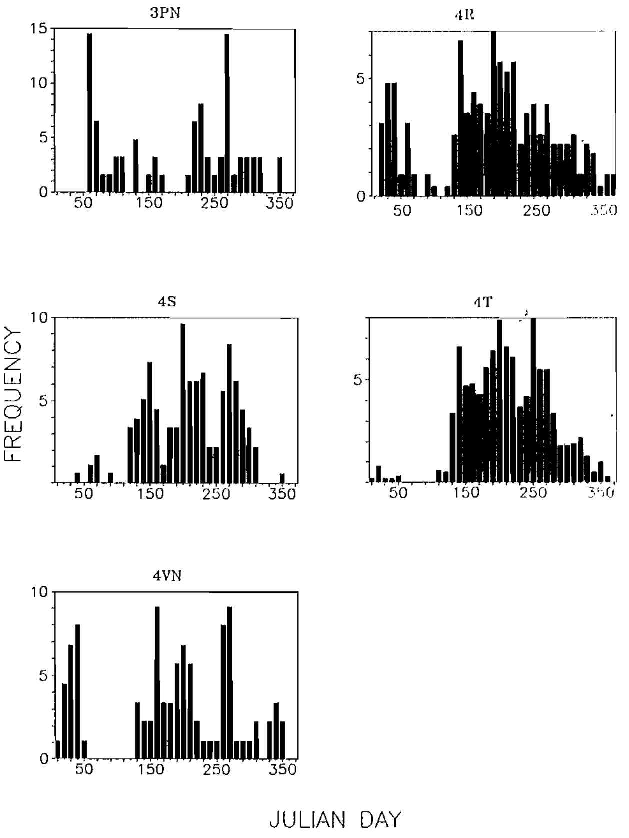

FIG. 8. Distribution of median dates for cod, plaice, herring, redfish, mackerel and white hake fisheries in NAFO Divisions of Gulf of St. Lawrence. Data were combined for 10 years, 1978-87.

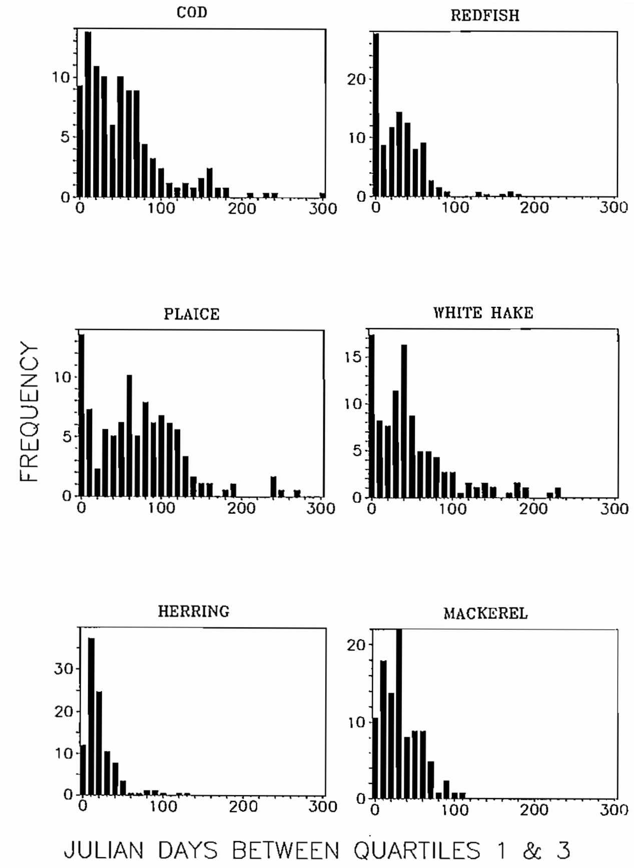

FIG. 9. Distribution of duration of cod, plaice, herring, redfish, mackerel and white hake fisheries in Gulf of St. Lawrence. Data were combined for all 24 NAFO unit areas and 10 years, 1978–87. Duration was measured as the number of days between the first and third quartiles.

herring was a relatively mobile species. Over 50% of mackerel fisheries had 10–30 d between the two quartiles, which again indicated that mackerel was a mobile species. There were 10–60 d between the two quartiles for 50% of cod, white hake and redfish fisheries. For 50% of plaice fisheries, there were 10–100 d between the first and third quartiles, which indicated that plaice was the least migratory species.

There appeared to be two kinds of species: those which were caught in all areas of the Gulf at the same time and those which had significant area effects. Herring was the only species that did not have a significant area effect (Figure 10). Herring arrived on their spawning-grounds in all areas of the Gulf at the same time, around day 140 (mid-May) in spring and day 250 (early September) in fall. This observation suggested that herring were sub-divided into many stock units. Later catches of herring were observed in purse seine fisheries that catch overwintering aggregations in 3Pn, 4Vn and 4R.

By contrast, the other species tended to arrive in each area at different times (Fig. 10). This lack of synchrony suggested that these species comprised only a few large stocks, which made extensive migrations throughout the Gulf. Cod arrived following herring in areas 4Tf and 4Tg, then it arrived in areas 4Si, 4Ss,4Sv,4Tn,and 4Vn. These arrival dates were coincident with herring. Of all species, cod remained longest in the Gulf, with peak catches on day 320 in 4Tf and 4Tg. Plaice follow closely behind cod, but arrived first in north-central Gulf, areas 4Si, 4Ss, 4Sv, and 4Sw. Peak catches occurred in almost all areas before day 200. Plaice were last caught in 4Sx and 4Tm. Mackerel arrived at different times, but tended to leave all areas at the same time, about day 270. There were two peaks to redfish catches: they were caught first between days 180 and 220 and then day 260 to 280, about the same time as mackerel catches. White hake arrived latest; in most years, catches peaked after day 200. Generally, there was little annual variation in the timing of catches for white hake.

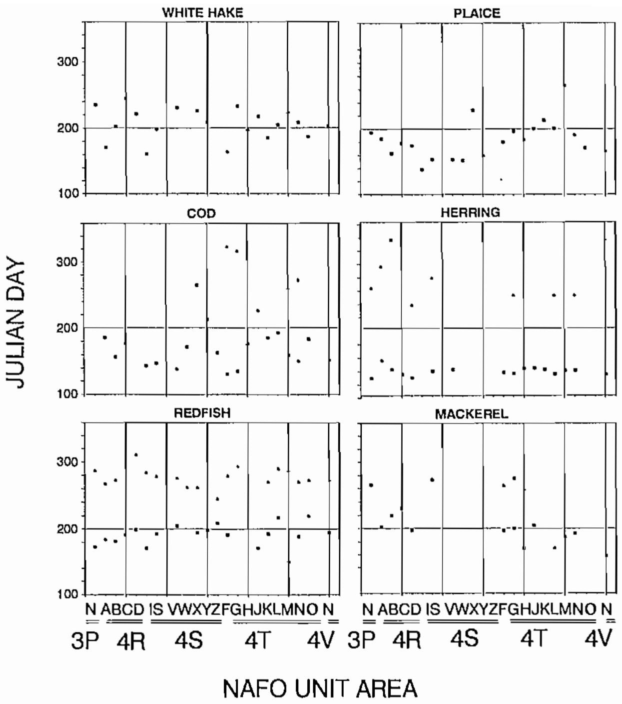

FIG. 10. Median dates for cod, plaice, herring, redfish, mackerel and white hake fisheries in 24 NAFO unit areas of Gulf of St. Lawrence. Data were combined for 10 years, 1978–87. The line at Julian Day 200 is for reference only.

Run timing of anadromous species had the following patterns (Fig. 11). Smelt arrived in 4Tg and 4Tl simultaneously, which suggested that stocks from these areas overwintered separately. It should be noted that numbers of fish counted at weirs for anadromous species were not necessarily equivalent to catches. For example, there were very important winter fisheries for smelt that occurred at times different from when this species was counted at weirs during its spawning migrations. These winter fisheries, which occur in shallow waters, indicated that smelt overwinter in the Gulf (Cairns 1989).

By contrast, gaspereau arrived in 4Tg about 20 d before it arrived at rivers in 4Tl (Fig. 11). The delay between the two areas suggested that gaspereau had a different overwintering behaviour than smelt. It is possible that gaspereau stocks overwinter together in the same area. Gaspereau therefore appeared to have spawning times that were unique to each river.

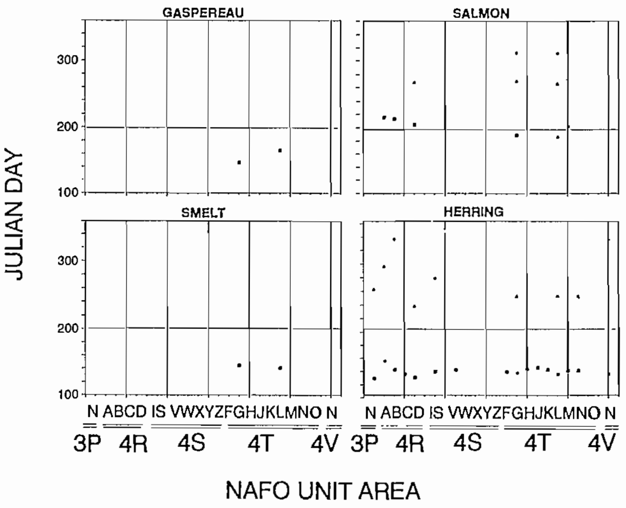

FIG. 11. Median dates for upstream counts of gaspereau, Atlantic salmon and smelt for rivers located within NAFO unit areas of the Gulf of St. Lawrence. Data were combined for 5 years, 1983–87. Median dates in herring fisheries from Fig. 10. are included for comparison.

Although there were three distinct migrations, Atlantic salmon from different areas arrived at natal rivers at the same time. There was one exception, stocks from 4Ra and 4Rb on the northwest coast of Newfoundland arrived 10–20 d later than other stocks (Fig. 11). It was likely that the northern salmon stocks had entirely different migration routes from stocks in the southern Gulf. In general, it appeared that smelt and salmon could be loosely classified with herring as species that demonstrated some spatial synchrony in the timing of their spawning migrations. On the other hand, gaspereau was more akin to cod, plaice, mackerel and white hake and had significant area effects in migration timing.

In addition, each of the latter four marine species appeared to have different migration routes. The migration routes were inferred by following the sequence of median catch dates (Fig. 10). For example, plaice appeared to migrate into the southern Gulf from Gaspé and Sydney Bight at about the same time, and then into shallower waters of upper Chaleur Bay and north shore of Prince Edward Island. By contrast, cod migrations started around Magdalen Islands, splitting into two groups: one group moving north and into Chaleur Bay; the other moving towards eastern Prince Edward Island, then along the north shore of the island towards Cape Breton. These inferred movements of cod are generally supported by the studies of Jean (1964) and Templeman (1979). White hake migrations appeared to begin south of Magdalen Islands, branching into three groups that moved at the same time into Chaleur Bay and the eastern and western ends of Northumberland Strait. Finally, mackerel were caught as they migrated southwards along the west coast of Newfoundland and as they were leaving Northumberland Strait and Chaleur Bay. Thus, the timing of catches in fisheries suggested that each species has a unique migration route.

Annual Variation

There was very little annual variation in the migration timing of the major fish species in the Gulf. Year effects were significant for only three species: mackerel, herring and cod (Fig. 12). For mackerel, the early summer catches in 1985 were significantly earlier than other years. There was no significant year effect for timing of late summer mackerel catches. Significant year effects were found for the timing of catches of fall spawning herring, where in 1984 they were significantly later than the reference year. For cod, significant year effects were found for spring and fall catches. For spring catches, 1983 was significantly earlier than the reference year. For fall catches, 1985 was significantly later than the reference.

There was no anomalous year that had a significantly later or earlier migration timing for all species. At best, 1984 was a late year for several species. However, it was clear that there was no pattern among species; each species appeared to be independent of the others and annual variation in timing of catches was always less than the variation due to species and area effects.

An example of the slight annual variation in timing of catches for some species in Miramichi Bay (4Tl) is shown in Fig. 13. Annual variation in timing of herring and

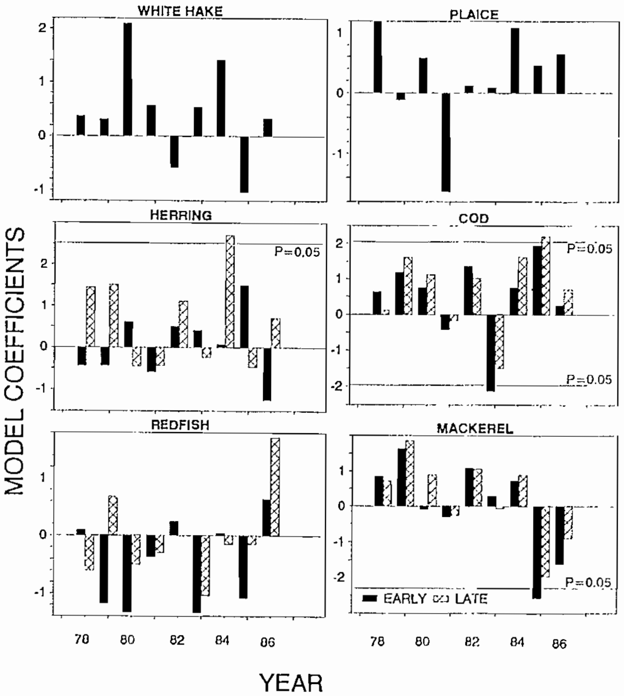

FIG. 12. Year effects for median catch dates of six Gulf finfish species, 1978–87. Year effects are expressed as regression coefficients for all years relative to 1987: positive values indicate that the median catch date in a particular year was later than 1987; negative values indicate that the median was earlier. Data are shown for early and late cod, redfish, mackerel and herring fisheries. Only four coefficients were significantly different from 1987: late or fall spawning herring were late in 1984; early or spring mackerel fisheries were early in 1985; early cod fisheries were early in 1983; and, late cod fisheries were late in 1985. Horizontal lines indicate significance, $P = 0.05$.

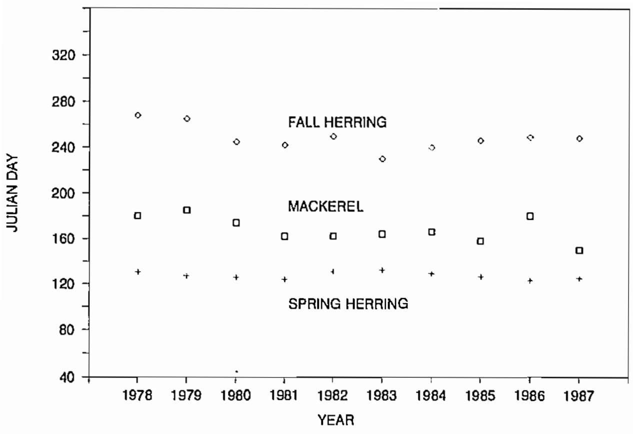

FIG. 13. Annual variation in the median catch date of herring and mackerel fisheries in Miramichi Bay (4Tl).

mackerel catches was very small and similar to the small variation in run timing that has been described for gaspereau, smelt and salmon (Chadwick and Claytor 1989). It appeared that, at least in Miramichi Bay, migration time of herring and mackerel was highly predictable.

Conclusions

In this paper, we have drawn inferences about the dynamics of aquatic resources in the Gulf of St. Lawrence almost exclusively from catch data. Although the analysis is not exhaustive, several important conclusions can be made. First, trends in total catch from six geographic areas in the northwest Atlantic indicated that the Gulf was somewhat unique in comparison to other coastal areas. This was consistent with a study by Koslow (1984) who, in an analysis of environmental forcing on recruitment of northwest Atlantic cod and haddock stocks, noted that the cod stocks in the southern Gulf did not conform to the general pattern of stocks outside the Gulf. While the different trends in catches may have been partly due to differences in fishing effort within and outside the Gulf, they may also indicate that the Gulf responds differently to large-scale forcing.

Second, about 80% of the commercial finfish and invertebrate biomass in the Gulf comprised three species, cod, herring and redfish. This conclusion was based on an analysis of catch and exploitation rates. While catches of invertebrate species such as snow crab, lobster and shrimp have been high, these species are exploited at much higher rates than fish.

We have also demonstrated that catch alone is a poor approximation to total production. At equilibrium, a fishery would be cropping surplus production, and catch would not provide any estimate of the biomass of fish dying from natural causes throughout the year. Comparisons of catch among areas, therefore, would only be indicative of relative production. When populations are not in equilibrium, catch and production become more different. For example, since 1975, catch of Gulf cod, herring and redfish varied between 0.21×10^6 t and 0.25×10^6 t (Fig. 3) while production varied between 0.4×10^6 t and 0.9×10^6 t (Fig. 5). In addition, these were minimum estimates of production, because we were unable to account for non-commercial species, the production of reproductive materials, or the production of young fish.

Third, there was synchrony in production of the two cod stocks in the Gulf and between two of the four herring stocks studied. This was largely because of similar, low-frequency trends in recruitment. However, there was no synchrony in production among species.

Fourth, timing of catches, which was used as a proxy for migration timing, had strong season and area effects, but small year effects. In other words, there was little annual variation in the timing of fisheries. It was clear that each species had its unique migration route into and out of the Gulf. For most species, timing of fisheries varied around the Gulf, except herring and smelt, which appeared to arrive in all areas of the Gulf at the same time.

Finally, there was no anomalous year that affected production or migration timing of all species together, thus it was concluded that any studies on how environmental factors influence the dynamics of fish populations would require careful understanding of the life history of each individual species. Given the richness of interspecific variation in growth and migration, the extensive data on fisheries and oceanography and the closed nature of the system, the Gulf of St. Lawrence provides a unique area for studying the effects of oceanographic processes on commercial catch.

Acknowledgements

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CHAPITRE IV.
LES CONTRIBUTIONS SCIENTIFIQUES

CHAPTER IV.
CONTRIBUTED PAPERS

Changes in the Temperature–Salinity Characteristics of the Deeper Waters of the Gulf of St. Lawrence over the Past Several Decades[1]

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BUGDEN G .L. 1991. Changes in temperature–salinity characteristics of the deeper waters of the Gulf of St. Lawrence over the past several decades, p. 139–147. *In* J.-C. Therriault [ed.] The Gulf of St. Lawrence: small ocean or big estuary? Can. Spec. Publ. Fish. Aquat. Sci. 113.

Changes of up to 2°C in the temperature of the deeper waters of the Gulf of St. Lawrence have been observed over the past several decades. Temperatures were very low during the middle 1960's and have recently reached the highest sustained values attained over the last half century. The temperature variations are very coherent along the Laurentian Channel from Cabot Strait to the St. Lawrence Estuary, a distance of over 1000 km. The temperature changes are largely density compensated through changes in salinity. Observed along channel gradients and phase lags are consistent with forcing which originates at the edge of the continental shelf. The phenomenon of shear dispersion allows the up-channel propagation of the changes to be described by a simple advection–diffusion equation. The forcing at the continental slope is a result of varying proportions of Labrador and Western North Atlantic Water supplied along density surfaces to the mouth of the channel. This may be monitored by the position of the shelf–slope water boundary giving some predictive capability.

Une variation atteignant jusqu'à 2°C de la température des eaux plus profondes du golfe du Saint-Laurent a été observée au cours des quelques dernières décennies. Les températures qui étaient très faibles au milieu des années 60 ont récemment atteint de manière soutenue les valeurs les plus élevées du dernier demi-siècle. Les variations de la température sont très cohérentes le long du chenal Laurentien, du détroit de Cabot jusqu'à l'estuaire du Saint-Laurent, soit sur une distance de plus de 1000 km. Les modifications de la température sont en grande partie compensées par la densité, par l'entremise de modifications de la salinité. Les gradients et les retards de phase observés le long du chenal sont conformes à une entraînement dont l'origine se situe au rebord du plateau continental. Le phénomène de la dispersion par cisaillement permet la propagation vers l'amont du chenal des modifications décrites au moyen d'une équation simple d'avection-diffusion. L'entraînement au talus continental résulte des proportions variable d'eau du Labrador et de l'Atlantic Nord occidental apportées à l'embouchure du chenal le long des surfaces de densité, ce qui peut être surveillé par l'entremise de la position de la limite entre l'eau du plateau et l'eau du talus qui offre ainsi certaines possibilités de prévision.

Introduction

The Laurentian Channel (Fig. 1) is a deep trough which extends from the edge of the continental shelf through the Gulf of St. Lawrence and into the St. Lawrence Estuary, separating the Grand Banks of Newfoundland and the Scotian Shelf. This trough, which maintains depths of over 300 m throughout most of its 1100 km length, provides the only deep access to the Gulf for waters of oceanic origin.

The waters of the Laurentian Channel (Fig. 2) may be divided into three layers: a surface layer approximately 50 m deep which displays large variations in temperature and salinity in response to vernal changes in surface heat flux and freshwater discharge, an intermediate cold layer extending from about 50 to 150 m with lesser seasonal variations merging with the surface layer in winter, and a deeper, warmer layer extending to the bottom which undergoes only longer term changes (Bugden 1981).

The deeper layer generally exhibits a weak temperature maximum at a depth of approximately 250 m (Fig. 2). Variations in the value of the temperature maximum over several years were first noted by Lauzier and Trites (1958) at Cabot Strait, the entrance to the Gulf of St. Lawrence. Using data from irregularly-spaced cruises, some extending back as far as 1915, they described changes in the maximum temperature from the 1920's to the early 1950's. They assumed the deeper waters of the Laurentian Channel to be formed of a mixture of Labrador and Slope Water in essentially constant proportions, steadily

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[1] This paper forms part of the Proceedings of a Workshop/Symposium held at the Maurice Lamontagne Institute, Mont-Joli, Quebec, 14–17 March 1989.

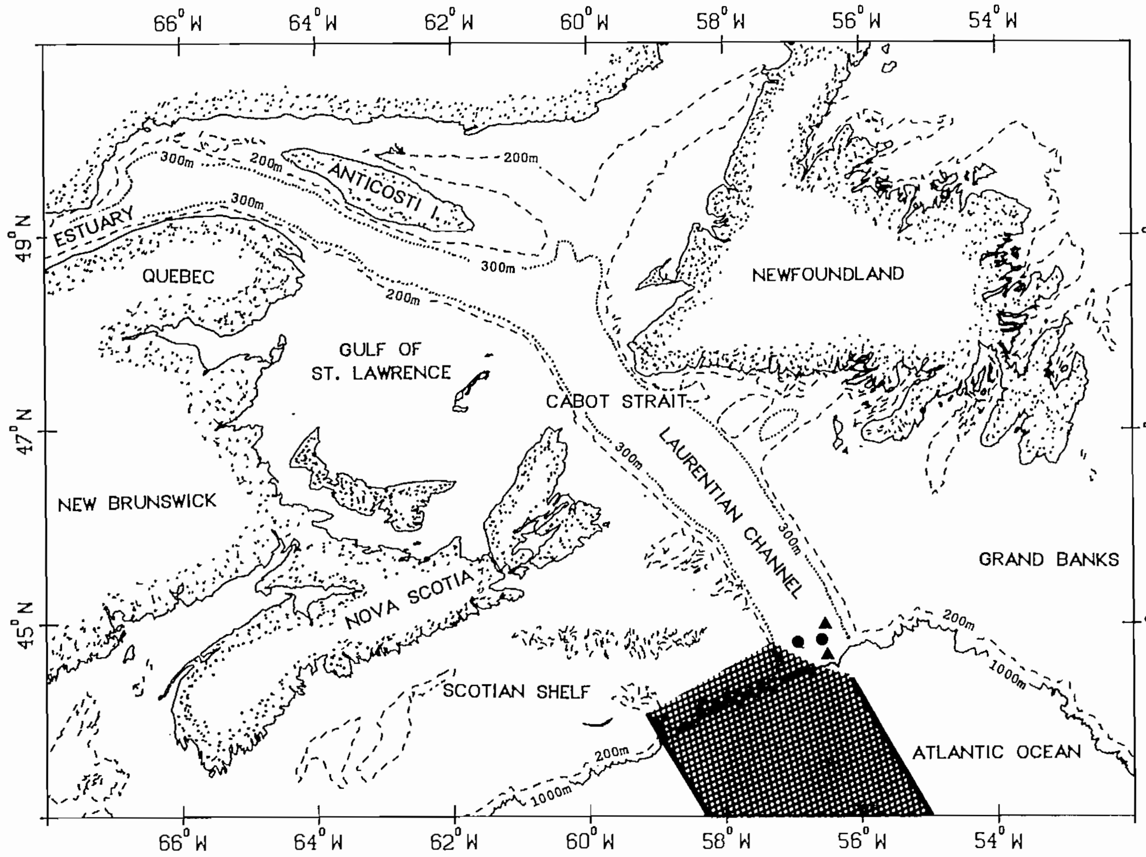

FIG. 1. The Gulf of St. Lawrence showing the Laurentian Channel as delineated by the 200 and 300 m isobaths. Also shown are hydrographic station positions at the mouth of the channel (circles-1976, triangles-1960). The shaded region is an area where satellite imagery was analyzed.

supplied to the Gulf from the edge of the continental shelf. On the basis of T–S analysis they attributed the observed temperature variations to changes in the temperature of the Labrador Water.

El-Sabh (1973) extended the work of Lauzier and Trites (1958) through to 1971 and also showed that lateral differences in the T–S characteristics of the deeper waters exist between the two sides of the channel.

In many flow regimes the rate of separation of fluid parcels by turbulent diffusion is greatly exceeded by the rate of separation caused by the different advection velocities experienced by the parcels as they are randomly diffused along vertical or horizontal velocity gradients. This enhanced separation may sometimes be expressed as a shear-dependent Fickian diffusion coefficient. Since the publication of G. I. Taylor's classic papers on the dispersion of dissolved tracers in shear flows (Taylor 1953, 1954) the concept of "shear dispersion" has been applied to a wide variety of environmental flows (e.g. Young et al. 1982).

In this paper, I will describe changes in the characteristics of the deeper waters of the Gulf of St. Lawrence, enlarging upon the analysis of Lauzier and Trites (1958) and that of El-Sabh (1973). The propagation of these changes along the Laurentian Channel will be examined in the context of shear dispersion. I will show how these changes move slowly up the channel in a manner such that the along channel evolution of the cross-channel average may be described by a simple one-dimensional advection-diffusion equation. The changes will be shown to be largely density compensated, suggesting that they originate from variations in along-isopycnal mixing near the mouth of the Laurentian Channel at the edge of the continental shelf.

Variations in Water Properties

Variations at a Fixed Depth

All bottle and bathythermograph data for the Gulf of St. Lawrence were obtained from the Marine Environmental Data Service in Ottawa. For recent years, these observations were supplemented by CTD data from files at the Bedford Institute of Oceanography. Seven rectangles along the Laurentian Channel, named for nearby geographic features, were chosen for data selection (Fig. 3). The rectangles were, as much as possible, located to encompass traditional hydrographic sections. For stations within each of these rectangles, average variables at 250 m for each month for the years 1950 to the present were calculated.

Figure 4 shows the resulting time series of temperature, salinity and sigma-theta from two rectangles separated by approximately 450 km along the axis of the Laurentian

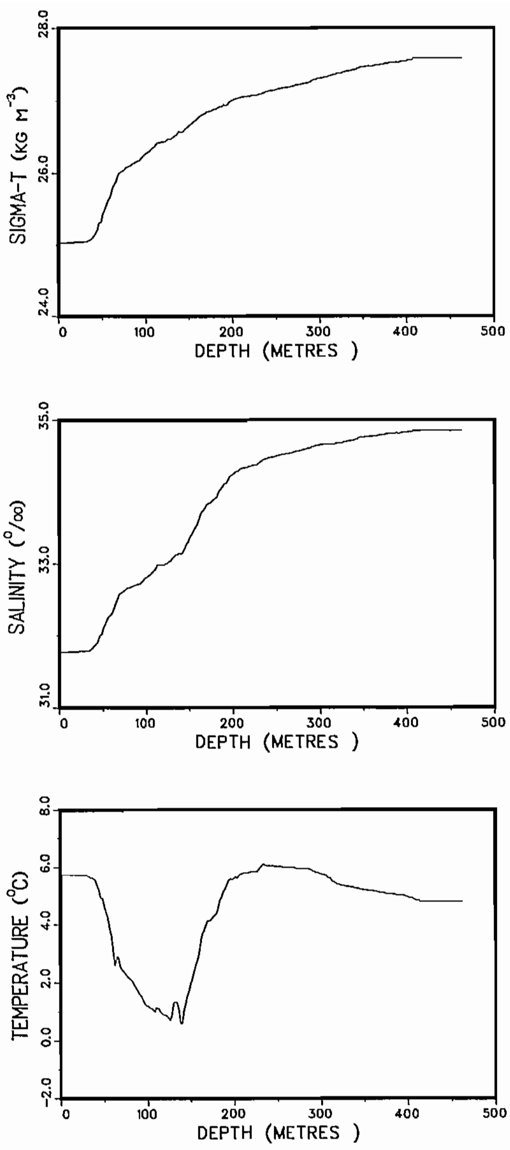

FIG. 2. Typical temperature, salinity and density profiles from the Laurentian Channel from data obtained in November 1983.

Channel. To illustrate only the longer time scale changes, the filtered series was prepared by filling data gaps with linearly interpolated values and applying a 37-mo running average filter. Several significant and well-resolved temperature excursions are evident in Fig. 4. The temperature at Cabot Strait rises from a low of about 4.5°C in mid 1966 to about 6.1°C in late 1985. Also apparent in Fig. 4 is an along-channel temperature gradient of about 1.8×10^{-3} °C km^{-1}, the difference in the average of the two time series being about 0.76°C. The temperature signal is seen to be very coherent along the channel with phase lags suggesting an advection velocity of about 0.5 cm s^{-1}.

It is evident from Fig. 4 that significant changes in salinity also occur and that they are positively correlated with temperature. The salinity data are not of as high a quality as the temperature data for several reasons. Salinity is more difficult to measure accurately than temperature and, in addition, a profiling instrument for salinity (conductivity) similar to the bathythermograph for temperature did not become generally available until the early 1970's. This reduces the amount and vertical resolution of the salinity data as only discrete bottle observations are available for earlier years. However, the along-channel phase lag and gradient indicated in the temperature series are also clearly discernible in the salinity series.

Both temporal and along-channel temperature changes appear to be density compensated through the salinity changes. The density, displayed as sigma-theta in Fig. 4, suffers from the same quality problems as the salinity because of the intimate relationship between these two variables. In spite of this, it is evident from the figure that the density at this depth is essentially constant both in time and along the channel. The mean value of all density points shown in Fig. 4 is about 27.26 and the scatter can be explained by vertical isopycnal displacements of only about 15 m given the average vertical density gradient at this depth (Fig. 2). On the other hand, at the Cabot Strait average 250 m salinity of 34.49, the previously described temperature change of about 2°C implies a sigma-theta change of about 0.2 which is not apparent in the data. There is also no apparent along-channel phase lag in the density series as is present in the temperature and salinity. This seems to suggest that the small density changes which are observed at this depth are the result of a different mechanism than the temperature and salinity changes. The observed identical, near-simultaneous changes at widely separated sites suggests that they may be the result of large scale set-ups or set-downs due to atmospheric or upper layer forcing.

Vertically Averaged Temperature Data

As the temperature data are of higher quality and more abundant than salinity data, further analysis concentrates on this variable. The average monthly temperature from 200 to 300 m was calculated for each of the rectangles. The resulting time series from the Cabot Strait rectangle is displayed in Figure 5. The filter used in this case was only a 13-mo running average because of the smoothing effect of the vertical averaging. The relatively densely sampled period from the late 1960's to the early 1970's illustrates that changes on time scales of less than a few years are much smaller than those on decadal scales. Figure 6 shows the filtered time series from two other rectangles in addition to that from Cabot Strait. The gap in the South Point series near 1980 is the result of an absence of data over about five years. The along channel coherence, phase lag and gradient are even more evident in the smoother vertically averaged data. The vertical arrows in Fig. 6 connect common features in the Cabot Strait and Port Menier signals by a lag corresponding to an advection velocity of 0.5 cm s^{-1}. The pattern of the temperature variations exhibited in Figure 6 suggests that a one-dimensional advection-diffusion equation might be used to describe the along-strait evolution of the cross-channel averaged temperature. Such an equation, combining vertical and horizontal diffusion with advection, could reproduce the observed along-channel phase lag and gradient.

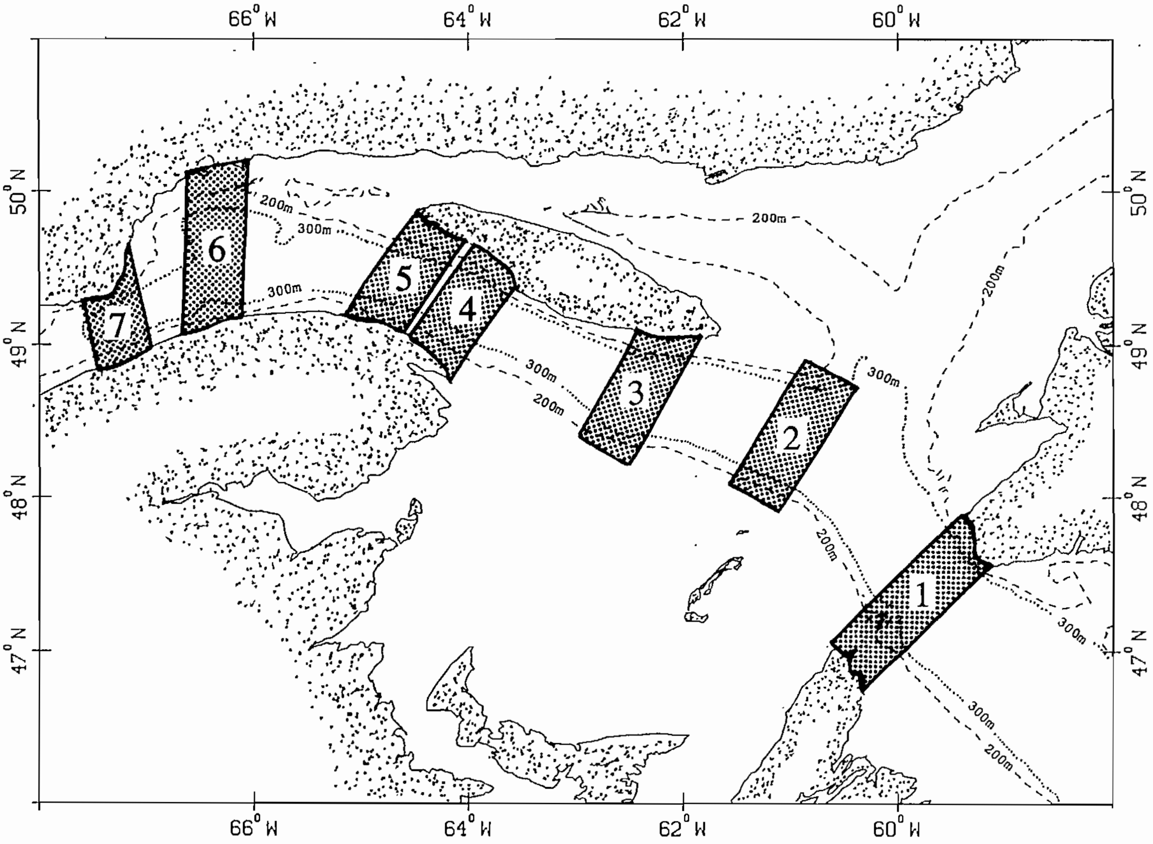

FIG. 3. Rectangles for abstraction of temperature-salinity data. 1. Cabot Strait, 2. Esquiman, 3. South Point, 4. Southwest Point, 5. Port Menier 6. Sept-Iles, 7. Pointe-des-Monts.

Dynamics in the Channel

Average Currents in the Channel

The mean currents at depths of over 200 m in the Laurentian Channel are dominated by cross-channel shear with a small average inward transport. The direction and magnitude of the cross-channel averaged current is consistent with the approximately 0.5 cm s^{-1} advection velocity implied by Fig. 6. Figure 7 shows average current vectors from all the current meter records from the Gulf available from the archives at the Bedford Institute of Oceanography with deployments of greater than 20 days and from depths greater than 200 m. These data are widely separated in space and time with record lengths varying from slightly more than 29 d to more than two years. A strong cross-channel shear is apparent with inward flow on the northeastern side of the Laurentian Channel and outflow on the southwestern side. Near the edges of the channel, the currents tend to parallel the local topography. Currents closer to the centre of the channel are seen to be weaker than those near the edges. Figure 8 shows the currents plotted as average current speed vs distance from the axis of the channel. Speed was chosen to eliminate the effects of local topography. This is equivalent to choosing the local coordinate system of the flow to be in the direction of the local average current. Inward flow is plotted as negative, and positive displacement from the axis of the channel is to the northeast. A linear least squares fit of current speed vs distance from the axis of the channel yields an average speed of 0.13 cm s^{-1} inward with a cross-channel shear of 0.13 cm • s^{-1} • km^{-1}. The correlation coefficient was 0.86. Dropping the one outlying point gives an average speed of 0.71 cm s^{-1} inward with a shear of 0.10 cm • s^{-1} • km^{-1}. The correlation coefficient rises to 0.94. The calculated value of the average inward current is seen to be relatively sensitive to the choice of data points, perhaps to be expected at these low values which are of the same order as the instrument accuracy. However, the sign and order of magnitude of the average current and value of the cross-channel shear are quite robust. Taking the average width of the channel to be 75 km, the volume transport implied by a 0.5 cm s^{-1} current over a depth of 300 m is 0.11×10^6 m^3 s^{-1} which is of the same order as the upwelling from below 50 m of 0.24×10^6 m^3 s^{-1} as calculated by Bugden (1981) to balance near surface salt and heat budgets in the Northwestern Gulf and Estuary.

Implications of the Cross-Channel Shear

Analysis of the enhanced horizontal dispersion of tracers by a sheared flow in the ocean generally considers the interaction between vertical shear and vertical diffusion (Young et al. 1982). This is due to the fact that in steady unbounded shear flows where no-flux boundary

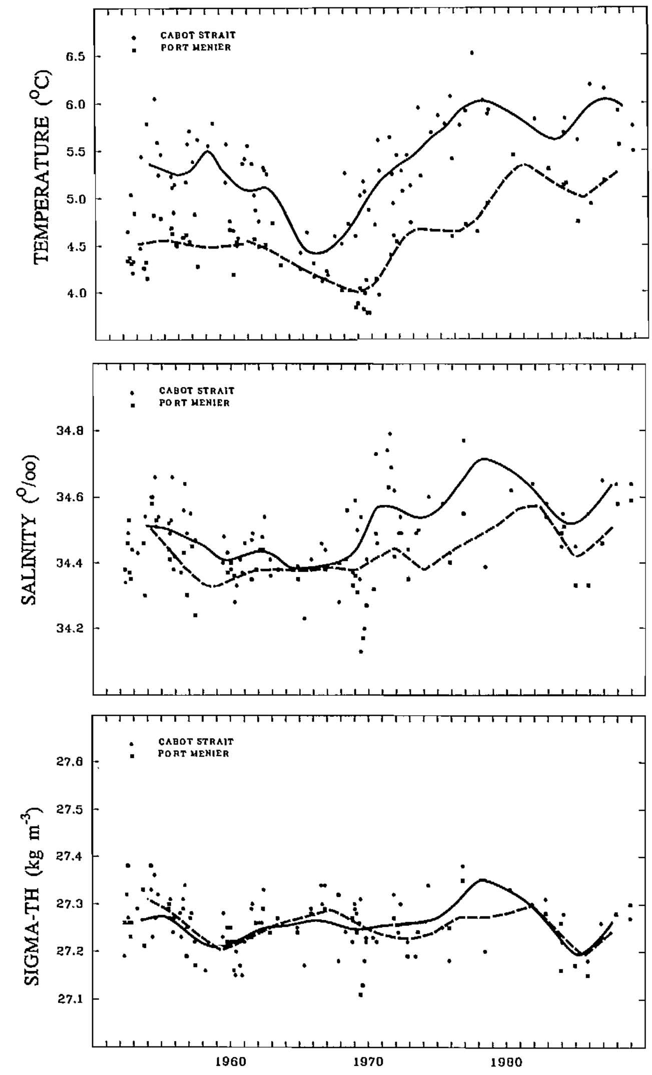

FIG. 4. Temperature, salinity and density at a depth of 250 m from rectangles #1 (Cabot Strait) and #5 (Port Menier) separated by 450 km. Filter is described in the text.

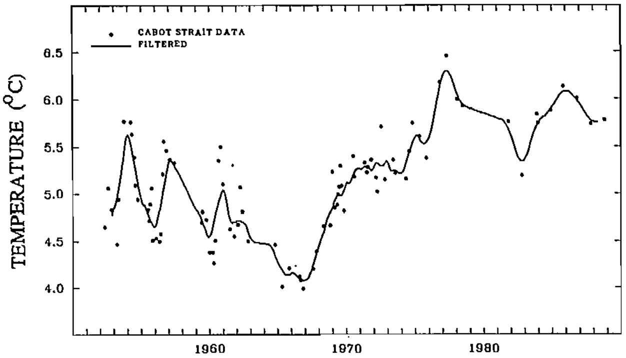

FIG. 5. Temperature averaged from 200 to 300 m at Cabot Strait. See text for explanation of filtering.

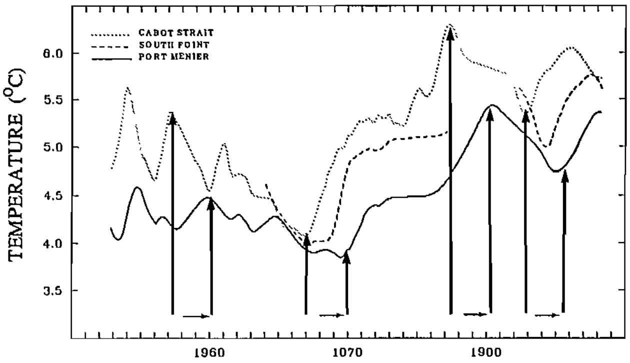

FIG. 6. Temperature averaged from 200 to 300 m from three rectangles along the Laurentian Channel. The vertical arrows connect common features with a time lag corresponding to an advection velocity of 0.5 cm s^{-1}.

conditions cannot be applied the concentration field of the tracer generally expands more rapidly than can be represented by a constant Fickian diffusivity (Okubo 1967). However, in laterally bounded regions such as the deeper portions of the Laurentian Channel the steady laterally sheared flow described in the previous section can be shown to be the dominant mechanism for along-channel dispersion and to be representable by a Fickian diffusion coefficient. As noted by Fischer et al. (1979) for river flows, horizontal shear will be much more effective at along-channel dispersion than vertical shear because the lateral scale is so much larger than the vertical scale. The results of Young et al. (1982) also indicate that time varying flows are not as effective as steady flows even when the period of oscillation is much greater than the cross-channel mixing time scale. As most cross-channel flows are likely to be transitory in nature, we will ignore them in the subsequent analysis.

The equation for the evolution of a tracer θ may be written

$$\theta_t + u\theta_x = K_\ell\theta_{yy} + K_v\theta_{zz} \quad (1)$$

where the subscripts denote differentiation. Here θ is some tracer, t time, u the deviation of the along-channel velocity from the cross-channel mean, (we have chosen axes moving with the mean flow), x the along-channel coordinate, y the cross-channel coordinate and z the vertical coordinate. K_ℓ is the cross-channel diffusion coefficient and K_v the vertical diffusion coefficient. Both are assumed due to processes on smaller scales than those we are trying to resolve and to be representable by Fickian diffusion coefficients. We have ignored the along-channel diffusion due to these processes as the shear dispersion coefficient is expected to be much larger. We have also assumed that the channel is infinite in extent, ignoring any recirculation which may take place near the ends of the channel. Integrating Equation (1) vertically, assuming u does not change appreciably over the range of integration, we obtain

$$\bar{\theta}_t + \overline{u\theta_x} = K_\ell\bar{\theta}_{yy} + \frac{K_v\theta_z\big/^{top}}{h} \quad (2)$$

where the overbar denotes a depth average over the layer of interest which has thickness h. We have ignored diffusion out of the bottom of the layer because of the limited depth available below 300 m and the smaller vertical

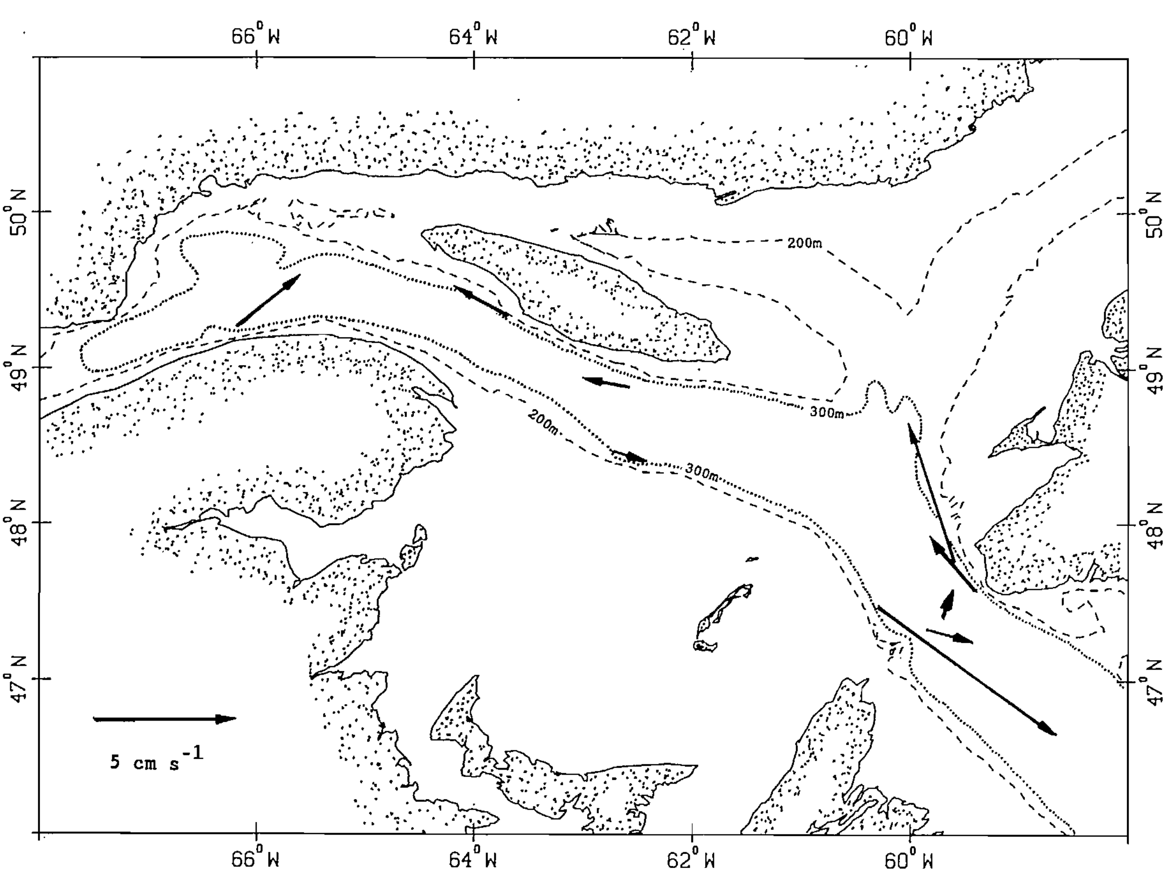

FIG. 7. Average current vectors for current meter deployments in the Laurentian Channel which were longer than 20 d and deeper than 200 m.

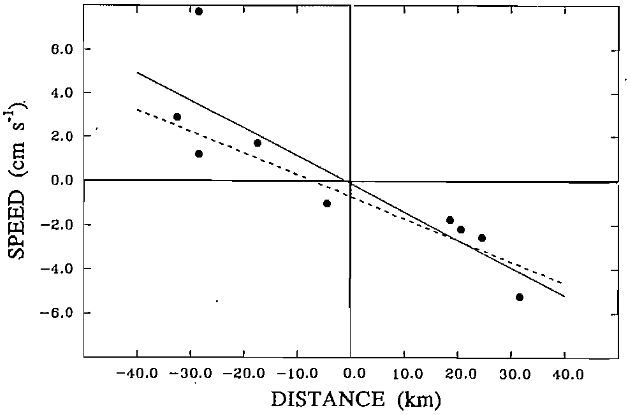

FIG. 8. Currents plotted as average current speed vs distance from the axis of the channel. The lines are linear fits. See text for explanation.

gradients which exist there. We will approximate the last term in Equation (2) by a constant, assuming that the large vertical gradient above the layer under consideration will be relatively unaffected by the small temporal and spatial changes within the layer. We will then write

$$\bar{\theta} = \bar{\theta}' + \frac{K_v \theta_z}{h}\Big|^{top} t \tag{3}$$

to remove the assumed uniform cooling due to vertical diffusion. Non-dimensionalizing, we obtain

$$\frac{W^2}{K_\ell \, \tau} \bar{\theta}'_{t'} + \frac{U \, W^2}{K_\ell \, L} u' \bar{\theta}'_{x'} = \bar{\theta}'_{y'y'} \tag{4}$$

where W is the cross-channel length scale, τ the time scale of interest, L the along-channel scale and U the velocity scale.

The coefficient of the first term of Equation (4) is seen to be the ratio of the cross-channel mixing time scale to the time scale of interest. Taking the width of the channel to be 75 km, assuming that for this horizontal scale K_ℓ is about 100 m^2 s^{-1} (Smith 1989) and recognizing that we wish to resolve decadal time scales (Fig. 6) this coefficient is O(0.1). Assuming an along-channel length scale of 500 km (a typical rectangle separation) and a velocity scale of 5.0 cm s^{-1} (the scale of the velocity shear), the coefficient of the second term, the ratio of the cross channel mixing time scale to the advective time scale, is O(1.0). Dropping the first term of Equation (4) yields the balance between cross-channel diffusion and along-channel advection assumed by Taylor (1953) which leads to description of the shear-enhanced dispersion in terms of a constant Fickian diffusion coefficient.

Fischer et al. (1979), following the analysis of Taylor (1953), develop an expression for the shear dispersion

TABLE 1. Parameters obtained by a least squares fit of model parameters to temperature data.

Parameter	Symbol	Value
Advection velocity	$\overline{U}$	4.9×10^{-3}m/s
Horizontal diffusion	K_{eff}	8.2×10^{2}m^2/s
Vertical diffusion	K_v	2.2×10^{-4}m^2/s

coefficient describing the development of a tracer field in a channel with a linear velocity profile.
They obtained

$$K_{eff} \approx \frac{U^2 W^2}{120\, K_\ell} \qquad (5)$$

where K_{eff} is the effective horizontal diffusion coefficient for the cross-channel averaged tracer and U/W is the cross-channel shear.

Simple Slab Model

The results of the previous section suggest that the evolution of the cross-channel average temperature in the Laurentian Channel may be described by a simple advection-diffusion equation. Returning to a fixed coordinate system, we may write

$$T_t + \overline{U}\, T_x = K_{eff} T_{xx} + \frac{1}{h} K_v\, T_z / top \qquad (6)$$

Here T is the temperature averaged over the width and thickness of the layer, $\overline{U}$ is the cross-channel averaged velocity and K_{eff} is the shear dispersion coefficient. We shall again assume that the vertical diffusion term is constant.

Equation (6) was cast in finite difference form and a fully-explicit, space-centered, forward time step scheme (Richtmyer and Morton 1967) used for numerical integration. The model grid was initialized using a quadratic approximation to temperatures observed near August 1952 and was subsequently driven by the Cabot Strait observations with data gaps filled by linear interpolation. An IMSL non-linear least squares routine then used the model output to determine the parameters U, K_{eff} and the vertical diffusion term by fitting the model output to the observed temperatures at the other 6 rectangles.

The parameters selected by this objective procedure are shown in Table 1. The fitted average advection velocity is seen to agree very well with that obtained from the current meter observations. The vertical eddy diffusivity K_v was obtained using a vertical temperature gradient of 2.5×10^{-2} °C m^{-1} at 200 m. A linear regression on the temperature data in the depth range 150–250 m yielded an average gradient of 2.4×10^{-2} °C m^{-1} for the Cabot Strait rectangle and 2.5×10^{-2} °C m^{-1} for the South Point rectangle. The root mean square error between the model output and the 164 temperature observations fitted is 0.21°C. The success of this simple model in duplicating at least the longer time scale temperature variations over several hundred kilometres is indicated in Fig. 9.

Using the effective dispersion coefficient from the model fitting process and the shear from the linear fit to the velocity observations we obtain a lateral diffusion coefficient $K_\ell \approx 322$ m^{2}s^{-1}. This in turn implies a cross channel mixing time scale of the order of 200 d. At the fitted mean advection velocity of 0.5×10^{-2} m s^{-1}, the distance the center of mass of a tracer distribution would be advected before Equation 5 became appropriate would be less than 87 km which is comfortably less than the 385 km from the edge of the continental shelf to Cabot Strait. Thus Equation (6) is applicable to the cross channel averaged temperature from Cabot Strait inward as well as several hundred kilometres to seaward.

Origin of the Variations

Mixing at the Mouth of the Channel

Variations in horizontal or along-isopycnal mixing at the edge of the continental shelf near the mouth of the Laurentian Channel can produce large changes in the characteristics of the water entering the Channel. This region is known to be an area of active and highly variable mixing where the waters of the Gulf Stream meet

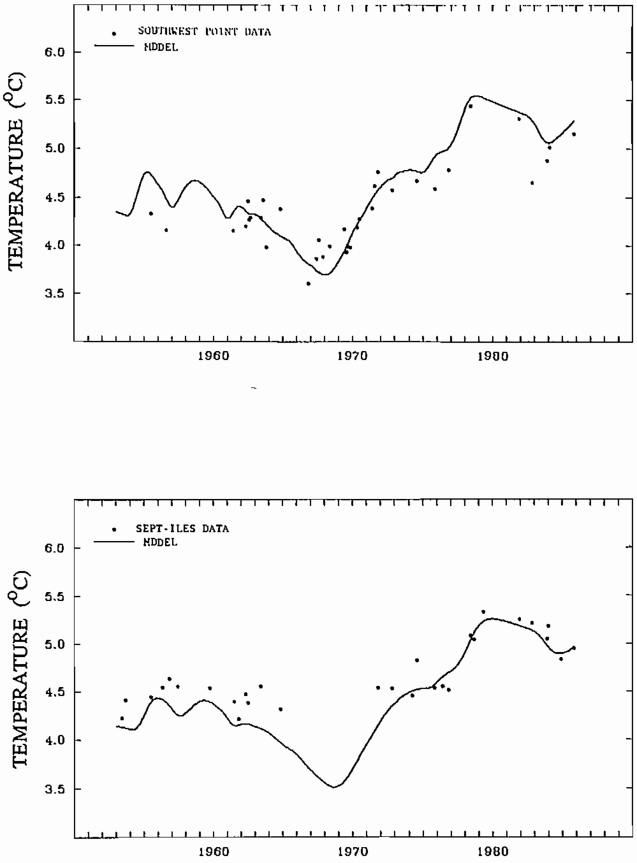

FIG. 9. Vertically and laterally averaged temperature observations and model output from the Southwest Point rectangle(#4), 390 km from the driven model boundary at Cabot Strait, and the Sept-Iles rectangle(#6), 570 km from the boundary.

waters of Labrador origin flowing around the southeastern corner of the Grand Banks. Gulf Stream meanders and eddies shed by the Gulf Stream can produce large variations in exchange across the continental slope in this area (Smith and Petrie 1982). Sharp fronts whose onshore–offshore position can vary over more than 150 km on a time scale of months are also known to exist (Horne 1978).

As mentioned previously, Lauzier and Trites (1958) believed the deeper waters of the Gulf to be composed of a mixture of Labrador and Slope waters in relatively constant proportions supplied continuously to the Laurentian Channel. Variations were attributed to changes in the temperature of the Labrador water. Subsequent work has disputed the existence of Slope Water with a constant T–S correlation (Gatien 1976). Rather, in the region east of the Scotian Shelf, appreciable variations in T–S properties occur, generally related to location. The waters found in the Slope Water region below about 150 m appear to be formed of a mixture of Labrador and Atlantic Waters in varying proportions, the proportion of Labrador Water generally decreasing with alongshore distance from the Grand Banks as well as offshore distance from the Scotian Shelf (Lee 1970).

Figure 1 indicates the positions of two sets of profiles obtained at the mouth of the channel at different times. One set was taken in 1960, the other in 1976. Examination of Fig. 5 shows that conditions at Cabot Strait during the early 1960's were relatively cool, while those in the late 1970's were quite warm. Figure 10 shows the T–S relationships from these two groups of stations. The two solid curves shown in Fig. 10 are T–S curves for Western North Atlantic Water (Armi and Bray 1982) and for the waters of the Labrador Shelf and Slope (Lazier 1982). The 200–300 m layer in the Laurentian Channel generally lies between σ_θ values of 26.9 and 27.4. Although the effects of vertical mixing are evident above a σ_θ of about 27.30 where the profiles tend toward the colder and fresher surface waters of the Scotian Shelf, the denser waters are seen to be formed of a mixture of Labrador and Western North Atlantic Waters. The proportions of each parent water mass are very different between the two sets of stations. At an initial σ_θ of 27.40 the proportion of Western North Atlantic Water ranges from about 65% in 1960 to about 80% in 1976. This difference in proportions produces a temperature change of about 2°C at the densities found in the 200–300 m layer in the Laurentian Channel.

Monitoring the Variations in Mixing

Myers and Drinkwater (1989) using satellite infrared imagery have analyzed the position of the surface front between the "shelf water" and the "slope water" in relation to the 200 m isobath at the edge of the continental shelf. Their data from the area shown in Fig. 1, expressed as average distance from the 200 m isobath, reduced to monthly averages and filtered with a 7 point boxcar filter to show longer term trends, is shown in Fig. 11. A large excursion of nearly 300 km on a time scale of about 5 yr is apparent. Also shown on Fig. 11 is the Cabot Strait averaged temperature plotted on an inverted scale and advanced 2.5 yr, the advective lag using the velocity from the model and the distance from Cabot Strait to the shelf break. There appears to be a strong relationship between the lower frequency components of the two signals at the lag predicted by the measured velocities and model analysis. Although relatively few data points are involved at the Cabot Strait rectangle, the same disturbances are apparent propagating up the channel in Fig. 6.

Satellite infrared imagery indicates the surface position of the shelf–slope water boundary. However, on the time scales presently under consideration its motion over several hundred kilometres must be reflected in the deeper waters. The horizontal temperature gradients in the area imply that large scale shoreward motion of the frontal system will result in warmer waters near the mouth of

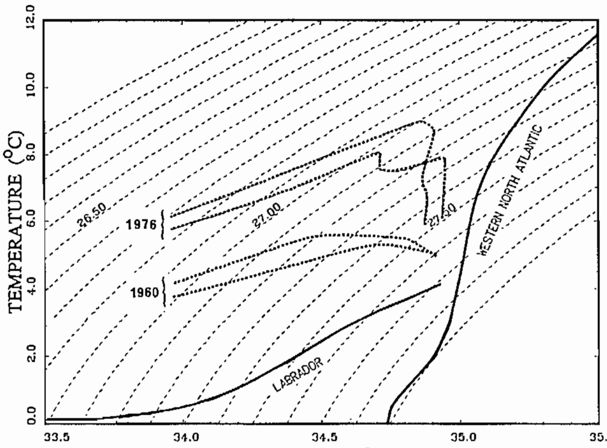

FIG. 10. Temperature–salinity relationships from the two sets of stations shown in Fig. 1 showing the difference in characteristics along constant density surfaces.

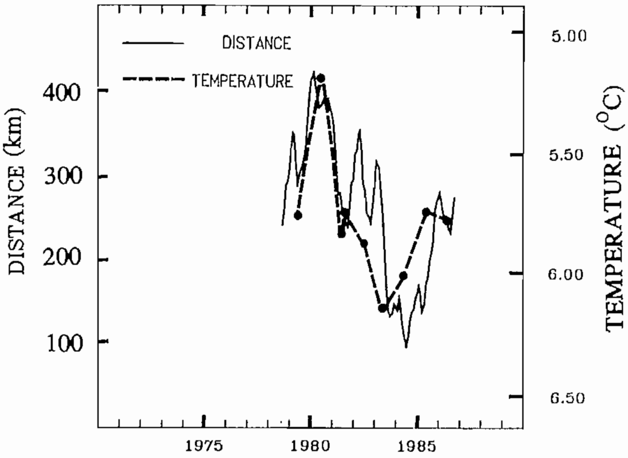

FIG. 11. Average distance from the 200 m isobath to the shelf-slope water boundary. (after Myers and Drinkwater (1989)) Also shown are the Cabot Strait average temperatures plotted on an inverted scale and advanced 2.5 yr, the lag time predicted by the model.

the Laurentian Channel. It is unfortunate that satellite imagery for the region east of the Scotian Shelf is unavailable prior to about 1975. Given the convoluted form of the various fronts and the path of the Gulf Stream, traditional oceanographic sections provide little information on the large scale motion of these features. Even large surveys such as "Gulf Stream '60" (Fuglister 1963) take several weeks to perform and provide only one isolated data point of use in the present context.

Discussion

The results of the present study indicate that conditions in the deeper waters of the Gulf of St. Lawrence are the result of a slow but relatively steady advection of water from outside the Gulf in addition to some vertical diffusion. The effects of the average flow pattern and lateral diffusion within the channel may be represented as an effective horizontal diffusivity. The mean advection velocity in the deeper Laurentian Channel appears to be relatively slow and constant, the main variations in the characteristics of the deeper waters being determined by mixing at the mouth of the channel. Other processes such as changes in advection velocities or vertical mixing are unable to reproduce the observed phase lags and horizontal gradients as the disturbances propagate inward from the edge of the shelf. This puts the Gulf somewhat in the role of a sampler equipped with a low pass filter (shear dispersion) which samples conditions on a constant density surface at the edge of the continental shelf.

The deeper waters of the Laurentian Channel appear to be made up of a mixture of Labrador and North Atlantic waters in varying proportions. The proportions vary on time scales of several years and may be monitored by remote sensing through the position of the Shelf-Slope water boundary. The applicability of a simple advection-diffusion equation to the propagation of parameter anomalies provides some forecasting ability as the disturbances move slowly inward at the mean advection velocity.

The large freshwater discharge received by the Gulf of St. Lawrence has been considered to be one of the main influences in the determination of the marine environment in the Gulf. Concern has been raised that natural and anthropogenic changes in the discharge pattern may exert less than desirable influences on the Gulf ecosystem (Neu 1975). Correlations have been found between freshwater discharge and landings of commercial fish species with lags appropriate to the species age at maturity (Sutcliffe 1973). This study of deep water circulation of the Gulf of St. Lawrence was motivated in large part by the hypothesis that changes in freshwater outflow would result in changes in the rate of entrainment of deep water into the upper layers. The results of this analysis indicate that the primary factor determining the variation of at least the deep water properties is the variation of the oceanic waters at the mouth of the Laurentian Channel.

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On the Seasonal Cycle of the Gaspé Current[1]

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A recently published box model inverse calculation, based on archived temperature and salinity data from the Gulf of St. Lawrence, has shown that the Gaspé Current has a summer transport minimum. This is somewhat contrary to one's expectation that the transport should peak with the spring–summer freshet. We show that the summer minimum is likely due to the summer relaxation of eastward wind stress in the northwest Gulf of St. Lawrence.

Une récente publication de calculs inverses à l'aide d'un modèle en boîte et de données archivées de salinité et température en provenance du golfe du Saint-Laurent a démontré que le transport d'eau par le Courant de Gaspé atteint un minimum en Juillet. A première vue, ceci semble être en contradiction avec le fait que l'apport d'eau douce au Golfe est près de son maximum en Juillet. Nous démontrons que ce transport minimum en Juillet est dû à la relaxation de la tension des vents d'ouest durant l'été.

Introduction

The Gaspé Current is probably the most prominent feature of the circulation of the Gulf of St. Lawrence (GSL, Fig. 1). This jet originates in the lower St. Lawrence Estuary (LSLE) where the discharge of the St. Lawrence River drives a pair of coastal jets (Koutitonsky and El-Sabh 1985). These jets merge at the mouth of the St. Lawrence estuary, and during summer conditions combine with the general cyclonic circulation of the northwest GSL to form the Gaspé Current (Tang 1980). This current is indeed a powerful jet, exhibiting surface speeds of up to 100 cm s^{-1} (Benoit et al. 1985) during the summer period. Mertz et al. (1988) and Mertz and El-Sabh (1989) have shown that instability events, with periods on the order of 1 wk, are common features of this current. The Gaspé Current apparently leaves the coast at the tip of the Gaspé Peninsula, and carries relatively light waters across the Magdalen Shallows, one of the most biologically productive areas of the GSL. Its trajectory however is not well known as it traverses this southern region. We examine here the variability in transport of the current at seasonal time scales, a scale also of interest to fishery dynamics research (Sinclair et al. 1987).

Bugden (1981) found that the Gaspé Current has a minimum transport in July, conflicting with one's expectations that the transport should be maximum during the spring–summer runoff peak. Here, we present data to show that the transport minimum is likely due to the abatement of eastward wind stress during summer.

The July Water Transport Minimum

Figure 1 from Bugden (1981) shows that the Gaspé Current achieves a transport of about 3×10^5 m^3s^{-1} as it enters the southern GSL (region 4). This transport consists largely of water upwelled in the Lower St. Lawrence estuary (LSLE) – Gaspé Current zone (0.7×10^5 m^3s^{-1}), and in the northwest Gulf (1.7×10^5 m^3s^{-1}). Bugden arrived at these figures through a box model inverse calculation, using all archived temperature and salinity data, via application of the relevant conservation equations. Figure 2 shows his monthly estimates of the transport of the Gaspé Current and the salinity of the upper 20 m for zone 3 (the LSLE and Gaspé region). Transports were calculated, by Bugden, only for the months of March to December, since in the winter season property gradients are too small to allow reliable

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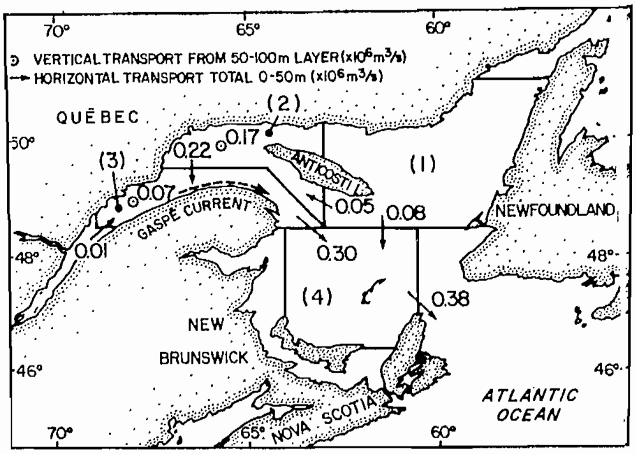

FIG. 1. The study area with transports estimated by Bugden (1981) for the upper 50 m of the water column. (1) = Northeast Gulf of St. Lawrence; (2) = Northwest Gulf of St. Lawrence; (3) = Lower St. Lawrence Estuary and Gaspé Current zone; (4) = Southern Gulf of St. Lawrence (Magdalen Shallows).

transport estimates. Note that Bugden smoothed his results with a 3-mo running mean so that only estimates from April to October are shown. Figure 2 defines the theme for this note: why does the Gaspé Current have its minimum transport in July, the period of high runoff and low salinity? (In Bugden's estimates, freshwater input to the LSLE peaks in May; see his fig. 6).

Tee and Lim (1987) have presented a recent analysis of the response of the LSLE to seasonal runoff variations. They employed a laterally-averaged numerical model of the LSLE, forced by freshwater input at the head of the estuary. As expected, their results show a surface outflow which thickens downstream due to vertical entrainment of the underlying fluid. Their calculated vertical velocities produce upwelling estimates in good agreement with Bugden's value for region (3). Figures 9 and 26 of Tee and Lim indicate that the upwelling velocity at 50 m depth is about 8×10^{-6} m s^{-1} for the LSLE.

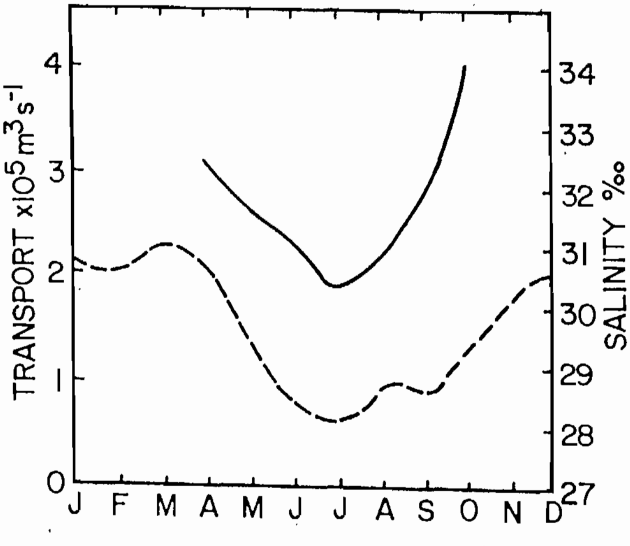

FIG. 2. The transport of the Gaspé Current (solid line) and the seasonal salinity cycle for the region 3, the Estuary and Gaspé coast (dashed line). Adapted from Bugden (1981).

This implies a transport into the upper 50 m estimated at $8 \times 10^{-6} \times 40$ km (width) $\times$ 200 km (length) = 6.4×10^4 m^{3}s^{-1}. Bugden found a vertical transport of 7×10^4 m^{3}s^{-1} for all of region (3) while Tee and Lim's value applies to the LSLE alone. Now, the key point is that fig. 26 of Tee and Lim shows that the upwelling speed only increases by about 0.6×10^{-6} m s^{-1} at 50 m during the freshet pulse, achieving its peak in June. Thus the change in transport due to changes in upwelling is probably no larger than 7×10^4 m^{3}s^{-1} $\times$ 0.6×10^{-6} / (8×10^{-6}) = 5×10^3 m^{3}s^{-1}. This change is negligible compared to the estimated transport of the Gaspé Current, 3×10^5 m^{3}s^{-1}, and explains why no spring-summer peak in transport is observed in the Gaspé Current. This does not, of course, explain why the Gaspé Current has a July minimum in transport.

The Wind Stress Cycle

Figure 3 shows the annual wind stress cycle for the western GSL and the LSLE. This figure has been drawn from data presented in Saunders (1977) who employed ship reports and grouped the data by Marsden square. Monthly mean wind stress estimates over the GSL were also computed by Koutitonsky and Toro (personal communication, 1989; INRS-Océanologie, Rimouski, Québec), using monthly mean sea-level pressures averaged over 39 yr. Their monthly mean sea-level pressures have been added to Fig. 3 (using January, April, July, and October to represent winter, spring, summer and fall, respectively). The wind stress field over the northwest GSL is predominantly oriented in an easterly direction; it has maximum amplitudes in winter and minimum ones in summer.

Over open seas the geostrophic winds should lie about 15° counterclockwise of the isobars (Thompson et al. 1983). Clearly, this is not the case in the northwest Gulf. The wind vectors, particularly in winter, lie up to 90° counterclockwise of the isobars. Orographic steering by the coastal mountains is certainly affecting the winds here. The unusually large rotation of the wind vectors in the northwest Gulf probably reflects the sharp relief of the south coast due to the Chic-Choc mountain ranges on the Gaspé Peninsula, and that shipping lanes are within 20 km of the Gaspé coast. [Recall that wind vectors in Fig. 3 are based on ship reports]. To amplify this point, the comparison between results of the geostrophic wind stress model at Sept-Iles with 39 yr of wind data measured at the same point yielded good agreement between geostrophic and measured wind directions (Koutitonsky and Toro, personal communication, 1989). So, it is conceivable that due to the gentler relief there winds along the north shore blow towards the south (along isobars), but are deflected towards the east near the Gaspé Current area.

Wind-Induced Upwelling in the Northwest Gulf of St. Lawrence

We will now estimate the volume flux of water upwelled by the eastward wind stress. If the wind stress was uniform across the northwest GSL, then upwelling

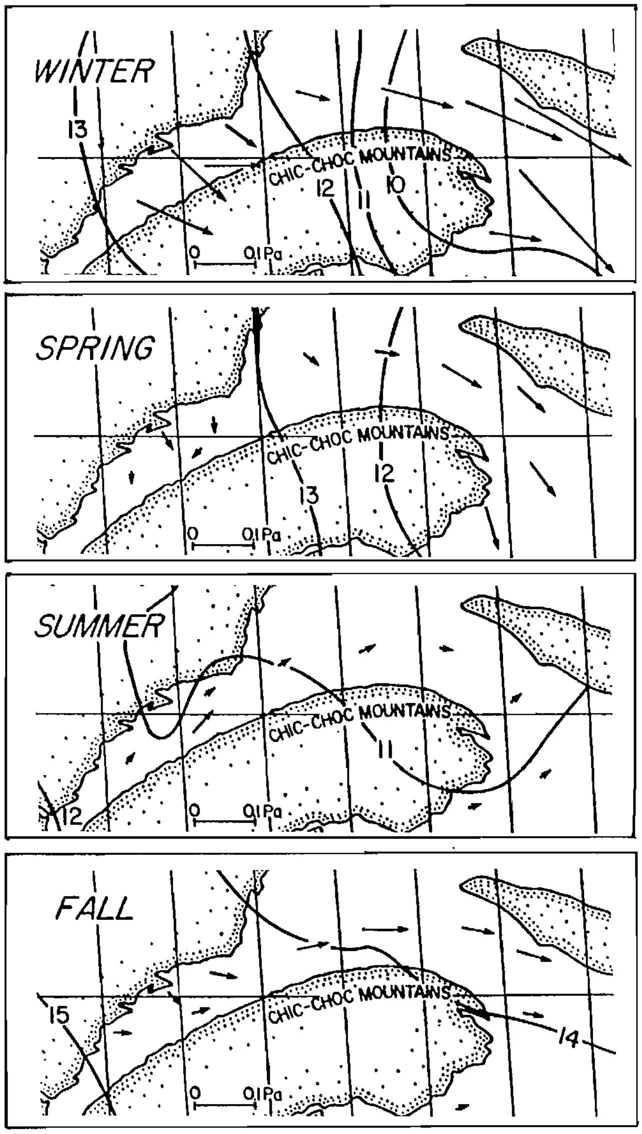

FIG. 3. The seasonal wind stress cycle for the western Gulf of St.Lawrence, by Marsden square (drawn from Saunders 1977). Also shown are surface isobars, P – 1000 mbars, for climatological January, April, July and October. (Winter = December to February, Spring = March to May, Summer = June to August, Fall = September to November.)

would take place on the north shore (again for an eastward wind stress), surface waters would drift across the northwest GSL with the Ekman transport, and enter the Gaspé Current near the south coast. This scheme is valid because the northwest GSL is much wider than an internal Rossby radius, about 10 km in this region (Tang 1980). Indeed, wind driven upwelling along the north shore has been detected in satellite images (eg. Lacroix 1987). At a distance from the coast greater than a Rossby radius, the movement across the northwest GSL has a speed equal to the Ekman drift $U_E = \tau / (\rho f h)$, where τ is the eastward wind stress, ρ is the density of water, f is the Coriolis parameter, and h is the thickness of the upper layer. The transport ψ across the northwest GSL is then:

$$\psi = U_E\, h\, L = L\, \tau / (\rho f) \tag{1}$$

where L is the length of coastline under consideration, about 200 km, for the northwest GSL. This transport ψ is equal to the flux of water upwelled.

However, when the wind is not uniform across the northwest GSL, as may be the case due to topographic steering by the Chic-Choc mountains, then upwelling will occur in the interior of the northwest GSL, rather than along the north shore. Suppose the wind stress is uniformly eastward within a strip (say) 20 to 30 km wide along the south shore, and that outside this strip the wind vectors rotate into a more north–south orientation. Then the eastward wind stress will decrease to zero beyond this strip along the south coast. This implies that there will be a wind stress curl equal to $\tau / \Delta y$, where Δy is the width of the zone over which the eastward wind stress goes to zero. Since the north–south wind stress is generally much weaker than the eastward wind stress we ignore any possible contribution to the curl from the north–south component of the wind stress. The curl of the wind stress will induce upwelling of magnitude $w_E = \tau / (\rho f \Delta y)$, (see, eg., Gill 1982). Thus the total volume flux of upwelled water is $w_E L \Delta y = L \tau / (\rho f)$, which is equal to the upwelling calculated assuming that the wind stress is uniform across the northwest GSL. Thus, whether or not the eastward wind stress is uniform across the northwest Gulf does not affect the total volume flux of upwelled water. It is the location of the upwelling zone within the northwest GSL that changes according to the meridional wind stress profile.

Using the Saunders data, shown in Fig. 3, we have set τ (spring) = 0.04 Pa, τ (summer) = 0.02 Pa, and τ (fall) = 0.07 Pa. The north and south coasts of the northwest Gulf do not deviate more than ± 30° from due east, so that eastward and alongshore wind stress are equal to within 15 % . With these values and eq. (1), we can calculate the wind-induced upwelling in the northwest GSL: ψ (spring) = 0.8×10^5 m^{3}s^{-1}, ψ (summer) = 0.4×10^5 m^{3}s^{-1}, and ψ (fall) = 1.4×10^5 m^{3}s^{-1}. We estimate the

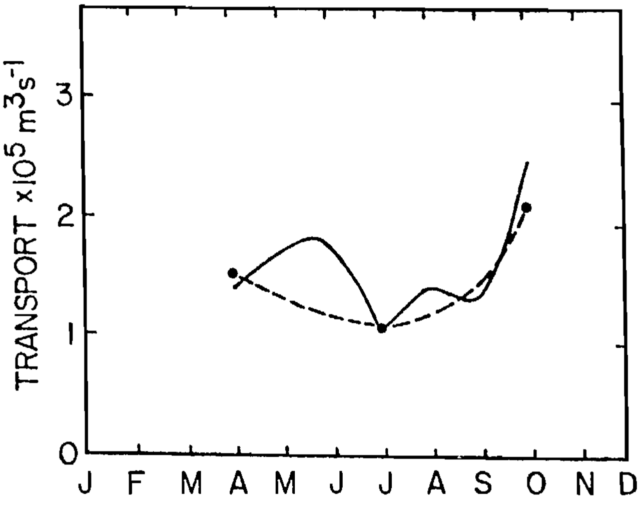

FIG. 4. The upwelling cycle for the northwest Gulf, region 2, calculated by Bugden (solid line) and estimated from the seasonal wind stress (dashed line).

average eastward wind stress from March to December to be 0.05 Pa, implying an upwelling flux of 1 × 10^5 m^3s^{-1} versus Bugden's value of 1.7 × 10^5 m^3s^{-1}. Our calculated mean upwelling underestimates Bugden's value by 0.7 × 10^5 m^3s^{-1}. However, when this missing transport is added to the seasonal values calculated above, the estimates presented on Fig. 4 (dashed-lines) are obtained. The agreement between the seasonal cycle of wind-driven upwelling and Budgen's estimates (solid lines) is quite good. Our figures do not account for the May-June peak in Budgen's estimates; this peak is in phase with the runoff from the north shore rivers in the northwest GSL (see fig. 6 of Budgen 1981).

To conclude this section, we offer a number of caveats: It should be noted that the wind stresses have statistical errors of up to 30 % (Saunders 1977) due to the strong variations of the wind stress about the mean. For the transport values, Bugden has estimated the uncertainty of his calculations as "probably less than 50 %". And, of course, our calculations here are far from being a complete treatment of the physics; eventually, numerical models will be used to study wind driven motions in the Gulf in detail.

Conclusion

Based on the results of section (3), we claim that wind stress variations explain the seasonal cycle of upwelling in the northwest Gulf, but leave a steady contribution of 0.7 × 10^5 m^3s^{-1} unexplained. Since Fig. 1 shows that just over half of the transport of the Gaspé Current arises from upwelling in the northwest Gulf, it seems that the July transport minimum is due to the summer minimum in wind stress.

Acknowlegements

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The Possible Role of the Surface Circulation in the Spread of PSP in the Western Gulf of St. Lawrence in 1988[1]

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Almost every year the toxins that produce paralytic shellfish poisoning (PSP) are found in shellfish along the north and south shores of the St. Lawrence Estuary seaward from the Saguenay River. In 1988, toxic shellfish were detected for the first time along the northeast coastline of New Brunswick and on the western and northern shores of Prince Edward Island. The pattern of the toxin outbreaks within the Gulf of St. Lawrence suggests the possibility that currents may have transported the toxic phytoplankton (*Alexandrium*) that is responsible for the contamination of the shellfish. A model is developed to examine possible plankton drift trajectories assuming the plankton are concentrated at the surface, exhibit passive behavior, and are transported by the mean residual surface drift plus the time-dependent wind-driven currents. The model results are consistent with the pattern and timing of the buildup of the toxins within the shellfish.

Presque tous les ans, les toxines responsables de l'intoxication paralysante par les mollusques (IPM) font leur apparition dans les mollusques des rives nord et sud de l'estuaire du Saint-Laurent, en aval de l'embouchure du fleuve Saguenay. En 1988, on a décelé pour la première fois des mollusques toxiques le long de la côte nord-est du Nouveau-Brunswick et des côtes ouest et nord de l'Île-du-Prince-Édouard. D'après les conditions d'apparition des toxines dans le golfe du Saint-Laurent, il semble que les courants transportent le phytoplancton (*Alexandrium*) responsable de la contamination des mollusques. On a établi un modèle des trajectoires possibles de cheminement du plancton, en tenant pour acquis que ce dernier est concentré à la surface, qu'il a un comportement passif et qu'il est transporté par la dérive de surface résiduelle médiane plus les courants de vents à variations chronologiques. Les résultats fournis par le modèle correspondent aux caractéristiques et aux périodes d'accumulation des toxines dans les mollusques.

Introduction

Paralytic shellfish poisoning (PSP) caused by the consumption of toxic shellfish is common in eastern Canada and, over the past hundred years, has resulted in several hundred illnesses and a number of deaths (Prakash et al. 1971; Medcof 1985). The contaminated shellfish are normally found in the middle and lower reaches of the Bay of Fundy and the St. Lawrence Estuary seaward of the Saguenay River (Fig. 1). They occur mainly during summer and are associated with the appearance of high concentrations of the planktonic marine dinoflagellate *Alexandrium* (alternative nomenclature *Protogonyaulax* and referred to in earlier literature as *Gonyaulax tamarensis, Gonyaulax excavata,* or *Protogonyaulax tamarensis*). The shellfish acquire the PSP toxins through filter feeding on the dinoflagellates. Indeed, shellfish toxicity data closely reflect the status of *Alexandrium* blooms and serve as indicators in time and space of *Alexandrium* populations (Prakash et al. 1971; Therriault et al. 1985; White 1987).

High temperature, high light intensity, low salinity, and strong vertical stratification of the water column are some of the factors necessary for, or which stimulate, the growth of these dinoflagellates. Prakash (1967) found that low salinity and high temperature promoted growth in laboratory cultures of *Alexandrium* (*Gonyaulax tamarensis*), with salinity appearing to be the more important ecological factor. Field observations have shown that dinoflagellates thrive in highly stratified, low salinity water (Therriault et al. 1985; Prakash 1987). Therriault et al. (1985) reported that the August bloom of *Alexandrium* (*Protogonyaulax tamarensis*) in the low salinity plume formed by the discharge of the Manicouagan and the Aux-Outardes Rivers into the Lower St. Lawrence Estuary occurred during periods of low wind speeds and neap tides. This led the authors to conclude that reduced mixing and the associated strong vertical stratification of

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[1] This paper forms part of the Proceedings of a Workshop/Symposium held at the Maurice Lamontagne Institute, Mont-Joli, Quebec, 14–17 March 1989.

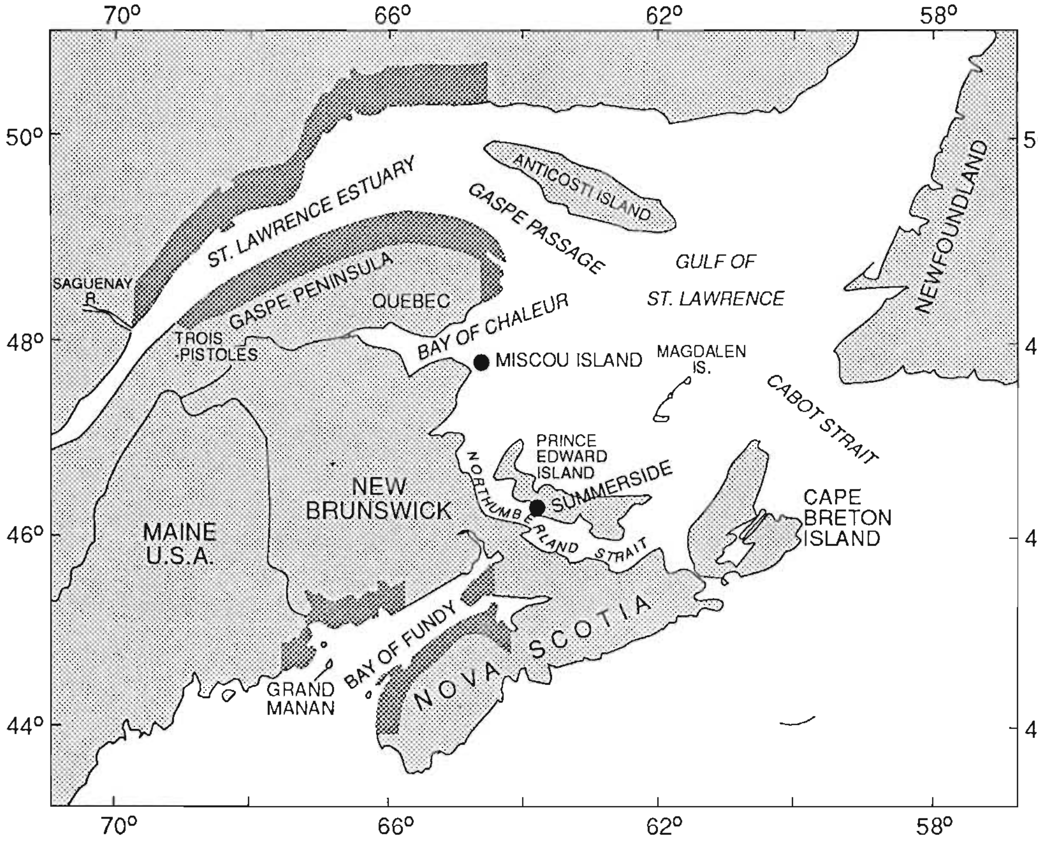

FIG. 1. Canadian Atlantic coast showing the two regions (shaded) commonly affected by PSP (adapted from Prakash et al. 1971). • denotes wind stations at Miscou Island and Summerside.

the water column are important for bloom incidence. They also found that the spatial distribution of the dinoflagellate coincided with the extent of the low salinity plume.

Relationships between shellfish toxicity and environmental data for the Bay of Fundy over a 40 yr period were recently examined by White (1987). No simple picture emerged but a number of statistically significant correlations were found between interannual variations in summer toxicity and salinity, the amount of sunshine and the wind speed during the previous January and February and with the 18.6 y cycle of lunar modulation of the tide. A positive relationship between shellfish toxicity levels and sunshine duration had been found earlier for the Bay of Fundy by Prakash and Medcof (1962) using a shorter time series and in the St. Lawrence by Beaulieu and Ménard (1985).

Alexandrium form cysts when subjected to temperatures below their limits for growth (<5°C; Prakash 1967). Shortly after the formation of cysts, they lose their buoyancy, sink to the bottom, and become incorporated into the surficial sediments where they will remain over the winter or longer (Martin and White 1988). Laboratory studies by Anderson (1980) indicate that excystment is initiated after an applied stimulus, such as a rapid temperature change. Recent studies suggest that an annual biological clock may also play a significant role in excystment in some areas (Anderson and Keafer 1987). In the Bay of Fundy resting cysts of *Alexandrium* (*G. excavata*) are widely distributed from the intertidal zone to deep waters offshore (White and Lewis 1982). The highest concentrations, however, were reported in an area of sediment deposition of fine brown mud to the northeast of Grand Manan Island (Fig. 1). This area is believed to serve as the major source of *Alexandrium* motile cells for the initiation of the annual summer bloom within the Bay of Fundy. Similarly, Cembella et al. (1988) suggested that the high concentration of cysts found along the north shore of the St. Lawrence Estuary near the mouths of the Manicouagan and Aux-Outardes may serve as a source of *Alexandrium* for the entire lower estuary.

In the spring of 1988 PSP toxins were found in shellfish along the northern Gaspé coast, a relatively common phenomenon. However, by the beginning of June contaminated shellfish were also reported in the Bay of Chaleur in the Gulf of St. Lawrence. Toxicity levels within the Bay rose during the month and toxic shellfish began to appear along the northeast coastline of New Brunswick (N.B.) and eventually on the western and northern shores of Prince Edward Island (P.E.I.). This was the first time PSP toxins had ever been recorded in these areas. The location of the toxic shellfish "downstream" of the St. Lawrence Estuary raises the possibility that surface currents may have transported *Alexandrium* from the Estuary into the western and southwestern Gulf. A similar mechanism of transport of motile cells by the surface circulation has been proposed to explain, in part, the general distribution of toxic shellfish in both the Bay of Fundy (Martin and White 1988) and within the St. Lawrence Estuary (Cembella et al. 1988). The lack of data on the currents and *Alexandrium* distributions during 1988 prevents us from testing directly the hypothesis that phytoplankton transport was important in the spread of PSP toxins through the southwestern Gulf of St. Lawrence. Undaunted, we decided to explore whether the sequential timing and location of PSP toxins within the Gulf of St. Lawrence were, at least, consistent with transport by the surface currents. We assume that *Alexandrium* drift passively and are transported by the near-surface currents. While they do possess some mobility that allows them to vertically migrate, the highest concentrations are found at, or near, the sea surface (Martin and White 1988; A. Cembella, personnel communication). Possible drift tracks of *Alexandrium* during May and June of 1988 are derived from a simplified trajectory model based upon the historic residual surface-layer flows and the time-dependent wind-driven currents.

A further description of the temporal and spatial patterns of the PSP outbreaks in the Gulf of St. Lawrence is provided in the next section. Details of the surface drift model are then presented along with some possible drift trajectories of *Alexandrium.* The last section discusses the results and possible consequences, together with the major conclusions of the study.

PSP Data

In 1988, PSP toxins were first found in several clam species at Trois-Pistoles, Quebec, a short distance seaward of the Saguenay on the south side of the St. Lawrence Estuary (Fig. 1). All toxicity data were derived from mouse bioassays (see Cembella et al. 1988 for details on methods). On 1 April, a value of 320 μg Saxitoxin equivalents (STXeq)/100 g of clam meat was reported. Detectable levels (>42 μg STXeq/100 g) were also reported from a number of other sites further seaward along the Gaspé coast. During May and June, toxins were reported in both clams and mussels from many sites along the Gaspé coast and at the northeastern entrance to the Bay of Chaleur (Fig. 2). By mid-June the level in mussels at some sites exceeded 7000 μg STXeq/100 g of shellfish meat. The toxins spread through the southwestern Gulf of St. Lawrence during June. They were found in mussels on the New Brunswick side of the Bay of Chaleur during the first week, along the northeastern coast of New Brunswick and on the western shore of Prince Edward Island by mid-month, and on the north shore of P.E.I. by late June (Fig. 3). The highest toxicity levels occurred in mussels at the western end of P.E.I. and nearby on the New Brunswick coast where they exceeded 1000 μg STXeq/100 g during the last week of June. Although toxin levels generally declined during July and August, values in various clam and mussel beds in both provinces sporadically exceeded 80 μg STXeq/100 g, necessitating their closure until such time as the levels dropped below the acceptable limit.

Surface Drift Model

Mean Residual Currents

In the absence of direct current observations in the Gulf of St. Lawrence for May–June, 1988, a grid (10′ × 10′) of mean surface-layer currents was constructed from historical data (Fig. 4). Currents were obtained from geostrophic computations for June by Keyte and Trites (1971) and El-Sabh (1976). They were augmented by surface drifter release and recovery data obtained over several years during the spring and summer (Bumpus and Lauzier 1965; Lauzier 1965; Boudreault 1971; Keyte and Trites 1971; Messieh 1974; BIO data files) and published charts of summertime surface circulation patterns (Trites 1972; De Lafontaine et al. 1984). These data were the primary sources for the nearshore regions of the Bay of Chaleur, off northeast New Brunswick, and in Northumberland Strait where geostrophic data were unavailable. Currents were then compared with measured current meter observations obtained during the spring and summer (in Northumberland-Strait, Farquharson 1959; in the Gaspé Passage, Farquharson 1963; and on the Magdalen Shallows, Keyte and Trites 1971, BIO data files) and adjustments made where necessary. Further minor adjustments were finally made to obtain a relatively smooth velocity field and to ensure approximate conservation of volume within the grid system.

The main features of the residual circulation pattern include the strong eastward-flowing Gaspé Current along the north shore of the Gaspé Peninsula, a general southeastward flow in Northumberland Strait and over much of the southwestern Gulf of St. Lawrence, a westward drift off southern Anticosti Island, and cyclonic eddies west of Anticosti Island and in the Bay of Chaleur.

Winds

Hourly wind measurements were available for May, 1988, at Miscou Island, N.B., and for May and June for

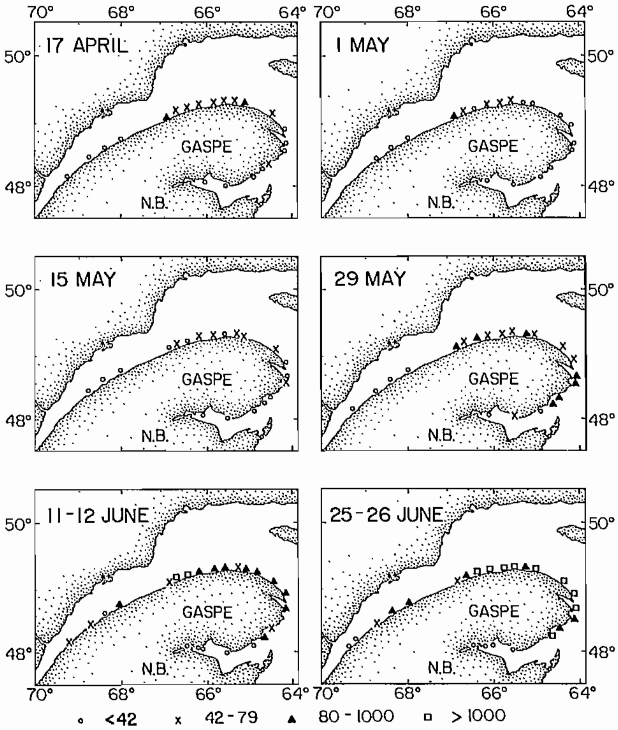

FIG. 2. PSP toxin levels (μg STXeq/100 g) during 17 April to 26 June, 1988, in shellfish sampled on the south side of the lower St. Lawrence Estuary and extending to the north shore of the Bay of Chaleur.

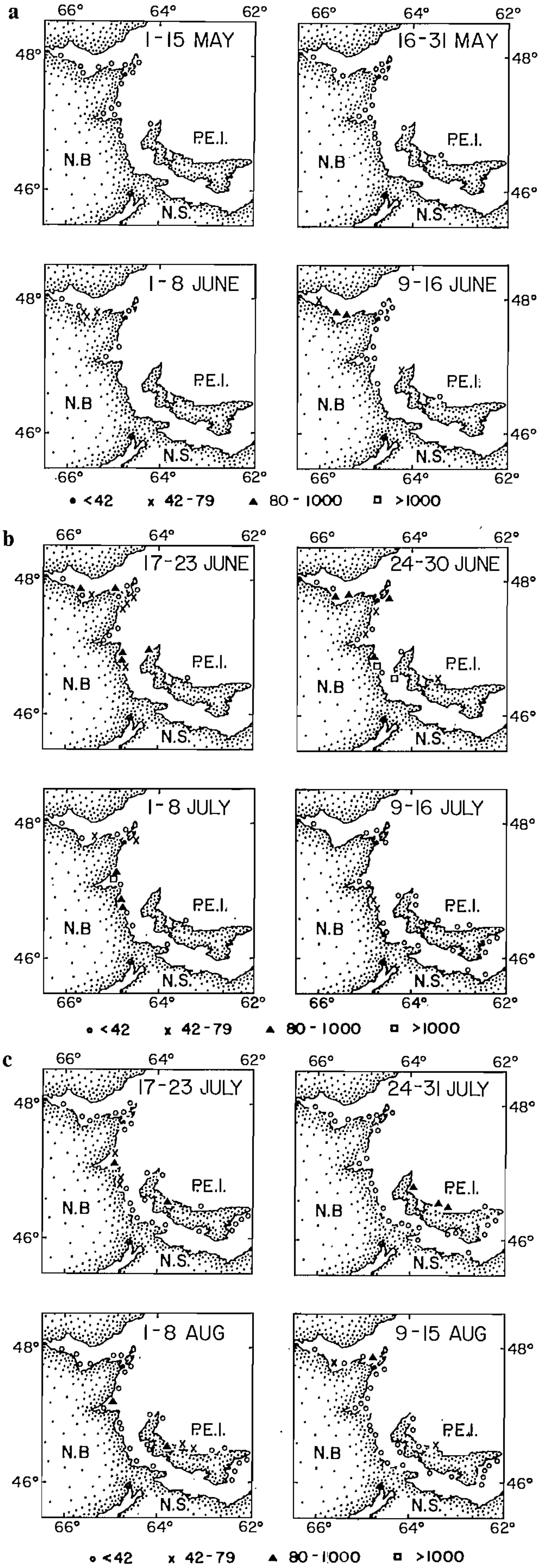

FIG. 3. PSP toxin levels (μg STXeq/100 g) in the southwestern Gulf of St. Lawrence during (a) 1 May to 16 June, (b) 17 June to 16 July, and (c) 17 July to 15 August, 1988.

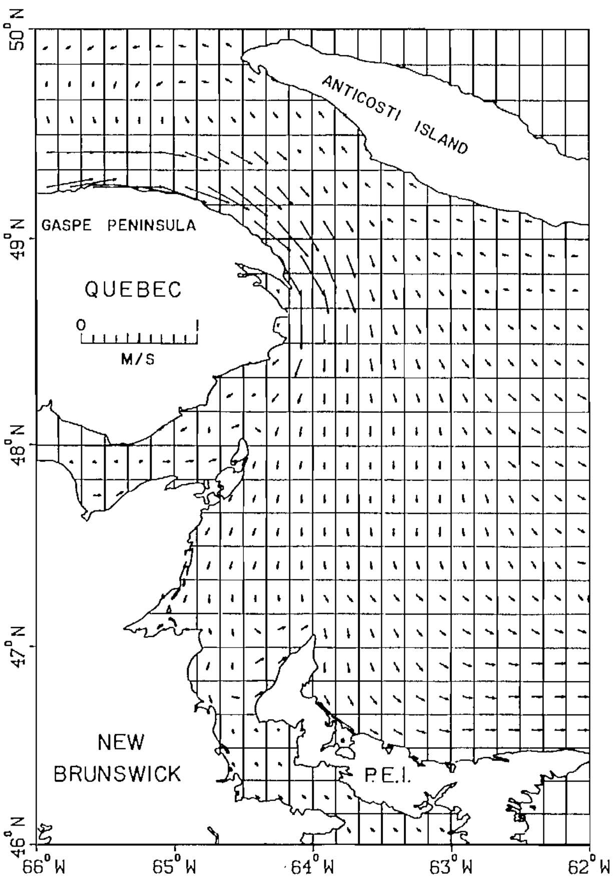

FIG. 4. Surface residual current grid derived from historical data.

Summerside, P.E.I. (Fig. 1). The data were vector averaged and filtered to produce 6 h averages. The wind-induced drift at the surface was assumed to be 3% of the wind speed without any deflection. Trajectories were determined by the vector addition of the residual current for the appropriate grid square and the computed wind drift using the 6 h time step. The winds were applied uniformly across the grid. Although very simplified, a similar model was found to be relatively successful in reproducing the observed drift of oil for a 30 d period following a spill in Cabot Strait in 1979 (Trites et al. 1986).

Results

Surface drift trajectories were initially constructed using only the residual currents. The net drift over a two month period for several start points are shown in Fig. 5. These paths reflect the general southward flow throughout the region. Of particular note is the eastward flow from the New Brunswick coast towards Prince Edward Island.

A series of drift trajectories were then calculated using both the mean currents and the wind-driven flow. Separate runs with Miscou Island and Summerside winds for

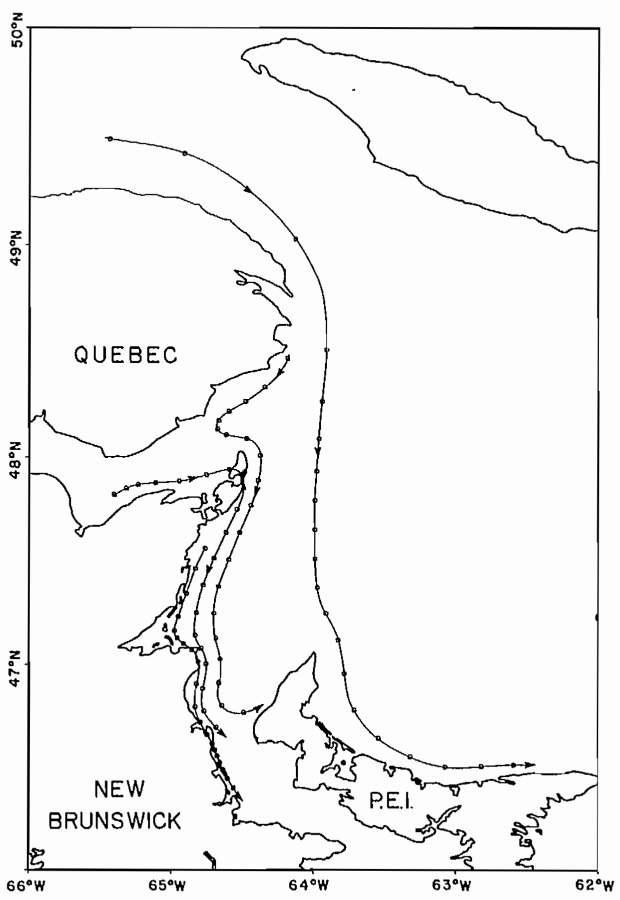

FIG. 5. Drift trajectories based on the residual currents for a two month period from different starting locations. The circles are placed on the paths at 3 d intervals.

the same period and start points showed similar drift patterns confirming the visual observation that the wind records at the two sites were highly correlated. From a start point in the Gaspé Current on 3 May (Julian day 124) and using wind data from Miscou Island, the model predicts that the flow would have rounded the Gaspé coast, crossed the mouth of the Bay of Chaleur, drifted slowly southward parallel to the New Brunswick shoreline, and eventually reached the mouth of Miramichi Bay on 2 June (day 154; Fig. 6a). This pathway is closer inshore than that predicted solely on the basis of the mean residual flow (Fig. 5). In a second case study, beginning three days earlier (30 April, day 121) from a starting point further to the southeast along the Gaspé coast, there was significant penetration into the Bay of Chaleur and containment within the bay throughout May (Fig. 6b). Additional model runs beginning in the Gaspé Current during early May generally showed that the trajectories remained nearshore and that by the beginning of June were located within the Bay of Chaleur or near the northeast coast of New Brunswick between Miscou Island and Miramichi Bay. The reason for the tendency towards shoreward movement can be seen from the monthly wind anomaly for May (Fig. 7). The vector-averaged monthly mean wind (1964–80) at Miscou Island is 0.34 m s^{-1} from 204°T. By contrast the 1988 resultant was 0.69 m s^{-1} from 68°T. Therefore, in 1988, there was a wind anomaly

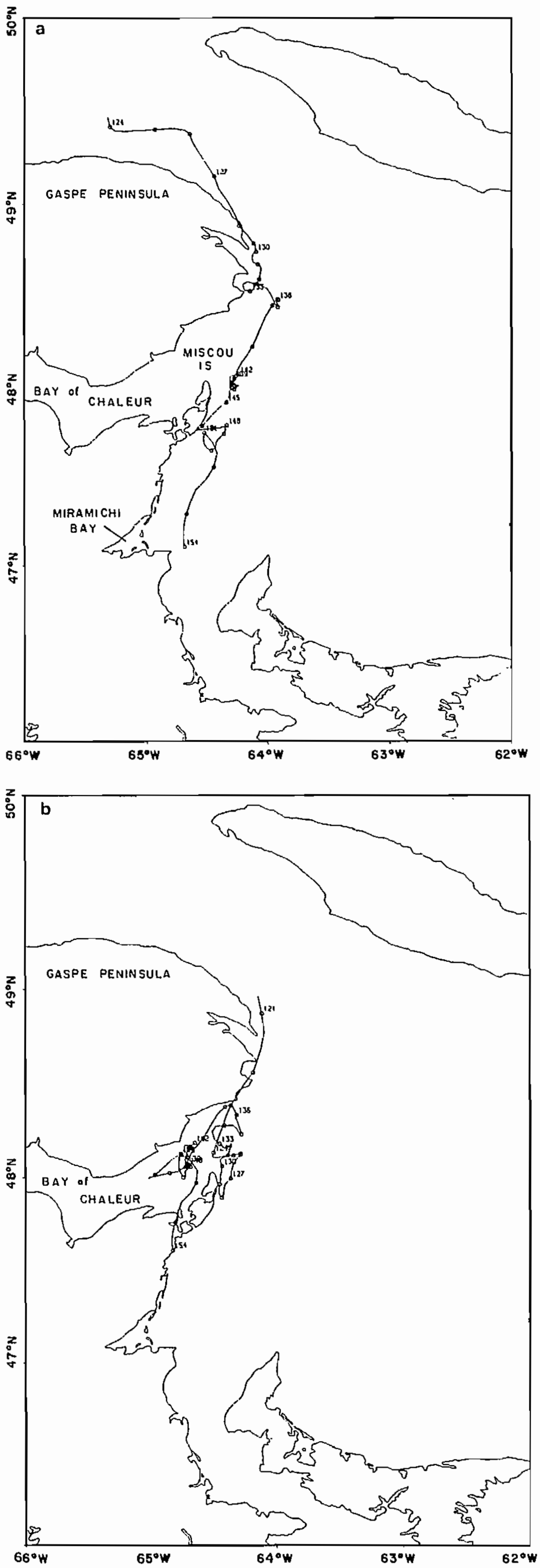

FIG. 6. Surface drift trajectories using Miscou Island winds for (a) a 30 d period commencing in the Gaspé Current on Julian day 124 (May 3), 1988, and (b) a 33 d period commencing at the eastern tip of the Gaspé Peninsula on Julian day 121 (April 30), 1988

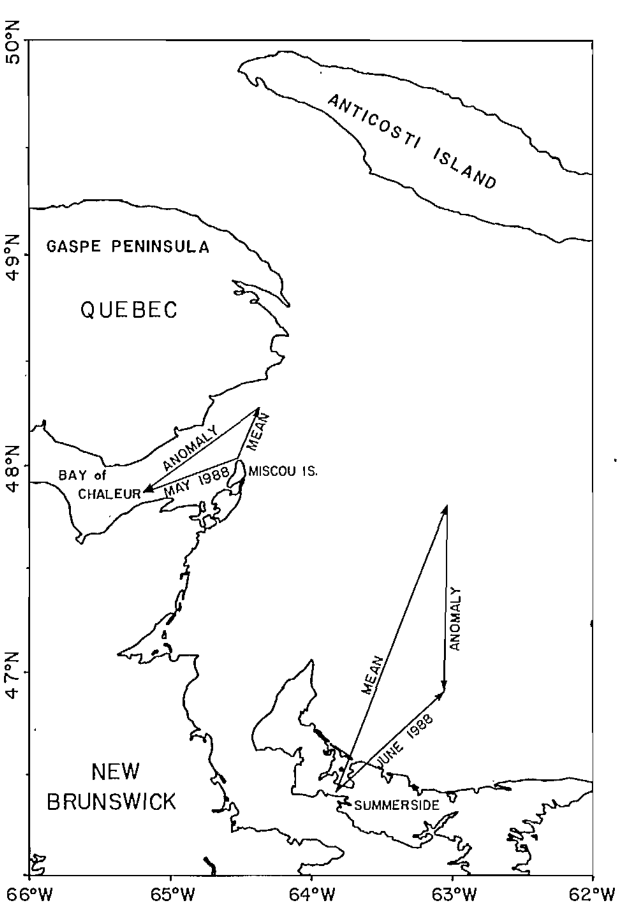

FIG. 7. Monthly mean wind-induced displacement of surface waters assuming 3% of the resultant wind during May using Miscou Island winds and June using Summerside winds. The resultant wind vectors for the long-term mean, the 1988 monthly means, and the 1988 anomalies are plotted to chart scale.

of 0.97 m s^{-1} from 52°T. Assuming a wind-induced surface drift of 3% of the wind speed, this would produce an anomalous surface displacement of 78 km towards the southwest (232°T) during the month (Fig. 7).

Not all of the model runs that started in the Gaspé Current showed nearshore drift, however, as is evident from Fig. 8. This trajectory began at approximately the same position as that shown in Fig 6b but two days later (4 May, day 125). The trajectory moved offshore, showing no movement towards the Bay of Chaleur or the coastlines of New Brunswick or Prince Edward Island.

To determine possible subsequent drift paths of water that may have entered the Bay of Chaleur, several model runs were made that began within the inner half of the Bay of Chaleur in mid-May. All trajectories remained within the Bay through to at least the beginning of June and typically longer.

The winds in June were generally weaker than normal (relative to the 1955–80 mean), resulting in an anomalous monthly mean wind of 1.25 m s^{-1} from the north (Fig. 7). This would have produced an anomalous southward displacement of water of 97 km over the month (assuming 3% of the wind speed). In addition, the weaker winds would reduce the observed upwelling along the northeast coast of New Brunswick (Lauzier 1967).

Discussion

The drift trajectories produced by the circulation model suggest that in May and early June of 1988 water from the Gaspé Current would, in general, have been forced by the residual and wind-driven currents into the Bay of Chaleur and southward toward the northern entrance of Northumberland Strait. The one to two month travel times from the northern Gaspé coast to the Bay of Chaleur, eastern New Brunswick and Prince Edward Island match closely the time between the first occurrences of PSP toxin in these regions. Assuming that *Alexandrium* blooms are carried with the surface currents, the model results suggest that a portion of the blooms which developed in the St. Lawrence Estuary in April–May, 1988, may well have been subsequently advected into Chaleur Bay and southward along the New Brunswick and Prince Edward Island coastlines, giving rise to the measured PSP toxins in the June–August period. Our model results further suggest that any *Alexandrium* blooms transported to the northeast coast of New Brunswick and Prince Edward Island would have been carried by the currents directly from the Gaspé region rather than taking a more circuitous route through Chaleur Bay.

Although PSP toxins have never previously been reported southward of the Gaspé peninsula, it may have occasionally occurred there in the past but not been

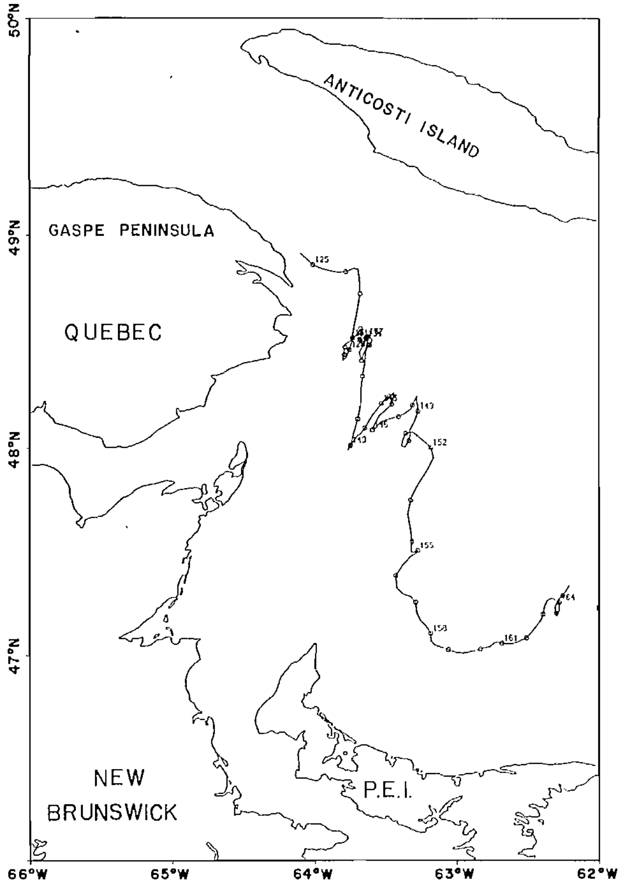

FIG. 8. Surface drift trajectory for a 45 d period commencing near the eastern tip of the Gaspé peninsula on Julian day 125 (May 4) using Summerside winds.

detected owing to limited monitoring. While the May-June wind pattern in 1988 varied significantly from normal, such anomalies have occurred in the past. Winds over the southwestern Gulf of St. Lawrence undergo a marked seasonal shift in prevailing wind direction (Blackford and Tsang 1964; Anonymous 1982). Typically, relatively strong winds blow from the northwest quadrant from September to April and weaker winds from the southwest quadrant from May to August. The switch in wind pattern commonly occurs over a period of a few weeks but displays considerable interannual, as well as decadal, variability in its timing. For example, during the decade 1940–49 winds over the Gulf of St. Lawrence in May were more characteristic of the summer wind pattern whereas during 1951–60 they were similar to the winter pattern (Blackford and Tsang 1964). In order to produce an *Alexandrium* bloom in Chaleur Bay or along the northeast coast of New Brunswick and Prince Edward Island, it may be that the timing of oceanographic and hydrological events, together with the biological mechanisms, which trigger bloom development in the Estuary must be accompanied by anomalous wind patterns at the time a bloom is developing in the Gaspé Current.

Although highly speculative, the long-term changes in wind pattern may produce long-term changes in the pattern of PSP outbreaks. For example, the average 1-mo delay in the change-over from NNW to WSW winds in May between the 1951–60 decade compared to the 1940–49 decade could have resulted in an increase in the amounts of St. Lawrence Estuary water moving seaward along the Gaspé coast and subsequently reaching the shores of New Brunswick and Prince Edward Island. In general, higher concentrations of *Alexandrium* are expected in May, compared to April, so that years when the change-over from a winter to summer wind pattern is delayed, the probability of *Alexandrium* being transported from the Estuary to Chaleur Bay and the northeast New Brunswick coast would be increased.

In this paper we have only considered the possible role of the surface circulation in the outbreak of PSP in the Gulf of St. Lawrence although we recognize that other environmental and biological factors may have been influential. We also realize that the trajectory model we have used is highly simplified. It ignores changes in the residual flow induced by interannual variations in the amplitude and timing of the freshwater discharge from the St. Lawrence and other rivers as well as the propagating wave-like low-frequency motions of the Gaspé Current described by Tang (1980) and Mertz et al. (1988). Both processes could significantly influence any drift trajectories. The mean residual drift used in the model contains seasonal wind effects and therefore we may be overemphasizing the effect of the wind. We know that the rate and magnitude of toxin accumulation in mussels and clams depend not only on the appearance of *Alexandrium,* but also upon the concentration, persistence, and specific toxicity per cell of these dinoflagellates. In spite of the shortcomings in our model, we believe it represents a first order approximation of the surface circulation and supports the hypothesis that *Alexandrium* from the St. Lawrence Estuary were transported by the surface currents into the southwestern Gulf of St. Lawrence.

Acknowledgements

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Effets du climat et de l'hydrographie sur le recrutement du homard américain *(Homarus americanus)* dans le nord du golfe du Saint-Laurent[1]

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L'examen de la partie nord du golfe du Saint-Laurent au moyen d'images satellites NOAA permet d'y observer plusieurs phénomènes hydrographiques tels que des tourbillons et des remontées d'eau froide, engendrant un gradient thermique de la Côte Nord du Québec (froide) à la côte ouest de Terre-Neuve (chaude). Ces phénomènes peuvent être reliés à certaines conditions climatiques, en particulier à la direction et à la force des vents dominants. Ces observations suggèrent un mécanisme précis par lequel les facteurs climatiques et hydrographiques pourraient exercer un impact direct sur l'advection et la survie des larves de crustacés planctoniques, en particulier celles du homard. Nous réexaminons ainsi, dans un cadre défini, l'hypothèse de Sutcliffe (1973) concernant l'existence d'une relation entre les facteurs physiques (dont dépend la survie larvaire) et les débarquements de homards, en tenant compte du décalage temporel qui existe entre la phase larvaire et le homard débarqué.

Dans un premier temps, nous examinons les hypothèses implicites à ce type de relation, soit (1) l'évaluation du recrutement annuel au moyen des statistiques de débarquement, (2) la perte de larves par advection des masses d'eaux, (3) la survie larvaire dans le plancton, (4) le nombre d'années de croissance benthique avant la taille minimale légale, (5) l'existence d'une relation stock-recrutement. Dans un second temps, les mécanismes pouvant être à l'origine de ce genre de corrélations sont évalués pour la phase critique de la vie larvaire planctonique, au moyen de données pour le nord du golfe. La modélisation des échanges de larves entre les différentes régions au moyen d'une matrice de Markov suggère que l'exportation de larves provenant de la Côte Nord et de l'île d'Anticosti vers la côte ouest de Terre-Neuve pourrait être importante pour y assurer le maintien des débarquements. La persistance de l'effet des apports de larves jusqu'à la taille minimale légale est évaluée au moyen de données physiques historiques régionales (température, vent, débit), en combinaison avec les statistiques détaillées de débarquement de homards sur la côte ouest de Terre-Neuve, l'île d'Anticosti, la Côte Nord du Québec et les Îles-de-la-Madeleine. Les relations entre les facteurs physiques et les débarquements de homards sont décrites au moyen de régressions multiples, permettant d'expliquer de 0 à 70 % de la variance des débarquements entre 1953 et 1982, selon les régions. La validation des modèles avec les débarquements de 1983–1988 montre que les prédictions sous-estiment toujours les débarquements observés. La démarche indique que l'identification d'un cadre conceptuel, la fiabilité et l'homogénéité des données de débarquement et des données physiques, ainsi que la connaissance des particularités physiographiques de chaque région, sont des éléments critiques pour le succès de la modélisation.

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[1] Cet article fait partie des Compte rendus d'un atelier/symposium tenu à l'Institut Maurice-Lamontagne, Mont-Joli (Québec) du 14 au 17 mars 1989.

A study of the northern Gulf of St. Lawrence using NOAA satellite imagery reveals a number of hydrographic phenomena such as gyres and coastal upwelling. These phenomena maintain a thermal gradient from the Québec North Shore (cold) to the west coast of Newfoundland (warm) and may be related to specific climatic conditions, such as the direction and speed of prevailing winds. These observations suggest a mechanism by which climatic and hydrographic factors could exert a direct impact on the advection and survival of planktonic crustacean larvae, particularly lobster. In that context we reexamine Sutcliffe's (1973) hypothesis concerning the existence of a relationship between physical factors (on which larval survival depends) and lobster landings.

In the first part of this paper, we examine the implicit assumptions to this type of relation: (1) the use of annual landing statistics to evaluate recruitment into the fishery, (2) the loss of larvae via water mass advection, (3) the survival of larvae in the plankton, (4) the number of years of benthic growth prior to minimum legal size, (5) the existence of a stock-recruitment relationship. In the second part of the paper, the potential mechanisms at the origin of such correlations are evaluated for the critical phase of the planktonic larval phase, using data from the northern Gulf of St. Lawrence. A model of larval exchange among the different regions using a Markov transition matrix suggests that larval exports from the Québec North Shore and Anticosti Island could explain the stability of landings off the west coast of Newfoundland. The persistence of the effects of larval exchange until recruitment into the fishery is evaluated using historical physical data (temperature, wind, freshwater flow) in conjunction with detailed landing statistics for the west coast of Newfoundland, Anticosti Island, the Quebec North Shore and Îles-de-la-Madeleine. The relationships between various physical factors and lobster landings are described using multiple regressions, explaining from 0 to 70% of the variance of landings between 1953 and 1982, depending on the region. Validation of the models using the 1983–1988 landings shows that predicted values always underestimate the observed landings. This study indicates that the definition of a conceptual framework, the reliability and homogeneity of landings and physical data, as well as the knowledge of the physiographic characteristics of each region, are critical to the success of modelling.

Introduction

La délimitation des populations biologiques formant des unités de recrutement distinctes représente l'un des fondements de la gestion des pêches dans l'Atlantique canadien. À défaut de pouvoir circonscrire des cellules de recrutement homogène, la gestion des stocks du homard américain (*Homarus americanus*) se fait présentement selon des unités géographiques. L'influence commune de certains facteurs physiques et/ou biologiques affectant le recrutement dans des unités géographiques a déjà été utilisée pour expliquer les fluctuations parallèles des statistiques historiques de débarquement de homard (Robinson 1979; Campbell et Mohn 1983; Harding *et al.* 1983). Les statistiques de débarquement peuvent servir d'indice du recrutement puisque les populations de homard sont sujettes à un taux d'exploitation suffisamment élevé (Campbell 1980) pour que les prises annuelles reposent essentiellement sur les individus ayant mué à la taille commerciale la saison précédente (Ennis 1982), ce qui lie très fortement les débarquements annuels au succès de la déposition larvaire plusieurs années auparavant (Ennis 1983a; Campbell et Mohn 1983).

La prédiction de l'abondance d'une population à partir de certaines variables physiques déterminantes pour la déposition larvaire représente aussi un objectif important de la gestion à long terme des pêches maritimes. Les effets possibles des débits d'eau douce (Sutcliffe 1973; Trites 1970; Sheldon *et al.* 1982; Bugden *et al.* 1982; Sinclair *et al.* 1986), des vents dominants (Caddy 1979), des patrons de circulation (Îles 1975; Dadswell 1979; Robinson 1979), ainsi que de la température de surface (Scarratt 1964; Dow 1977; Flowers et Saila 1972; Boudreault *et al.* 1977; Fogarty 1988) sur le recrutement du homard ont été étudiés pour différentes régions de la côte Atlantique.

La relation proposée par Sutcliffe (1973) entre le débit du fleuve Saint-Laurent en avril et les débarquements de homards neuf années plus tard fut de loin la plus fréquemment utilisée; on en a subséquemment tiré une équation prédictive expliquant 77 % de la variance des débarquements de homards au Québec entre 1950 et 1979 (Sheldon *et al.* 1982). Des hypothèses quant aux mécanismes à l'origine de cette corrélation furent élaborées par Bugden *et al.* (1982), puis revues par Sinclair *et al.* (1986) et par Drinkwater et Myers (1987). De toute évidence, la relation entre les débits d'eau douce et les débarquements présuppose plusieurs mécanismes intermédiaires, certains d'une grande complexité. Parmi les facteurs affectés par les variations de débit se trouvent la circulation et l'intensité du mélange des masses d'eau, la formation et la distribution de la glace, la rétention thermique (température à la surface), l'apport direct de sels nutritifs, la salinité, la turbidité, la pénétration de la lumière et l'intensité de la stratification. Ce genre de relation suppose que la survie accrue des larves lors d'une année aux conditions physiques favorables se reflètera plusieurs années plus tard par un plus grand nombre de homards adultes dans la pêche.

Le nord du golfe du Saint-Laurent est la limite nordique de la distribution du homard (Huntsman *et al.* 1954) (fig. 1) ce qui rend l'espèce plus sensible aux fluctuations du milieu physique. Ceci pourrait expliquer au moins en partie pourquoi les patrons de débarquement à long terme sont très différents de ceux des autres régions du golfe et de la côte Atlantique (Campbell et Mohn 1983; Harding *et al.* 1983). Le nord du golf comprend les districts statistiques de la Côte Nord du Québec et de l'île d'Anticosti, ainsi que la côte ouest de Terre-Neuve (districts statistiques K, L, M, N). Les Îles-de-la-Madeleine ont été incluses dans notre analyse pour permettre des comparaisons avec une région préalablement étudiée.

Notre étude a pour objectifs (1) d'élaborer des hypothèses quant aux mécanismes physiques déterminant l'advection et la survie des larves de homard dans le nord du golfe; (2) de décrire les échanges potentiels de larves entre les régions du nord du golfe; (3) de produire un modèle prédictif quantitatif de l'effet des facteurs physiques sur l'advection et la survie larvaire à l'aide de données historiques, ce qui permet d'évaluer les variables physiques susceptibles d'exercer un effet critique dans chacune des régions; et enfin, (4) de tester ce modèle avec les valeurs récentes de débarquements (1983–1988) pour en déterminer la validité et la sensibilité et évaluer les éléments critiques au succès de la démarche.

Hypothèses sous-jacentes d'un modèle de prédiction des débarquements de homards à partir des facteurs environnementaux

Les modèles visant à prédire les débarquements à partir de variables physiques reposent sur plusieurs hypothèses de base que nous allons d'abord examiner, en vue de déterminer comment elles en affectent les résultats. Cette démarche nous permettra de déterminer *a priori* les éléments critiques à la modélisation, les variables physiques et biologiques devant être incluses ainsi que le décalage annuel devant être utilisé.

Hypothèse #1 : Les statistiques de débarquements de chaque région sont un indice fiable du nombre de homards atteignant la taille minimale légale de capture chaque année.

Cette hypothèse comporte plusieurs éléments sous-jacents :

a) Les statistiques de débarquement sont fiables.
b) le taux d'exploitation est si élevé que la capture est indépendante de l'effort déployé.
c) Les captures reposent principalement sur les individus qui viennent de muer à la taille légale, plutôt que sur un

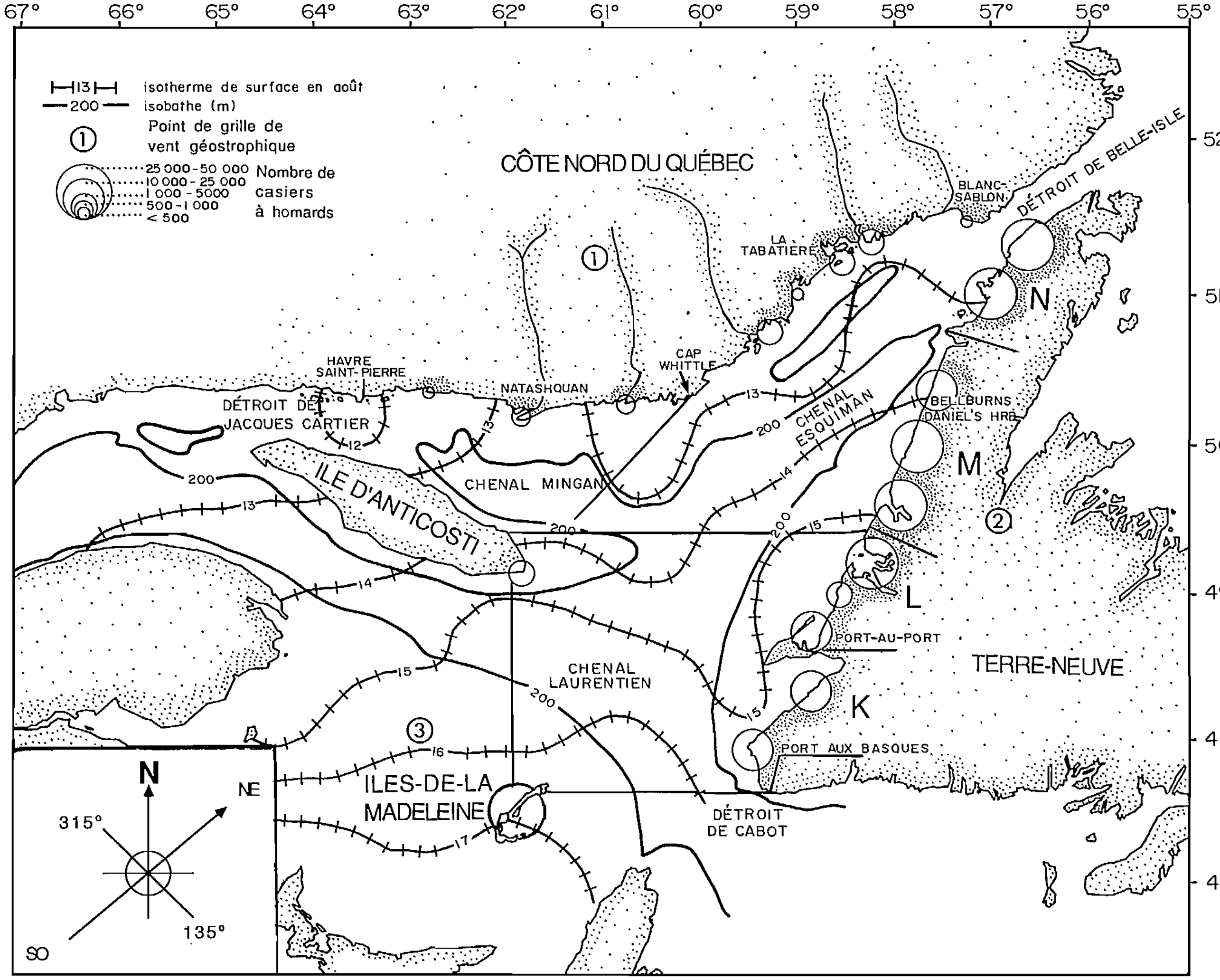

FIG. 1. Principales caractéristiques morphologiques et physiques du nord du golfe du Saint-Laurent. Les isothermes des eaux de surface pour le mois d'août ont été tracées d'après Vigeant (1987). La répartition du nombre de casiers a été obtenue à partir des statistiques des pêches maritimes de 1986 (Ministère des Pêches et des Océans). Les points numérotés 1, 2, 3 réfèrent à la grille de Swail (1985) utilisée pour le calcul des vents géostrophiques. L'axe 135°–315° (encadré) a été utilisé pour distinguer les vents à dominance NE de ceux du SO dans le calcul de la fréquence des vents favorables à la rétention locale. Les vents et les températures ont été calculées initialement pour les régions du chenal Mingan, du chenal d'Esquiman et du chenal Laurentien, délimitées à partir de la pointe est de l'île d'Anticosti (voir le texte pour explications).

groupe d'âge mixte comprenant des individus plus âgés (i.e., de plus grande taille) ayant échappés à plusieurs années de pêche.

La côte ouest de Terre-Neuve est divisée en quatre régions (K, L, M, N, fig. 1) pour lesquels des statistiques détaillées de captures sont disponibles depuis 1953 (tableau 1). Plusieurs auteurs (Templeman 1939; Squires 1970; Ennis 1974; Anthony et Caddy 1980; Campbell 1980) rapportent que le régime de capture des 50 dernières années semble autant, sinon plus, lié au recrutement annuel qu'à l'effort de pêche comme tel. En outre, l'interruption de la pêche pour des périodes allant de 6 à 3 années consécutives n'a accru la taille des individus et le volume des captures que pour l'année suivant la réouverture, tant sur la côte ouest de Terre-Neuve (Wilder 1965; Squires *et al.* 1974) que sur la Côte Nord du Québec (Huntsman *et al.* 1954).

Par comparaison, la pêche est très sporadique le long de la Côte Nord du Québec, où elle se concentre surtout entre Blanc-Sablon et le cap Whittle. Les homards capturés sur la Côte Nord et à l'île d'Anticosti comportent une proportion élevée d'individus de grande taille (observ. pers.), indiquant que les débarquements annuels reflètent plus que la production annuelle de recrues. C'est aux Îles-de-la-Madeleine que les débarquements sont les plus importants (tableau 1); la taille moyenne des individus y est faible, particulièrement sur la face SO.

Les données de débarquements souffrent de nombreuses imprécisions, dont l'importance semble être en relation inverse avec le volume des captures. Ainsi, une proportion variable des ventes locales est privée, particulièrement dans les régions isolées telles que la Côte Nord du Québec et la côte ouest de Terre-Neuve (observ. pers.; D. Maynard, Ministère des Pêches et des Océans, région du Golfe, comm. pers.). Une partie des captures peut être vendue et enregistrée dans une région adjacente, mal rapportée ou entièrement omise des statistiques (ventes locales et braconnage).

La variabilité inter-annuelle des débarquements, exprimée par le coefficient de variation, est élevée pour la Côte Nord et l'île d'Anticosti (54 et 128 %, respectivement), tandis que les régions M (18 %), N (27 %) et les Îles-de-la-Madeleine (18 %) montrent des débarquements plus stables (tableau 1). Il est impossible de déterminer la relation entre les captures et l'effort de pêche, puisqu'aucune donnée historique de nombre de casiers • jour^{-1} n'est disponible. Le nombre de casiers utilisés annuellement, tel que rapportés pour le côte ouest de Terre-Neuve, ne peut pas être considéré comme une mesure adéquate de l'effort de pêche déployé.

Pour la côte ouest de Terre-Neuve, Ennis (1983a) a évalué que 90 % des homards atteignant la taille légale sont capturés chaque année, ce qui représente une valeur très élevée et rend cette région très sensible à la surexploitation (Templeman 1939, 1941; Huntsman *et al.* 1954; Wilder 1965). Nous avons employé la valeur de 16 % pour corriger l'estimation d'abondance du homard à l'île d'Anticosti (Gauthier 1988) et un taux approximatif de 20 % pour la Côte Nord pour laquelle aucune donnée n'est disponible. Ces faibles taux indiquent que les statistiques des débarquements sous-estiment nettement l'abondance annuelle des recrues. Aux Îles-de-la-Madeleine, nous avons utilisé un taux d'exploitation de 80 % (Campbell 1980).

La correction pour les taux d'exploitation estimés dans chaque région n'altère pas significativement l'ordre d'importance des régions (tableau 1, colonne 5) et corrige quelque peu les effets dus aux disparités régionales de taille de casiers, de type de mouillages et de puissance de la flotte de pêche. En somme, les taux d'exploitation indiquent que l'hypothèse liant les captures au recrutement annuel semble assez bien se vérifier pour les Îles-de-la-Madeleine, modérément pour la côte ouest de Terre-Neuve, et fort peu pour l'île d'Anticosti et la Côte Nord.

Hypothèse #2 : Le nombre de larves se déposant dans une région donnée est fonction de la dérive des masses d'eau dans lesquelles les larves se trouvent.

Au cours de leur séjour dans le plancton, les larves se trouvent principalement dans les 5 m supérieurs de la

TABLEAU 1. Tableau comparatif des captures annuelles moyennes entre 1953 et 1985 pour chaque région dans le nord du golfe du Saint-Laurent, corrigées en fonction du taux d'exploitation (colonne 4) et ramenées à un dénominateur commun (région $N = 1{,}00$, colonne 6). Ces valeurs doivent être comparées avec les contributions théoriques obtenues par la matrice de transition de Markov initiale (colonne 7) et après itérations (colonne 8). Le coefficient de variation (100 × s/x) permet de comparer la variabilité annuelle des débarquements des régions (colonne 3).

Région (1)	Captures moyennes (tm) (2)	Coefficient de variation (%) (3)	Taux d'exploitation (%) (4)	Quantité estimée (tm) (5)	Proportion de N (6)	Matrice de Markov	
						initiale (7)	finale (8)
Îles-de-la-Madeleine	1 239,73	18,82	80[b]	1 549,66	7,35	1,30	2,99
Côte	14,92	53,99	20[a]	74,55	0,35	0,30	0,11
Anticosti	13,96	128,42	16[c]	87,18	0,41	0,60	0,16
K	142,96	38,33	90[d]	158,77	0,75	0,80	0,71
L	249,56	37,99	90[d]	277,23	1,30	0,90	0,94
M	277,90	18,07	90[d]	307,88	1,46	1,25	1,29
N	189,88	27,99	90[d]	210,95	1,00	1,05	0,96

[a] Taux d'exploitation approximatif
[b] Campbell (1980)
[c] Gauthier (1988)
[d] Ennis (1983a)

colonne d'eau (Hudon *et al.* 1986). Les mouvements des masses d'eau engendrés par les courants et les vents dominants pourraient donc avoir une grande influence sur le succès du recrutement larvaire, déterminant si les larves produites en un lieu donné atteindront le stade benthique sur place ou seront exportées vers l'autres régions.

Plusieurs études ont déjà mentionné l'effet favorable des vents dominants du SO sur la rétention des larves de homard le long de la côte ouest de Terre-Neuve (Templeman 1939; Templeman et Tibbo 1945; Huntsman *et al.* 1954; Squires 1970; Ennis 1983b). L'abondance de larves de homard ainsi que de leurs proies le long des côtes est significativement plus grande lorsque le vent souffle vers la côte plutôt que vers le large (Ennis 1983b). L'examen de la figure 1 suggère que la force et la direction des vents devraient avoir un effet différent sur des côtes rectilignes (régions M et N), et des côtes indentées de baies profondes orientées vers le SO (K) ou le NE (L). Les Îles-de-la-Madeleine ont déjà été identifiées comme une zone de recrutement homogène (Robinson 1979) où l'on observe un déplacement vers la face SE des larves produites sur la face NO, sous l'influence d'un vent du SO (Hudon *et al.* 1986).

Par conséquent, notre modèle doit inclure le kilométrage cumulatif des vents dans les axes NE et SO, pour tenir compte des déplacements des larves dans les masses d'eaux de surface.

Hypothèse #3 : La survie des larves est liée aux conditions du milieu physique pendant leur phase planctonique.

La température : Le développement du premier stade larvaire peut s'effectuer dans des eaux de 7 à 20°C (Templeman 1936). À une température inférieure à 10°C, le passage des stades larvaires IV à V ne peut être complété (Templeman 1936). En raison de ces contraintes thermiques, les larves de homard devraient séjourner dans le plancton du nord du golfe de juillet à la fin de septembre, leur survie étant proportionnelle à leur vitesse de croissance, qui est elle-même une fonction de la température locale.

La salinité : Les larves de homard tolèrent mal les salinités inférieures à 19–20‰ (Templeman 1936), quoiqu'elles puissent éviter activement les eaux de salinité inférieure à 21 ou 22‰ (Scarratt et Raine 1967) en migrant vers le fond. Sur la côte ouest de Terre-Neuve, la salinité varie entre 30 et 31.5‰ (Squires 1970; Squires *et al.* 1974). Sur la Côte Nord, des salinités inférieures à 21‰ sont parfois observées dans les 3 premiers m entre juillet et septembre (Gaudet 1986; Thomas 1989), alors que les valeurs habituelles oscillent entre 25 et 29‰, ce qui n'affecte les larves que dans certains cas particuliers.

Le mélange vertical et la production primaire : L'apport d'éléments nutritifs par les débits d'eau douce et le mélange vertical dû au vent ont pour conséquence d'augmenter la production planctonique, pouvant ainsi contribuer indirectement à la survie des larves (Bugden *et al.* 1982). Les larves de homard sont carnivores, utilisant des proies d'une taille qui croît avec la séquence des stades larvaires (Harding *et al.* 1983). La survie des larves est affectée par la quantité et la qualité du zooplancton (Scarratt 1964; Templeman 1936) dont l'abondance est mal connue dans le nord du golfe (Steven 1974). Cependant, une production secondaire accrue peut engendrer soit une meilleure production de nourriture pour les larves (survie), soit une production accrue de prédateurs des larves de homard (mortalité), ce qui nous empêche de déterminer *a priori* la direction de l'effet attendu.

Les variables physiques devant être incluses dans le modèle pour évaluer la survie des larves sont donc la température, les apports de sels nutritifs via les débits d'eau douce et le mélange vertical dû au kilométrage cumulé des vents de toutes directions.

Hypothèse #4 : Le nombre d'années de décalage entre la déposition larvaire et les débarquements est déterminé par le taux de croissance benthique dans la région de déposition larvaire.

Le taux de croissance du homard varie entre les régions, étant une fonction directe de la température au fond. Cette dernière est beaucoup plus élevée aux Îles-de-la-Madeleine que sur la côte ouest de Terre-Neuve, où elle est supérieure à celle de la Côte Nord. La croissance des homards étant directement reliée au régime thermique, on devrait s'attendre à ce que les homards provenant des régions froides prennent un plus grand nombre d'années à atteindre la taille commerciale.

Sur la côte ouest de Terre-Neuve, Ennis (1980) estime que les homards atteignent la taille commerciale après 8 à 9 années de croissance. Compte tenu des différences de température entre les régions, nous avons fixé le décalage dû à la période de croissance benthique, entre la période de déposition des larves et la taille minimale de pêche légale, à 8 ans pour les régions K et L et à 9 ans pour les régions M et N dont les eaux sont plus froides. Ce même décalage de 9 ans a été utilisé pour la Côte Nord et l'île d'Anticosti, où la température au fond est au moins aussi froide, sinon plus froide, que dans les régions M et N (fig. 3a). Aux Îles-de-la-Madeleine, le décalage dû à la croissance benthique a été fixé à 7 ans, quoique la période de croissance avant l'atteinte de la taille minimale légale puisse être différente sur les faces nord-est et sud-ouest, cette dernière étant nettement plus chaude (Hudon 1987).

La production de larves repose essentiellement sur le nombre et la taille des femelles ovigères, qui sont en principe exclues de la pêche durant toute la période où elles portent leurs œufs. Le homard femelle porte les œufs sous son abdomen pour une période d'environ 10 à 12 mois (voir la revue d'Aiken et Waddy 1986). La durée de développement des œufs permet de déterminer que la survie des larves produites par la population de homards pêchés au cours de l'année (*t*) sera une fonction des conditions physiques lors de l'éclosion des œufs au cours de l'année (*t* + 1 an). Il en découle que le décalage utilisé pour calculer la relation entre le stock et la production de recrues sera d'une année de plus que celui utilisé pour les variables physiques ayant un effet sur la survie des larves.

Au sein d'une même région, la déposition benthique peut s'étendre sur plus de deux mois, avec pour conséquence que l'intervalle de taille d'une cohorte pourrait couvrir quatre stades de mue dès la fin de la première saison de croissance (Hudon 1987). Cet écart, combiné à la forte variabilité individuelle des taux de croissance (Hughes et Mathiessen 1962; Wilder 1953), pourrait avoir pour résultat que différents individus d'une même cohorte pourraient entrer dans la pêche au cours de plusieurs années successives (Hudon 1987). Les bénéfices d'une seule année favorable au recrutement larvaire pourraient donc être dilués dans le temps. Cette relation assume de plus que la mortalité a surtout lieu au stade planctonique plutôt que lors des premiers stades benthiques (post-larves et juvéniles), ce qui reste à démontrer en nature (Hudon 1987).

Hypothèse #5 : Il existe une relation entre le stock adulte exposé à l'exploitation et le nombre de larves, et éventuellement d'adultes produits par ce même stock.

La nature exacte de la relation stock-recrutement reste toujours à déterminer pour le homard américain. L'existence d'une rétroaction positive entre le nombre de larves produites par le stock et l'abondance même de ce stock devrait induire la non-indépendance des valeurs des séries temporelles de données de débarquement, susceptible de se manifester sous la forme de cycles d'abondance (autocorrélation positive). Le calcul de cette relation suppose l'existence d'une relation de proportionnalité entre les différents segments de la population d'une région donnée, en tenant compte du décalage entre la ponte et la taille adulte : débarquements adultes ∝ femelles ovigères ∝ oeufs ∝ juvéniles

Une analyse de l'autocorrélation temporelle des débarquements bruts de chacune des régions n'indiquait aucune fluctuation cyclique significative aux périodes comprises entre 5 et 11 ans, qui représentent les valeurs extrêmes des périodes pouvant correspondre à la durée de croissance du homard. Des fluctuations cycliques d'abondance auraient possiblement indiqué une forte rétention locale de larves; celles-ci auraient cependant pu être masquées par un apport de larves provenant d'autres régions, selon le régime de circulation engendré par les vents et les courants (Hypothèse 2), par une survie différentielle des larves dans le plancton (Hypothèse 3) ou par l'arrivée d'une même cohorte à la taille minimale légale au cours de plusieurs années successives (Hypothèse 4).

Sources des données et méthodologie

Les données historiques de débarquement et d'effort de pêche au homard ont été fournies par le Ministère des Pêches et des Océans (régions de Terre-Neuve, du Golfe et du Québec) et par le Bureau de la Statistique du Québec. L'autocorrélation des débarquements de chaque région a été calculée sur les données brutes avec un décalage annuel croissant pour détecter la présence de cycles d'abondance. Les échanges de larves entre les régions ont été modélisés à l'aide d'une matrice de transition de Markov (8 × 8 cellules); aux sept régions du tableau 1 a été ajoutée une huitième région « au large » rendant compte des larves exportées hors des zones de pêche. Cette matrice a été multipliée par elle-même jusqu'à sa stabilisation asymptotique pour déterminer si le réseau d'échange élaboré pouvait correspondre à l'importance relative des débarquements observés dans chaque région.

Relation climat-hydrographie

Dans le cadre d'une étude précédente (Lavoie *et al.* 1986), 17 images des satellites NOAA 6 et 7 ont été obtenues pour 1981 et 1984. Six de ces images (fig. 2) sont présentées au tableau 2. La plupart d'entre elles couvrent une partie du secteur à l'étude, entre Natashquan et Saint-Augustin, selon le couvert de nuages. Il s'agit d'images infrarouges thermiques qui permettent de visualiser les variations de température de l'eau à la surface de la mer. L'interprétation de ces images a été faite en fonction des patrons de répartition des températures de l'eau (Lavoie *et al.* 1986). Les informations présentées ici mettent plutôt l'accent sur les relations avec les conditions météorologiques.

Ces images satellite ont été corrigées géométriquement et sont donc superposables. On a appliqué une correction radiométrique à partir des valeurs obtenues pour des corps noirs servant à l'étalonnage du radiomètre qui enregistre les images. Pour les images de 1981, nous avons employé les valeurs moyennes de la correction obtenues du Service de l'Environnement Atmosphérique d'Environnement Canada à Toronto. Une correction atmosphérique additionnelle a été réalisée à partir de données de température de la surface de l'eau relevées lors d'une campagne océanographique (D. Lefaivre, MPO, Région du Québec, comm. pers.), et à partir de mesures provenant de navires (Vigeant 1987).

TABLEAU 2. Caractéristiques climatiques au moment de la prise des images NOAA présentées à la figure 2 (A–F). L'intervalle des températures enregistrées à la surface des eaux est indiqué après calibration. Les phénomènes hydrographiques observés sur chaque image sont indiqués (x). Le code de l'image indiqué entre parenthèses fait référence au code utilisé dans l'étude de Lavoie et al. 1986. T : présence de tourbillons; R : présence de remontées d'eau profonde le long de la côte; Grad. : présence d'un gradient thermique dans l'axe E–O.

Image et code	Date Jr/mo/an	Heure GMT	Température		Vent		Pression Barométrique	T	R	Grad.
			Min	Max	Vitesse km • h^{-1}	Direction N-S-E-O				
A (B)	22 mai 81	11:41	2,18	6,97	15	NE	Haute	x		
B (J)	27 sep. 81	07:48	9,13	15,77	10–20	NO	–			x
C (K)	8 mai 84	19:14	-0,13	8,16	10–25	O	Haute	x	x	x
D (L)	27 mai 84	18:41	2,46	11,05	30–40	O-SO	–	x	x	x
E (M)	24 juin 84	19:38	5,49	12,98	15–25	S-SO	Haute		x	
F (Q)	30 sep. 84	19:34	3,52	11,98	15–30	SO	Haute	x	x	x

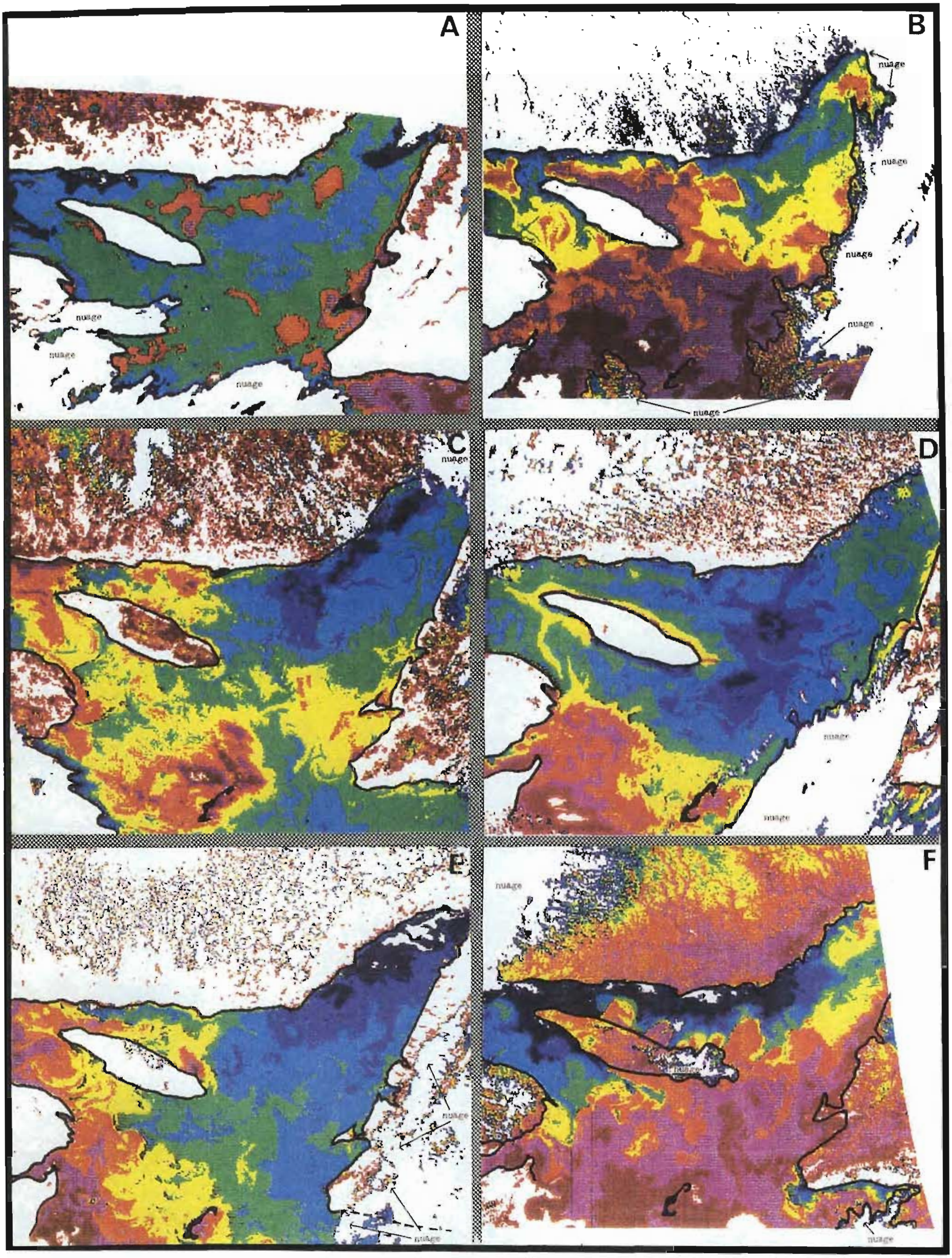

FIG. 2. Images satellite NOAA montrant les différentes caractéristiques de la circulation dans le nord du golfe du Saint-Laurent. Les teintes de couleur allant du bleu foncé au rouge clair indiquent des températures de plus en plus élevées. Les dates et conditions climatiques dans lesquelles les images ont été prises ainsi que les minima et maxima de l'échelle des températures sont indiqués au tableau 2.

Variables physiques

L'examen des hypothèses présentées précédemment, ainsi que l'analyse des relations climat-hydrographie ont permis de déterminer que la température de l'eau, la vitesse et la direction du vent, ainsi que les débits d'eau douce provenant du Saint-Laurent et des grandes rivières de la Côte Nord du Québec devaient être considérées lors de l'élaboration des modèles prédictifs des débarquements. Les données climatiques ont été fournies et analysées par le service de statistiques maritimes du Service de l'environnement atmosphérique (Environnement Canada). Les modèles prédictifs des débarquements de chaque région par les variables physiques ont été calculés à l'aide de régressions multiples.

Vitesse et direction des vents — Les statistiques de vent pour les régions ont été obtenues au moyen des calculs de vents géostrophiques à partir des données de pression en surface aux 6 h à des points de grille séparés de 381 km et fournis par le Fleet Numerical Oceanography Center (Mendehall *et al.* 1978). La banque de vents géostrophiques aux 6 h entre 1946 et 1986 pour les trois points de grille utilisés (les plus rapprochés du secteur à l'étude, fig. 1) est accessible au Centre climatologique canadien (Swail 1985) et a été utilisée ici pour calculer le kilométrage parcouru par le vent au cours des mois de juillet à septembre selon les deux directions divisées selon l'axe 135°-315°, soient NE et SO (fig. 1). Le lien entre le vent géostrophique et celui réellement observé en surface est complexe et dépend entre autres de la latitude, de la stabilité atmosphérique, de la baroclinicité, de la rugosité du terrain, de la courbure des isobares et de la variabilité du champ de pression. Malgré ces contraintes, Swail *et al.* (1984) montrent que les vitesses des vents géostrophiques sont en moyenne 11 % supérieures aux valeurs mesurées et que les écarts dans les directions sont en moyenne de 15° environ. Donc, l'emploi de la banque des vents géostrophiques aux points 1, 2 et 3 pour estimer le kilométrage parcouru par le vent et son influence sur le transport des eaux en surface constitue un choix logique.

Température de l'eau — L'estimation de la température mensuelle de l'eau en surface a été faite au moyen des observations météorologiques recueillies depuis 1860, en subdivisant le nord du golfe du Saint-Laurent en trois zones (fig. 1), pour lesquelles toutes les observations de température de l'eau en surface, recueillies à bord des navires en transit, ont été groupées par année et par mois. Ces zones correspondent au chenal de Mingan (5022 obs.), au chenal d'Esquiman (20182 obs.) et au chenal Laurentien (23991 obs.). Afin de s'assurer que les données de température de l'eau de chaque zone soient raisonnablement réparties au cours du mois, celles-ci ont été regroupées selon le choix arbitraire des trois périodes de 10 jours (décades) de chaque mois. Pour les mois où on possède au moins une observation pour chaque décade, la température moyenne mensuelle a été calculée en faisant la somme des valeurs moyennes décadaires du mois divisée par 3. Cette température moyenne mensuelle devrait physiquement s'approcher plus de la vraie valeur climatologique puisque chaque décade se voit attribuer le même poids lors du calcul de la moyenne.

Faisant l'hypothèse que la température de l'eau d'une zone est directement liée au régime thermique des masses d'air de chaque région, on a élaboré un modèle de régression linéaire pour calculer les températures de surface pour les années où la couverture par les navires n'était pas suffisante :

$$T_{eau} = T_{eau}(i) - T_{eau}(i\text{-}1) = a + b * [T_{air}(i) - T_{air}(i\text{-}1)]$$

où $T_{eau}(i)$ et $T_{air}(i)$ sont respectivement les températures moyennes mensuelles de l'eau et de l'air observées au mois i; $T_{eau}(i\text{-}1)$ est la température moyenne mensuelle de l'eau observée au cours du mois précédent; a et b sont les coefficients de régression. Ce modèle exige donc que l'on connaisse les températures moyennes de l'eau durant deux mois consécutifs, ainsi que les températures moyennes mensuelles de l'air à des stations terrestres considérées comme représentatives des trois zones maritimes à l'étude, soit Natashquan (1913-1986) pour le chenal de Mingan, Daniels Harbour (1946-1986) pour le chenal d'Esquiman, et enfin les Îles-de-la-Madeleine (1871-1986) pour le chenal Laurentien (tableau 3). Les données des stations terrestres sont archivées au Centre climatologique canadien, SEA. La pente des équations correspondant à chacune des zones (tableau 3) indique qu'en moyenne, la température de l'eau augmente d'un °C pour une augmentation de deux °C de la température de l'air.

Les valeurs de température et de vent obtenues pour les trois secteurs décrits à la figure 1 ont été extrapolées pour chacune des régions statistiques en faisant la moyenne des valeurs pour les secteurs adjacents. Par exemple, la température moyenne à l'île d'Anticosti a été calculée comme la moyenne des températures estivales des trois secteurs (Esquiman, Jacques-Cartier et Laurentien), puisque les eaux des trois secteurs baignent la pointe est où se pêche le homard.

Débits d'eau douce — Les données historiques de débit des rivières de la Côte Nord ($m^3 \cdot s^{-1}$) ont été fournies par le Service des Relevés hydrologiques d'Hydro-Québec; celles-ci sont disponibles pour les années de 1946 à 1986. Un indice de débit estival a été calculé à partir des valeurs centrées-réduites des débits de juillet, août et septembre pour les six plus grandes rivières de la Côte Nord (Brosseau 1979). Les données historiques de débits du Saint-Laurent ($1000\ m^3 \cdot s^{-1}$) pour les mois de juillet, août et septembre telles que rapportées par Bugden *et al.* (1982) ont été utilisées. Ces mois ont été choisis parce qu'ils correspondent à la période larvaire proprement dite en l'absence d'information objective sur le décalage exact entre le débit et la production.

TABLEAU 3. Valeurs obtenues pour les équations de régression entre les différences de température de l'air et de l'eau de surface pour deux mois consécutifs de l'année pour les données historiques de température. La valeur moyenne de température mensuelle a été obtenue en faisant la moyenne des valeurs obtenues par période de 10 jours, pour tous les mois de l'année sans couvert de glace.

Région	Ordonnée à l'origine (a)	Pente (b)	r^2	P	n
Chenal Mingan	0,1087	0,5042	0,768	0,0001	72
Chenal d'Esquiman	-0,0078	0,4978	0,748	0,0001	182
Chenal Laurentien	0,3841	0,4711	0,802	0,0001	309

Élaboration d'une hypothèse quant aux effets du climat et de l'hydrographie sur l'advection et la survie larvaire du homard dans le nord du golfe

Relation climat–hydrographie et conséquences sur l'advection larvaire

Les images satellite apportent une vue intégrée des patrons généraux des mouvements des masses d'eau, tout en permettant de visualiser les variations synoptiques des températures de surface. Il est également possible grâce aux images satellite de déterminer l'interaction entre les conditions climatiques et l'hydrographie pour l'ensemble du secteur d'étude, ce qui permet d'inférer où se trouvent les conditions favorisant, ou non, le recrutement larvaire du homard.

Les images satellites (fig. 2, tableau 2) permettent d'identifier deux types de phénomènes hydrographiques ayant un impact potentiel sur l'advection et la survie des larves de homards. Ces phénomènes sont la circulation tourbillonnaire dans le nord du golfe et les remontées d'eau froide; ils engendrent le gradient thermique observable dans l'axe est-ouest entre la Côte Nord du Québec et la côte ouest de Terre-Neuve.

La présence de tourbillons est suggérée sur les images satellite du nord du golfe, où l'on observe des masses d'eau de forme curvilinéaire dans le chenal d'Esquiman (fig. 2c, d, f) (Huntsman *et al.* 1954) ainsi qu'entre l'île d'Anticosti et la côte ouest de Terre-Neuve (fig. 2c, f) (Murty et Taylor 1970; El-Sabh 1976). Une fois exportées vers le large, les larves de homard pourraient être maintenues par une circulation tourbillonnaire dans les eaux du large, les empêchant de regagner les eaux côtières où la déposition benthique aurait le plus de chances de se produire avec succès. Ces larves exportées et maintenues au large seraient perdues pour le recrutement de leur région d'origine sans pouvoir contribuer au recrutement d'une autre région (Templeman 1939).

Les remontées d'eau profonde le long de la Côte Nord du Québec, dues à l'effet du vent (Huntsman *et al.* 1954; Lauzier *et al.* 1957; Bailey 1958), sont observables sur quatre images (fig. 2c, d, e, f), correspondant à des vents parallèles à la côte (O et SO) (Rose et Leggett 1988, tableau 2). L'étendue de la nappe d'eau froide de surface semble proportionnelle à la force et à la durée de l'épisode de vent : elle s'étend généralement de 4 à 25 km en direction SSE, quoiqu'elle ait atteint 55 km en conjonction avec des vents de 25 à 50 km • h^{-1} (tableau 2, fig. 2f).

La présence d'un fort gradient thermique dans les eaux de surface (Lauzier *et al.* 1957; Messieh et El-Sabh 1979; Weiler et Keeley 1980; Vigeant 1987), dans l'axe est-ouest, est visible sur plus de la moitié des images (fig. 2 b, c, d, f). La Côte Nord du Québec affiche des températures inférieures de 1 à 7°C à celles observées sur la côte ouest de Terre-Neuve (fig. 2, 3, tableaux 2, 4). Chez les larves, la température joue un rôle important pour leur croissance et leur survie, qui se trouve compromise à moins de 10°C (Templeman 1936). Dans ces conditions, les larves produites dans les eaux de la Côte Nord du Québec pourraient être (1) soit exposées à des eaux froides si elles sont retenues sur la Côte Nord, ce qui aura pour effet de diminuer leur croissance et d'augmenter leur taux de mortalité, ou encore (2) exportées vers les eaux plus chaudes de la côte ouest de Terre-Neuve. Ce même gradient existe au fond (10–15 m) entre avril et octobre (fig. 3A) avec pour conséquences probables d'augmenter la taille à maturité sexuelle et, de diminuer le taux de croissance (voir la revue par Aiken et Waddy 1986) et la vulnérabilité à la capture dans les zones plus froides (McLeese et Wilder 1958).

On peut généraliser ces observations en utilisant (1) les statistiques historiques (1946–1986) de direction de l'axe NE–SO des vents dominants dans le nord du golfe de juillet à septembre, en considérant de plus (2) la direction de la dérive d'Ekman selon laquelle le mouvement des masses d'eau se fait dans une direction perpendiculaire à celle du vent. Ceci permet d'évaluer que la direction et la fréquence des vents favorisant la rétention des larves produites localement pour chacune des régions (tableau 4) correspond aux vents du NE pour les Îles-de-la-Madeleine (fréquence de 25 % de juillet à septembre), la Côte Nord (31 %) et l'île d'Anticosti (27 %), et du SO pour la côte ouest de Terre-Neuve (74–78 %). Le kilométrage cumulé des vents de direction favorable reflète la dominance des vents du SO, indiquant que le régime normal de vents encourage les pertes par advection des larves de la Côte Nord et de l'île d'Anticosti vers la côte ouest de Terre-Neuve.

Les observations précédentes indiquent une importante interaction entre les facteurs climatiques et le régime hydrodynamique local, qui ont tous deux des effets potentiels importants sur l'advection et la survie des larves de homard durant leur phase planctonique.

Effets du régime thermique sur la survie larvaire

Les différences régionales de température de surface permettent de comparer la durée des stades larvaires et la date de déposition benthique des larves produites dans chaque région. Une revue des études précédentes (Harding *et al.* 1983) nous a permis de calculer que l'apparition de larves de stade I se produit à une température moyenne de 12.7°C en surface et de 9.1°C au fond. On peut donc estimer que les premières larves devraient éclore dès la fin mai à Port-au-Port Bay (région L), plus d'un mois avant le début de l'éclosion à La Tabatière (région CN) (fig. 3B). Les larves écloses à Port-au-Port devraient atteindre le stade benthique (V) dès le début d'août, soit juste avant le maximum estival de température. L'éclosion hâtive et la déposition benthique en conditions optimales de température ont été précédemment observées aux Îles-de-la-Madeleine, et permettent sans doute de maximiser la survie larvaire en diminuant la période de vulnérabilité planctonique (Hudon et Fradette 1987). De plus, une déposition benthique hâtive permet aux post-larves de continuer de croître sur le fond avant leur premier hiver (Hudon 1987). D'autre part, les premières larves écloses à La Tabatière n'atteindront le stade IV qu'à la fin août, époque trop tardive pour permettre leur mue au stade V, étant donné le refroidissement rapide des eaux. Par conséquent, les faibles

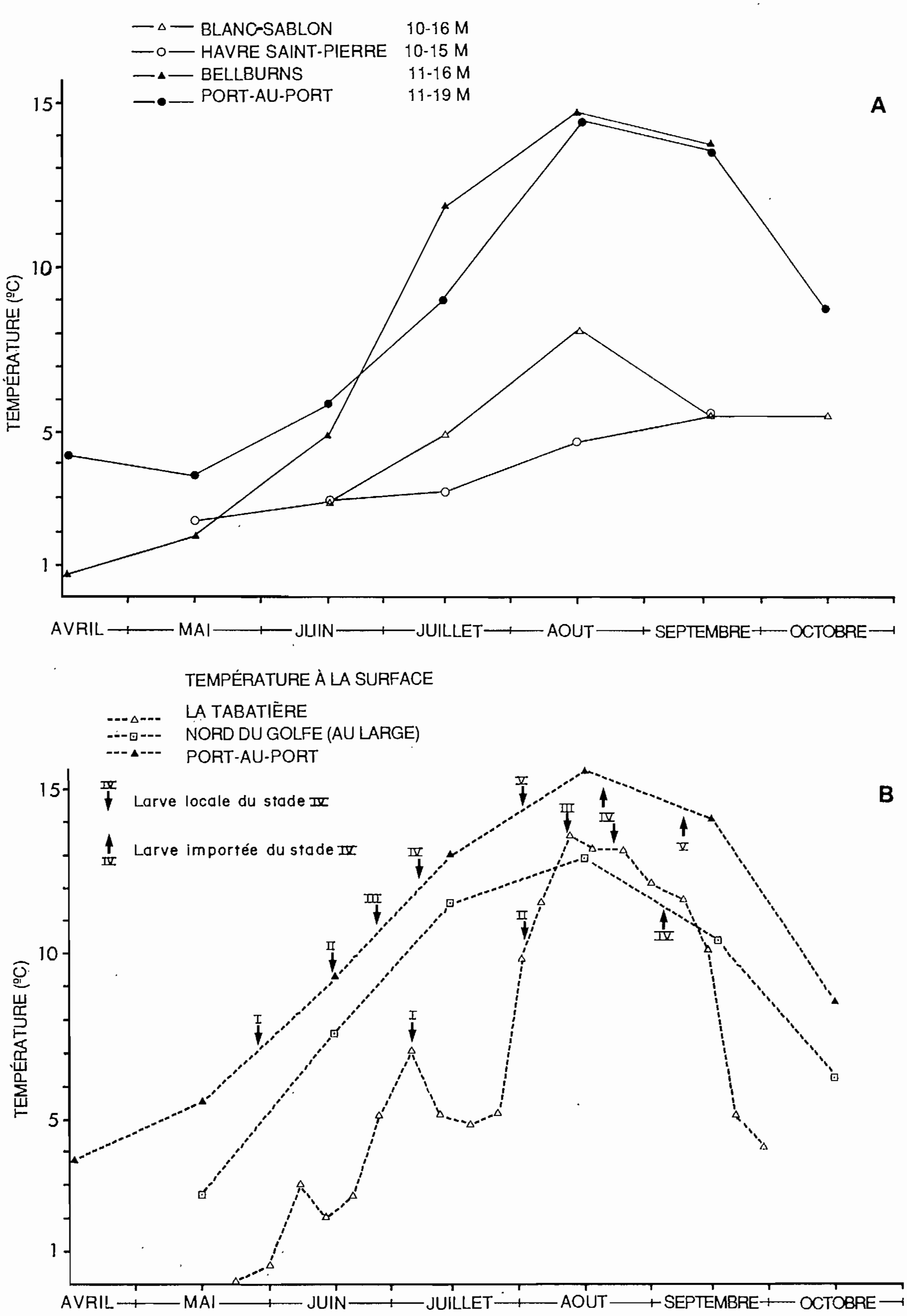

FIG. 3. Variations saisonnières (avril à octobre) de température au fond (A) et à la surface (B) à différentes stations côtières dans le nord du golfe. (B) Les flèches indiquent la date à laquelle les larves locales (flèches vers le bas) ou importées depuis la Côte Nord du Québec (flèches vers le haut) atteindraient chaque stade. Les valeurs de température au fond proviennent des publications suivantes : La Tabatière : Gaudet 1986; Havre Saint-Pierre, Blanc Sablon, Bellburns : Dobson et Petrie 1982, 1983, 1984, 1985; Baie de Port au Port : Squires 1970.

températures de surface enregistrées pour l'été 1985 à la Tabatière ne devraient pas avoir permis la croissance des larves produites localement jusqu'à leur déposition benthique. La température de surface locale apparaît donc comme un facteur critique du succès du recrutement larvaire.

Cependant, si les larves produites à La Tabatière avaient été exportées vers le large en direction de Terre-Neuve après avoir atteint le stade III, leur développement en aurait été modifié (fig. 3B). D'abord, les larves exportées au large et maintenues dans les tourbillons auraient atteint le stade IV au début de septembre, peu après celles retenues dans les eaux côtières du Québec, sans toutefois pouvoir passer au stade V. Quant aux larves exportées du Québec jusque dans les eaux côtières de Terre-Neuve, elles auraient atteint le stade IV à la mi-août, se déposant sur le fond à la mi-septembre (fig. 3B). Par conséquent, les effets défavorables des faibles températures de surface sur la Côte Nord pourraient être compensés par l'exportation des larves par le vent jusqu'à la côte ouest de Terre-Neuve.

Élaboration de modèles

Modèle d'échange de larves entre les régions du nord du golfe

L'apport de larves provenant d'autres régions, selon le régime de circulation engendré par les vents et les courants (Hypothèse 2), est modélisable sous la forme d'une matrice de transition de Markov dont les 8 cellules correspondent aux 7 régions à l'étude, plus une région additionnelle désignée comme la région centrale (AL) du nord du golfe (tableau 5). Cette région (AL) représente les eaux du large vers lesquelles les larves peuvent être exportées par les vents et les courants, entraînant leur perte pour les zones côtières (2^e ligne); elle rend compte des pertes différentielles de larves entre les régions, quoique les différences réelles de mortalité entre les régions ne puissent être évaluées ici. L'absence de population de homard hauturier dans le chenal d'Esquiman suggère l'absence de survie des larves entraînées vers et retenues dans les eaux du large.

TABLEAU 4. Moyenne et écart type (entre parenthèses) des variables physiques (1946–1986) utilisées pour chaque région dans le modèle de régression multiple entre les débarquements de homards et les facteurs physiques.

Région	Température °C	Vents favorisant la rétention: Direction	Fréquence %	Force km cumulatif	Mélange : vent toutes directions km cumulatif
Îles-de-la-Madeleine	13.8	NE	25,5	45 412	60 966
	(0,6)		(6,4)	(4 757)	(4 127)
Côte Nord	11,2	NE	31,3	19 220	61 596
	(0,6)		(9,2)	(5 635)	(4 862)
Anticosti	11,8	NE	26,7	16 942	64 110
	(0,5)		(7,5)	(4 892)	(4 464)
K	13,8	SO	74,5	45,412	60,966
	(0,6)		(6,4)	(4 757)	(4 127)
L	12,5	SO	76,2	48 677	63 786
	(0,6)		(6,3)	(5 061)	(4 336)
M et N	11,2	SO	77,9	14 664	66 605
	(0,6)		(6,7)	(4 444)	(5 021)

TABLEAU 5. Matrice de transition de Markov simulant l'hypothèse que les débarquements du nord du golfe varient en fonction d'un échange de larves d'une région à l'autre. Les sept régions sont représentées avec une région additionnelle représentant les eaux du large (AL). Les valeurs en caractères gras indiquent la proportion des larves retenues dans leur région d'origine.

		Larves provenant de la région								
		Îles-de-la-Madeleine (IM)	Au Large (AL)	Côte Nord (CN)	Île d'Anticosti (AN)	Côte ouest de Terre-Neuve K	L	M	N	Somme
Larves exportées vers les régions	IM	**0,9**	0,1	0	0	0,3	0	0	0	1,3
	AL	0	**0,1**	0,5	0,6	0,1	0,1	0,2	0,2	1,8
	CN	0	0,1	**0,2**	0	0	0	0	0	0,3
	AN	0	0,1	0,1	**0,4**	0	0	0	0	0,6
	K	0,05	0,05	0	0	**0,6**	0,1	0	0	0,8
	L	0,05	0,1	0	0	0	**0,75**	0	0	0,9
	M	0	0,2	0,1	0	0	0,05	**0,6**	0,3	1,25
	N	0	0,25	0,1	0	0	0	0,2	**0,5**	1,05
Somme		1	1	1	1	1	1	1	1	

Les proportions de larves exportées ont été évaluées empiriquement, en considérant la fréquence des vents engendrant des mouvements des masses d'eau dans cette direction (tableau 4), la possibilité d'échanges selon les mouvements des masses d'eau (fig. 2) ainsi que l'abondance relative du homard dans chaque région (tableau 1). Par exemple, pour les régions M et N, les vents qui engendrent un déplacement des eaux côtières vers le large sont du nord-est; ceux-ci prévalent à 22 % durant les mois au cours desquels les larves sont présentes dans le plancton (juillet, août, septembre), ce qui nous fournit une estimation de 0,2 pour la probabilité qu'une larve soit exportée vers le large. Des contributions peuvent aussi se faire directement vers une autre région; par exemple, le patron des courants dans le golfe nous permet d'estimer qu'une faible proportion des larves de la Côte Nord du Québec pourrait contribuer au bilan de l'île d'Anticosti (0,1) et des régions M et N (0,1). Le taux de perte de larves de la région L est comparativement plus faible (0,1 + 0,1 + 0,05) en raison de la configuration des baies de cette région, qui l'abritent quelque peu de la dérive due au vent.

Les larves entraînées au large dans le nord du golfe (AL) ne sont pas toutes perdues et une certaine proportion pourrait contribuer au bilan d'autres régions (2^{e} colonne). D'après le patron de vent SO favorisant le transport des masses d'eau, cet apport pourrait être plus élevé à mesure que l'on se déplace vers le nord de la côte ouest de Terre-Neuve (0,05, 0,1, 0,2, 0,25), étant donné le patron de circulation général du secteur. La région K est pour sa part orientée directement vers le sud du golfe et pourrait bénéficier de l'apport de larves des Îles-de-la-Madeleine (0,3) ou des régions I et J (côte sud de Terre-Neuve) (non incluses ici). La rétention des larves aux Îles-de-la-Madeleine est la plus élevée (0,9) puisque la configuration de l'île produit une circulation gyratoire, quelle que soit la direction du vent (Hudon *et al.* 1986).

La matrice n'est pas symétrique, puisqu'elle représente les mouvements potentiels de larves produites dans une région donnée (colonnes), lesquelles sont exportées vers chacune des autres régions (lignes). Ainsi, les patrons de courants favorisent l'exportation unilatérale de larves provenant de la Côte Nord du Québec (0,1) vers l'île d'Anticosti, mais non l'inverse (0). Enfin, une fois déterminés les échanges entre les régions, la diagonale (caractères gras) a été ajustée pour que la somme de chaque colonne soit égale à 1, et représente la proportion de larves retenues dans leur région d'origine. La somme des lignes équivaut au bilan des contributions en larves à chacune des régions, et reflète l'importance des populations de homards dans chacune des régions (tableau 1, colonnes 6 et 7).

La stabilité de ce modèle dans le temps est évaluée en multipliant la matrice par elle-même jusqu'à sa stabilisation asymptotique, laquelle indique le niveau auquel les populations locales devraient se maintenir si le processus en chaîne était homogène au cours du temps. Le bilan des contributions après stabilisation (tableau 1, colonne 8) indique qu'un tel modèle pourrait reproduire l'importance relative des débarquements dans chacune des régions. Deux éléments affectent fortement le niveau de convergence du bilan des contributions des régions après itération du modèle : (1) l'importance de la rétention locale et (2) la proportion de larves importées depuis le large (région AL). Ainsi, le bilan après itération atteint rapidement de très fortes valeurs aux Îles-de-la-Madeleine (2,99, tableau 1) où la rétention est de 0,9 (tableau 5). Outre leur niveau de rétention locale relativement élevé (0,75 et 0,6), les régions L et M atteignent des contribution finales plus élevées (0,94 et 1,29, tableau 1) en raison des apports de larves provenant du large (0,1 et 0,2). Quoique basé sur des valeurs très approximatives, cet exercice suggère qu'il existe des échanges de larves suffisamment importants entre les régions statistiques du nord du golfe pour justifier son identification comme une seule unité de stock, puisque ces échanges pourraient contribuer de façon non négligeable aux débarquements dans la plupart des régions.

Modèles explicatifs des débarquements à partir des variables physiques et biologiques

L'interaction entre les facteurs climatiques et hydrographiques d'une part, leurs effets sur l'advection et la survie des larves de homards d'autre part, et leurs conséquences ultérieures sur les débarquements impliquent un grand nombre d'étapes intermédiaires, résumées à la figure 4. Par exemple, le nombre de larves se déposant en un site donné est lié au nombre de larves produites localement (présumément en fonction du nombre d'œufs produits), ainsi qu'aux mouvements des masses d'eau dans lesquelles elles se trouvent, étant soit exportées par advection, ou retenues localement dans les tourbillons gyratoires. D'autre part, la survie proprement dite des larves repose sur des températures de surface et sur une concentration de proies zooplanctoniques suffisamment élevée pour leur croissance et leur développement jusqu'au stade benthique.

Ce modèle nous permet de faire des prédictions quant aux effets de certaines combinaisons climatiques-hydrographiques sur le succès du recrutement dans les régions du nord du golfe. D'une manière générale, le recrutement larvaire devrait être favorisé sur la côte ouest de Terre-Neuve dans les conditions de vents SO qui prédominent dans ce secteur. Ces vents provoquent la remontée d'eau profonde froide le long de la Côte Nord du Québec, y engendrant des températures faibles et contribuant à l'exportation des larves locales vers Terre-Neuve. Ces conditions semblent expliquer les différences d'importance du homard sur la côte ouest de Terre-Neuve et de sa comparativement faible abondance le long de la Côte Nord du Québec. Le réseau d'influences des variables physiques et biologiques sur le succès du recrutement larvaire du homard (fig. 4) permet en outre de déterminer les variables devant être incluses dans le modèle prédictif des débarquements, ainsi que les décalages devant être utilisés pour chaque type de variable. Les variables exerçant un effet sur la survie larvaire doivent être décalées d'une année de moins que celles décrivant les apports de larves des régions, puisque l'apport de larves est fonction de la densité de population adulte porteuse d'œufs, dont l'éclosion ne survient qu'une année plus tard.

Pour la plupart des variables physiques, nous avons émis *a priori* des hypothèses quant au signe que devraient avoir les coefficients de régression, si bien que la plupart des tests de signification sont unilatéraux. Ainsi, nous

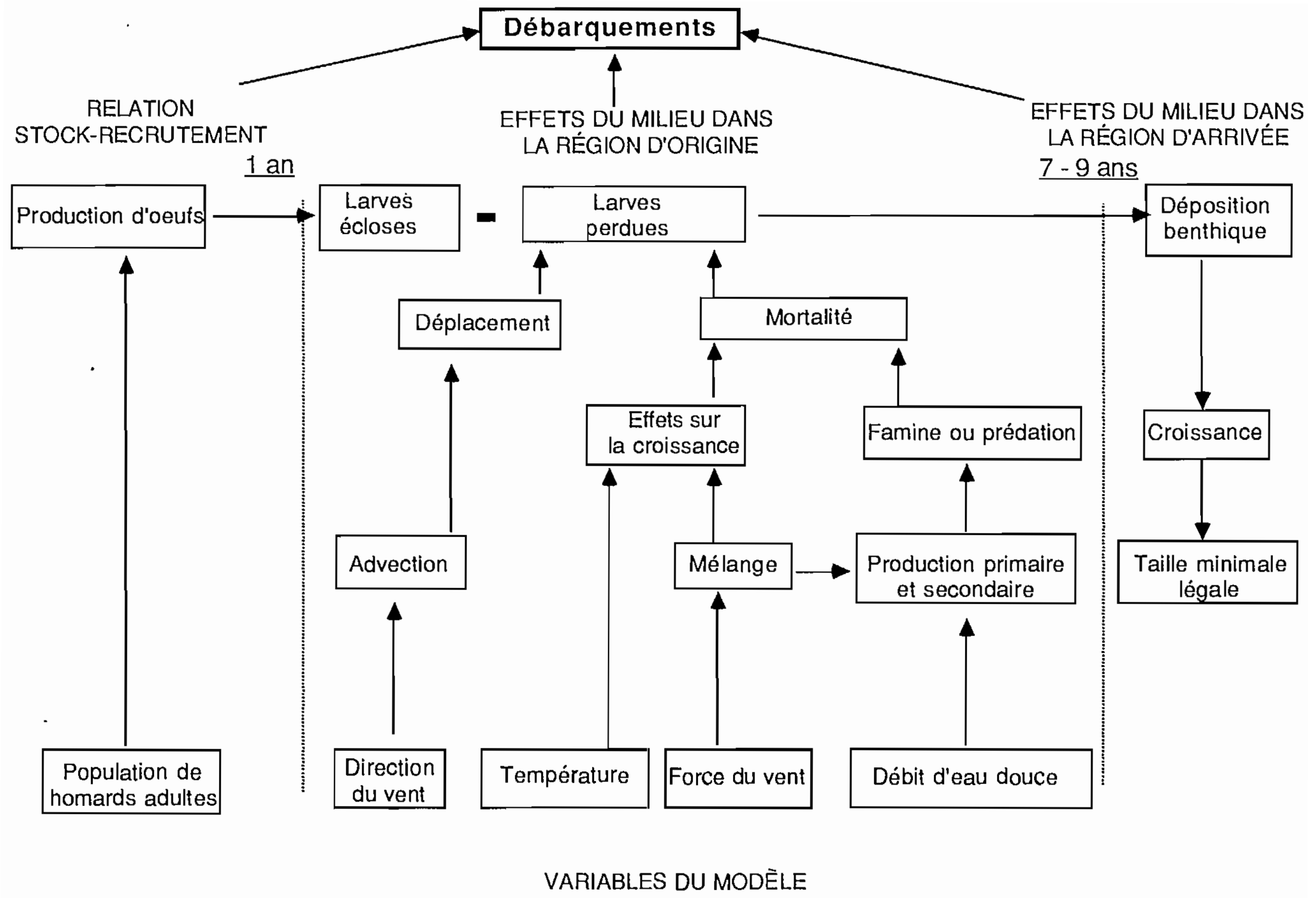

FIG. 4. Modèle intégrant l'ensemble des interactions prévues entre le climat, l'hydrographie et le recrutement larvaire du homard dans le nord du golfe, avec les décalages devant être utilisés pour les facteurs physiques et biologiques.

nous attendions à ce que les facteurs physiques aient un effet plus marqué dans la région d'origine des larves que dans la région d'arrivée; par exemple, l'exposition à des températures froides devrait affecter la croissance et la survie des larves dès l'éclosion, peu importe les mouvements des masses d'eau dans lesquelles elles se trouvent. La température devait donc toujours exercer un effet positif, que ce soit dans la région de départ ou dans la région d'arrivée des larves. D'autre part, les coefficients associés aux vents favorables à la rétention provenant de la région d'origine devraient avoir un signe négatif, tandis qu'ils devraient avoir un signe positif lorsqu'ils proviennent de la région d'arrivée. Enfin, les coefficients de régression des variables de mélange (kilométrage cumulé du vent total) et de débit d'eau douce peuvent prendre un signe positif ou négatif (test bilatéral) puisque ces variables peuvent avoir des effets indirects, parfois même dans des directions opposées (production secondaire, remontée d'eau profonde, effets thermiques, etc.), ce qui rend ces effets plus difficiles à prévoir.

Pour chaque région, l'équation de régression retenue (tableau 6) est celle qui maximise la signification du coefficient de détermination (r^2) et qui ne contient que des coefficients de régression significativement différents de zéro, en tenant compte de la signification biologique des signes des coefficients de chaque variable selon les hypothèses énoncées ci-dessus. Ainsi, et comme le suggère Lefkovitch (1965), tous les coefficients de régression négatifs pour l'apport de larves et pour la température ont été forcés à zéro, puisqu'un coefficient de régression négatif n'aurait aucun sens, même si cela entraîne une diminution subséquente de la quantité de variance expliquée par le modèle (r^2).

En utilisant les 30 premières années de données à notre disposition, soit les débarquements de 1953 à 1982, des modèles significatifs ont pu être calculés pour toutes les régions, sauf celles de la Côte Nord et de l'île d'Anticosti. Les équations de régression résultantes pour les cinq autres régions affichent des coefficients de détermination (r^2) allant de 0,47 à 0,70 et contiennent de deux à trois variables explicatives significatives (tableau 6). Aux Îles-de-la-Madeleine, les débarquements sont expliqués par une relation négative avec la fréquence des vents SO, ainsi que par les débits estivaux du Saint-Laurent. Les débarquements de la région K sont le mieux expliqués par l'apport de larves retenues dans les eaux locales (K) ainsi que par les larves importées des Îles-de-la-Madeleine. Les vents soufflant des régions K et Côte Nord, ainsi qu'un faible apport de larves de cette dernière région, expliquent en bonne partie les débarquements de la région L. Pour les régions M et N, la température et le mélange sont, avec l'apport de larves de l'île d'Anticosti vers M, les variables explicatives des débarquements.

TABLEAU 6. Comparaison des coefficients de régression linéaire simple obtenus pour le modèle optimal permettant de prédire les tendances des débarquements avec le décalage annuel approprié pour chaque région au moyen d'un sous-ensemble des variables étudiées. Les coefficients sont comparables entre eux étant donné que toutes les variables ont été préalablement centrées et réduites. La proportion de la variance expliquée (r^2) est indiquée. La signification du r^2 et des coefficients de régression est indiquée par : ns, non significatif; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

Région	r^2	Larves	Temp °C	Déplacement km cumulatif	Mélange : vent toutes directions km cumulatif	Débits du Saint-Laurent	Décalage (années)
Îles-de-la-Madeleine	0,555**	—	—	-1,388 K *** -1,324 AN***	—	0,469**	7
Côte Nord	ns	—	—	—	—	—	9
Anticosti	ns	—	—	—	—	—	9
K	0,474***	0,831 IM*** 0,615 K**	—	—	—	—	8
L	0,617***	0,285 CN^{ns}	—	-1,219 CN*** -1,064 K***	—	—	8
M	0,697***	0,458 AN*	0,474 AN*	-	0,537 CN**	—	9
N	0,605**	—	0,440 L*	—	2,066 L***	—	9

Discussion

Notre étude cherche d'abord à établir des relations entre les débarquements de homards et les facteurs physiques et biologiques dans le golfe du Saint-Laurent; son originalité réside dans le fait qu'elle tient compte des relations spatiales qui existent entre les régions, relations qui sont établies par la circulation hydrologique. Les modèles décrits ci-dessus devraient donc être perçus comme un moyen d'explorer ces relations de manière générale et d'établir des parallèles et/ou des contrastes entre les régions, afin de discerner les grandes lignes des mécanismes qui les affectent et leur confèrent leurs caractéristiques propres. Nous désirons enfin évaluer la pertinence de chercher à établir de tels modèles, considérant la précision des données présentement à notre disposition ainsi que l'absence d'autres données qui pourraient s'avérer utiles.

L'examen des coefficients de régression centrés-réduits (tableau 6) pour la relation prédictive des débarquements de chaque région indique que la fiabilité des données de base a une importance primordiale sur le succès d'élaboration d'une relation. Il était de rigueur d'essayer de développer un modèle pour les régions de la Côte Nord et de l'île d'Anticosti, quoique le manque de succès en ait été prévisible. En effet, les tendances à la hausse récemment observées dans les statistiques de débarquements de la Côte Nord résultent de l'amélioration de la prise des statistiques elles-mêmes plutôt que de captures accrues (G. Chantigny, Ministère des Pêches et des Océans, région du Québec, comm. pers.).

Les coefficients de régression calculés pour les Îles-de-la-Madeleine supportent l'importance de l'apport d'eau douce du Saint-Laurent, quoique nous ayions utilisé ici les valeurs cumulées de juillet à septembre, plutôt que les débits du fleuve au mois d'avril, comme le faisaient Sheldon *et al.* (1982). Les valeurs cumulatives estivales (juillet–août–septembre) de débit du Saint-Laurent sont d'ailleurs corrélées positivement (*r* de Pearson = 0,548***), avec celles du mois d'avril. Le débit du Saint-Laurent affiche de plus une forte co-linéarité avec l'apport de larves provenant des Îles-de-la-Madeleine (*r* de Pearson = 0,76701***), de la Côte Nord (*r* = 0,65338**), ainsi que de la région K (*r* = 0,43155*). Ce phénomène engendre l'élimination soit du débit ou encore de l'apport de larves de ces régions, lorsqu'on les introduit ensemble dans un modèle. La complexité des relations explicatives ainsi que les différences de signes des corrélations rendent leur interprétation hasardeuse. Il est à noter que la relation empirique de Sheldon *et al.* (1982) expliquait une proportion plus importante de la variance (77 %) que celle obtenue ici pour les Îles-de-la-Madeleine (56 %). Ceci est probablement lié à notre utilisation du critère de Lefkovitch (1965), qui force à zéro les coefficients n'ayant pas de signification biologique évidente et élimine de l'équation les coefficients non significatifs.

L'importance des apports de larves locales ou provenant des autres régions est perceptible dans les équations de régression pour les régions K, L et M. La configuration en une baie allongée tournée vers le sud du golfe pourrait favoriser les apports de larves vers la région K, d'origine locale, ou encore provenant des Îles-de-la-Madeleine ou de la côte sud de Terre-Neuve. Les régions L et M semblent aussi être liées à des apports extérieurs de larves de la Côte Nord et de l'île d'Anticosti, respectivement, quoique le peu de fiabilité de ces statistiques rende difficile la prédiction à long terme. Notons que dans ces deux cas, les coefficients de régression sont peu ou pas du tout significatifs.

Les régions L et Îles-de-la-Madeleine sont les seules où la fréquence des vents favorables à la rétention dans d'autres régions intervient. Dans ces deux régions, les coefficients sont négatifs, du même ordre de grandeur, et d'origine opposée (AN et CN: vent NE; K: vent SO, tableau 4), ce qui est difficile à interpréter. Or, ces deux régions sont celles où la configuration des côtes est susceptible de permettre une rétention locale comparativement élevée.

L'effet de la force du vent intervient dans les équations des régions M et N, qui sont celles situées à l'extrémité nord de la péninsule d'Avalon, et sont donc les plus susceptibles de recevoir des apports des autres régions par la dérive d'Ekman des masses d'eaux sous l'influence des vents dominants estivaux SO. Ces deux régions nordiques sont aussi les seules pour lesquelles la température semble jouer un rôle dans le succès du recrutement larvaire. La corrélation positive entre la température et les débarquements de plusieurs espèces marines à la limite nord de leur distribution avait déjà été soulignée par Drinkwater et Myers (1987). Des corrélations positives avec la température ont aussi été rapportées au Maine par plusieurs auteurs (Flowers et Saila 1972; Dow 1977; Fogarty 1988). Notons que les variables qui expliquent les débarquements des régions M et N sont très similaires, ce qui concorde avec la corrélation élevée des débarquements entre ces deux régions (r de Spearman = 0,54303 ***).

L'examen des prédictions du modèle pour les six années gardées en réserve pour la validation des modèles (1983–1988) montre que, pour toutes les régions, les modèles se mettent rapidement à diverger des niveaux de captures observés, prédisant toujours des captures inférieures à celles obtenues. L'examen de l'intervalle de confiance de 95 % des prédictions indique cependant que celles-ci correspondaient bien aux captures jusqu'à 1979; la divergence débute dès 1980, alors même que les années de 1980 à 1982 font partie des données ayant servi aux calculs des paramètres des modèles.

Plusieurs raisons peuvent être invoquées pour expliquer cette divergence. Une première raison est que les vents ont été calculés à partir d'un modèle théorique depuis 1978, alors qu'auparavant les données provenaient d'un modèle ajusté à partir d'observations directes; le résultat est un ensemble de données de vent dont la qualité n'est pas homogène, ce qui peut fort bien affecter les prédictions des années 1985–1987, selon les régions. Cependant, la divergence est observée depuis 1980 pour toutes les régions, même celles où le facteur vent n'intervient pas dans les modèles retenus; elle ne peut donc être expliquée à moins d'invoquer un autre type de changement, à plus grande échelle spatiale. Il est intéressant de noter que ce même genre de divergence sous-estimant les débarquements se trouve aussi dans les prédictions de Sheldon *et al.* (1982) à compter de 1985. Il est possible que ces divergences soient dues à un changement du patron d'effort de pêche ou de la qualité des statistiques de débarquement au cours des années 1970, ce qui, encore une fois, rendrait la série non homogène. Nous n'avons pas jugé bon de présenter les coefficients de régressions réels ou une courbe comparant les valeurs prédites et observées puisque là n'est pas le but de notre exercice. La présentation de relations malgré les limitations discutées ici pourrait inciter le lecteur à donner aux modèles une valeur prédictive qui ne peut leur être accordée.

À cet effet, il importe de mentionner les limites statistiques de modèles tels que ceux que nous avons présentés. Avant que de tels modèles puissent être employés pour réaliser des prédictions fiables, un certain nombre de conditions doivent être réalisées, et leur réalisation vérifiée. Les principales sont la constance des méthodes de prise des données servant de variables prédictives dans les modèles (i.e., leur stabilité temporelle), ainsi que l'assurance que le processus peut être décrit par un seul et même modèle, aussi bien dans l'intervalle de temps à prédire que dans celui où le modèle a été calibré. Les remarques ci-dessus montrent qu'à partir de 1978, la première de ces conditions n'est plus réalisée pour les variables vents, et portent à croire que depuis les années '80 la condition de stationnarité pourrait ne plus être respectée, ce qui expliquerait la dérive des prédictions par rapport aux observations.

La diversité des variables affichant des coefficients significatifs dans les différentes régions à l'étude, ainsi que ceux obtenus par d'autres auteurs pour d'autres régions, suggèrent que les facteurs affectant le recrutement sont spécifiques aux conditions physiographiques de chaque région et qu'en conséquence chaque secteur doit être interprété en fonction d'un modèle qui lui est propre. Il est aussi possible que d'autres facteurs limitants, tels que la disponibilité d'habitats propices aux post-larves et juvéniles (Hudon, 1987) puissent agir dans certaines régions. Une étape essentielle à la suite de ce travail serait d'entreprendre une campagne de terrain pour vérifier la plausibilité des mécanismes que nous proposons.

Conclusion

L'examen des hypothèses qui sous-tendent l'élaboration des modèles a permis de mettre en relief la complexité du cycle vital du homard et des facteurs susceptibles d'affecter son recrutement. Il importe de sélectionner les éléments qui engendrent la variabilité maximale des débarquements pour les modéliser, mais cette décision ne saurait se faire sans connaissances de la région à l'étude. La modélisation décrite ici montre l'effet potentiel des échanges de larves, de la direction des vents dominants, du mélange et de la température dans certaines régions. La tentative de validation de nos modèles avec les données récentes met cependant en évidence l'importance primordiale de disposer de données de débarquements et de données physiques de qualité homogène. Celà ne garantit cependant pas le succès d'une modélisation, puisqu'un modèle ne conserve sa valeur prédictive que si le processus à modéliser reste lui-même homogène au cours du temps.

Au-delà de la mise au point de modèles, notre étude fait ressortir la possibilité d'une forte dépendance du recrutement régional sur les échanges de larves à l'échelle du nord du golfe. La gestion inconsidérée d'une région donnée pourrait donc avoir des conséquences importantes sur les débarquements, non seulement dans cette région, mais également dans les secteurs avoisinants, bien au-delà des limites arbitraires de juridiction administrative. Ces considérations devraient pousser le gestionnaire à chercher à définir des cellules de recrutement homogènes dans le golfe et le long de la côte Atlantique. Ce concept s'apparente mieux à l'approche stock par stock préconisée pour la gestion des autres ressources marines que le système actuel de régions arbitrairement définies géographiquement. Le maintien des populations de homards sur la côte ouest de Terre-Neuve pourrait ainsi être critiquement lié à l'apport constant de larves provenant de la Côte Nord du Québec ainsi que de l'île d'Anticosti. Une augmentation de l'intensité d'exploitation dans ces deux régions pourrait avoir des conséquences importantes sur l'ensemble de la pêcherie de homard dans le nord du golfe du Saint-Laurent.

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The Relationship of Quebec Lobster Landings to Freshwater Runoff and Wind Storms[1]

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The relationship, discovered by W.H. Sutcliffe, between Quebec lobster landings and the lagged discharge from the St. Lawrence River system successfully predicted lobster catches from the early 1970's to the mid-1980's. The river-derived estimates failed, however, to forecast the steady increase in lobster landings since 1984. Changes in the geographical distribution of the reported landings and fishing effort, the age at recruitment, and the possibility that lobster landings are regulated more by storm incidence than runoff are examined but none can explain the recent deviation between predicted and observed landings. The expansion of lobster populations at the same time elsewhere in eastern North America suggests a response to a widespread environmental or ecosystem change.

Le rapport entre les débarquements de homard du Québec et l'écoulement différé provenant du bassin hydrographique du fleuve Saint-Laurent, établi par W.H. Sutcliffe, a donné des prévisions justes des prises de homard du début des années 1970 jusqu'au milieu des années 1980. Toutefois, les estimations fondées sur l'écoulement du fleuve n'ont pas permis de prévoir la hausse soudaine des débarquements de homard qui s'est produite depuis 1984. On examine ici les changements dans la distribution géographique des débarquements déclarés et dans l'effort de pêche, l'âge du homard recruté à la pêche, et l'hypothèse selon laquelle les débarquements de homard sont davantage influencés par les tempêtes que par le ruissellement. Aucun de ces phénomènes n'explique cependant l'écart récent entre les débarquements prévus et les débarquements réels. Le fait que la population de homard se soit également accrue en d'autres endroits de l'est de l'Amérique du Nord pendant la même période semble indiquer qu'elle réagit ainsi à une vaste transformation de l'environnement ou de l'écosystème.

Introduction

In an exploratory study of the possible role of the St. Lawrence River discharge on major commercial fish and shellfish species off eastern Canada, Sutcliffe (1972) found a positive relationship between the annual mean run-off and the number of cases of canned American lobster (*Homarus americanus*) packed in the province of Quebec (Table 1). The maximum correlation coefficient occurred when the lobster landings lagged the river discharge by 6 yr; a time considered to approximate the average age at which the small canner lobsters entered the fishery. Sutcliffe (1972, 1973) hypothesized that increased larval survival occurred during years of above-average river discharge because of increased food production resulting from river-induced nutrient entrainment into the euphotic layer. If the timing of the run-off was critical to specific stages in the life history of the species then higher correlations should result using monthly, rather than annual, means of river discharge (Sutcliffe 1972). This was subsequently shown to be correct with April discharges, 9 yr earlier, correlating most closely with the Quebec lobster catches (Sutcliffe 1973; Table 1). The longer lag time was still considered consistent with an effect on lobster larvae because the total catch included the older market size lobsters. On the basis of the 9-year lag time and the river discharge records, Sutcliffe (1973) successfully predicted the pattern of Quebec lobster landings during the 1970's (Ennis 1986). Lobster landings are considered a reasonable index of recruitment because of

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[1] This paper forms part of the Proceedings of a Workshop/Symposium held at the Maurice Lamontagne Institute, Mont-Joli, Quebec, 14–17 March 1989.

TABLE 1. Summary of the data sets, statistical methods and results from the major papers that established the relationship between lobster landings and river discharge.

	Sutcliffe (1972)	Sutcliffe (1973)	Sheldon et al. (1982)
Lobster data	Annual # cases canned lobsters 1939–68	Annual Quebec lobster catch 1939–70	Annual Quebec lobster catch 1950–79
River data	St. Lawrence River annual means	St. Lawrence River monthly means	RIVSUM monthly means
Statistical method	Correlation analysis	Correlation analysis	Multiple regression
Filter applied	2-yr running mean	3-yr running mean	None
Maximum r^2	0.56	0.69	0.77
Lag (yr)	6	9	9-10
Month for river	—	April	Feb.–Mar., July–Sept.

the high (70–95%) annual exploitation rates (Robinson 1979; Ennis 1986).

Sheldon et al. (1982) speculated that the mechanism linking the St. Lawrence River discharge and Quebec lobster landings may be a river-induced temperature effect on larvae rather than an influence on food production. They went on to develop a multiple regression model between the annual Quebec lobster landings (1950–79) and the lagged runoff from the combined St. Lawrence, Ottawa, and Saguenay Rivers (termed RIVSUM; Sutcliffe et al. 1976). Their model accounted for 77% of the variations in the Quebec lobster landings (Table 1) and was used to predict landings from 1980 to 1988. These predictions corresponded closely to recorded landings up to and including 1984 (Drinkwater 1987a).

Whatever the underlying mechanism, these studies clearly demonstrated a close relationship between lobster landings and lagged river discharge over a period of 40 yr. Indeed, in the 15 yr following the pioneering work by Sutcliffe (1972), river-based predictions of lobster landings performed better than predictions based on extrapolation of previous catch data (Drinkwater and Myers 1987) which is rare in marine fish and shellfish species (Roff 1983; Drinkwater and Myers 1987).

Since 1984 Quebec lobster landings have risen steadily to an all time high in 1989 (Department of Fisheries and Oceans 1989). This, however, contrasts with the river-derived prediction that catches would remain relatively constant (Sheldon et al. 1982). What can account for the recent deviation between the predicted and observed landings? The present paper evaluates three possible explanations. First, we examine whether a shift has occurred in the distributional pattern of lobster landings within the province of Quebec or if the increase in landings resulted from greater fishing effort. A shift in the distribution of lobsters could result in a significant proportion of the total landings now coming from regions other than those used to establish the relationship with river runoff and where the river's influence may be less important. Secondly, we estimate the mean age of the lobster catch to determine whether it corresponds to the empirically-derived lags from the river-lobster correlations, as was originally suggested by Sutcliffe (1972, 1973). If there is no biological rationale for the time lag from the correlation analysis, the lobster-river runoff relationship must be disregarded as coincidental. Finally, we consider an alternate hypothesis discussed at a national workshop on recruitment held in St. John's, Newfoundland, that Quebec lobster recruitment is dependent more upon storm-induced mortality than by river discharge (Sinclair et al. 1988).

Data and Statistical Methods

Recent lobster landing data for Quebec were obtained from annual fisheries summaries published by the Department of Fisheries and Oceans in Ottawa. River discharge records were updated from the Historical Streamflow Summaries for the provinces of Ontario and Quebec published by the Department of the Environment in Ottawa. Fishing effort, measured by the number of lobster traps, was obtained from Bergeron (1967) and for later years from the number of active lobster licenses multiplied by the maximum allowable number of traps per license. Although the number of traps does not account for increases in catch efficiency through improvements in technology, it is considered to be a reliable measure of fishing pressure.

To examine the relationship between storms and lobster landings, 6 h geostrophic wind data for the period 1946 to 1987 were obtained for a site located at 47°54′N, 63°06′W, approximately 100 km northwest of Îles-de-la-Madeleine (Fig. 1). A reduction of 20% in wind speed and a cyclonic rotation of 20° was applied to the data to account for frictional influences near the sea surface. In general, there is good agreement between these frictionally adjusted geostrophic winds and those measured at Grindstone on Îles-de-la-Madeleine (Swail et al. 1984). We chose to use the geostrophic wind estimates because they represent a better areal average of the wind field than the measured winds, especially under extreme wind speeds (Swail et al. 1984). Also, the time series for the geostrophic winds is longer since the wind measurements at

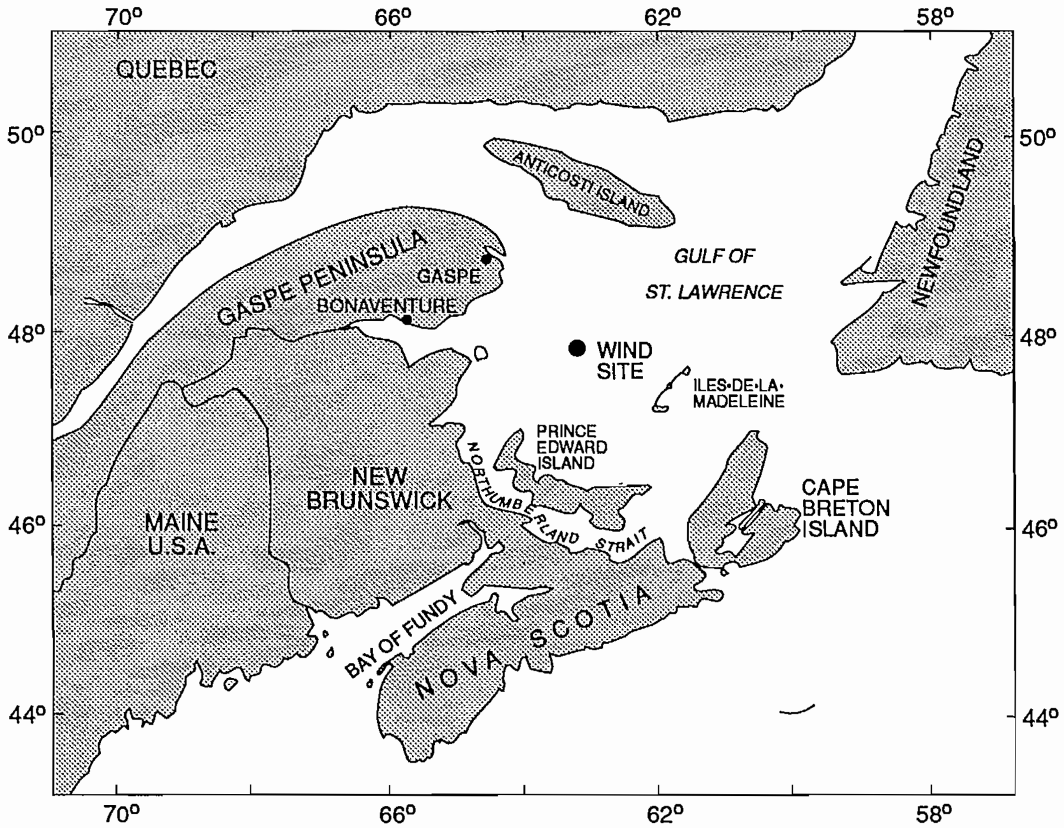

FIG. 1. Gulf of St. Lawrence.

Grindstone only began in 1955. Wind stress was calculated from the adjusted geostrophic winds using the stress formulation of Large and Pond (1981).

To test the hypotheses relating lobsters, river discharge, and wind, the lag correlation method was used. The procedure of correlating annual landing data with lagged monthly environmental data has been described by Sutcliffe et al. (1977). Results are reported in terms of the square of the correlation coefficient (r) and the significance level, P, i.e. the approximate probability that $r = 0$. The latter were determined using the number of independent data points (n^*) in the time series. For a time series of n points, n^* is given by

$$(1) \quad \frac{1}{n^*} = \frac{1}{n} + \frac{2}{n^2} \sum_{j=1}^{n-1} (n-j)\,(r(jt))$$

where $r(jt)$ is the autocorrelation of the product of the two variables being correlated (e.g. river discharge and lobster landings) at the jth lag for period t (Bayley and Hammersley 1946; Garrett and Toulany 1981). In the present study, $t = 1$ yr. To avoid large errors in r due to the decreasing number of points as the number of lags increases, the summation in equation (1) was taken to the lag corresponding to the first zero crossing in the autocorrelation function or to $j = 10$, whichever was less. Correlations were determined from both annual data and 3-yr equally weighted running means. In the case of the latter, the running mean was applied not only to the annual lobster landings but also to the monthly river discharge data, e.g. the January discharge value for year j was the average of the January RIVSUM for years $j-1$, j, and $j+1$. Analysis using the 3-yr running means allows direct comparison with the results of Sutcliffe (1973). Such filters reduce the high-frequency variance and increase the autocorrelation of the resultant time series, which in turn lowers its n^*. Therefore, to achieve a given significance level, r must be higher. The standard Fisher's Z transformation was used to determine the statistical difference between correlation coefficients.

Results and Discussion

Comparison of Observed and Predicted Landings

Quebec lobster landings between 1950–89 are plotted in Fig. 2 together with the river-derived estimates from Sheldon et al. (1982). The latter are labelled as "calculated" for those years used to establish the regression relationship (1950–79) and as "predicted" for subsequent years (1980–88). We added the predicted catch for 1989 based on available river runoff data and the regression equation of Sheldon et al. (1982). As previously noted, the predictions followed closely the recorded catches from 1980 to 1984 but thereafter vastly underestimated the catch.

Lobster Landing Patterns and Fishing Effort

One factor contributing to higher-than-average lobster landings in Quebec in recent years has been the increased

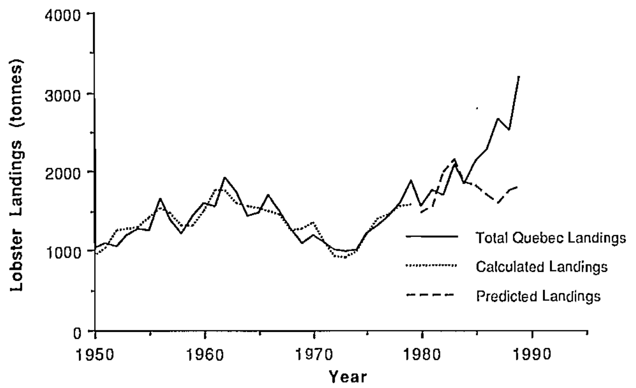

FIG. 2. The observed Quebec lobster landings together with the calculated and predicted landings based on river discharge (RIVSUM) using the regression equation of Sheldon et al. (1982).

catch from regions of the province where traditionally landings were low. From the early part of this century to the mid-1970's the Îles-de-la-Madeleine landings typically accounted for over 80% of the total Quebec catch (Fig. 3a,b). In the late 1970's the landings from other fishing districts increased and through the 1980s they contributed approximately 30–40% of the total catch (Fig. 3a,b). The majority of this increase was caught in Fishing Districts 9–12 along the Gaspé coast from Gaspé to Bonaventure (see Fig. 1 for location).

The increase in landings from the Gaspé Peninsula does not appear, however, to be responsible for the recent divergence between the observed total Quebec landings and the river-derived predictions. First, the relatively steady increase in landings along the southern Gaspé during the late 1970's precedes the deviation of the predicted and observed catches by almost a decade. Second, the sharp rise in the Quebec landings beginning in 1985 was principally due to increased catches off the Îles-de-la-Madeleine (Fig. 3a).

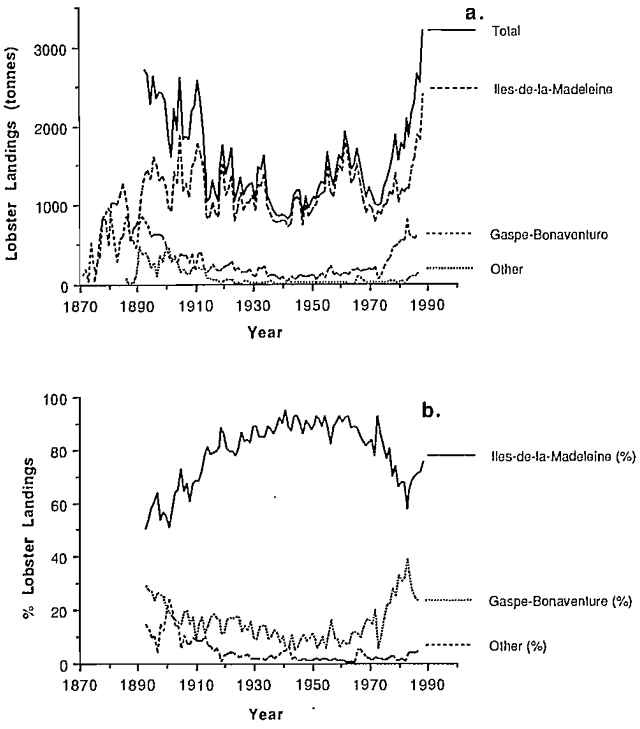

FIG. 3. Quebec lobster landings by fishing districts measured (a) in tones and (b) as percentage of the total provincial catch.

If the catch from regions other than the Îles-de-la-Madeleine were altering the relationship between river discharge and the Quebec lobster landings in recent years, then higher correlation coefficients would be expected when the non-Madeleine portion of the landings was subtracted from the total Quebec landings. To test this, correlations were calculated between the annual Îles-de-la-Madeleine lobster landings for the years 1939 to 1989 and lagged monthly means of RIVSUM. The beginning year was chosen to correspond to that of Sutcliffe (1973) although similar results were obtained using data from 1950 to 1989. The pattern of the correlation matrix of RIVSUM with Îles-de-la-Madeleine landings was similar to that with the total Quebec catch, i.e. maximum correlation coefficients (significant at $P < 0.05$ level) for similar months of RIVSUM and at similar lags. No statistical difference ($P = 0.05$) was found between these correlations, although the magnitude of those obtained with the Madeleine lobster landings were slightly lower than for the total Quebec landings (Table 2).

During the recent period of rapidly rising lobster landings on Îles-de-la-Madeleine, the total number of traps used by the fishermen remained relatively constant (Fig. 4). This indicates a steady fishing pressure and, therefore, the increased catches must have been due to a greater abundance of lobster.

We conclude that neither changes in the geographical distribution of the lobster landings or fishing effort are responsible for the recent failure of the river-derived lobster landing predictions.

Age at Recruitment

Sutcliffe (1973) suggested that the 9-yr lag between RIVSUM and lobster landings found from his correlation analysis reflected the approximate age at recruitment. This was consistent with the conventional wisdom at the time that lobsters in the Gulf of St. Lawrence reached market size (84–86 mm C.L.) at 8.25 yr (Wilder 1953).

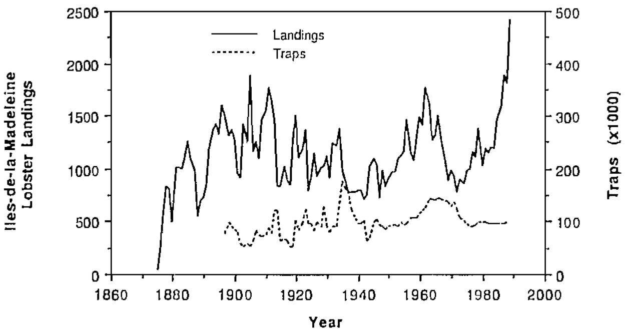

FIG. 4. The lobster landings and number of lobster traps from the Îles-de-la-Madeleine fishery.

TABLE 2. The maximum r^2 values from the correlation analysis between the monthly RIVSUM estimates and annual lobster landings (in t) from Quebec and Îles-de-la-Madeleine (1939–89).

	Region	Month	Lag (yr)	r^2
No smoothing	Quebec	March	8	0.56
	Madeleine	March	8	0.47
3-yr running mean	Quebec	March	10	0.72
		March	9	0.72
	Madeleine	March	10	0.62

Recent growth data for lobsters from Îles-de-la-Madeleine (Dubé 1986; Hudon 1987) has led to the questioning of the validity of this biological interpretation of the lag (p. 201, Sinclair et al. 1988). To examine this controversy, we estimated the average age of the commercial lobster catch. In the case of highly exploited fisheries, such as lobster, the average age should match closely the age at recruitment.

Aging of crustaceans in the wild is uncertain because the calcareous parts that are normally used to age vertebrates through depositional growth rings are lost during the moulting process (Shelton and Chapman 1987). Because measurements of moult frequency and growth increment of captive animals (Hughes and Matthiessen 1962) can not be equated to lobsters occurring in natural conditions, indirect methods are used to obtain growth and age estimates in the wild (Wilder 1953; Thomas 1973; Conan and Gundersen 1979; Aiken 1980; Campbell 1983; Hudon 1987). However, such techniques have to contend with an absence of information between the planktonic settlement and pre-recruitment stages.

Several authors have fit von Bertalanffy growth equations to lobster data (generally for sizes > 60 mm C.L.) but no clear geographic pattern in growth rates of inshore stocks has resulted (Russell 1980; Campbell 1983; Dubé 1986). Lobsters do appear to grow faster offshore than inshore by maintaining the most optimal conditions possible through spring and fall migrations on and off the continental shelf, respectively (Cooper and Uzmann 1980). Temperatures below approximately 5°C are known to inhibit moulting in lobsters whereas moult frequency increases linearly between 5 and 20°C (Aiken and Waddy 1976; Aiken 1980). Temperature differences, as measured by the number of degree-days above 5°C (Table 3), may explain the observation that growth rates of lobsters above 60 mm C.L. are slower in the Îles-de-la-Madeleine region (Dubé 1986) than those obtained in the Bay of Fundy (Campbell 1983).

TABLE 3. The mean annual number of degree-days above 5°C.

Îles-de-la-Madeleine[a]		Bay of Fundy[b]	
Depth	Degree-days	Depth	Degree-days
0	1978	0	2117
20	1166	25	1989
30	205		
50	0	50	1950

[a] Data source Petrie (1990).

[b] Data source Drinkwater (1987b).

To estimate the average age of the commercial catch off Îles-de-la-Madeleine we modelled the growth of recruits through successive years in the fishery. We began by calculating the age of first entry into the fishery. From observations of the size-frequency distributions and moulting stages off Îles-de-la-Madeleine, Hudon (1987) estimated that lobsters typically reach stage XIV (≅ 50 mm C.L.) at the beginning of their third winter (≅ 2.5 yr since hatching). Tag-recapture studies indicate that Îles-de-la-Madeleine lobsters are recruited annually into the fishery between 76 and 89 mm C.L. (Dubé 1986). This finding is supported by the abrupt decrease in size frequency curves of the commercial catch (Fig. 5a). To estimate the time required to reach this size range from 50 mm C.L. we assumed one moult per year and a growth rate per moult equivalent to that estimated by Wilder (1953) for lobsters in eastern Northumberland Strait. Evidence for a single annual moult comes from Wilder (1953) who found that 99% of the lobsters in the size range

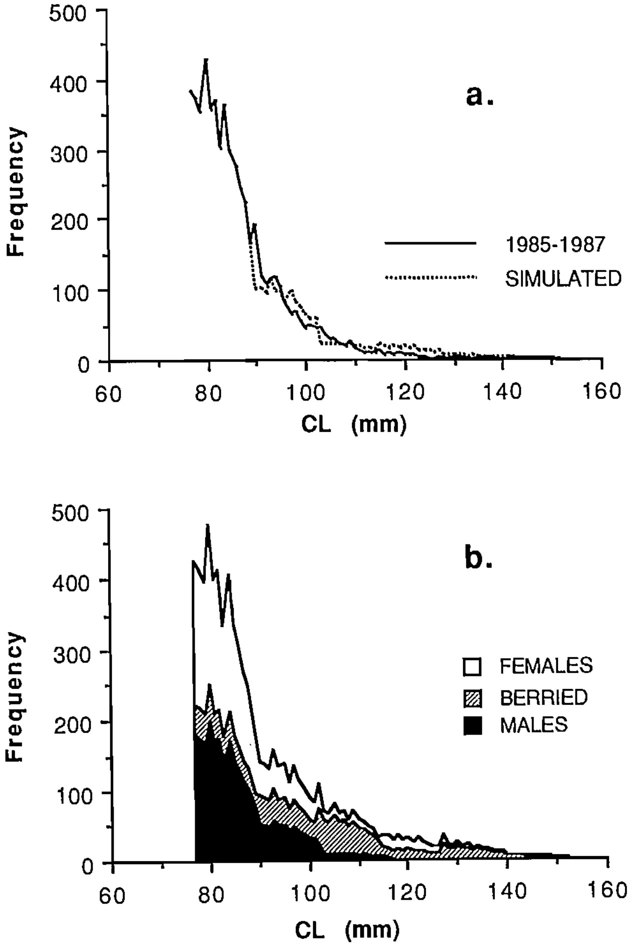

FIG. 5. (a) The observed and modeled size-frequency distribution used to calculate the average age of the commercial lobster catch in the 1980's from Îles-de-la-Madeleine (see text). (b) The relative contribution of male, female and berried female lobsters to this simulated population.

52–55.2 mm C.L., marked off Lismore, N.S., were recaptured the following year having moulted only once. Based upon the above assumptions, we estimate that, on average, lobsters enter the Îles-de-la-Madeleine fishery (76–89 mm C.L.) at an age of approximately 6 yr.

Next we took the size-frequency distribution of lobsters between 76 and 89 mm C.L. from the commercial catch for 1985–87 (Fig. 5a) and assumed that 47% were male (Dubé 1986). These lobsters were then grown based on one moult per year and size increments per moult of 12.5 mm C.L. for females and 13.5 mm C.L. for males (Dubé 1986). We also incorporated the size-dependent changes in the proportion of male and females moulting (Dubé 1986) and the proportion of females extruding eggs (Dubé and Grondin 1985). An annual 70% exploitation rate by the fishery (Axelsen and Dubé 1978; Attard 1985) was used for mortality. Berried females were assumed to be unaffected by the fishery because they are protected by law (DeWolf 1974). The resultant size-frequency distribution of the surviving lobsters from this cohort was used to obtain next season's growth and survival. This procedure was repeated to simulate 10 growth seasons and the results added to form a size-frequency distribution of the lobster population. It closely matches the observed size-frequency distribution (Fig. 5, comparison of sizes > 89 mm C.L.) giving us confidence in the parameters used. Based on the model results, we calculate an average age of 6.6 yr for the commercial lobster catch around the Îles-de-la-Madeleine.

An important question, given the long time series of lobster data used in the correlation analyses, is whether the average age may have varied significantly over the years. The largest change is expected to have occurred between 1953 and 1957 when the minimum legal size was increased annually by approximately 3 mm C.L. from 62.5 mm C.L. to the present 76 mm C.L. (Pringle et al. 1983). To determine the possible effect of this change we estimated an average age of the commercial catch prior to 1953 using the above model but subject to the following altered premises: (1) an estimated entry age of 4.5 yr for lobsters 62.5 mm C.L., (2) a size-frequency distribution measured in 1945 (Corrivault and Tremblay 1948), and (3) a 40% exploitation rate (derived from tag returns in 1951–53; Bergeron 1967). The average age was estimated to be 6.2 yr which is close to that calculated for the 1980's. The effect of the capture of the smaller, younger lobsters on the average age of the catch before 1953 was largely offset by a lower exploitation rate.

Our estimates of the average age of the catch may be low because the first couple of years of lobster growth are based on larvae that settled in warm shallow waters close to shore (Hudon 1987). If settlement was random, the majority of larval recruits would descend to cool deep waters. Although Hudon et al. (1986) found most of the final planktonic stage lobster larvae near shallow rocky bottom along the shore and in the bay to the southeast of the islands, the geographical coverage of that study was not sufficient to exclude the occurrence of substantial larval settlement in deep waters surrounding the Îles-de-la-Madeleine. Indeed, evidence for spatial differences in growth rates around Îles-de-la-Madeleine comes from observations that the lobsters residing to the northwest are generally larger than those located to the southeast (average size of 87.6 mm C.L. compared to 85.1 mm C.L. based on measurements from commercial catches during 1985–87; unpubl. data) and reach maturity at a slightly larger size (Dubé and Grondin 1985). Also, fewer of the lobsters from the northwest sector moult each summer and those that do, moult later in the year (Dubé 1986). In spite of these differences Dubé (1986) could find no statistical difference in the growth parameters for lobsters greater than 60 mm C.L. measured at different locations around the islands. This suggests that the difference in growth rates must have occurred earlier, i.e. at smaller sizes. Given these uncertainties and others associated with the assumptions in the model, we believe that the average age could range anywhere from approximately 0.5 yr earlier to 1 to 2 yr later than our estimate.

The lag of 9 yr between river discharge and Quebec lobster landings found by Sutcliffe (1973) corresponded to the maximum coefficient in the correlation analysis using 3-yr running means. He noted, however, that statistically significant correlations also occurred at other time lags. Similar results were found by Budgen et al. (1982) using annual means of both lobster and river discharge data. To examine this in more detail, we calculated correlations between lagged monthly RIVSUM and annual Quebec lobster landings, with and without 3-yr running means, for lags of 0–15 yr. Two trends were clearly evident from the correlation matrices. First, the majority of the correlation coefficients were positive (>95% of the total and 100% above a lag of 3 yr) and second, the maximum correlations tended to occur in spring at a lag of 8–9 yr. The latter were statistical significant at the $P = 0.05$ level. Of importance to the present discussion, there was no significant difference ($P = 0.05$) between these maxima and surrounding correlation coefficients over a wide range of lags (generally 7–12 yr) and months (October to April, i.e. autumn to early spring). This was true using either the unsmoothed data or the 3-yr running means. We repeated the analysis using Îles-de-la-Madeleine lobster landings and found similar results. The lack of statistical distinction between the correlation coefficients at different lags means any estimate in the timing of the river's effect on lobster from the correlation analysis has an uncertainty of several years.

Within the uncertainties of the estimates, the lags suggested from the correlation analysis are indistinguishable from the average age of the commercial catch. Therefore, the river discharge–lobster relationship can not be disregarded as a statistical coincidence on the argument that the lags are too long to make biological sense.

Storm-Induced Mortality

Massive storm-induced mortality of lobsters was a common occurrence within the southwestern Gulf of St. Lawrence in the latter part of the last century. Lobsters were found after storms along considerable lengths of the New Brunswick coast, with up to 1000 lobsters being recorded on 10 m of beach (Prince 1897). D.J. Scarratt (pers. common., Dept. Fisheries and Oceans, Halifax, N.S.) recalled that lobsters were infrequently washed up on the northern beaches of P.E.I. during his summer field studies in the 1960's and early 1970's. A particularly severe hurricane on September 11, 1972 stranded approximately 20 to 30 lobsters of various sizes per 100 m of shoreline on Pond Beach, North Rustico (D.J. Scarratt, pers. comm.). More recently, Maynard and Chiasson (1987) reported lobsters, ranging in size from 22 to 135 mm C.L., were washed up on the beaches along the northern coast of P.E.I. following an intensive storm on November 22, 1986. The same phenomenon has been reported by local fisherman on Îles-de-la-Madeleine (C. Hudon, pers. comm., Dept. Fisheries and Oceans, Halifax, N.S.)

At the National Workshop on Recruitment held in St. John's, Newfoundland, in February 1988, G. Conan proposed that fall and winter storms could disrupt the early benthic stages of the lobsters on shallow grounds around Îles-de-la-Madeleine and that this might lead to reduced recruitment 4 or 5 yr later (p. 198–199 in Sinclair et al. 1988). He suggested that in the absence of ice cover, lobsters in shallow water would be vulnerable to storm generated turbulence and, eventually, to beaching. This vulnerability is enhanced under cold water conditions due to the lobsters low activity level (McLeese and Wilder 1958). Conan also suggested that storm incidence and river runoff might themselves be positively correlated but they would be expected to have opposite effects on recruitment and at different time lags because they would effect different phases in the life history of the lobster.

To test the hypothesis of storm-induced effects on lobster recruitment yearly indices reflecting fall and winter storm activity were constructed. These were based upon the number of hours between September and January, inclusive, during which wind speeds exceeded (a) 20 m s^{-1} (38 knots, gale force) and (b) 25 m s^{-1} (48 knots, storm force). Data from February and March were not included because the Gulf of St. Lawrence is normally ice-covered during these months (Sowden and Geddes 1980). The winds were not separated according to direction because of the relatively long fetch (> 80 km) in all directions surrounding Îles-de-la-Madeleine. Indices based upon the total number of storms between September and January were also generated but were found to be strongly correlated with those derived from hours of wind (r^2 = 0.53 and 0.84 for wind speed thresholds of 20 and 25 m s^{-1}, respectively). The criteria of hours of wind was chosen because it is a more objective measure of storm activity.

Correlations between these fall–winter storm indices and Îles-de-la-Madeleine lobster landings at lags of 4 and 5 yr were non-significant ($P > 0.05$; Table 4). They were also positive, contrary to the hypothesis that storm incidence would reduce landings. Since juvenile lobsters may be vulnerable to storms over several years rather than any particular year, storm indices were summed over periods of 3 and 5 yr and again correlated with the lobster landings using an average lag of 4 and 5 yr. For example, for a summation period of 3 yr and an average lag of 4 yr, lobsters landings in year *j* were correlated with the sum of the September to January storms in years j-3, j-4 and j-5. These correlation coefficients were higher than for the single year case but were again positive and not significant ($P > 0.5$).

TABLE 4. The correlation coefficients between the storm index (wind speed threshold of 20 m s^{-1}) and lobster landings (1950–87) from the Îles-de-la-Madeleine as a function of lag time and the summation period.

Lag (yr)	Period (yr)	Correlation coefficient
4	1	0.17
5	1	0.16
4	3	0.32
5	3	0.35
4	5	0.37
5	5	0.43

Similar results were obtained from correlation analysis using storm indices formed from the monthly means of the amplitude of the wind stress (τ), the cube of the wind speed (w^3), and the standard deviation of the cube of the wind speed. τ represents the force of the wind on the water while w^3 and its standard deviation are measures of the wind energy available for mixing and its degree of variability, respectively.

D.J. Scarratt's observations of mass mortalities along the northern beaches of P.E.I. in summer led us to consider the possible influence of summer storms. Lobsters are also known to be closer to shore in this area during the summer (Templeman 1935; Munro and Therriault 1983) possibly making them more susceptible to storms. Examination of the data revealed that only on 6 occasions did the geostrophic winds exceed 20 m s^{-1} during the months May to August, inclusive, between 1946–87. This was too few to use in a standard correlation analysis. Visual examination of the data shows no obvious relationship between these summer storms and lobster landings on Îles-de-la-Madeleine.

In conclusion, while observations have established that storm-induced mortality of lobsters does occur, our results do not support the hypothesis that storm incidence negatively affects the overall recruitment level of lobsters on the Îles-de-la-Madeleine. Storm incidence cannot, therefore, explain the recent divergence between river-derived estimates and observed landings.

Concluding Remarks

The connection between St. Lawrence River discharge and Quebec lobster catch is another in a long list of environment–fish relationships that were correlated for a period of time but eventually failed (Walters and Collie 1988). No doubt debate will ensue as to whether this was a causal relationship or if the correlations were simply spurious. The biological rationale for the lags from the correlation analysis provide support for, but not confirmation of, such a linkage. That the river-derived predictions of lobster landings failed to reproduce recent increased catches may not necessarily indicate a lack of influence of river runoff but rather the existence of an overriding event (or events) not previously experienced.

In this regard, the recent rise in Quebec landings has coincided with similar increases in lobster catches throughout most of eastern Canada and northeastern United States (Pezzack 1990). The wide-spread nature of this rise suggests a common, presently unknown, cause due to a combination of environmental or ecological factors. Examination of sea surface temperature trends (K. Drinkwater, unpub. data) shows no general pattern throughout the region, suggesting that the increased lobster landings are not temperature related. Analysis of subsurface data is required to confirm if this lack of surface temperature pattern is representative of the water column. A possible cause of the widespread rise in lobster landings may have been a general decrease in predation, perhaps due to a reduction in either the size or abundance of predators, such as fish. Further analysis of the data are required to examine this hypothesis.

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Distribution of Organic Walled Microfossils in Recent Sediments from the Estuary and Gulf of St. Lawrence: Some Aspects of the Organic Matter Fluxes[1]

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The palynomorph content of surface sediments from the Estuary and Gulf of St. Lawrence has been analysed to trace the origin of microscopic organic matter, terrestrial (pollen & spores) *vs* marine (dinoflagellate cysts), or allochthonous *vs.* autochthonous. Throughout the Estuary and the Gulf, the abundance of pollen and spores ($>10^4 \bullet \mathrm{cm}^{-3}$) suggests large fluvial inputs of terrestrial organic matter. However, a continentality index, defined by the ratio (pollen + spores)/dinocysts (P&S/D) shows a steep gradient from the Lower Estuary (>100) to the downstream end of the Gulf (<1), indicating a relative decrease in terrestrial organic matter deposition between the Estuary and Cabot Strait. In the Lower Estuary, a north-south gradient in the P&S/D ratios as well as a north to south increase in thermophilic pollen percentages point to preferential fluvial inputs along the south shore of the Estuary.

Marine palynomorph abundances, notably the dinocyst concentrations, vary from $<10^2 \bullet \mathrm{cm}^{-3}$ in the Upper Estuary up to $>10^5 \bullet \mathrm{cm}^{-3}$ in the Gulf, due to the higher production of downstream marine autochthonous dinoflagellate communities. This trend is accompanied by a change in dinocyst assemblages, which are composed almost exclusively of Peridiniales taxa in the Estuary, but which contain abundant Gonyaulacaceae cysts in the Gulf. The palynological analyses allow to characterize organic fluxes and lead to the distinction of different zones of organic matter production and sedimentation in the transitional environment of the Estuary and the Gulf of St. Lawrence.

Le contenu palynologique des sédiments de surface de l'estuaire et du golfe du Saint-Laurent a été analysé dans le but de retracer l'origine de la matière organique microscopique, terrestre (pollen & spores) *vs* marine (kystes de dinoflagellés), soit allochtones *vs* autochtone. L'abondance de pollen et de spores ($>10^4 \bullet \mathrm{cm}^{-3}$) traduit d'importants apports fluviatiles de matière organique terrestre non seulement dans l'Estuaire mais aussi dans le Golfe. Cependant, un indice de continentalité, défini par le rapport (pollen + spores)/dinokystes (P&S/D), suggère un gradient marqué de l'estuaire maritime (>100) à l'extrémité aval du Golfe (<1), indiquant une diminution relative des apports de matière organique d'origine terrestre de l'estuaire au détroit de Cabot. Dans l'estuaire maritime, des gradients nord-sud du rapport P&S/D et des pourcentages de pollen d'essences thermophiles révèlent par ailleurs des apports fluviatiles préférentiels le long de la rive sud de l'estuaire du Saint-Laurent.

Les concentrations des palynomorphes marins, en particulier celles des dinokystes, varient de $<10^2 \bullet \mathrm{cm}^{-3}$ dans l'Estuaire Moyen à $>10^5 \bullet \mathrm{cm}^{-3}$ dans le Golfe, illustrant ainsi l'augmentation de la productivité des dinoflagellés de l'amont vers l'aval. Ce gradient s'accompagne de changements dans la nature des assemblages de dinoflagellés qui se singularisent par la dominance presque exclusive des Péridiniales dans l'Estuaire et par d'abondants kystes de Gonyaulaceae dans le Golfe. L'analyse palynologique autorise la caractérisation des flux de matière organique et permet de distinguer différents domaines de production et de sédimentation organique dans le milieu de transition que constituent l'estuaire et le golfe du Saint-Laurent.

Introduction

The Estuary and Gulf of St. Lawrence constitute a major transitional environment between continental (St. Lawrence River) and oceanic (North Atlantic) poles. The Estuary–Gulf system is marked by a pronounced salinity gradient and by inputs and fluxes of particles from both terrigenous and marine origin. The distribution and transportation of organic and inorganic suspended particulate matter in the Estuary and Gulf of St. Lawrence have been intensively studied since the early works of d'Anglejan (1969), d'Anglejan and Smith (1973), and Sundby (1974), notably with respect to the chemical (C,H,N, lignin) and isotopic ($\delta^{13}C$, $\delta^{15}N$) composition of the organic matter (*cf.* for ex. Pocklington

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1973; Tan and Strain 1979). However, little attention has been paid to the specific biological nature of the organic matter deposited in the Estuary and Gulf of St. Lawrence. Herein, we intend to focus on the nature and origin of the microscopic organic matter in sediments, using a palynological approach which consists of quantitative and qualitative analyses of organic walled microfossils. These palynomorphs may result from both terrestrial and marine biogenic production and therefore constitute a natural tracing method to determine the origin and the nature of a significant component of the organic fluxes to sedimentary environments (*e.g.,* Mudie 1980; de Vernal 1986). In terrestrial environments, organic walled microfossils consist mainly of pollen and spores produced by vascular and non-vascular plants for their reproduction, and are therefore a function of continental primary productivity. In oceanic environments, palynological assemblages are generally dominated by cysts of dinoflagellates which constitute the main source of primary organic carbon in marine environments (*e.g.,* Parsons *et al.* 1984). In addition to pollen, spores and dinocysts, several other biogenic organic products are fossilisable as palynomorphs, notably copepod eggs, foraminifera and thecamoebian organic linings, prasinophyte phycoma, freshwater algae such as *Pediastrum* or *Botryoccocus*. . . etc. Absolute and relative counts of the palynomorphs of sedimentary records may therefore be used to quantify and characterize organic fluxes and paleofluxes.

Palynological analyses have been performed in surface sediments collected in the Laurentian Channel along an upstream–downstream gradient, from the head of the Trough to Cabot Strait (Fig. 1; Table 1). In the Trough, surface deposits are relatively uniform and consist mostly of accoustically semi-transparent hemipelagic pelites (Loring 1974). According to estimates based on sediment trap data (Silverberg and Sundby 1986), sedimentation rates in the Laurentian Channel are *ca.* 0.5–1 mm • yr^{-1} in the Gulf and may attain several mm • yr^{-1} in the Estuary. The Estuary is marked by a strong seasonality and by complex hydrodynamical processes (EL-Sabh 1976). As a consequence, a spatial and temporal variability is recorded in the suspended matter transportation and deposition (*e.g.,* Nota and Loring 1964; d'Anglejan and Smith 1973), and in the autochthonous primary productivity (*e.g.,* Therriault and Levasseur 1985; Legendre and Demers 1985). In order to examine the spatial variation of organic matter deposition in the Estuary, surface sediments were collected in the Upper Estuary and along several north–south transects in the Lower Estuary (Fig. 2; Table 1).

Method

Surface sediments from the Estuary and Gulf of St. Lawrence were collected by box coring or grab sampling (Table 1). The upper cm of sediment was subsampled and prepared for palynological analyses using the following technique: (1) a measured volume (5 cm^3) of the sample was sieved at 10 and 125 μm to eliminate coarse sand, fine silt and clay particles; (2) a cold HCl (10%) treatment was used to remove carbonates; (3) a

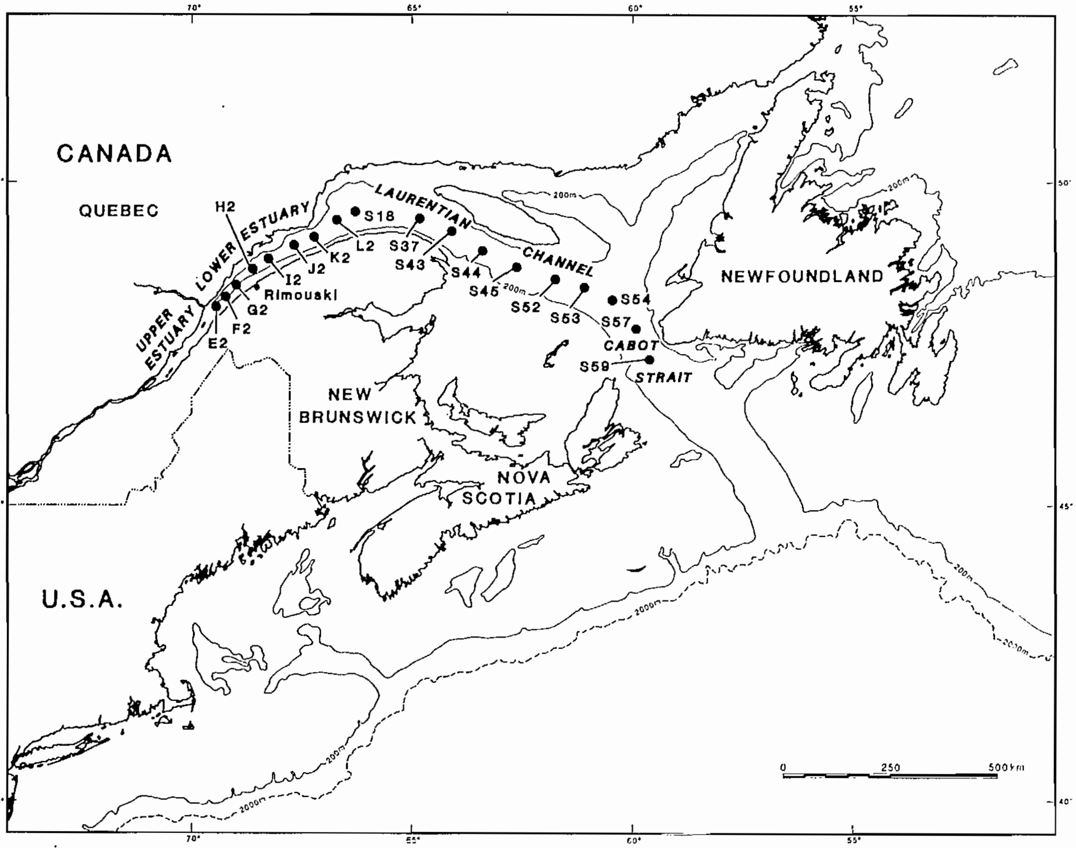


Fig. 1. Location of the sampling sites in the Laurentian Channel.

TABLE 1. Sampling location and characteristics.

Sites no.	Latitude north	Longitude west	Water depth (m)	Lab no. UQP	Sample type[a]	Cruise	Sediment type[b]
19C	47°00.40'	70°37.40'	15	175-6	A	*LM Lauzier* 85-001	3
9A	47°40.60'	70°00.70'	100	175-5	A	*LM Lauzier* 85-001	3
15	47°46.40'	69°43.30'	20	196-3	A	*LM Lauzier* 85-001	3
B1	47°49.67'	69°39.69'	17	300-1	A	*PétrelV* 88-013	3
13	47°58.30'	69°30.00'	30	196-2	A	*LM Lauzier* 85-001	3
E2	48°10.26'	69°31.81'	190	300-2	A	*PétrelV* 88-013	3
E3	48°11.92'	69°34.62'	132	300-3	A	*PétrelV* 88-013	3
F1	48°13.70'	69°16.00'	44	300-4	A	*PétrelV* 88-013	3
F2	48°16.90'	69°20.86'	329	300-5	B	*PétrelV* 88-013	1
F3	48°17.00'	69°26.50'	212	300-6	A	*PétrelV* 88-013	3
11	48°19.00'	69°20.00'	200	196-1	A	*LM Lauzier* 85-001	3
G1	48°24.50'	68°57.50'	45	295-1	A	*LM Lauzier* 88-004	3
G2	48°28.60'	69°02.40'	320	295-3	A	*LM Lauzier* 88-004	2
G3	48°31.40'	68°06.50'	50	195-4	A	*LM Lauzier* 88-004	3
H1	48°36.83'	68°27.76'	65	301-3	B	*PétrelV* 88-013	2
H2	48°45.25'	68°33.91'	351	301-4	B	*PétrelV* 88-013	1
H3	48°51.35'	68°40.05'	121	295-5	A	*LM Lauzier* 88-004	2
I1	48°43.59'	68°04.56'	47	301-5	A	*PétrelV* 88-013	2
I2	48°54.92'	68°14.52'	336	301-6	B	*PétrelV* 88-013	1
I3	49°01.42'	68°21.69'	71	302-1	C	*PétrelV* 88-013	3
J1	48°53.34'	67°30.90'	55	302-2	C	*PétrelV* 88-013	2
J2	49°03.86'	67°42.07'	284	302-3	B	*PétrelV* 88-013	1
J3	49°14.83'	67°52.40'	115	302-4	A	*PétrelV* 88-013	3
K2	49°09.42'	67°14.55'	327	302-5	B	*PétrelV* 88-013	1
L1	49°52.35'	66°41.10'	107	302-6	B	*PétrelV* 88-013	2
L2	49°16.69'	66°16.50'	330	303-1	B	*PétrelV* 88-013	1
S12	50°00.00'	66°18.00'	188	305-1	A	CHAV *Sackville* S46	3
S15	49°44.00'	66°15.00'	338	305-2	A	CHAV *Sackville* S46	1
S18	49°36.00'	66°12.00'	366	305-3	A	CHAV *Sackville* S46	1
S23	49°14.00'	66°06.00'	187	305-4	A	CHAV *Sackville* S46	3
S34	49°39.18'	64°24.00'	75	305-5	A	CHAV *Sackville* S46	3
S35	49°32.43'	64°27.00'	280	305-6	A	CHAV *Sackville* S46	1
S37	49°20.69'	64°36.00'	390	306-1	A	CHAV *Sackville* S46	1
S38	49°13.65'	64°48.00'	325	306-2	A	CHAV *Sackville* S46	1
S43	49°12.65'	64°00.00'	365	306-3	A	CHAV *Sackville* S46	1
S44	48°58.00'	63°31.20'	365	306-4	A	CHAV *Sackville* S46	1
S45	48°48.40'	63°06.00'	405	306-5	A	CHAV *Sackville* S46	1
S52	48°34.00'	62°06.00'	405	300-6	A	CHAV *Sackville* S46	1
S53	48°24.80'	61°34.80'	410	307-1	A	CHAV *Sackville* S46	1
S54	48°10.00'	60°43.20'	450	307-2	A	CHAV *Sackville* S46	1
S57	47°53.20'	60°07.20'	475	307-3	A	CHAV *Sackville* S46	1
S59	47°24.00'	59°31.80'	463	307-4	A	CHAV *Sackville* S46	1

[a] A = grab (surface); B = box core (surface). C = trigger weight core (surface).

[b] 1 = clayey mud; 2 = silty mud; 3 = sandy mud.

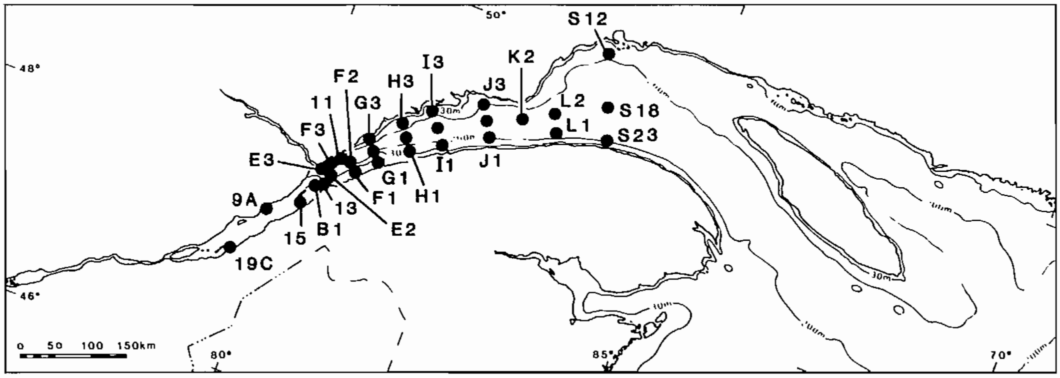


Fig. 2 Location of the sampling sites in the Upper & Lower St. Lawrence Estuary (including the entrance of the Gulf).

repeated treatment with hot HF (52%) was done to dissolve silicates. The prepared samples were mounted in glycerine gel on microscope slides for counting. Palynomorph concentrations (numbers • cm^{-3}) were evaluated on the basis of the marker-grains method (Matthews 1969), which involves spiking the sample with a calibrated *Eucalyptus globulus* suspension. This method is accurate to 10–12% for a 0.95 confidence interval (de Vernal *et al.* 1987). Palynomorph counts were greater than 500 individuals in each sample. Because of the large number of taxa (>100), the results are summarized for the purpose of this paper. Detailed palynomorph counts are reported by Giroux (1989).

The pollen and spore taxonomy refers to the modern flora nomenclature (*e.g.*, Marie-Victorin 1964). The Index to Genera and Species (Lentin and Williams 1989) was used as reference for the nomenclature of most dinoflagellate cyst taxa. Two dinoflagellate cyst taxa, which have been described after cultures, are however designated by their thecal name: *Peridinium faeroense* (*cf.* Dale 1977) and *Protoperidinium americanum* (Lewis and Dodge 1987). Foraminifera lining concentrations refer exclusively to multichamber forms.

Pollen and Spore Distribution

In any marine environment, pollen and spore assemblages result from an allochthonous productivity and subsequent transportation through air and/or water. Although atmospheric transportation plays an important role in pollen dispersion, pollen concentration in air generally decreases asymptotically with distance from the vegetation source (*e.g.*, Tauber 1965; Jacobson and Bradshaw 1981). According to Traverse (1988), at least 95% of all pollen normally settles well within a kilometre of the vegetation source. As a consequence, in open oceanic environments (*i.e.*, continental rise and abyssal plain), where pollen results mainly from atmospheric transportation (*cf.* Mudie 1982; de Vernal 1986; de Vernal and Hillaire-Marcel 1987), the terrestrial palynomorph content is generally sparse ($<10^3 \cdot cm^{-3}$; $<10 \cdot cm^{-2} \cdot yr^{-1}$). In neritic environments, where pollen and spores are generally abundant, studies of suspended particulate matter and sediments have demonstrated that the main pathway of pollen transportation is by fluvial mechanisms (Muller 1959; Groot and Groot 1966a, 1966b; Cross *et al.* 1966; Heusser and Balsam 1977; Heusser 1978). Based on the above considerations, the St. Lawrence River runoff can be considered as the main source of pollen and spores inputs to the Estuary and Gulf of St. Lawrence.

The Laurentian Channel

Pollen and spores are abundant in all samples from the Laurentian Channel, especially in the Gulf region. Concentrations (numbers • cm^{-3}), which relate to both fluxes (numbers • $cm^{-2} \cdot yr^{-1}$) and sediment accumulation rates (cm • yr • $^{-1}$), vary from a minimum of 11 100 • cm^{-3} at the head of the Channel, to a maximum of 164 990 • cm^{-3} downstream in the Gulf. Concentrations along the transect may be subdivided into two main groups: from the head of the Channel to the mouth of the Lower Estuary, concentrations average $23.10^3 \cdot cm^{-3}$ ($\pm 7.10^3$), whereas the open Gulf region is characterized by much higher concentrations (mean = $107.10^3 \pm 29.10^3 \cdot cm^{-3}$; Fig. 3A). Because pollen influx in marine environments usually decreases with the distance from the vegetational source areas (Heusser 1983; Mudie 1982), the pollen and spore concentration gradient in the Laurentian Channel must be considered with respect to both the hydrodynamical behavior of palynomorphs and the sediment accumulation rates. The downstream increase in pollen concentrations may result from a differential settling due to stronger surface currents in the Estuary as compared to the Gulf. It is probably also a response to the much lower sedimentation rates of the Gulf as compared to the Estuary, as indicated by sediment trap data (Silverberg and Sundby 1986). The abundant pollen content in surface sediments from the deep channel of the Gulf is a clear evidence of the important inputs of organic matter from terrestrial origin. Assuming sedimentation rates of 0.5 - 1 mm • yr^{-1} (Silverberg and Sundby, 1986), the pollen concentrations

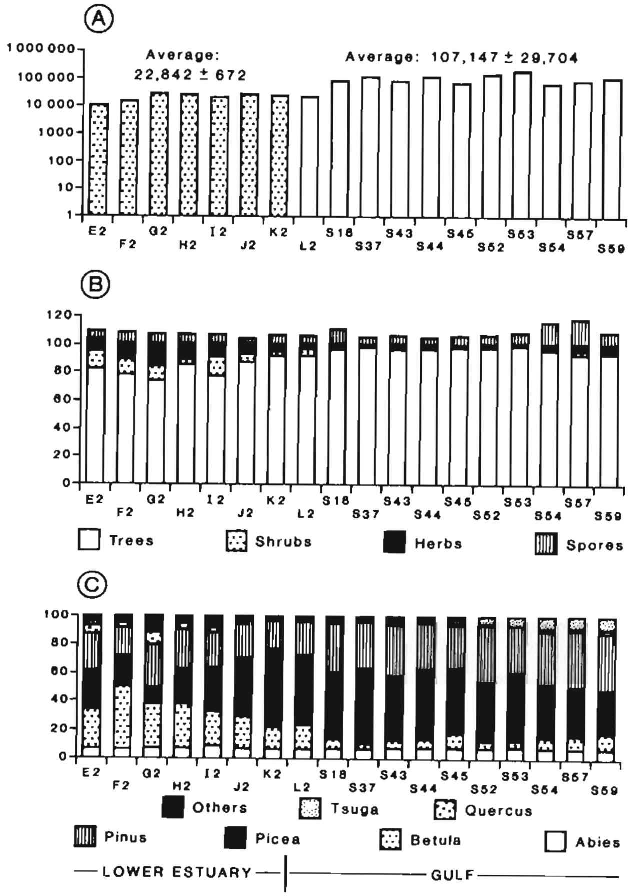


Fig. 3 Pollen and spore content in surface sediments from the Laurentian Channel along an upstream–downstream transect from the head of the channel (E2) to the Cabot Strait (S59). A. Concentrations (pollen grains and spores • cm^{-3}). B. Percentages of tree, shrub and herb pollen grains. Spores of Pteridophytes and *Sphagnum* are not included in the pollen sum. Their percentages are calculated to the pollen sum. C. Percentages of the main tree taxa.

lead to flux estimates of the order of 5.10^3-10^4 grains • cm^{-2} • yr^{-1}. For comparison purposes, such a flux range is more than 3 orders of magnitude higher than those normally observed in deep ocean basins (*e.g.*, Labrador Sea: de Vernal and Hillaire-Marcel 1987) and comparable or slightly lower than those measured in lake sediments (*e.g.*, southern Québec: Richard 1978; Labelle and Richard 1981).

Pollen and spore assemblages from the Laurentian Channel (Fig. 3B-C) are mainly composed of tree taxa (70%): *Pinus*, *Picea* and *Betula* are dominant; *Abies* and *Tsuga* are relatively well represented; the occurrence of pollen from thermophilic deciduous trees is sparse, with the exception of *Quercus*. Shrub taxa, notably *Alnus rugosa* and *Salix*, are represented by low percentages (<12%). Within the herbaceous component of the assemblages, the occurrence of *Ambrosia* and Gramineae pollen grains is significant (up to 20%). These taxa are related to agriculture (Gramineae) or to anthropogenic occupation (*Ambrosia*) and therefore imply that analysed sediments correspond to recent or sub-recent accumulations. In addition to pollen grains, Polypodiaceae, *Lycopodium* and *Sphagnum* spores are common (∿10% to the pollen sum). On the whole, these pollen and spore assemblages reflect inputs from the mixed forest vegetation occupying southeastern Canada. (Fig. 4). Pollen assemblages in samples from the Laurentian Trough show a downstream trend of increasing tree percentages, notably those of vesiculate pollen grains such as *Pinus*, *Picea* and *Tsuga*. As already mentioned by Mudie (1980, 1982), the over-representation of vesiculate pollen in marine sediments off eastern Canada results from selective long distance transportation.

The St. Lawrence Estuary

In the St. Lawrence Estuary, pollen and spore concentrations range between 7 580 • cm^{-3} and 32 230 • cm^{-3} (mean = 18 677 • cm^{-3}; Fig. 5A). The assemblages are similar to those of the Laurentian Trough with respect to species composition. However, the percentages of the main taxa vary significantly (Fig. 5B-C), indicating differential fluvial pollen inputs from the St. Lawrence River and its tributaries. The variation in percentages of taxa having an ubiquitous distribution in southeastern Canada (*Pinus, Picea, Betula, Alnus..*) cannot be used to identify the precise source vegetation area. Nevertheless, some taxa in the assemblages are characterized by a more restricted distribution in modern vegetation. For example, *Quercus* and *Tsuga* grow only in the mixed forest domaine south of the 47th parallel in Quebec (Fig. 4). These taxa may therefore be attributed to inputs originating from southern Quebec and to a subsequent transportation *via* the St. Lawrence River. The significantly higher *Tsuga* and *Quercus* percentages recorded in samples collected on the southern shelf of the estuary (Fig. 5D) appear related to the surface circulation outflow of the St. Lawrence River along the southern shore of the Estuary.

Dinoflagellate Cyst Distribution

In most marine sediments, dinoflagellate cysts are the dominant organic walled microfossils. These cysts are hypnozygotes or resting spores (*cf.* for example Wall and Dale 1968; Dale 1983) and play an important role in the

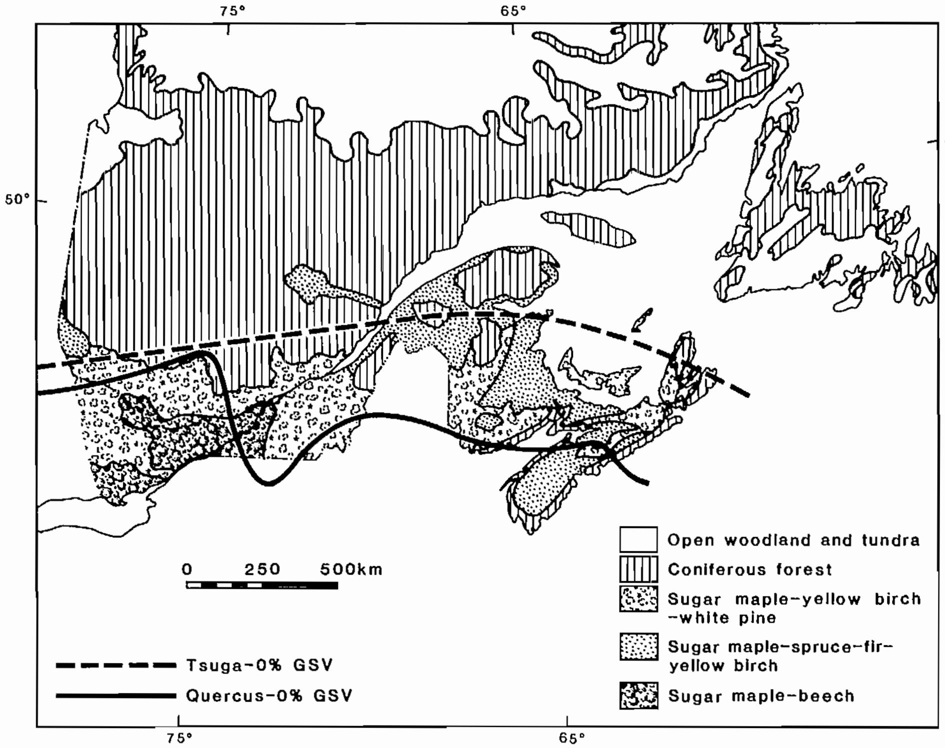


Fig. 4. Schematic map of the vegetation in eastern Canada (simplified from the National Atlas of Canada, 1973; GSV = growing stock volume after Delcourt *et al* 1984).

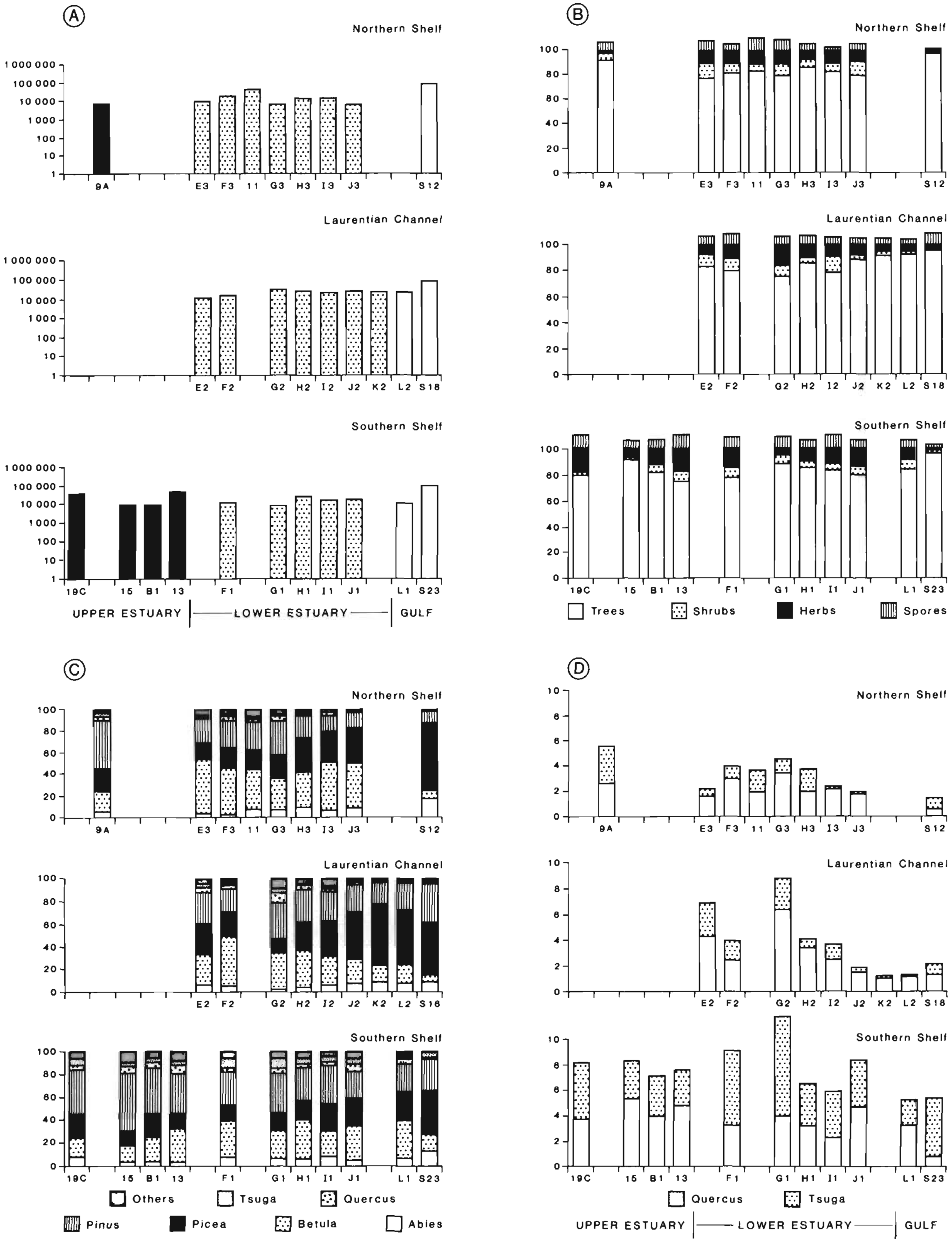


Fig. 5 Pollen and spore content in surface sediments from the Upper & Lower St. Lawrence Estuary, including the entrance of the Gulf. A. Concentrations (pollen grains and spores • cm^{-3}) in the Upper Estuary (black), the Lower Estuary (stippled) and at the entrance of the Gulf (white); B. Percentages of tree, shrub and herb pollen grains. Percentages of spores of Pteridophytes and *Sphagnum* are calculated to the pollen sum; C. Percentages of the main tree taxa; D. Percentages of *Tsuga* (stippled) and *Quercus* (white).

reproduction of the Dinophyceae. Since only a fraction (*ca.* 20%; *cf.* Dale 1976) of dinoflagellates produce acid resistant organic walled cysts, palynological assemblages cannot be used for direct reconstruction of dinoflagellate biocenoses. Although providing only a fragmentary picture of the total productivity, organic walled dinocyst assemblages are nevertheless related to planktonic production. Most fossilisable dinocysts, notably the Gonyaulacaceae, are produced by autotrophic taxa and are therefore a reflection of the primary productivity of the photic zone. Some fossilisable dinoflagellates, in particular those belonging to the genus *Brigantedinium*, are heterotrophic (*e.g.*, Gaines and Taylor 1984). These feed on diatoms and their cyst abundance also relates to biological production of the upper water masses.

Dinoflagellate cysts are rare to common in sediments collected in the Estuary (Fig. 6) and are generally abundant in the Laurentian Channel, especially toward the marine end of the Gulf (Fig. 7A). Dinocyst concentrations vary from 0 at some stations in the Upper Estuary to a maximum of 174 910 • cm^{-3} in Cabot Strait (Fig. 6 and 7A). The downstream increase in dinocyst abundance appears to be progressive, with the exception of a few sites. Although sedimentation rates are known to be variable in the Estuary and Gulf of St. Lawrence (*cf.* Silverberg and Sundby 1986), the downstream increase in dinocyst concentrations by more than three orders of magnitude is indicative of spatial variability in dinoflagellate productivity. In the Upper Estuary, the low dinoflagellate production suggested by the sparse dinocyst occurrences may be related to low and variable salinities and/or turbulence, which inhibits dinoflagellate production (*e.g.*, Taylor 1987). In the Lower Estuary and the Laurentian Channel, higher dinocyst concentrations no doubt indicate significant dinoflagellate production. In the Gulf, dinocyst fluxes of $10^3 • cm^{-2} • yr^{-1}$ have been calculated based on sedimentation rate estimates of 0.5-1 mm • yr^{-1} (*cf.* Silverberg and Sundby 1986). This flux magnitude is of the same order as that recorded in areas of high primary productivity such as the southwest Greenland rise (*e.g.*, de Vernal and Hillaire-Marcel 1987; de Vernal and Mudie 1989).

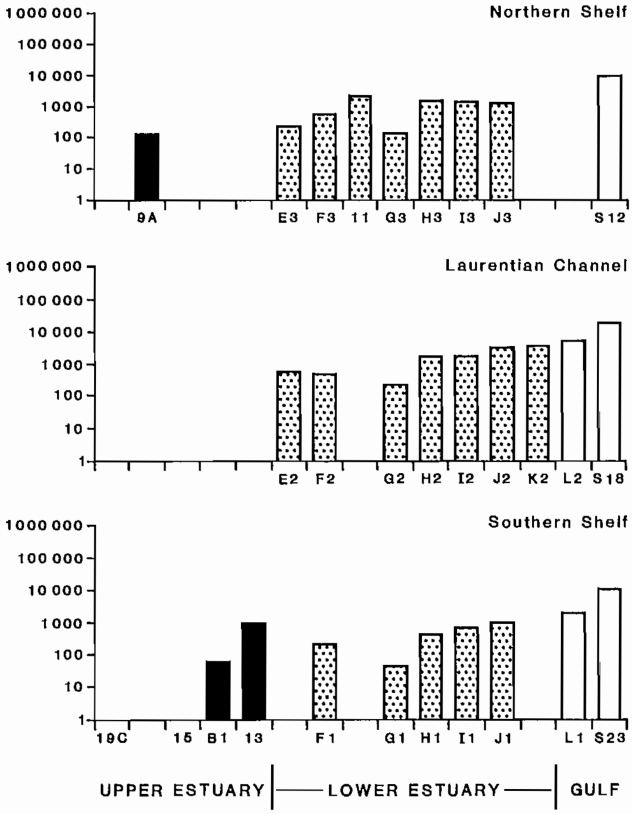


Fig. 6. Dinoflagellate cyst concentrations (in cysts • cm^{-3}) in surface sediments from the Upper Estuary (black), the Lower Estuary (stippled), and the entrance of the Gulf (white).

The upstream-downstream increasing trend in dinocyst concentrations is accompanied by significant changes in the assemblage composition and species dominance (Fig. 7B,C,D). Changes in dinocyst taxa percentages (Fig. 7B) show the existence of distinct dinoflagellate populations in the Estuary and the Gulf. Peridiniales largely dominate in the Estuary, whereas Gonyaulacales constitute approximately half of the assemblages in the Gulf (Fig. 7C). Peridiniales are generally associated with inner neritic environments while Gonyaulacales often dominate exclusively in open ocean sediments as shown by the modern assemblages from the North Atlantic Ocean and adjacent seas (*e.g.*, Wall *et al.* 1977; Harland 1983; Mudie and Short 1985). The Peridiniales to Gonyaulacales ratio gradient recorded along the Laurentian Channel (Fig. 7C) appears therefore representative of the transition from a continental to an oceanic environment. The slope of this gradient is especially steep at the mouth of the St. Lawrence Estuary.

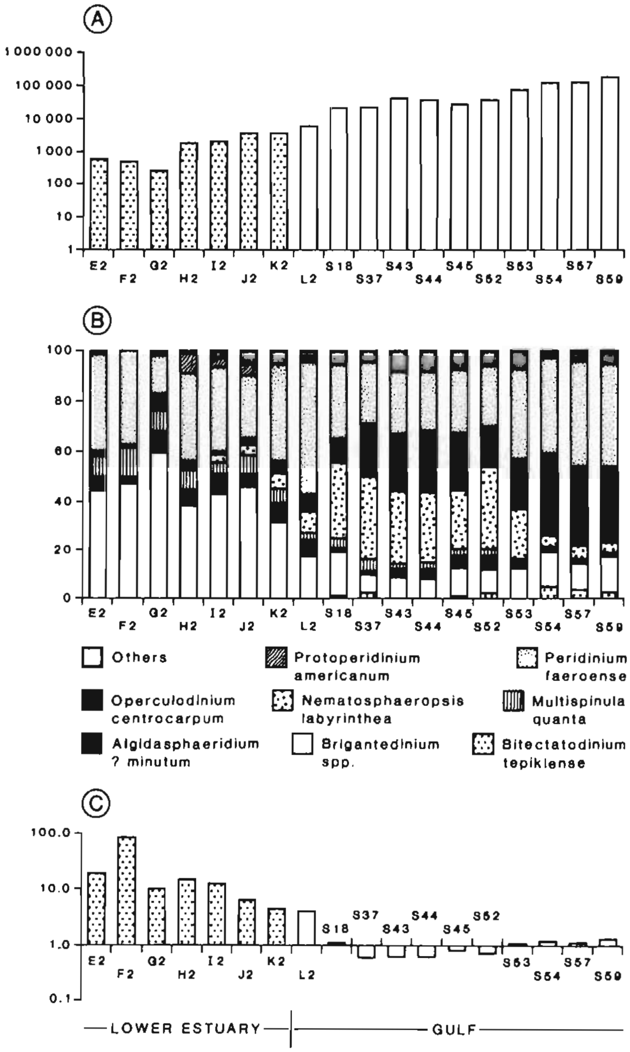
Four main dinocyst assemblage zones can be distinguished along the Laurentien Channel transect based on species percentages, diversity and abundance (Fig. 7B,C,D).

Zone I: Surface sediments from the upstream part of the Lower Estuary are characterized by sparse assemblages that are dominated largely (>85%) by Peridiniales taxa, notably *Brigantedinium* spp. and *Peridinium faeroense* in addition to *Algidasphaeridium ?minutum* and *Multispinula quanta*. The occurrence of Gonyaulacaceae is rare with the exception of a few *Operculodinium centrocarpum*. Zone I corresponds approximately to region II of Therriault and Levasseur (1985), in which surface waters are characterized by a salinity range of 25-30‰ and by relatively low summer temperatures (<7°C).

Zone II: This zone corresponds to the downstream part of the lower Estuary (including the mouth). The assemblages are also characterized by very high proportions (>80%) of Peridiniale cysts. However, zone II differs from zone I in regard to its increased species diversity and abundance. *Brigantedinium* spp. and *Peridinium faeroense* still dominate and *Multispinula quanta* and *Algidasphaeridium ?minutum* are subdominant. A peculiar attribute of zone II is the exclusive occurrence of *Protoperidinium americanum*. In addition, the Gonyaulacaceae taxa *Nematosphaeropsis labyrinthea* and *Spiniferites elongatus* occur in significant numbers. Zone II corresponds to the high primary production area of the Lower Estuary (*cf.* regions III and IV of Therriault and Levasseur, 1985), where the salinity range is 27–32‰ and summer temperatures may exceed 9°C in surface waters.

Zone III: This zone includes the open Gulf region, from the mouth of the Estuary to the area west of Cabot Strait. It is characterized by rich dinocyst assemblages with abundant Gonyaulacaceae, notably *Nematosphaeropsis labyrinthea* and *Operculodinium centrocarpum*. *Brigantedinium* spp. is still abundant but occurs in much lower percentages than in zones I and II. *Algidasphaeridium, ?minutum* and *Multispinula quanta* are still present and *Peridinium faeroense* remains relatively abundant. The occurrence of *Ataxiodinium choanum* and *Bitectatodinium tepikiense* is characteristic of this zone. Zone III corresponds to a marginal marine environment where salinity is >30‰ and where summer temperatures exceed 9°C in surface waters (*e.g.*, Forrester 1964).

Zone IV: The dinocyst assemblages from the Cabot Strait area are similar to that of zone III with respect to taxonomic diversity. However, the high percentages of *Operculodinium centrocarpum, Peridinium faeroense* and *Bitectatodinium tepikiense,* as well as relatively low occurrences of *Nematosphaeropsis labyrinthea* and *Multispinula quanta* are typical of zone IV. Zone IV corresponds to an open marine environment that is very much under the influence of surface North Atlantic waters (El-Sabh 1976).



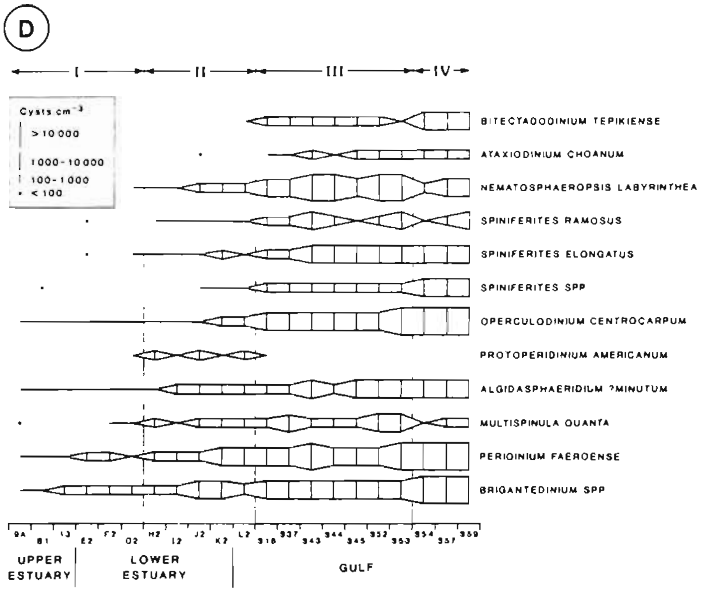


Fig. 7. Dinoflagellate cyst content in surface sediments from the Laurentian Channel. A. Concentrations (in cysts • cm^{-3}) in the Lower Estuary (stippled) and the Gulf (white); B. Schematized percentage diagram; C. Peridiniales to Gonyaulacales ratios in the Lower Estuary (stippled) and the Gulf (white). (genera *Peridinium, Brigantedinium, Multispinula* and *Algidasphaeridium* belong to Peridiniales; genera *Spiniferites, Nematosphaeropsis, Operculodinium, Bitectatodinium* and *Ataxiodinium* belong to Gonyaulacales); D. Upstream to downstream concentrations of dinocyst species in the Estuary and the Gulf. The roman numbers refer to assemblage zones discussed in the text. Note: According to cluster analyses performed on percentage data set from the Estuary and Gulf of St. Lawrence, similarity coefficients of 0.81, 0.88 and 0.99, respectively, characterize the assemblages of zones I & II, III and IV (*cf.* Giroux 1989).

Foraminifera Lining Distribution

In addition to dinoflagellate cysts, the most common marine organic walled microfossils in sediments are the chitinous linings of Foraminifera. These linings corresponds to the organic membrane of the inner chambers of Foraminifera. Comparison of microfaunal and palynological counts has shown that Foraminifera lining concentrations are proportional to benthic Foraminifera abundance in sediments (de Vernal 1986; Bilodeau *et al.* 1990). Therefore, the Foraminifera linings abundance may be considered as indicator of benthic production. Foraminifera linings are moderately abundant in surface sediments from the Laurentian Channel (Fig. 8) and from the Estuary (Fig. 9). Concentrations are relatively uniform in the Gulf, but vary in the Estuary, where an upstream–downstream gradient is recorded. Downstream from Rimouski, the concentrations are of the order of $10^3 \cdot cm^{-3}$. According to sedimentation rates of ∼1 mm • yr^{-1} (Silverberg and Sundby 1986), a benthic production of the order of 10^2 foraminifera • cm^{-2} • yr^{-1} may be estimated.

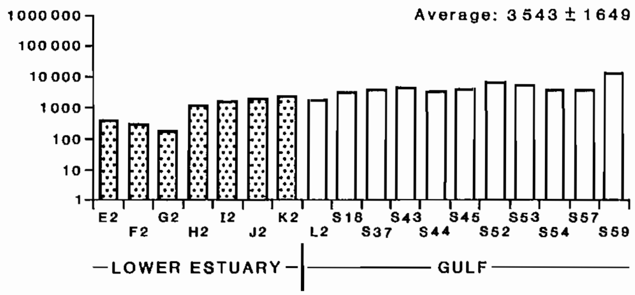


Fig. 8 Concentrations (number • cm^{-3}) of foraminifera linings in sediments from the Laurentian Channel in the Lower Estuary (stippled) and the Gulf (white).

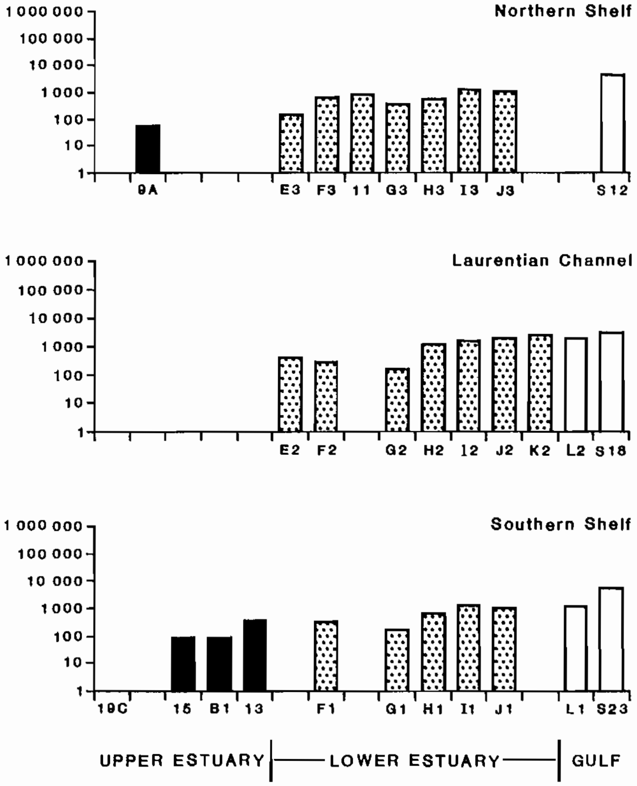


Fig. 9. Concentrations of foraminifera linings (number • cm^{-3}) in sediments from the Upper Estuary (black), the Lower Estuary (stippled) and the entrance of the Gulf (white).

Relative Fluxes of Terrestrial to Marine Palynomorphs

The palynomorph content in sediments provides a picture of the microscopic organic matter inputs. However, unless the sedimentation rates are precisely known, these data cannot be directly transformed to actual fluxes, and only order of magnitude estimates can be soundly proposed. Relative measurements are therefore required to evaluate the fluxes, at least from a qualitative viewpoint. Palynomorphs, which are composed of chitin and/or sporopollenin and behave similarly as sedimentary particles (*e.g.*, Traverse 1988), may be used for this purpose. Pollen & spore (P&S) to dinocyst (D) ratios (P&S/D) may be considered as an indicator of the organic flux origin, i.e. terrestrial *vs* marine, or allochthonous *vs* autochtonous. In terrestrial aquatic basins this ratio is infinite while in the open ocean it tends towards 0 (*e.g.*, $<10^{-2}$ in the Labrador Sea basin; de Vernal and Hillaire-Marcel 1987). Such a terrestrial to marine palynomorph ratio may therefore be viewed as a "continentality index". In the Laurentian Channel, the downstream decreasing trend of the P&S/D ratio (Fig. 10) indicates a dowstream increase in the flux of autochthonous marine particles relative to lateral terrestrial inputs. It is notable that the minimum P&S/D values are recorded in Cabot Strait area, which is also characterized by a distinctive dinoflagellate cyst assemblage (zone IV), marking the penetration of surface North Atlantic waters. Also of interest is the reverse tendency in the P&S/D ratios recorded at the head of the Laurentian Channel, perhaps related to locally higher marine bioproductivities in response to the local upwelling (Greisman and Ingram 1977).

In the St. Lawrence Estuary a P&S/D ratio average of 37.14 indicates the predominance of organic matter fluxes from a terrestrial source (Fig. 11). The P&S/D ratios are however highly variable (6 to 122; Fig. 11)

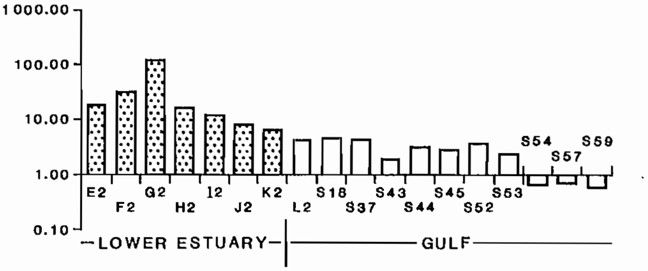


Fig. 10. Pollen and spore to dinocyst ratios in sediments from the Laurentian Channel in the Lower Estuary (stippled) and the Gulf (white).

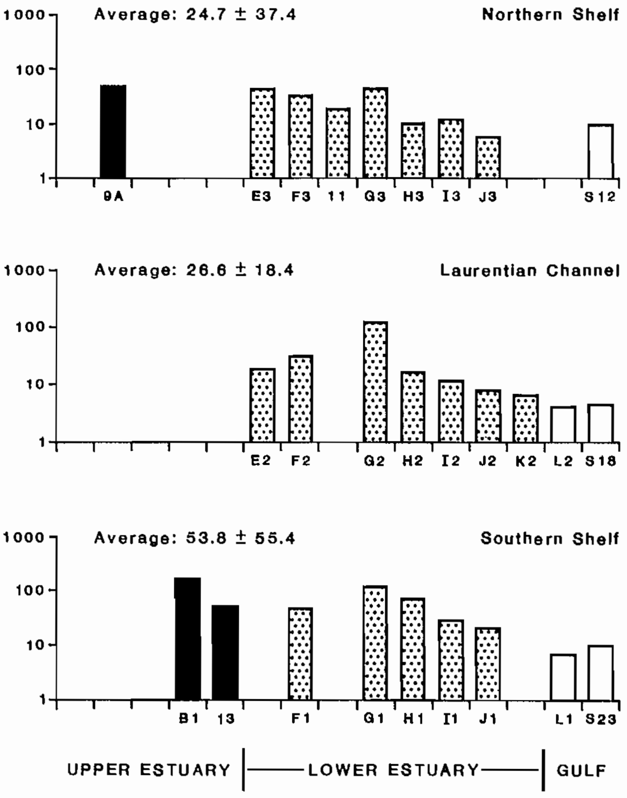


Fig. 11. Pollen and spore to dinocyst ratios in sediments from the Upper Estuary (black), the Lower Estuary (stippled) and the entrance of the Gulf (white).

throughout the lower estuary, but show a consistent pattern with respect to upstream-downstream and south-north gradients. Mean P&S/D ratios are 60.3 upstream and 19.7 downstream from Rimouski. They vary between 53.8 and 24.7 from the south to the north. The P&S/D ratios therefore reflect relatively higher terrestrial organic matter inputs along the southern coast of the Estuary and a relatively stronger marine signature of the organic matter fluxes for the downstream areas and for the northern shelf of the Lower Estuary.

Conclusion

Although palynological assemblages provide a fragmentary picture of the organic matter inputs and fluxes to marine systems, they enable the characterization of marine environments. The more relevant features of the palynomorph distribution exposed above lead to the following conclusions:

1) The pollen and spore concentrations (and orders of magnitude flux estimates) reveal very high terrestrial organic matter inputs to the Estuary and to the Gulf of St. Lawrence, which mark the epicontinental character of this transitional marine environment.

2) In addition to high terrestrial organic matter inputs, the Gulf, and to a lesser extent the Estuary, are characterized by high fluxes of autochthonous organic matter as demonstrated by abundant dinoflagellate cysts in sediments. An upstream-downstream gradient of cyst concentrations in the Laurentian Channel appears to reflect spatial variations in dinoflagellate production.

3) From an ecological point of view, dinoflagellate cyst assemblages also display some regionalism within the transitional environment of the Estuary-Gulf system. With respect to species composition and abundance, distinct assemblages are observed in the Upper Estuary, in the upstream and downstream Lower Estuary and in the open Gulf domaine suggesting correlations with the salinity gradients of the surface water masses. Another distinct assemblage characterizes the Cabot Strait area which is under influence of North Atlantic surface waters.

4) The complexity of lower Estuary water masses and sedimentary processes is shown by both pollen assemblages, benthic Foraminifera concentrations, dinocyst assemblages and terrestrial to marine palynomorph ratios. These data, taken together, illustrate the preferential southern outflow of the St. Lawrence River in the Lower Estuary, and the increased marine signature downstream from Rimouski.

5) The progressive transitional character of the Estuary-Gulf system is shown by terrestrial to marine palynomorph ratios (P&D/S), which also clearly evidences the epicontinental nature of the Gulf environment right down to Cabot Strait.

The multiplicity of indications provided by palynological assemblages seems useful for the characterization of modern sedimentary environments. Further studies are needed, particularly with the aim to develop transfer functions between palynological assemblages and physico-chemical parameters of the water masses. Valid transfer functions would aid in the investigations of environmental changes in the Estuary and Gulf during the Holocene, and would provide quantitative data on organic matter flux variations in response to climatic and anthropogenic influences.

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Nutrient Dynamics and Biological Variables of Ice Biota from the Gulf of St. Lawrence, Magdalen Islands Area[1]

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Ice biota nutrient dynamics were studied in relation to growth and ice algal biomass at six landfast ice stations and one drifting ice station in the Magdalen Islands area, Gulf of St. Lawrence. Nitrate and silicic acid concentrations in the ice were low ($NO_3 \leq 2.0$ μM, Si $(OH)_4 \leq 2.0$ μM), and became depleted in seawater with time to less than 1.0 μM at landfast ice stations. Ice soluble reactive phosphorus levels were also low, (PO_4: 0.1–0.2 μM), but concentrations increased with time to ≥ 0.4 μm and no depletion was observed in under ice seawater. Further, SRP enrichment in ice suggested *in situ* regeneration in bottom ice sections. Low nitrogen concentrations ($NO_2 + NO_3 + NH_4$), N:P ratios <16 and POC/PON ratios >10 suggest nitrogen limitation, while N:Si ratios >1 and poorly silicified frustules indicate silicic acid limitation. Mean chlorophyll *a* concentration in bottom ice was 12.91 (± 10.36 *SD*) mg • m^{-3} with lowest concentrations for drifting ice. Specific growth rates averaged 0.10 ± 0.05 d^{-1}. The instability of the ice substrate is suggested as the dominant factor responsible for the limitation of algal growth and biomass accumulation of ice biota in the Gulf of St. Lawrence.

La dynamique des sels nutritifs associés aux biocénoses de la glace a été étudiée en relation avec les taux de croissance et la biomasse des algues épontiques, à six stations de glaces côtières et à une station de glace de dérive aux Îles-de-la-Madeleine, dans le golfe Saint-Laurent. Les concentrations de nitrates et d'acide silicique étaient faibles dans la glace ($NO_3 \leq 2.0$ μM, Si $(OH)_4 \leq 2.0$ μM), et atteignaient des valeurs inférieures à 1.0 μM dans l'eau de mer aux stations de glaces côtières. Les concentrations en orthophosphates étaient aussi faibles dans la glace, (PO_4: 0.1–0.2 μm) mais augmentaient avec le temps jusqu'à ≥ 0.4 μM dans les sections de fond des glaces et aucune diminution n'était notée dans l'eau de mer. L'enrichissement en orthophosphates suggère des processus de régénération *in situ* particulièrement dans les couches de fond des glaces. Les faibles concentrations en azote ($NO_2 + NO_3 + NH_4$), des rapports N:P <16 et POC:PON >10 suggèrent que l'azote est limitant, alors que des rapports N:Si >1 et des frustules faiblement silicifiées suggèrent que la silice est limitante. Les concentrations moyennes de chlorophylle *a* dans les sections de fond des glaces étaient de 12.91 (± 10.36 *SD*) mg • m^{-3}, avec concentrations minimum à la station de glace de dérive. Les taux de croissance spécifique moyens étaient de 0.10 ± 0.05 d^{-1}. L'instabilité des glaces est considérée comme le facteur dominant limitant l'accumulation de la biomasse et la croissance des algues épontiques des biocénoses de la glace dans le golfe du Saint-Laurent.

Introduction

Sea ice algae, predominantly diatoms, are significant contributors to marine primary production in Arctic and Antarctic waters (Horner 1976; Horner and Schrader 1982; Palmisano and Sullivan 1983). They form dense populations in the lower few centimetres of annual sea ice (the skeletal layer), often attaining standing crops of 100 mg Chl*a* • m^{-2} or more despite chronically low temperatures (roughly −1.0°C to −1.8°C) and irradiance (a few percent or less of incident surface irradiance) in their growth environment (Smith et al. 1987). Sea ice microalgae have been estimated to contribute as much as 30% of the total annual carbon production in the Arctic Ocean (Alexander 1974; Horner 1976).

In the Gulf of St. Lawrence, the most southerly region in the North Atlantic in which sea ice is regularly formed, Dunbar and Acreman (1980) found chlorophyll *a* concentrations in bottom sections of drifting ice floes to be an order of magnitude less than from higher latitudes such as Hudson Bay, Barrow Strait and Robeson Channel. Differences between the Gulf and Arctic

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regimes were attributed to the duration of the ice cover (8 months in the Arctic, 2–3 months in the Gulf of St. Lawrence), the extreme density stratification of the uppermost layer of water in the Arctic, and latitude differences in light regimes coupled with thinner ice in the Gulf. Similar results were observed by Demers et al. (1984), from drifting ice floes in the St. Lawrence estuary. Cell densities were comparable to those of higher latitudes but chlorophyll *a* content per cell was much lower than ratios observed in Arctic regions (Cota 1985), suggesting that higher under ice light intensities in the Gulf were not propitious to the extreme shade adaptation characteristic of polar ice algae.

Apart from duration of ice cover and light intensities, nutrient limitation might be involved in reduced ice algal biomass. There is actually growing evidence that the supply of inorganic nutrients may limit production of ice algae in Arctic and some Antarctic regions (Grainger 1977; Gosselin et al. 1985; McConville et al. 1985; Palmisano et al. 1985; Cota et al. 1987; Maestrini et al. 1986). Early development of ice algal blooms appears to be regulated by light availability, but later in the growth season the apparent nutrient consumption ratio (Grainger 1977), response to nutrient enrichment (Maestrini et al. 1986) and protein-poor pattern (McConville et al. 1985; Palmisano et al. 1985; Smith et al. 1987) of polar ice algae suggest limitation by nitrogen.

This study on ice biota from the Gulf of St. Lawrence was undertaken in view of the differences observed between the Gulf of St. Lawrence and Arctic regimes. The aim was to determine environmental variables responsible for reduced ice algal biomass in the Gulf of St. Lawrence. Distinction was made between landfast and drifting ice for a better comparison to Arctic ice studies, most of which were made in landfast ice, whereas the studies of Dunbar and Acreman (1980) and Demers et al. (1984) dealt with drifting ice only. Biological variables and nutrient concentrations in ice and seawater were monitored on a spatial and temporal basis. Nutrient limitation was investigated in view of the evidence of nutrient limitation observed for Arctic ice algae and of lower ice algal biomass from the Gulf of St. Lawrence.

Materials and Methods

Study Sites

The Magdalen Islands Archipelago is located approximately in the centre of the Gulf of St. Lawrence. Location of stations is illustrated in Fig 1. Stations 1 and 3 are located respectively at Hâvre-aux-Maisons and Bassin in shallow protected lagoons and bays. Station 2, located on the eastern coast of the Magdalen Islands, is exposed to northwesterly winds. Stations 4 and 5, located on the western coast, are exposed to prevailing northwesterly winds and to southeast drifting ice floes coming from the Gulf of St. Lawrence. At these two stations ice was sampled midway between shore and the edge of the landfast ice (Stations 4 and 5), as well as at the ice edge (Stations 4A and 5A), the boundary between landfast ice and drifting pack ice. Stations 4A and 5A were compared to stations 4 and 5 for ice boundary effects. Station 6, on the northwestern coast at Pointe-aux-Loups, is the most exposed to winds and drifting ice floes. Station 7, located approximately 20 km offshore west of Pointe-aux-Loups, is the drifting pack ice station which was used for comparison with landfast ice stations.

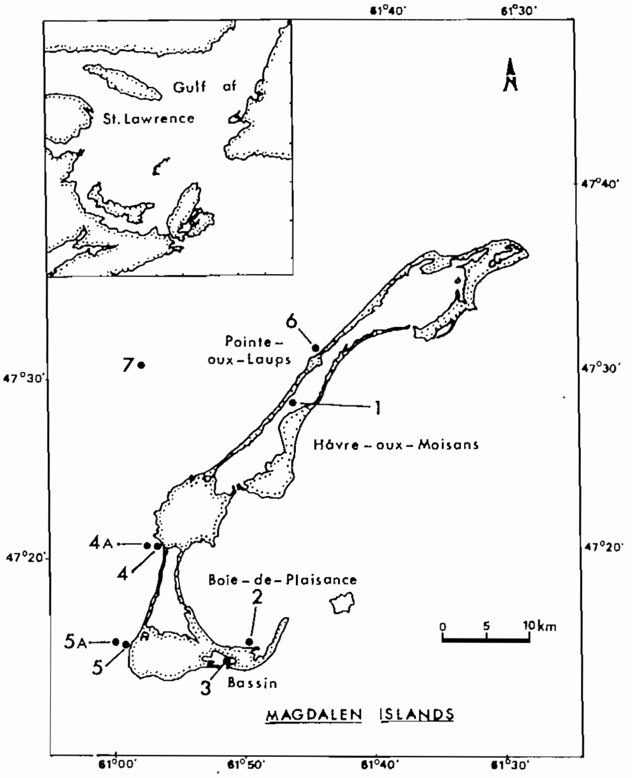


FIG. 1. The Magdalen Islands, Gulf of St. Lawrence. Sampling stations are designated by numbers 1 to 6 for landfast ice stations and by number 7 for the drifting ice station. Stations 4A and 5A are located at the edge of the landfast ice.

Sampling Procedures and Analysis

Seawater was sampled in January at stations 1, 4, 5 and 6 before ice formation. Landfast ice began to form in sheltered areas in the first week of February but ice sampling only started on the 27th of February, when the ice was thick and compact enough to work on. From that period until the 4th of April, ice and water samples were collected every 2 wk at stations 1 to 6. Ice and seawater were sampled only twice at station 7 by helicopter. Ice samples were collected with a SIPRE ice corer of 7.5 cm diameter. A minimum of two cores were collected within a 1 meter distance. Ice cores were cut into 20 cm sections, starting from bottom ice. Seawater was sampled by pumping underice water through holes made by the corer. All samples were placed in insulated containers and brought back to the laboratory for analysis of chemical and biological variables.

Ice core sections were melted slowly in warm water baths (approximately 16°C) immediately upon arrival to the laboratory. Volumes of 125 mL of the melted ice core sections and seawater samples were then filtered onto Whatman GF/C glass fiber filters for chlorophyll *a* and phaeopigments and onto Whatman GF/C glass fiber filters precombusted (for 6 h at 500°C to remove any contaminating C and N) for particulate organic carbon (POC) and nitrogen (PON) determinations, following Strickland and Parsons 1972. The filtrate was dispensed into 50 mL polyethylene bottles (prewashed with 0.15 *N* HCl) and stored frozen at −20°C for future (within 2 mo) determination of ammonia, nitrites, nitrates, soluble reactive phosphorus (PO_4-P) and silicic acid concentrations.

In the laboratory, spectrophotometric determinations of chl *a* and phaeopigments were performed using a Bausch and Lomb Spectronic 21 spectrophotometer. Carbon and nitrogen contents of the particulate matter collected on the filters were determined using a Perkin-Elmer model 240B CHN Elemental Analyser. Nutrient concentrations were determined using manual methods described in Strickland and Parsons (1972).

To determine statistical differences in the various environmental variables in ice and seawater among the stations, a SAS statistical package was used in all data analyses (Ray 1982a,b). The assumption for normal distribution was tested by computing the Shapiro-Wilk, *W*, statistic and probability plot for all environmental data sets using the Univariate procedure. Appropriate transformations were applied to data sets, when necessary. Single factor analysis of variance (ANOVA) was carried out to test the null hypothesis. Where parametric ANOVA rejected the null hypothesis, a specific among stations (or among seawater and ice sections at the same station) comparison of means (at the $P=0.05$ level), for each of the variables was carried out using Student-Newman-Keuls (SNK) multiple range test.

Results

Chemical Variables

Results on chemical variables are summarized in Table 1. They include mean, standard deviation and sample size of the different variables at stations 1 to 7, for seawater and bottom ice sections. Concentrations of silicic acid and of the nitrogen fractions (NO_3 and NO_2) are low in bottom ice sections. They are generally higher in seawater than in the ice and show an increasing trend in mean concentration values from station 1 to station 7. Statistical analysis reveals $Si(OH)_4$ mean concentration from station 7 to be significantly different from stations 1 to 6, and NO_3 mean concentration from stations 1, 2 and 3 to be significantly different from station 7, with intermediate concentrations at stations 4 to 6 ($P<0.05$ level, Student-Newman-Keuls multiple range test). Ammonia concentrations (Table 1) are low at station 1 (0.11-0.38 μM), and below the limit of detection at stations 2 to 7. Soluble reactive phosphorus (PO_4-P) concentrations are, however, somewhat similar for seawater and bottom ice sections, and no trend in mean seawater phosphorus concentrations is observed between the different stations. Lowest concentrations are found at station 1 (statistically

TABLE 1. Results of nutient analysis for sea water (W) and bottom ice section (B) at stations 1 to 7 (Fig.1). The variable are presented as means with standard deviation in parentheses and number of samples (*n*). Concentrations are in μM (μg − at/L) and the symbol * refers to NH_4 concentrations below 0.03 μM, the limit of detection.

Variables		Stations								
		1	2	3	4	4a	5	5a	6	7
NO_3-N	B	0.68	0.90	1.19	0.80	0.58	1.23	0.63	1.05	1.27
		(0.64)	(0.31)	(0.60)	(0.45)	(0.24)	(0.94)	(0.13)	(0.44)	(0.20)
	(*n*)	4	5	5	6	3	5	2	4	2
	W	1.19	0.94	1.30	3.77	3.40	3.12	3.02	1.90	7.19
		(1.62)	(0.80)	(1.96)	(2.03)	(1.12)	(2.58)	(2.66)	(3.61)	(2.17)
	(*n*)	6	6	6	7	3	6	2	5	2
NO_2-N	B	0.09	0.06	0.05	0.07	0.10	0.09	0.08	0.06	0.06
		(0.01)	(0.01)	(0.02)	(0.06)	—	(0.04)	—	(0.02)	(0.01)
	(*n*)	2	2	3	3	1	3	1	3	2
	W	0.09	0.12	0.58	0.19	0.19	0.13	0.17	0.21	0.0
		(0.11)	(0.02)	(0.98)	(0.07)	—	(0.11)	—	(0.20)	(0.03)
	(*n*)	3	2	4	3	1	3	1	4	2
NH_4-N	B	0.06	*	*	*	*	*	*	*	*
		(0.05)								
	(*n*)	4								
	W	0.15	*	*	*	*	*	*	*	*
		(0.11)								
	(*n*	6								
PO_4-P	B	0.28	0.46	1.09	0.37	0.45	0.37	0.50	0.29	0.41
		(0.18)	(0.22)	(1.57)	(0.15)	(0.15)	(0.13)	(0.23)	(0.14)	(0.30)
	(*n*)	4	5	5	6	3	5	2	4	2
	W	0.08	0.38	0.42	0.77	0.72	0.48	0.64	0.48	1.02
		(0.75)	(0.15)	(0.18)	(0.43)	(0.15)	(0.32)	(0.19)	(0.21)	(0.40)
	(*n*)	6	6	6	7	3	6	2	5	2
$Si(OH)_4-Si$	B	1.16	0.40	0.34	0.32	0.49	0.52	0.54	0.48	0.20
		(0.84)	(0.35)	(0.17)	(0.20)	(0.43)	(0.40)	(0.01)	(0.45)	(0.15)
	(*n*)	4	5	5	6	3	5	2	4	2
	W	0.37	1.04	1.57	3.25	3.49	2.91	3.70	2.44	4.72
		(0.13)	(1.77)	(1.61)	(2.86)	(1.58)	(3.23)	(3.61)	(3.04)	(3.84)
	(*n*)	6	6	6	7	3	6	2	5	2

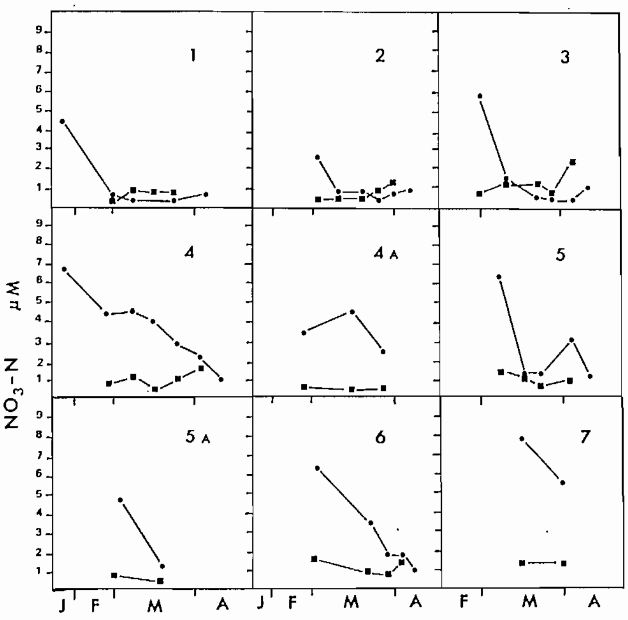


FIG. 2. Time scale evolution of nitrate concentrations (µM) in bottom ice sections (■——■) and in seawater (●——●) at stations 1 to 7.

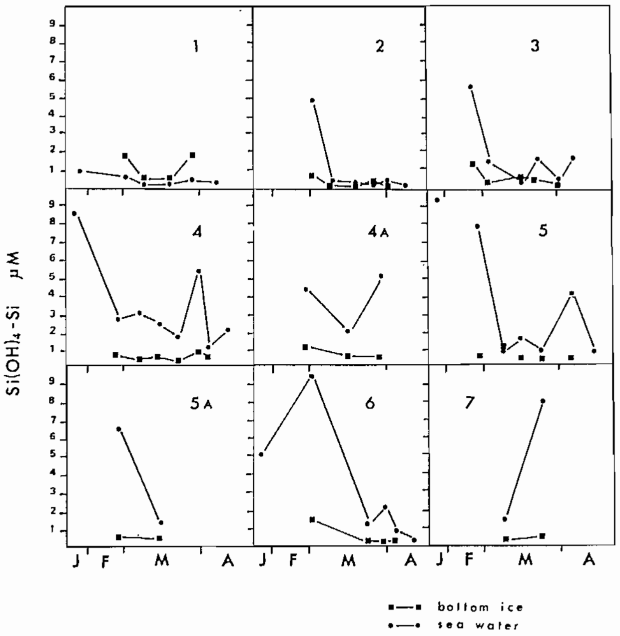


FIG. 3. Time scale evolution of silicic acid (µM) in bottom ice sections (■——■) and in seawater (●——●) at stations 1 to 7.

significant at the $P = 0.05$ level, Student-Newman-Keuls multiple range test), and highest ones at station 7.

Time scale evolution of the nutrients in bottom ice sections was then analyzed and compared to seawater concentrations for the different stations. For nitrates (Fig. 2), concentrations in bottom ice sections are less than 2.0 µM, and remain low throughout the ice season with a slight increase at some stations at the end of March and the beginning of April. In seawater, nitrate concentrations vary between 4 to 7 µM in January, before ice formation. After ice formation, i.e. middle of February, seawater nitrate levels decrease at all stations reaching concentrations of 1.0 µM or less, similar to bottom ice NO_3 levels. A trend in seawater nitrate depletion is observed from stations 1 to 7: depletion occurs earlier at stations 1, 2 and 3 (located in lagoons and on the eastern side of the Magdalen Islands) than at stations 4, 4A, 5, 5A and 6 (located on the western coast of the Magdalen Islands), and no depletion is observed at station 7. Time scale evolution of nitrites showed the same trends as for nitrates.

Similar trends were observed for silicic acid (Fig. 3). In bottom ice sections, silicic acid concentrations are low (1.0–2.0 µM) at the end of February and the beginning of March, and decrease to less than 0.05 µM by the end of March. In seawater, concentrations greater than 8 µm in January before ice formation (Fig. 3, stations 4, 5 and 6) decrease to less than 1.0 µM after ice formation at most stations, except for station 7. The pattern of seawater silicic acid depletion is similar to that of nitrates, with depletion occurring earlier at stations 1, 2 and 3 than at stations 4, 4A, 5, 5A and 6, and no depletion at station 7, the drifting ice station.

Time scale evolution of phosphorus (Fig. 4) reveals a different pattern. First, an increase in ice PO_4 concentrations is observed at most stations, from 0.1–0.2 µM at the beginning of March to more than 0.4 µM by the end of March. Second, seawater PO_4 concentrations do not become depleted after ice formation: from February on, PO_4 concentrations fluctuate highly but never reach levels below 0.20 µM. Again, seawater PO_4 concentrations remain much higher at station 7. Station 1 seems to stand out from the others, with significantly lower seawater PO_4 concentrations and with bottom ice levels higher than in seawater.

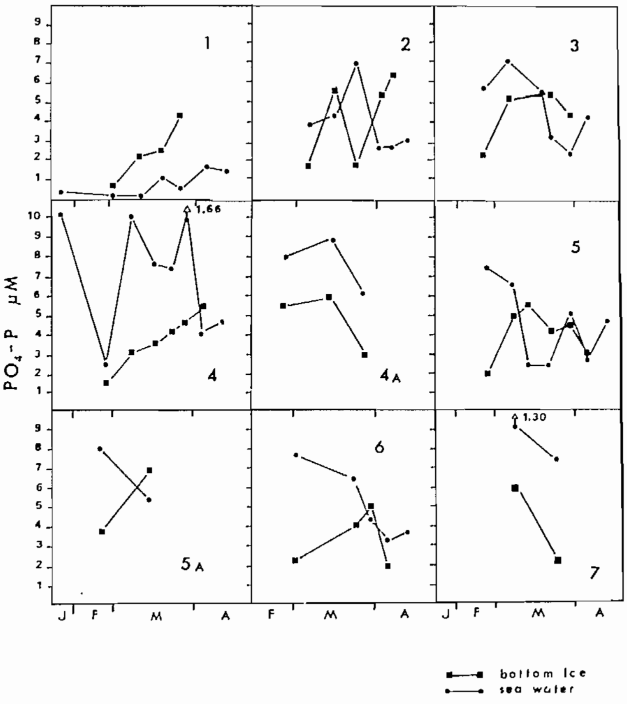
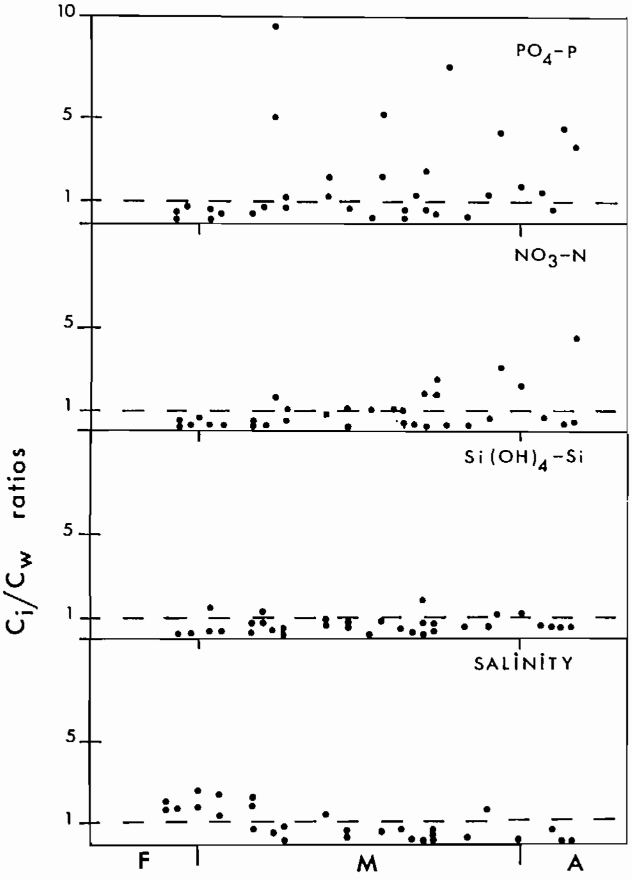


FIG. 4. Time scale evolution of soluble reactive phosphorus (µM) in bottom ice sections (■——■) and in seawater (●——●) at stations 1 to 7.

In summary, seawater and ice nutrients from the Magdalen Islands can be characterized by low NO_3 and $Si(OH)_4$ in ice, and depletion of these nutrients in seawater from February through April. Phosphorus, contrary to NO_3 and $Si(OH)_4$, increases in concentration in ice with time and shows no sign of depletion in seawater.



Ci/Cw nutrient ratios (Ci:concentration in bottom ice sections and Cw:concentration in seawater) was then computed for the different nutrients and compared to the Ci/Cw salinity ratios. The results (Fig. 5) indicate that Ci/Cw for silicic acid follow the same trend as for salinity ratios. Ci/Cw ratios for nitrates are somewhat higher than salinity ratios, particularly in the latter part of March and in April and some phosphate ratios are much higher, with values up to 9.

Biological Variables

Chlorophyll *a* levels in bottom ice vary from low mean concentrations of 5.45 mg • m^{-3} at station 7 to a high of 39.88 mg • m^{-3} at station 5A (Table 2) with significant

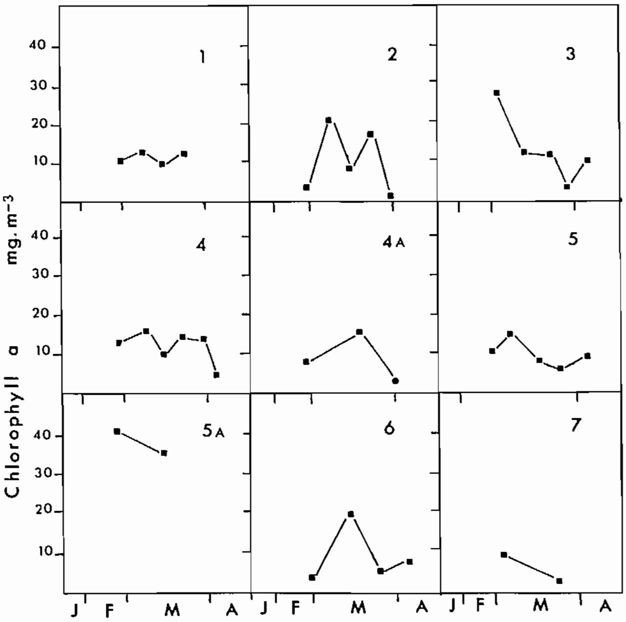


FIG. 5. Ci/Cw ratios (Ci:concentration in bottom ice, Cw:concentration in seawater) for salinity, silicic acid, nitrates and phosphates (SRP), grouping all stations.

FIG. 6. Time scale evolution of chlorophyll *a* concentrations (mg • m^{-3}) in bottom ice sections at stations 1 to 7. Seawater concentrations were too low to be included.

TABLE 2. Results of biological variables from sea water (W) and bottom ice section (B) at stations 1 to 7. The variables are presented as means with standard deviation in parentheses and number of samples (*n*). Negative specific growth rates are represented by *.

Variables		Stations								
		1	2	3	4	4a	5	5a	6	7
Chl *a*	B	10.55	9.57	12.22	12.74	8.33	9.85	39.88	7.62	5.45
(mg • m^{-3})		(1.86)	(8.76)	(8.90)	(5.41)	(8.26)	(4.65)	(4.30)	(6.29)	(5.34)
	(*n*)	4	5	5	6	3	5	2	4	2
	W	0.16	0.67	0.62	0.56	1.05	0.60	0.57	0.77	0.19
		(0.14)	(0.27)	(0.33)	(0.34)	(1.28)	(0.53)	(0.72)	(0.48)	(0.11)
	(*n*)	6	6	6	7	3	6	2	5	2
Phaeop.	B	2.49	3.43	6.97	1.37	2.78	1.08	2.70	2.08	1.29
(mg • m^{-3})		(3.21)	(4.04)	(9.27)	(1.32)	(—)	(0.92)	(1.27)	(1.63)	(1.12)
	(*n*)	4	5	5	6	1	5	2	4	2
	W	0.10	0.05	0.07	0.28	0.18	0.11	0.28	0.10	0.10
		(0.05)	(0.05)	(0.05)	(0.26)	(0.19)	(0.13)	(0.39)	(0.11)	(0.10)
	(*n*)	6	6	6	7	3	6		5	2
Growth	B	0.04	0.18	0.13	0.08	*	0.04	*	0.11	*
(d^{-1})		(.01)	(0.12)	(0.02)	(0.04)		(0.05)		—	
	(*n*)	3	3	4	4		4		3	

differences ($P = 0.05$ level, Student-Newman-Keuls multiple range test) from the other stations. Time scale evolution of chlorophyll *a* in bottom ice sections (Fig. 6) indicates an increase from the end of February until the first week of March for stations 1, 2, 3, 4 and 5, followed by a decrease in the second week of March, an increase in the third week of March followed again by a decrease in the last week of March. In seawater, chlorophyll *a* concentrations were generally less than 1.00 mg • m^{-3} (Table 2) with no significant variations in time.

Phaeopigment concentration varied from a mean of 1.08 mg • m^{-3} at station 5 to 6.97 mg • m^{-3} at station 6 (Table 2), but no significant differences were observed between the stations and no significant regression could be fitted through the data points over time. Seawater phaeopigment concentrations were low (Table 2), with no significant variations over time.

Specific growth rates, estimated as per Grossi et al. (1984) based on net increases in chlorophyll *a* (Table 2), gave positive estimate means of 0.10(±0.05 *SD*) d^{-1} for bottom ice sections. These estimates should be conservative because they are not corrected for biomass losses associated with sinking, grazing and erosion, and because apparent negative specific growth rates are not included.

Discussion

The results of the nutrient study can be interpreted with respect to the three major sources of nutrient supply to ice biota: desalination, *in situ* regeneration and underice seawater supply. Desalination was considered by Meguro et al. (1967) to be the most important mechanism of nutrient supply. An estimate of the potential nutrient supply derived from desalination was made by integrating nutrient concentrations over the whole ice thickness. For nitrates, average ice concentration of 0.89 mg−at NO_3- • m^{-3} multiplied by average ice thickness of 0.48 m gives a potential supply of 0.42 mg−at NO_3-N • m^{-2}. For silicic acid, average ice concentration of 1.00 mg−at $Si(OH)_4$ • m^{-3} gives a potential supply of 0.48 mg−at $Si(OH)_4$ • m^{-2}. Ice biota autotrophic nutrient demand, estimated for average bottom ice concentrations of 3.65 mg Chl*a* • m^{-3}, using N:Chl ratio of 9.1 and specific growth rate of 0.10 d^{-1} as mean values obtained in this study, and Si:Chl ratio of 10 (Nelson and Gordon 1982) gives an average daily nutrient demand of 0.24 mmol • m^{-2} • d^{-1} for nitrates and 0.13 mmol • m^{-2} • d^{-1} for silicic acid. These estimates indicate that nutrient supply from desalination would be used up in approximately 4 d. Cota et al. (1987) also found that nutrient supply from desalination represented only a small portion of the bloom's minimum demand for nitrogen and silicon for Arctic ice biota. Furthermore, the excluded desalination brine is not readily available to bottom ice algae since it leaves the ice in discrete plumes without appreciable diffusion and little mixing back into the seawater layer under the ice (Wakatsuchi and Ono 1983).

Ci/Cw nutrient ratios were used to determine the importance of *in situ* regeneration as a source of nutrient supply to the ice algae. Ci/Cw ratios higher than salinity ratios can result form either in situ regeneration or uptake from seawater. Ci/Cw ratios for phosphates indicate an important enrichment in bottom ice sections. Since no seawater phosphorus depletion through uptake is observed, contrary to the findings for nitrates and silicic acid, it can be concluded that the phosphorus enrichment in ice results from *in situ* regeneration. Phosphorus enrichment of bottom ice reported by Meguro et al. (1967), Mel'nikov and Pavlov (1978) and Tsurikov (1983) was thought to result from the desalination processes. In this study, Ci/Cw ratios for phosphorus were much higher than Ci/Cw salinity ratios, ruling out desalination as a possible source of nutrient enrichment. Thus *in situ* regeneration can explain the observed phosphorus enrichment, and this is even more apparent considering that enrichment is greatest in bottom ice sections where maximum ice algal biomass is found. With respect to Ci/Cw ratios for nitrogen (NO_3 + NO_2), some enrichment is observed but it could result from uptake since nitrates are depleted in seawater with time. Regeneration of nitrogen is, however, much slower than for phosphorus: Garber (1984) observed regeneration of P occurring after 2 wk, compared to 4 wk for N. In the Arctic, Cota et al. (1987) estimated that regenerative fluxes of nitrogen approached the estimated demand in Barrow Strait, but that this was not the case for silicic acid for which regeneration occurs through a dissolving process (Nelson and Gordon 1982).

The third source of nutrient supply for ice algae comes from the underice seawater column. Cota et al. (1987) reported that nutrient flux from the water column was the largest source of nutrient supply for ice algae in Barrow Strait. Results from this study bring indirect evidence to the fact that nutrient flux from the water column is the most important source of supply to ice algae. Nitrates and silicic acid from the water column are used up by ice algae to the point of depletion, especially at stations protected from winds or drifting ice floes where underice nutrient fluxes are reduced.

If we accept the fact that nutrient flux from the water column is the largest source of supply to ice algae, low seawater nitrate and silicic acid concentrations observed in seawater could act as a limiting factor to ice algal biomass production in the Magdalen Islands area. Nitrogen reaches concentrations in seawater that are less than the starvation level of 0.3 μM reported by Collos (1980). Furthermore, seawater N:P ratios are generally less than 10 with a mean value of 3.63(±6.55 *SD*), and C:N ratios from POC and PON data give cell ratios of 8–9 for February, increasing to more than 10 by March. Although it is misleading to interpret low seawater N:P ratios as indicative of N limitation (Heckey and Kilham 1988), C:N ratios ≥ 10 are considered to represent real subsaturation with nitrogen in marine diatoms (Sakshaugh et al. 1983). Limitation by silicic acid can also be considered in this study, with seawater $Si(OH)_4$ concentrations less than 1 μM and N:Si ratios greater than 1. Silicic acid starvation is reported to occur at $Si(OH)_4$ concentrations of 2.0–5.0 μM (Dugdale et al. 1981; Jacques 1983; Laing 1985) and Si limitation predicted for N:Si ratios >1 (Levasseur and Therriault 1987). Si limitation can also lead to an increase in C:N ratios as a result of lipid accumulation (Taguchi et al. 1987), and to the formation of thin walled frustules such as were frequently observed in this study.

Chlorophyll *a* concentrations vary from a minimum of 5.45 $\text{mg} \bullet \text{m}^{-3}$ of chl *a* at station 7 to a maximum of 39.9 $\text{mg} \bullet \text{m}^{-3}$ at station 5A. Such biomass values are one to two orders of magnitude lower than for higher latitude ice biota communities (Dunbar and Acreman 1980; Poulin et al. 1983; Cota et al. 1987). Furthermore, chlorophyll *a* values from the drifting ice station are significantly lower than at the landfast ice stations where nutrient depletion was observed. Dunbar and Acreman (1980) and Demers et al. (1984) reported similar chlorophyll *a* concentrations for drifting ice in the the Gulf and the St. Lawrence Estuary.

Despite indications of nutrient limitation, no correlation could be established between nutrients and chlorophyll *a* concentrations. Since the decrease in chlorophyll *a* of bottom ice sections coincided with a 20 cm reduction in ice thickness (De Sève 1989), the instability of the ice substrate with respect to ice melt, is considered responsible for reduced ice algal biomass in the Gulf of St. Lawrence. The low specific growth rates, in the order of $0.10 \pm .05$ *SD* d^{-1} which is in the lowest range of values reported for Arctic ice algae, can also be related to ice instability. Recent data indicate a range of 0.3–0.7 d^{-1} (Hegseth 1982), while Cota et al. (1987) estimated specific growth rates at 0.08–0.25 d^{-1}, with a maximum of 0.96 d^{-1} for natural assemblages, and Horner and Schrader (1982) reported values of 0.26 d^{-1}.

The importance of underice light regimes should also be considered. Dunbar and Acreman (1980) and Demers at al. (1984) considered that higher underice light intensity in the Gulf of St. Lawrence was responsible for the differences observed between the Gulf and Arctic ice biota. In this study, underice light intensity was estimated at 109–218 $\mu\text{Ein. m}^{-2} \bullet \text{s}^{-1}$, using Maykut and Grenfell (1975) light absorption spectra for an average ice thickness of 50 cm and an average surface irradiance of 1090 $\mu\text{Ein} \bullet \text{m}^{-2} \bullet \text{s}^{-1}$ (data obtained from Environment Canada, Montréal, P.Q. H4M 2N8). During the Arctic ice algal bloom, the underice light regime is in the order of 1–2 $\mu\text{Ein} \bullet \text{m}^{-2} \bullet \text{s}^{-1}$ (Grainger 1977). Shade adapted Arctic ice algae are reported to be light saturated at 23 $\mu\text{Ein} \bullet \text{m}^{-2} \bullet \text{s}^{-1}$ with photoinhibition at about 250 $\mu\text{Ein} \bullet \text{m}^{-2} \bullet \text{s}^{-1}$ (Bunt 1964; Sakshaugh et al 1983). Low compensation light intensities, achieved through increased numbers of photosynthetic units and chlorophyll *a* content per cell, is a critical adaptation permitting the growth of ice algae in the Arctic despite low light intensities. Demers et al. (1984) reported much lower values of chlorophyll *a* content per cell in the Gulf than ratios observed in Arctic regions (Cota 1985), and suggested that higher under ice light intensities in the Gulf were not propitious to the extreme shade adaptation characteristic of polar ice algae. The results of chlorophyll *a* content per cell found in this study were highly variable but C/chl*a* ratios of 99.6($\pm$64.3 *SD*) could be an indication of poor adaption to light intensities. C/chl*a* ratios of 38 are typical of bottom ice algal communities adapted to low light levels while ratios ≥ 100 are found when there is not sufficient time for adaptation to underice light regimes (Bunt 1964; Palmisano et al. 1985).

In summary, the results obtained from this study indicate the possibility of nutrient limitation with respect to nitrates and silicic acid. No correlation is found between nutrients and biomass in the bottom ice, based on chlorophyll *a* concentrations. However, the instability of the ice substrate, in relation to ice melt, is suggested as a limiting factor for biomass accumulation and reduced growth rates. The instability of the ice substrate in the Gulf of St. Lawrence was demonstated with respect to ice melt and short duration of ice cover (De Sève 1989). Analysis of community structure (De Sève and Dunbar 1990) are also in agreement with this, suggesting that the ice microalgal communities are in early stages of colonization. But more research is needed to clearly evaluate the effects of higher light intensities and the degree of shade adaptation of these ice algal communities.

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Environnement physico-chimique et trophique d'un site mytilicole, Île-de-la-Madeleine (Québec): I — Évolution estivale des composés de l'azote, du phosphore et du silicium[1]

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SOUCHU, P., P. MAYZAUD ET S. ROY. 1991. Environnement physico-chimique et trophique d'un site mytilicole, Îles-de-la-Madeleine (Québec) : I — Évolution estivale des composés de l'azote, du phosphore et du silicium, p. 209–218. *Dans* J.-C. Therriault [éd.] Le golfe du Saint-Laurent : petit océan ou grand estuaire? Publ. spéc. can. sci. halieut. aquat. 113.

Des études menées du printemps à l'automne 1988 sur la composition physico-chimique des eaux de la lagune de Grande-Entrée (Îles-de-la-Madeleine, Québec) confirment l'absence de stratification et une bonne oxygénation du milieu. Les mesures de sels nutritifs indiquent une quasi absence d'azote inorganique dissous (NID, amnonium + nitrates + nitrites <0,1 μM-N), des quantités faibles, mais jamais nulles, de phosphates (0,25 à 0,70 μM-P) et de sels du silicium (0,3 à 1,5 μM-Si). L'Azote et le Phosphore Organiques dissous (NOD et POD) se distinguent par des concentrations élevées variant respectivement de 7,2 à 29,1 μM-N et de 0,10 à 1,17 μM-P. Aucun enrichissement significatif en sels nutritifs provenant du golfe (courant de Gaspé) ou de sources tellurique et anthropique (lessivage des sols et rejets domestiques) n'est observé. Le système lagunaire des Îles-de-la-Madeleine est peu fertilisé et présente des caractéristiques de type oligotrophe. L'essentiel des apports en sels nutritifs semble donc reposer sur le recyclage, et pour l'azote et le phosphore sur la reminéralisation bactérienne et l'excrétion par les hétérotrophes. Les concentrations en azote et phosphore organiques particulaires ont globalement augmenté pendant la période d'étude (respectivement de 2,0 à 6,5 μM-N et 0,10 à 0,60 μM-P). Cependant, l'évolution des rapports N/P laissait supposer un changement dans la nature des particules au cours de l'été. Le stock d'azote (gaz exclus) était composé en moyenne de 72 % d'organique dissous et 28 % de particulaire; celui de phosphore de 41 % de phosphates, 38 % d'organique dissous et de 21 % de particulaire. Les moulières (*Mytilus edulis*), dans leur couverture actuelle, ne semblent pas avoir induit de différence significative dans la distribution des composés de l'azote et du phosphore dans la colonne d'eau.

Physical and chemical characterization of lagoon waters from Grande-Entrée (Magdalen Islands, Québec) show that, from spring to fall 1988, there is good oxygenation of this environment and no apparent stratification. Nutrient measurements indicate a virtual absence of inorganic nitrogen ($NH_4^+ + NO_3^- + NO_2^- < 0.1$ μM-N), and low values (but never undetectable) of phosphate (0.25–0.70 μM-P) and silicate (0.3–1.5 μM-Si). Concentrations of Dissolved Organic Nitrogen and Phosphorus (DON and DOP) are distinctly high, from 7.2 to 29.1 μM-N and 0.10 to 1.17 μM-P, respectively. We noticed no significant enrichment in inorganic nutrients originating from the Gulf of St. Lawrence during the study period. No other sources of inorganic nutrient from land drainage or domestic wastes were observed. The lagoon system of Magdalen Islands is not well fertilized, and, in that sense, it displays some oligotrophic features. Most of the nutrient input comes from recycling, in particular for nitrogen and phosphorus, from bacterial remineralization and excretion by heterotrophic organisms. Concentrations of Particulate Organic Nitrogen and Phosphorus (PON and POP) generally increase during summer (from 2.0 to 6.5 μM-n (and 0.10 to 0.60 μM-P)). However, N/P ratios suggest that changes occur in the types of particles found in suspended matter during the study period. Total nitrogen (gas excluded) was composed, on averaged, of 72% dissolved organic form and 28% particulate form; for phosphorus, we found 41% in the form of phosphate, 38% as dissolved organic P and 21% as particulate P. Actual mussel culture sites (*Mytilus edulis*) do not seem to significantly affect the distribution of N and P compounds in the water column.

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[1] Cet article fait partie des Compte rendus d'un atelier/symposium tenu à l'Institut Maurice-Lamontagne, Mont-Joli (Québec) du 14 au 17 mars 1989.

[2] À qui adresser la correspondance.

Introduction

Le développement de la mytiliculture en milieu lagunaire pose un double problème de connaissance du potentiel de production du site et d'influence de l'activité économique sur les caractéristiques du milieu. La mise en place dans le début des années 1980 d'entreprises mytilicoles dans les deux lagunes de Havre-aux-Maisons et Grande-Entrée aux Îles-de-la-Madeleine s'est heurté à diverses difficultés dont la moindre n'est pas la chute des rendements en chair des moules pendant la saison estivale et les mortalités massives des animaux de 2 ans. L'étude des relations entre les caractéristiques physiques, chimiques et biologiques de la lagune de Grande-Entrée et la production mytilicole implique : (1) de décrire la distribution des composés de l'azote, du phosphore et du silicium afin de connaître les mécanismes de fertilisation de l'écosystème; (2) d'évaluer la productivité du milieu et les qualités nutritives du matériel particulaire présent dans la lagune et (3) de mettre en relation les facteurs trophiques du milieu avec les paramètres physiologiques et alimentaires des moules cultivées. Le présent travail répond de façon préliminaire au premier des objectifs décrits. Un certain nombre de paramètres chimiques comme l'azote ammoniacal, les composés organiques dissous et particulaires, sont décrits pour la première fois dans cet écosystème.

Matériel et méthodes

Site d'étude

L'archipel des Îles-de-la-Madeleine est situé dans la partie Sud du golfe du Saint-Laurent (fig. 1). Il est composé principalement d'un groupe d'îles reliées entre elles par des cordons dunaires doubles entre lesquels se trouvent des lagunes peu profondes (0,5 à 6 m). Les lagunes sont recouvertes de glace permanente de décembre–janvier à avril–mai dont l'épaisseur varie de 0,6 à 1 m (C.R.E.M. 1979). L'absence de cours d'eau ne rend les apports d'eau douce possibles que par les précipitations humides. La présence d'un point amphidromique atténue l'influence de la marée dont l'amplitude moyenne est de 0,58 m (Bourget 1976). En revanche, les vents dont les vitesses peuvent atteindre 15 $m \cdot s^{-1}$, peuvent contribuer de façon efficace à l'homogénéisation de la colonne d'eau et aux échanges lagune-golfe. L'étude a été effectuée dans la lagune de Grande-Entrée qui est en communication avec la lagune de Havre-aux-Maisons dans sa partie Sud-Est, et avec le golfe dans sa partie Sud. Un chenal d'une profondeur moyenne de 6 m traverse la lagune de part en part et permettrait l'échange de 22 % des eaux lagunaires par cycle de marée (Munro et Therriault 1983). Le taux réel de renouvellement des eaux qui dépend aussi de l'influence des vents n'est cependant pas connu. Les fonds inférieurs à 2 m (20 % de la surface totale), sont recouverts par des herbiers à zostères dont la biomasse est de 760 g PS $\cdot$ m^{-2} (De Sève *et al.* 1978). Ces plantes marines sont de plus associées à une importante communauté d'épiphytes, cette dernière pouvant représenter 23 % de la biomasse totale de certains herbiers (Penhale 1977). Des moulières, dont la présence remonte à 1985, couvrent 7 % de la superficie avec un total de 37 600 lignes flottantes (ou boudins) d'une longueur moyenne de 2 m et comprenant environ 450 moules d'un an (B. Myrand, MAPAQ-I.D.M; communication personnelle).

Prélèvements et dosages

Des campagnes de prélèvements ont ét conduites une fois par semaine de mai à août 1988 aux différentes

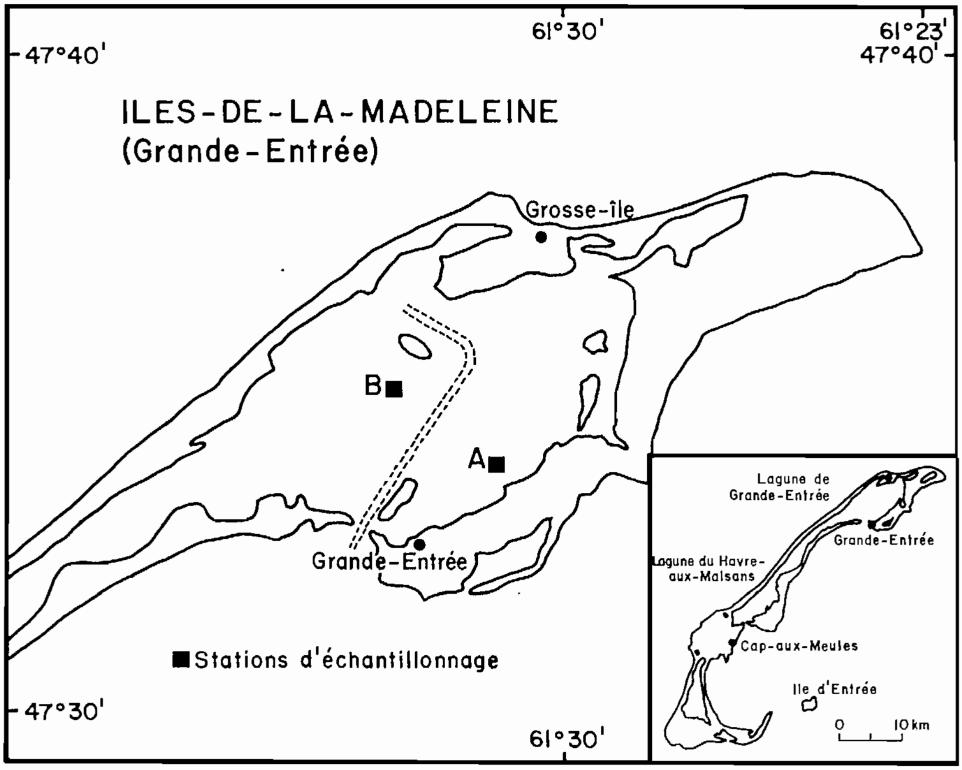

FIG. 1. Carte des Îles-de-la-Madeleine localisant les deux stations d'échantillonage.

stations de la lagune de Grande-Entrée (fig. 1). Les échantillons ont été prélevés en surface (1 m) et au fond (4 m) à l'aide de bouteilles Niskin. L'eau était aussitôt préfiltrée sur une toile de 200 μm (vide de maille) pour en retirer le zooplancton et les débris de grande taille.

La température était mesurée à l'aide d'une sonde YSI (précision : ± 0.1 °C) et les salinités analysées avec un salinomètre Autosal Guildline 8400 (précision : $\pm 0,01$ ‰). Les échantillons d'oxygène dissous étaient fixés à bord puis dosés au laboratoire par la méthode de Winkler selon Strickland et Parsons (1972) (précision : $\pm 0,01$ mL • L^{-1}). Le pourcentage d'oxygène dissous par rapport à la saturation a été ensuite calculé selon les équations de Weiss (1970).

Les échantillons d'azote ammoniacal étaient fixés à bord puis analysés manuellement selon Koroleff (1976) (précision : $\pm 0,1$ μM-N). Pour les autres sels nutritifs : nitrates + nitrites (NO_3^-), phosphates (PO_4^{3-}) et silicates (Si), les échantillons étaient filtrés sur membranes GF/C Whatman et les filtrats stockés dans des flacons de Pyrex à -20°C pour les phosphates et les nitrates, et à 4°C dans des flacons de polyéthylène pour les silicates. Ces trois paramètres ont été mesurés à l'aide d'un Auto-Analyser II Technicon selon Tréguer et Le Corre (1975) (précision : ± 1 %).

L'Azote et le Phosphore Organiques Dissous (NOD et POD), ont été déterminés selon Armstrong *et al.* (1966). L'eau de mer était filtrée sur membranes GF/C (brûlées au préalable à 450°C) puis irradiée 6 h au moyen d'une lampe U.V. de 1200 W dont le rendement d'oxydation était contrôlé à partir de standards de bipyridine (rendement >95 %). L'eau irradiée était ensuite dosée pour les nitrates et phosphates au moyen de l'Auto-Analyser (précision : ± 5 %). La précision sur les rapports N/P dans la Matière Organique Dissoute est de 10 %.

Pour la mesure des concentrations d'azote et de phosphore organiques particulaires (NOP et POP), trois échantillons de 250 mL étaient filtrés sur membranes GF/C (brûlées au préalable à 450°C). Les dosages de NOP étaient effectués selon Strickland et Parsons (1972) à l'aide d'un analyseur CHN Perkin-Elmer 240. (précision : ± 5 %). Pour les dosages de POP les molécules

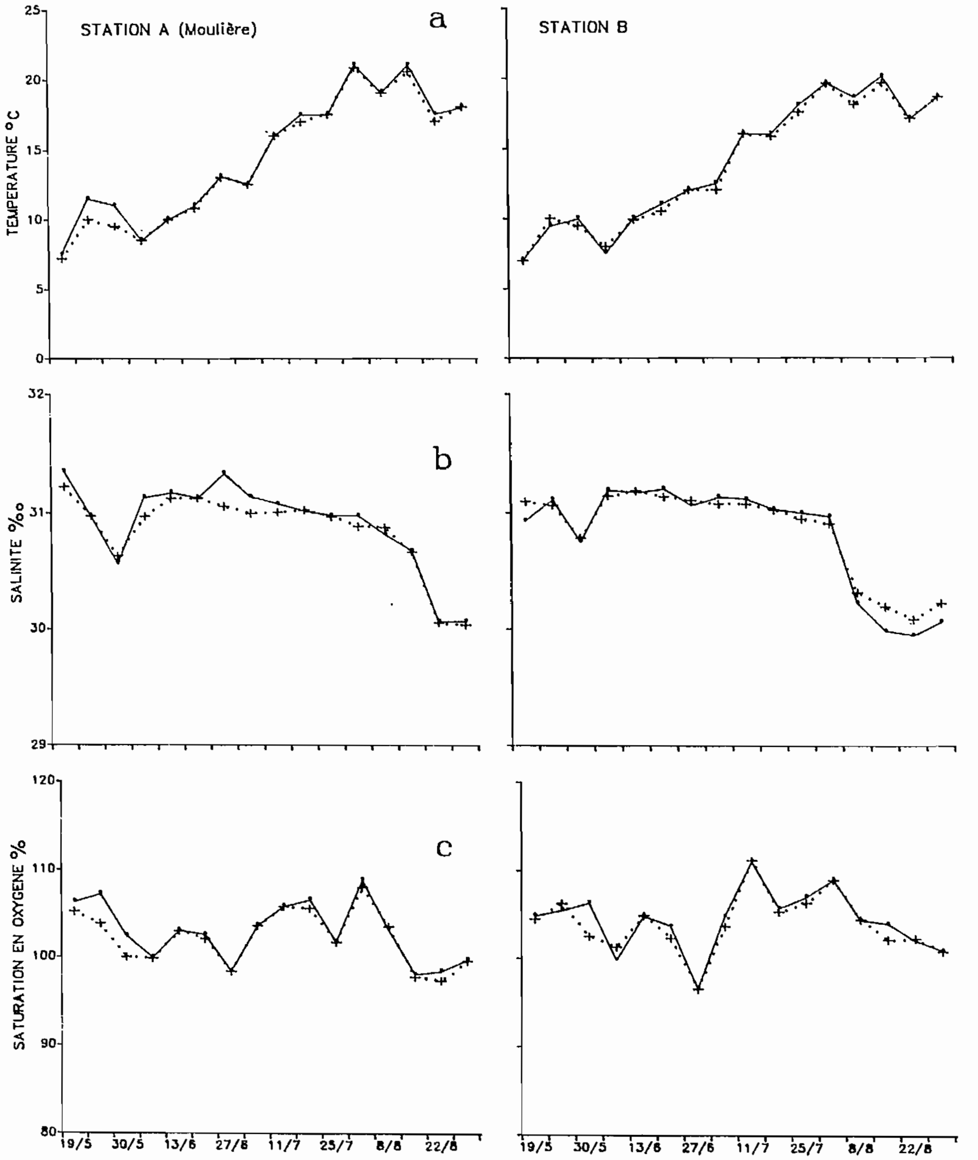

FIG. 2. Évolutions des températures (a), des salinités (b) et des pourcentages de saturation en oxygène dissous (c) en surface (. ___ .) et au fond (+ .. +) dans les eaux de la lagune de Grande-Entrée de mai à septembre 1988.

sion : ±5 %). Pour les dosages de POP les molécules phophorées étaient transformées en phosphates par oxydation à chaud au persulfate de potassium selon Menzel et Corwin (1965), puis dosées sur Auto-Analyser (précision : ±5 %). La précision sur les rapports N/P dans la matière organique particulaire est de 10 %.

Résultats

Température, salinité et oxygène dissous

Les températures (fig. 2a) varient de 7,5 à 21,5°C à la station A, le maximum thermique étant atteint au début du mois d'août. Les températures mesurées à la station A sont en moyenne supérieures de 1°C à celles de la station B.

Les salinités (fig. 2b) oscillent légèrement autour de 31 ‰ du printemps jusqu'au début du mois d'août. Toutefois, une légère inflexion se distingue à la fin du mois de mai. À partir du mois d'août, les salinités diminuent de 31 à 29,9 ‰ à la station B. La baisse est moins prononcée à la station A et se fait ressentir environ une semaine plus tard.

Les pourcentages d'oxygène dissous par rapport à la saturation (fig. 2c) varient de 98 à 108 % pour la station A et de 97 à 111 % pour la station B. Les eaux de la lagune sont donc en moyenne légèrement sur-saturées. Enfin, il n'y a pas de différence significative entre les échantillons de surface et ceux de fond pour les trois paramètres décrits.

Sels de l'azote, du phosphore et du silicium

Les concentrations en silicates (fig. 3a) sont inférieures à 1 µM-Si pendant les trois premiers mois de l'étude puis montrent une légère augmentation au mois d'août qui est plus sensible à la station A qu'à la station B.

Les phosphates (fig. 3b) présentent des concentrations variant entre 0,25 et 0,70 µM-P. Le mois d'août est caractérisé par des valeurs légèrement supérieures à la station A. Les concentrations mesurées sont du même ordre de grandeur que celles obtenues en 1987 lors d'une étude préliminaire (tableau 1).

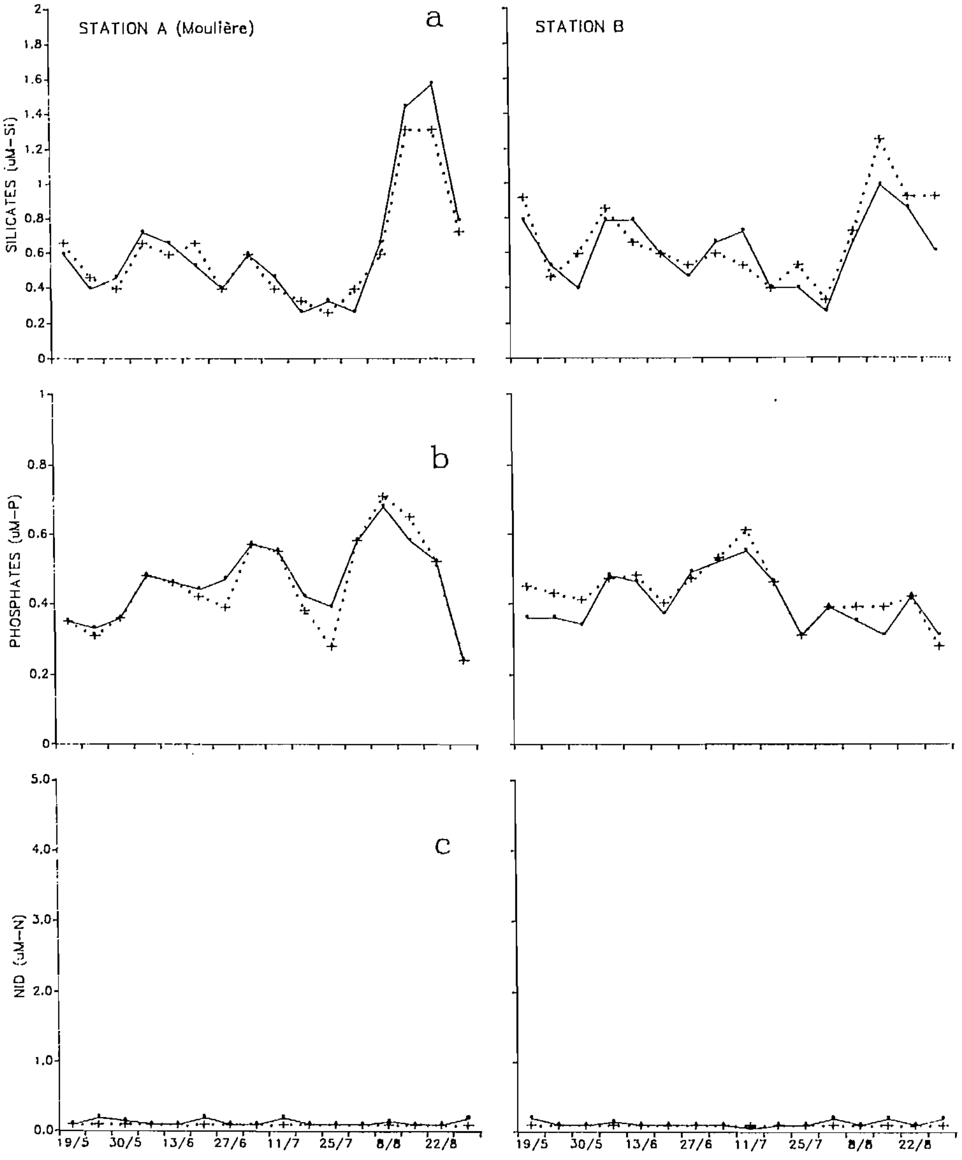

FIG. 3. Évolutions des concentrations en Silicates (a), phosphates (b) et Azote Inorganique Dissous (c) en surface (. ___ .) et au fond (+ .. +) dans les eaux de la lagune de Grande-Entrée de mai à septembre 1988.

TABLEAU 1. Concentrations moyennes en nitrates et en phosphates mesurées lors d'une étude préliminaire pendant l'été 1987 à la station A (moulière) de la lagune de Grande-Entrée. (Symboles : ± écarts-types; (n) : nombre d'observations.)

Dates	Concentrations — μM	
	Nitrates	Phosphates
Juin	0,05 ± 0,03 (15)	0,47 ± 0,11 (22)
Juillet	0,08 ± 0,04 (22)	0,62 ± 0,10 (22)
Août	0,08 ± 0,04 (12)	0,54 ± 0,09 (12)

L'Azote Inorganique Dissous (NO_3^- + NO_2^- + NH_4^+) n'est détecté que sous forme de traces dans les eaux de la lagune (fig. 3c). Ces résultats confirment les valeurs de nitrates obtenues pendant l'été 1987 (tableau 1). Les eaux de la lagune sont donc caractérisées par une quasi absence de NID du printemps à l'automne pendant les deux années étudiées.

Azote et Phosphore Organiques Dissous (NOD et POD)

Les teneurs en NOD (fig. 4a) oscillent autour de 10 μM-N avec un minimum de 7 μM-N au milieu du mois de juillet et une valeur extrême de 29,1 μM-N à la fin du mois d'août à la station A. Les variations ne montrent pas de tendance significative. En revanche, les concentrations de POD (fig. 4b) présentent les valeurs les plus faibles aux mois de mai et juin (environ 0,20 μM-P) et augmentent par la suite pour atteindre leur maximum à la fin du mois d'août (1,17 μM-P à la station A). Cette tendance est moins prononcée à la station B. Les rapports N/P dans la Matière Organique Dissoute (MOD) présentent des valeurs supérieures à 100 à la fin du mois de mai (fig. 4c) puis diminuent progressivement pour se stabiliser autour de 20 à partir de la mi-juillet.

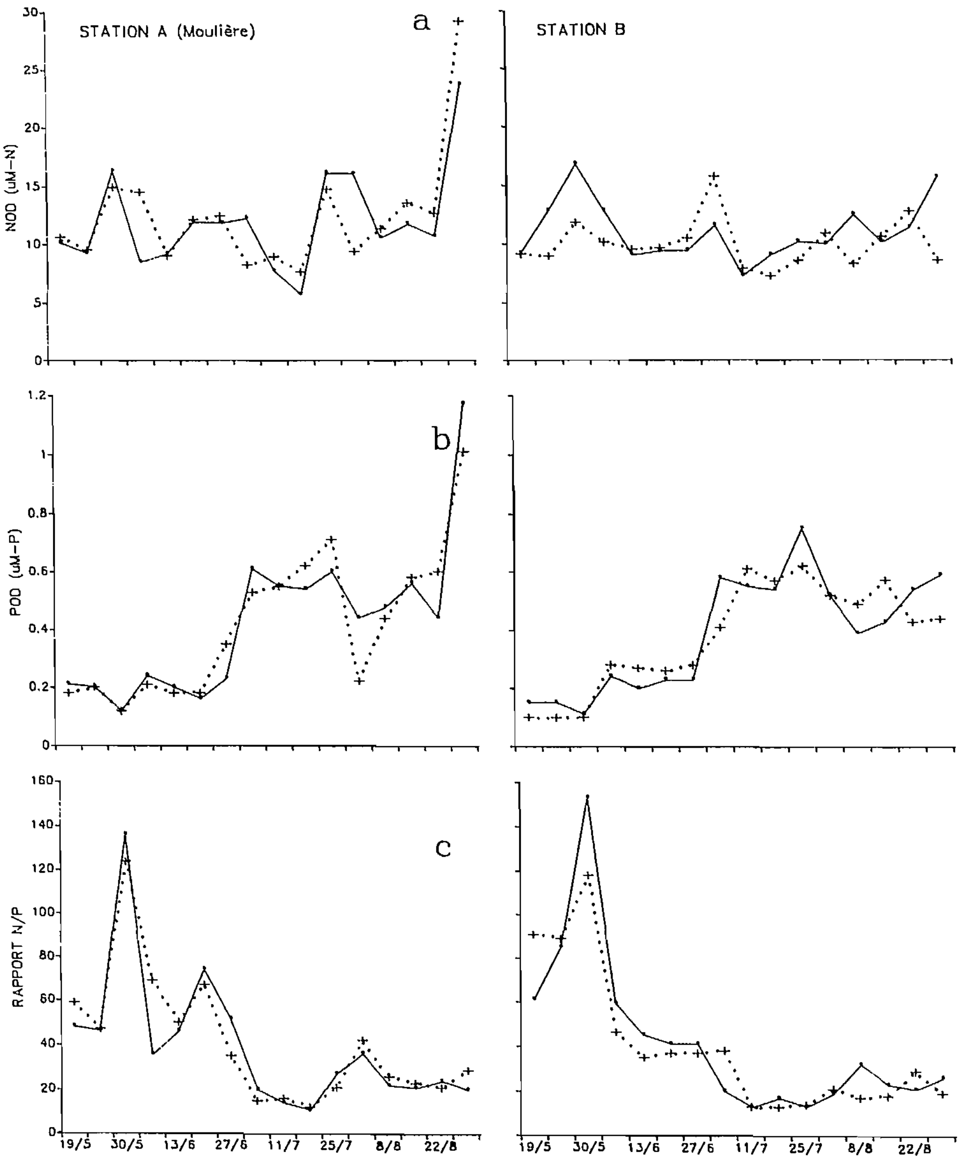

FIG. 4. Évolutions des concentrations en Azote Organique Dissous (a), Phosphore Organique Dissous (b) et des rapports N/P dans la Matière Organique Dissoute (c), en surface (. ___ .) et au fond (+ .. +) dans les eaux de la lagune de Grande-Entrée de mai à septembre 1988.

Azote et Phosphore Organiques Particulaire (NOP et POP)

Les concentrations de NOP (fig. 5a) augmentent progressivement de 2 μM-N au printemps à 6,5 μM-N à la fin du mois d'août pour la station A. L'augmentation est légèrement plus faible à la station B. Les teneurs en POP (fig. 5b) présentent une tendance différente : les concentrations sont relativement stables jusqu'à la mi-juillet ($<$0,2 μM-P) puis augmentent, plus brusquement à la station A qu'à la station B, pour atteindre des valeurs supérieures à 0,4 μM-P de la fin de juillet au début du mois d'août. Une diminution sensible des teneurs est observée en fin de période d'étude. L'évolution du POP semble contrôler les variations des rapports N/P dans la MOP (fig. 5c). Ces dernières sont marquées par une diminution de 35 à 10 du printemps à la mi-juillet puis suivies par une remontée progressive jusqu'à 20 à la fin de l'été.

Discussion

Température, salinité et oxygène dissous

Le milieu lagunaire, de par la faible profondeur de ses fonds, permet un réchauffement des eaux supérieur à celui des eaux du golfe en période estivale. La légère supériorité des températures à la station A semble indiquer que les moulières sont situées dans une aire de la lagune où les masses d'eaux ont un temps de résidence un peu plus long qu'à la station B. Les salinités présentent une gamme de variations en accord avec les mesures précédentes effectuées dans les lagunes (Munro et Therriault 1981). La légère diminution de salinité observée à la fin du mois de mai peut s'expliquer par les pluies importantes enregistrées à cette période. En effet, il est tombé plus de 100 mm de pluie sur les Îles-de-la-Madeleine entre le 17 et le 26 mai, ce qui représente une

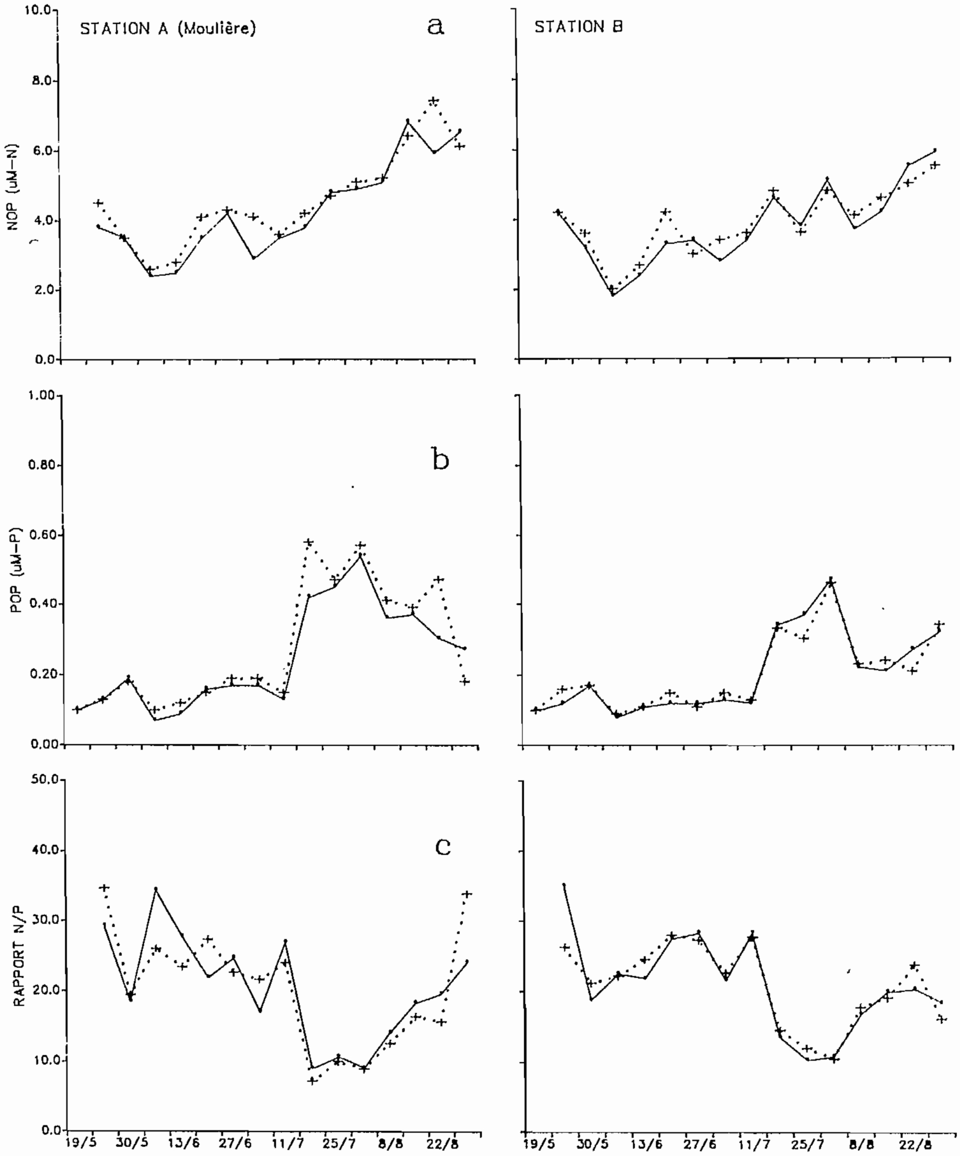

FIG. 5. Évolutions des concentrations en Azote Organique Particulaire (a), Phosphore Organique Particulaire (b) et des rapports N/P dans la Matière Organique Particulaire (c), en surface (. ___ .) et au fond (+ .. +) dans les eaux de la lagune de Grande-Entrée de mai à septembre 1988.

dilution d'environ 0,7 ‰, de la salinité dans la lagune. La baisse observée au mois d'août est trop importante pour avoir la même origine. Elle est probablement due à un changement des masses d'eau de surface du golfe qui alimentent le système lagunaire des Îles-de-la-Madeleine. Les importantes quantités d'eaux douces déversées par le fleuve Saint Laurent au printemps progressent lentement pendant la période estivale, en se diluant dans le golfe, par le biais du courant de Gaspé (Bugden *et al.* 1982). Le courant de Gaspé n'atteindrait le plateau Madelinot que vers le mois d'août (V. Koutitonsky, INRS-Océanologie; communication personnelle). Cependant l'influence de ces eaux d'origine fluviale ne semble se limiter qu'à une faible diminution de salinité (de l'ordre de 1 ‰ à la station B). La baisse moins prononcée à la station A et son décalage par rapport à la station B confirment l'hétérogénéité spatio-temporelle suggérée par les températures. Bien que cette hypothèse se doive d'être vérifiée à l'aide d'un modèle de circulation des eaux de la lagune, il semble que les eaux de la station A soient moins influencées par les échanges avec le golfe que celles de la station B. Cette situation permet d'expliquer en partie les évolutions plus contrastées observées à la station A pour l'ensemble des paramètres chimiques.

L'oxygène moléculaire dissous est un paramètre important des milieux aquatiques et gouverne la majorité des processus biologiques des écosystèmes marins. Sa concentration est la résultante des facteurs physiques, chimiques et biologiques. Ce sont les processus biologiques qui ont généralement une influence prépondérante sur les concentrations en oxygène. La production *in situ* par la photosynthèse peut engendrer des sur-saturations atteignant 150 voire 200 % (Aminot 1983), mais l'accumulation de détritus carbonés peut induire des phénomènes d'anoxie. Dans la lagune de Grande-Entrée, la saturation est restée proche de 100 % que ce soit en surface ou au fond. En conséquence, l'oxygénation des eaux lagunaire semble suffisamment contrôlée par les échanges air-océan pour éviter des risques d'anoxie.

Sels du silicium, du phosphore et de l'azote

Les silicates ne constituent un nutriment essentiel que pour les espèces phytoplanctoniques à tests siliceux (diatomées, chrysophycées, silicoflagellés, ainsi que les radiolaires parmi les protozoaires marins). En écosystème côtier, ces dernières constituent un stock de silice biogénique dont la redissolution intervient principalement dans le sédiment et dépend de la température (Aller et Benninger 1981). La légère augmentation des concentrations en silicates dans la colonne d'eau au mois d'août est sans doute due à la conjonction de plusieurs facteurs dont un accroissement des flux à l'interface eau-sédiment consécutif au maximum thermique, une diminution de la consommation par le plancton à test siliceux, mais aussi à une possible influence des eaux du courant de Gaspé. Les silicates n'étant jamais épuisés dans la lagune, il ne sont sans doute pas limitants pour les espèces phytoplanctoniques à tests siliceux.

En zone côtière peu profonde, les phosphates dissous dans les eaux marines sont généralement en équilibre avec les quantités présentes dans le sédiment par des phénomènes d'absorption-désorption (Pomeroy *et al.* 1965; Delmas et Tréguer 1983); de plus leur recyclage rapide permet à ces derniers de se maintenir à des concentrations variant de 0,5 à 0,9 μM-P (Pomeroy 1960). Dans la lagune de Grande-Entrée, les phosphates présentent des concentrations typiques des écosystèmes côtiers de l'Atlantique (Charpy-Roubaud *et al.* 1982; Wafar *et al.* 1983) et constituent en moyenne 41 % du stock total de phosphore dans la colonne d'eau. Les phénomènes de reminéralisation bactérienne et de désorption étant dépendants de la température, il n'est pas étonnant que les concentrations en phosphates aient eu tendance à augmenter avec le réchauffement des eaux malgré la pression consommatrice des organismes autotrophes. La plus grande stabilité des concentrations de phosphates à la station B s'explique aussi par des températures plus faibles couplées à un temps de résidence inférieur des eaux dans ce secteur de la lagune. Les eaux du courant de Gaspé ne semblent pas constituer un facteur d'enrichissement pour les eaux lagunaires. La lagune de Grande-Entrée n'étant jamais épuisée en phosphates, ces derniers ne limitent vraisemblablement pas la production primaire.

Si l'azote et le phosphore sont des éléments essentiels du contrôle de l'activité biologique marine, l'azote présente un cycle moins rapide que celui du phosphore et permet, selon Dugdale et Goering (1967), «une mesure satisfaisante de la productivité». L'épuisement du stock de nitrates pendant la saison estivale n'est pas exceptionnel; dans de nombreux écosystèmes côtiers ces derniers sont consommés en totalité pendant le bloom phytoplanctonique de printemps et ne sont renouvelés qu'à la fin de l'automne (Nixon et Pilson 1983). Les nitrates n'étant pas un produit d'excrétion, leur régénération n'est que bactérienne. En écosystème peu profond, la nitrification est un processus essentiellement intra-sédimentaire et se révèle rarement une source significative de nitrates pour la colonne d'eau. De plus, les apports importants de MOP au sédiment (biodépots issus de l'activité mytilicole, débris de zostères) induisent probablement des conditions anaérobies qui favorisent la dénitrification (consommation de nitrates). En l'absence d'apports telluriques et anthropiques, seuls les échanges avec les eaux du golfe pourraient constituer une source de nitrates pour les eaux de la lagune. Or, la faiblesse des courants de marée limite les entrées d'eaux du golfe à celles du plateau Madelinot. Ces dernières, au regard de leur faible profondeur (20 à 40 m), sont sans doute épuisées en nitrates dès le début de la saison estivale (Legendre 1971; Steven 1974; Coote et Yeats 1979). L'influence du courant de Gaspé ne s'étant pas accompagnée d'un enrichissement en nitrates, les eaux de la lagune ne sauraient être enrichies que par des remontées d'eau profonde du golfe dont les concentrations sont voisines de 20 μM-N (Legendre 1971; Yeats 1990). Cette hypothèse a été suggérée par Auclair (1977) pour interpréter des concentrations de nitrates supérieures à 14 μM-N dans la lagune de Grande-Entrée durant l'été 1975 (pour une température de 20°C). Les eaux profondes du golfe, plus riches en sels nutritifs, sont aussi beaucoup plus froides que les eaux de la lagune (4 à 6°C, Leim *et al.* 1957). Les remontées d'eaux auraient donc dues être accompagnées d'une baisse de plusieurs degrés dans les eaux lagunaires qui était absente des observations d'Auclair. Aucune augmentation dans les concentrations de nitrates n'ayant été observée pendant les périodes estivales de 1987 et 1988, l'hypothèse des remontées d'eaux ne saurait donc être évoquée qu'avec circonspection.

Dans la plupart des écosystèmes côtiers, les concentrations estivales en azote ammoniacal se maintiennent généralement entre 0,5 et 2,5 µM-N (Nixon et Pilson 1983) alors que celles mesurées dans les eaux de la lagune sont restées proches du seuil de détection de la méthode d'analyse. Les eaux du golfe, qu'elles soient superficielles ou profondes, ne possèdent pas des concentrations suffisantes d'azote ammoniacal pour enrichir la lagune (Legendre 1971). L'ammonium trouve principalement son origine dans la régénération par voie excrétionnelle (Henriksen *et al.* 1980; Regnault 1986), et par la reminéralisation de la matière organique particulaire à l'interface eau-sédiment (Zeitzschel 1980). La régénération de l'azote subit probablement la pression des autotrophes au point de ne pouvoir permettre l'établissement de niveaux détectables d'ammonium. Il faut ajouter que les zostères, qui peuvent absorber l'azote et le phosphore inorganiques dissous aussi bien par leur feuilles que par leurs racines (Brix et Lyngby 1985; Short et McRoy 1984), viennent s'ajouter à la pression consommatrice des organismes planctoniques. Dans la lagune de Grande-Entrée, l'azote semble bien être le facteur limitant de la production primaire pélagique, comme dans la plupart des écosystèmes côtiers des zones Atlantiques tempérées (Ryther et Dustan 1971; Charpy-Roubaud *et al.* 1982; Nixon et Pilson 1983; Graneli 1987).

Azote et Phosphore Organiques Dissous (NOD et POD)

La MOD rassemble un grand nombre de composés dont tous sont loins d'être connus et proviennent d'origines très diverses incluant l'excrétion directe par les organismes vivants, la dégradation physico-chimique ou microbienne de la MOP et les apports telluriques (Le Jehan et Tréguer 1984; Jackson et Williams 1985). Les concentrations en NOD dans la lagune présentent des teneurs importantes par rapport à celles rencontrées dans les eaux côtières et océaniques (2 à 7 µM-N; Wafar *et al.*; 1984; Jackson et Williams 1985) et constituent 72 % du stock total d'azote dans la colonne d'eau (gaz exclus). Parallèlement, les teneurs en POD sont supérieures aux moyennes observées en écosystèmes marins ($\leq 0,2$ µM-P; cf. précédents auteurs) et constituent 38 % du stock total de phosphore. En écosystèmes côtiers exempts de pollution, les concentrations de NOD et POD peuvent dépasser respectivement 10 µM-N et 0,2 µM-P lorsque les eaux sont soumises aux apports fluviaux (Le Jehan et Tréguer 1984). Des mesures directes de concentrations en NOD et POD dans les eaux du golfe n'ont pas été trouvées dans la littérature, mais au regard des concentrations du Carbone Organique Dissous (COD) mesurées par Pocklington (1985), il semble peu probable que le golfe soit une source de MOD pour les eaux lagunaires. La MOD est sans doute d'origine endogène et la haute variabilité des rapports NOD/POD (13 à 153) laisse entrevoir des changements importants dans sa composition. Des rapports variant de 15 à plus de 100 peuvent être calculés à partir des résultats de Wafar *et al.* (1983) obtenus dans des eaux côtières d'Europe Occidentale. Le recyclage plus rapide des composés phosphorés nous conduit à penser que les rapports supérieurs à 100 correspondent à des composés de nature détritique. Les détritus de zostères, disséminés après la fonte des glaces, ont tendance à s'accumuler dans les parties les plus profondes de la lagune ou sur le littoral et constituent une source de débris de tailles variables qui se dégradent lentement après avoir subi un lessivage intense de leur composés solubles (Harrisson et Mann 1975). Ces derniers sont dégradés en partie par les bactéries ou rallient la phase particulaire par agrégation (Pellikan 1984). Les herbiers à zostères pourraient donc constituer une source importantes de MOD pour la colonne d'eau et être à l'origine de la MOD détritique suggéré pour la période printanière. Les rapports les plus faibles correspondraient à du matériel fraîchement excrété par les organismes planctoniques.

Azote et Phosphore Organiques Particulaire (NOP et POP)

La Matière Organique Particulaire (MOP) des eaux lagunaires peut être constituée aussi bien de matériel détritique (décomposition d'organismes, biodépots, particules sédimentaires, etc.) que de matériel vivant (phytoplancton, bactéries, microzooplancton, etc.). Les concentrations de NOP qui n'ont jamais dépassé 8 µM-N sont restées plus faibles que les minimums enregistrés dans des eaux susceptibles de supporter des activités myticoles (Charpy-Roubaud *et al.* 1982; Kaspar *et al.* 1985). L'origine et la dynamique des particules dans la lagune sera discutée ultérieurement (Roy *et al.* 1991), mais la distribution du NOP et du POP dans la colonne d'eau nous suggère quelques remarques préliminaires. L'augmentation progressive des concentrations de NOP (28 % du stock d'azote total) est potentiellement reliée à un accroissement de la biomasse algale. L'évolution du POP (21 % du stock de phosphore total) met en évidence des changements structuraux complexes qui se reflètent dans la variation temporelle des rapports N/P. De la même manière que pour la MOD, les rapports N/P supérieurs à 15 semblent indiquer une composante détritique relativement importante au cours de la première moitié de la période d'étude. À partir de la mi-juillet les rapports sont inférieurs à 15, valeur rapportée pour des populations phytoplanctoniques en phase croissante (Parsons *et al.* 1977). À partir du milieu de la période estivale le stock particulaire a plus augmenté près des moulières qu'à la station B, ce qui pourrait suggérer un léger effet positif des moulières sur l'augmentation des concentrations de NOP et POP.

Influence des moulières sur les cycles de l'azote et du phosphore

La culture de moules dans les lagunes, par le biais de l'excrétion fluide, contribue à la régénération de l'azote et du phosphore et constitue une source d'azote et de phosphore dissous pour la colonne d'eau. Les évolutions estivales de l'excrétion des composés azotés et phosphorés par les moules de la lagune ont été mesurées pendant la période d'étude (P. Mayzaud, INRS-Océanologie, Rimouski, communication personnelle). Pour les 36 700 boudins de moules cultivées, les calculs des apports excrétionnels en ammonium et en phosphates à la lagune ont donné respectivement 5 kg-N • j^{-1} et 3,5 kg-P • j^{-1}. Les moulières ont excrété en moyenne 4,5 kg-N • j^{-1} de NOD et 1,1 kg-P • j^{-1} de POD. Sans la pression des autotrophes, et sans les échanges avec le golfe, l'excrétion fluide des moules cultivées n'enrichirait le volume de la lagune que de 3 10^{-3} μmole-N • L^{-1} • j^{-1} d'azote dissous et de 1,5 10^{-3} μmole-P • L^{-1} • j^{-1} de phosphore dissous. Bien qu'elles soient rapidement disponibles pour les consommateurs pélagiques (Kaspar *et al.* 1985), ces quantités semblent insuffisantes pour affecter significativement la production primaire au niveau de toute la lagune.

La présence de nombreux filtreurs est un paramètre important dans la dynamique des composées particulaires. Cloern (1982) a montré, qu'en une seule journée, les populations de bivalves présentes filtraient un volume équivalent à presque 2 fois le Sud de la baie de San Fransisco. Avec un taux moyen de filtration de 1,5 L • h^{-1} (P. Mayzaud, INRS-Océanologie, Rimouski, communication personnelle), les moules d'un an qui représentent plus de 90 % des classes d'âge en 1988 mettent environ un an à filtrer le volume total de la lagune. Bien que ce calcul soit tout a fait théorique, son ordre de grandeur indique que l'impact éventuel des moulières sur les concentrations en azote et phosphore particulaires ne devrait se ressentir que dans leur environnement proche (station A).

Les activités mytilicoles, par leurs biodépots, accroissent intensément les flux de matière organique particulaires vers le sédiment (Dahlback et Gunnarsson 1985) et intensifient les flux d'ammonium et de phosphates à l'interface eau-sédiment. Ces derniers n'ont pas encore été mesurés pour le site étudié mais Kaspar *et al.* (1985) ont évalué la contribution de la régénération benthique à plus de 90 % des apports totaux en ammonium (régénération benthique + excrétion) dans une moulière située dans un écosystème peu profond de Nouvelle Zélande. En revanche, l'intense reminéralisation des biodépots conduit à un déficit en oxygène (milieu réduit) et favorise la dénitrification aussi bien dans le sédiment sous-jacent que sur les boudins (Kaspar *et al.* 1985).

Les moulières et le sédiment sous-jacent constituent donc une source potentielle d'azote ammoniacal et de phosphore dissous, mais aussi un puit de nitrates et de matière particulaire pour leur environnement. Cependant les quantités actuelles de moules cultivées dans la lagune de Grande-Entrée ne semblent pas suffisantes pour induire des changements notables dans la distribution des composés de l'azote et du phosphore dans la lagune.

Du point de vue de la fertilisation, le système lagunaire des Îles-de-la-Madeleine ne saurait être comparé à d'autres écosystèmes des zones tempérées de l'hémisphère Nord supportant des activités myticoles. Dans ces derniers, la fertilisation des eaux est assurée en grande partie par des fleuves riches en nutriments. L'absence quasi totale de NID dans les eaux de la lagune est à mettre en parallèle avec les conditions d'oligotrophie rencontrées dans les eaux des atolls coralliens (Entsch *et al.* 1983) qui sont aussi des écosystèmes se ramenant à l'isolement partiel d'eaux océaniques superficielles sur des fonds peu profonds. Du printemps à l'automne, la productivité des lagunes dépend en grande partie de leur capacité à régénérer les nutriments et particulièrement les sels de l'azote qui limitent la production primaire. La présence d'un important stock de NOD va favoriser les espèces planctoniques capables d'utiliser les composés dissous comme source d'azote. La faible profondeur des fonds confère au sédiment un rôle fondamental dans le recyclage de la MOP. Les flux de sels nutritifs à l'interface eau–sédiment devront être mesurés afin de connaître leur contribution à la productivité de l'écosystème. Les zostères, qui contrôlent de façon étroite les cycles de l'azote et du phosphore de leur environnement immédiat, concurrencent le phytoplancton dans la consommation en nutriments (Kenworthy *et al.* 1982), et sont susceptibles d'affecter la production primaire dans la lagune de Grande-Entrée. Le rôle de ces plantes marines dans la dynamique de l'écosystème devra donc être déterminé. Enfin, les chimistes marins s'intéressent de plus en plus à l'impact des apports d'origine atmosphériques sur le cycle des nutriments (Correll et Ford 1982; Paerl 1985), et au regard des baisses de salinité observées dans les lagunes, les pluies pourraient s'avérer une source potentielle d'apports directs de NID et de phosphates pour cet écosystème démunis d'apports telluriques et anthropiques.

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Environnement physico-chimique et trophique d'un site mytilicole aux Îles-de-la-Madeleine (Québec) : II — Matière particulaire, composition biochimique et productivité primaire[1]

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ROY, S., P. MAYZAUD ET P. SOUCHU. 1991. Environnement physico-chimique et trophique d'un site mytilicole aux Îles-de-la-Madeleine (Québec) : II — Matière particulaire, composition biochimique et productivité primaire, p. 219–230. *Dans* J.-C. Therriault [éd.] Le golfe du Saint-Laurent : petit océan ou grand estuaire? Publ. spéc. can. sci. halieut. aquat. 113.

Cette étude décrit l'environnement particulaire (taille et type de particules en suspension, concentration et composition du matériel particulaire et activité photosynthétique des algues) de la lagune de Grande-Entrée (Îles-de-la-Madeleine), tel qu'observé pendant la période de juin à octobre 1987. Trois stations sont comparées : la station A, localisée au coeur d'une moulière, la station C, près du chenal central de navigation, à environ 1.5 km de la première station, et la station B, entre les deux autres. Les descripteurs de biomasse (carbone particulaire, chlorophylle, concentration particulaire totale) indiquent généralement des valeurs légèrement plus fortes au site de moulière. La composition floristique des trois stations montre une dominance des algues de taille inférieure à 10 μm (nanoplancton) et une augmentation de la diversité spécifique au cours de l'été. La composition biochimique du matériel particulaire reflète cette dominance du nanoplancton (flagellés hétérotrophes, cryptophycés, etc.), avec de fortes valeurs de protéines et de sucres totaux ne correspondant pas toujours aux valeurs de chlorophylle. Il n'y a pas d'évidence de déficience nutritive chez le phytoplancton, malgré l'absence virtuelle d'azote minéral dissous tout au long de l'été. Ces éléments suggèrent l'existence de «cycles microbiens». La comparaison générale des trois stations ne permet pas de conclure à un effet marqué de la moulière sur son environnement. Les faibles différences observées sont possiblement reliées à l'hydrographie du site. Les valeurs de chlorophylle et d'activité photosynthétique recueillies en 1987 sont comparables à celles récoltées en 1975 avant l'établissement de la mytiliculture commerciale (Auclair 1977). L'environnement particulaire de la lagune ressemble également à celui décrit pour le golfe du Saint-Laurent en été. En comparaison avec d'autres sites de mytiliculture dans le monde, la différence principale, pour l'environnement particulaire, semble résider dans le type de phytoplancton. Les effets de la composition et de la taille du phytoplancton sur la culture en suspension des moules restent à préciser.

This study, held from June to October 1987, describes the particulate environment of the Grande-Entrée lagoon (Magdalen Islands), in terms of size, type, quantity and quality of particles and photosynthetic activity. Three stations are compared: station A, located at a mussel culture site, station C, near the central navigation channel of the lagoon, at about 1.5 km from the first station, and station B, between the other two. Biomass evaluation (using particulate carbon, chlorophyll and total particulate concentration) generally shows slightly higher values at the mussel site. Phytoplankton identification indicates the predominance of algae of a size less than 10 μm (nanoplancton) at the three stations, and an increase in specific diversity during summer. Biochemical composition reflects this dominance of nanoplankton (heterotrophic nanoflagellates, cryptophytes, etc.), with elevated protein and total carbohydrate values, often with no relationship with chlorophyll concentration. There is no evidence of nutrient-deficiency in phytoplankton, even though inorganic nitrogen is virtually absent during the summer period. These elements suggest the presence of "microbial loops". Overall comparison among the three stations does not show a clear effect on the particulate environment caused by the presence of mussels. The small differences observed are probably related to hydrographic conditions. Our 1987 observations are comparable with chlorophyll and photosynthetic activity data collected in 1975, before the establishment of mussel farms (Auclair 1977). The particulate environment of this lagoon resembles that of the Gulf of St. Lawrence in summer. When compared with other mussel culture sites in the world, the main difference, in terms of the particulate environment, seems to reside in the type of phytoplankton present. Potential effects of taxonomical and size differences on the suspended culture of mussels have yet to be determined.

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[1] Cet article fait partie des Compte rendus d'un atelier/symposium tenu à l'Institut Maurice-Lamontagne, Mont-Joli (Québec) du 14 au 17 mars 1989.

Introduction

Le milieu lagunaire des Îles-de-la-Madeleine est un site de mytiliculture commercial depuis le début des années 1980. Les moulières, constituées d'environ 40 000 lignes verticales flottantes d'une longueur de 2 m, couvrent 7 % de la superficie de la lagune de Grande-Entrée. Chaque ligne peut compter jusqu'à 450 moules. Dans le cadre d'une étude de 3 ans (1987 à 1989) visant à définir le potentiel de production mytilicole de cet environnement et l'influence de la mytiliculture sur le milieu, nous présentons ici une série de résultats préliminaires récoltés à l'été 1987, concernant les particularités de l'environnement trophique des moules. Les données physiques et chimiques seront présentées ailleurs.

Dans plusieurs régions où les moules sont cultivées en suspension dans l'eau, un lien a été démontré entre l'activité nutritionnelle de ces organismes et la dynamique du phytoplancton (Tenore *et al.* 1982; Rosenberg et Loo 1983; Kaspar *et al.* 1985). Cette observation s'applique aussi aux moules non cultivées (Fréchette et Bourget 1985). Ces bivalves filtreurs ne sont pas indifférents au type de nourriture disponible, soit en termes de la qualité de cette nourriture (Cucci *et al.* 1985) ou de sa taille (Stuart et Klumpp 1984). Il est donc important de décrire précisément l'environnement trophique des moules en termes quantitatifs et qualitatifs et d'évaluer s'il existe un effet visible de la moulière sur son environnement.

Ce travail représente une première description des particules et du plancton depuis l'établissement de la mytiliculture commerciale aux Îles-de-la-Madeleine. L'étude d'Auclair (1977), effectuée avant l'implantation de cette industrie, fournit une base comparative pour certains critères communs aux deux études. Le niveau trophique primaire des Îles-de-la-Madeleine est également comparé avec celui d'autres sites de mytiliculture dans le monde, en termes de concentration de chlorophylle *a*, de productivité primaire et de composition floristique.

Matériel et méthodes

L'échantillonnage a été réalisé dans la lagune de Grande-Entrée, située au nord-est de l'archipel des Îles-de-la-Madeleine (fig. 1), pendant les mois de juin à octobre 1987. Les échantillons étaient prélevés à 1 et 4 m, à une fréquence d'une (carbone, azote, production primaire) à deux fois (tous les autres paramètres) par semaine. Trois stations étaient alors visitées entre 10h et 15h de la journée : la station A, représentant un site de moulière, la station C, en bordure du chenal de navigation, à 1.5 km du site de moulière, et la station B, entre les deux autres (fig. 1).

Les différentes mesures et analyses effectuées sont les suivantes : taille et concentration des particules en suspension (au moyen d'un compteur Coulter TA-II), contenu en carbone et azote organiques (détecteur CHN Perkin-Elmer 240, échantillons de 0.5 L filtrés sur filtres Whatman GF/C préconditionnés à 450°C pendant 1 h), contenu en chlorophylle *a* (fluorimètre Turner III, méthode de Yentsch et Menzel 1963). La composition biochimique du matériel particulaire a été évaluée à partir de la composition en protéines (Lowry *et al.* 1951), sucres (totaux : Dubois *et al.* 1956, solubles : Mayzaud *et al.* 1985) et lipides (extraction selon Bligh et Dyer 1959, analyse selon Barnes et Blackstock 1973). Les échantillons pour ces analyses provenaient de filtrations d'eau

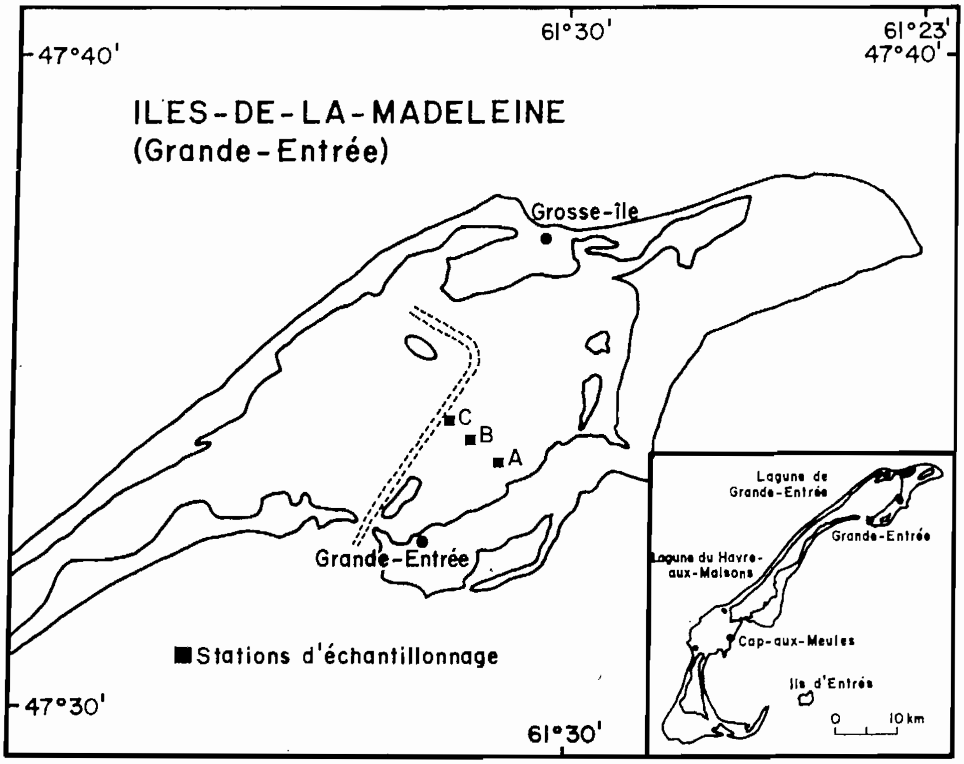

FIG 1. Carte indiquant la position des stations d'échantillonnage dans la lagune de Grande-Entrée, Îles-de-la-Madeleine.

récoltée à chaque période d'échantillonnage (volume filtré = 1 L, filtres Whatman GF/C). La composition floristique du phytoplancton a été étudiée par microscopie (Utermöhl 1931) sur des échantillons préservés au Lugol. L'activité photosynthétique des algues a été estimée au moyen de la méthode du carbone radioactif (Steemann Nielsen 1952), suivant le protocole de Strickland et Parsons (1972). Après inoculation de 5 μCi (185 kBq) d'une solution de bicarbonate de sodium – ^{14}C, les bouteilles de 300 mL d'eau de mer (deux bouteilles claires, une bouteille opaque) étaient incubées *in situ*, au site de provenance de l'eau échantillonnée, pendant 4 h. Leur contenu était alors filtré sur filtres Millipore AAWP, 0,8 μm, auxquels on ajoutait 1 mL d'une solution HCl, 0,1 M. Après 2 h d'évaporation du carbone radioactif non incorporé par les cellules, 12 mL de liquide à scintillation (Aquasol, NEN-DuPont) était ajouté. Le comptage des échantillons était effectué au moyen d'un compteur à scintillation liquide Beckman LS 5801. La plupart des analyses étaient réalisées en triplicata.

Résultats

Environnement physique

La lagune de Grande-Entrée est reliée au golfe du Saint-Laurent par une ouverture au sud de 2 km de large. La surface moyenne de cette lagune est d'environ 50 km^2 et sa profondeur maximale est de 6 m. Un chenal de navigation, d'une profondeur moyenne de 6 m, traverse la lagune (fig. 1); les échanges d'eau se font principalement le long de ce chenal (V.G. Koutitonsky, INRS-Océanologie, Rimouski, communication personnelle). L'influence de la marée est faible dans cet environnement (amplitude moyenne = 0.58 m: Godin 1979; courants de marée = 1 à 5 cm • s^{-1}: V.G. Koutitonsky, INRS-Océanologie, Rimouski, communication personnelle); ceci est causé par la présence d'un point amphidromique de la marée M2 à proximité, dans le golfe du Saint-Laurent. Par contre, cette région du golfe est reconnue pour la force et la fréquence de ses vents, dont les vitesses peuvent atteindre 15 m • s^{-1} (Anonyme 1987) et entraîner dans la lagune des courants d'une vitesse de 15 à 20 cm • s^{-1} (V.G. Koutitonsky, INRS-Océanologie, Rimouski, communication personnelle). A cause de la faible profondeur de la lagune, les vents entraînent une circulation verticale intense, qui se reflète par une grande homogénéité sur cet axe. Ainsi, la salinité et la température montrent des valeurs semblables aux 2 profondeurs échantillonnées (1 et 4 m, cf. Souchu *et al.* 1991). Pendant la période estivale 1987, la salinité variait entre 26 et 32 ‰ et la température entre 13 et 20°C, les valeurs sont maintenant au-dessus de 18° du 9 juillet au 13 août (données non publiées).

Sels nutritifs

Seuls les phosphates et les nitrates ont été mesurés pendant l'été 1987. Les concentrations de phosphates montrent des valeurs moyennes tout au cours de l'été 1987 (0,6 ± 0,1 μm). Les concentrations de nitrates sont, quant à elles, pratiquement au seuil de détection de la méthode d'analyse, ne dépassant pas 0,1 μm (Souchu *et al.* 1991). Les concentrations à 1m et 4m sont semblables pour l'ensemble des sels nutritifs. Un profil chimique plus détaillé a été obtenu à l'été 1988 pour la même lagune (Souchu *et al.* 1991). Les tendances observées sont les mêmes : valeurs identiques aux 2 profondeurs, valeurs extrêmement faibles de nitrates, valeurs de phosphates et silicates respectivement moyennes et faibles. L'azote ammoniacal, mesuré pendant l'été 1988, présente des valeurs extrêmement faibles (< 0,1 μm).

TABLEAU 1. Effets de la profondeur et de la station d'échantillonnage sur les variables biologiques étudiées dans la lagune de Grande-Entrée. Analyse de variance unidimensionnelle à deux facteurs (stations et profondeur) effectuée au moyen du programme 'ANOVA' (logiciel SPSS). a) Tableau d'analyse de variance pour la concentration des particules (mg • L^{-1}), b) Résumé des autres analyses de variance pour le reste des variables biologiques.

a)

Source de variation	ddl	SC	F	P
Profondeur	1	0.053	0.446	0.51
Station	2	1.960	8.223	0.01
Interaction	2	0.075	0.315	0.73
Residuelle	84	10.010		

b)

Variable	Profondeur		Station	
	F	P	F	P
Chlorophylle	0.380	0.54	4.775	0.01
Carbon	0.032	0.86	3.490	0.04
Azote	0.107	0.74	3.934	0.02
Protéines	0.223	0.64	8.581	0.01
Sucres totaux	0.656	0.42	7.053	0.01
Lipides	1.320	0.25	2.587	0.08
Photosynthèse	5.288	0.03	0.324	0.73

Matériel particulaire, carbone, azote et chlorophylle

L'homogénéité verticale de la lagune se traduit par une grande similitude des valeurs des différentes variables biologiques recueillies à 1 m et à 4 m, tel qu'illustré à la figure 2 pour la concentration des particules. Une analyse de variance à 2 critères de classification ('ANOVA', logiciel SPSS), appliquée à cette variable pour la totalité des données de l'été 1987 (tableau 1a), montre que la profondeur n'a pas d'effet significatif ici. La même conclusion s'applique pour les données de carbone, d'azote et de chlorophylle (tableau 1b). Par contre, le choix de la station affecte significativement ces mêmes variables (tableau 1b). Les stations A et C sont significativement différentes entre elles (test de Kolmogorov-Smirnov, $P < 0,05$) pour les quatre variables prémentionnées. Les valeurs moyennes estivales sont légèrement plus fortes à la station A.

Le profil temporel de la concentration des particules (fig. 2) montre une légère augmentation de la fin juin à la mi-août, avec des maxima les 7 juillet et 4 août 1987. La concentration en chlorophylle *a* (fig. 3) présente un maximum estival en date du 4 août au site de la moulière,

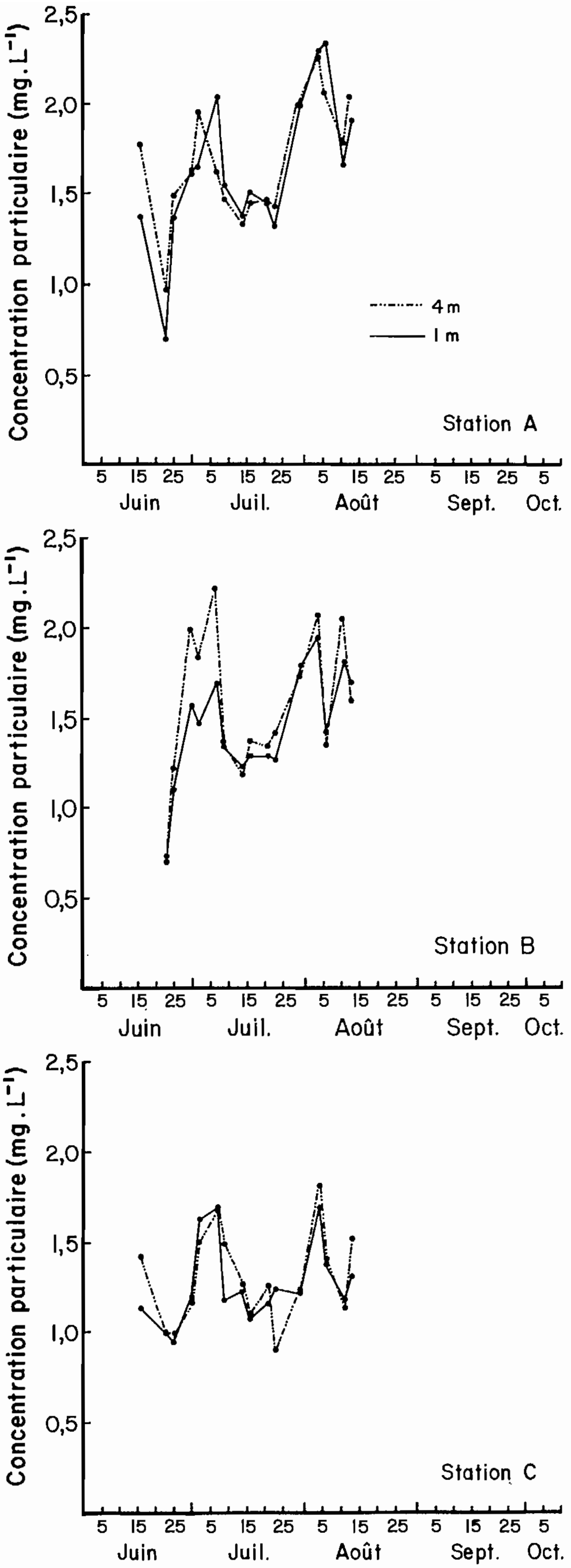

FIG. 2. Évolution saisonnière de la concentration particulaire (tailles de 1 à 100 μm) en mg • L^{-1}, représentée pour les trois stations d'échantillonnage, à 1 m et 4 m.

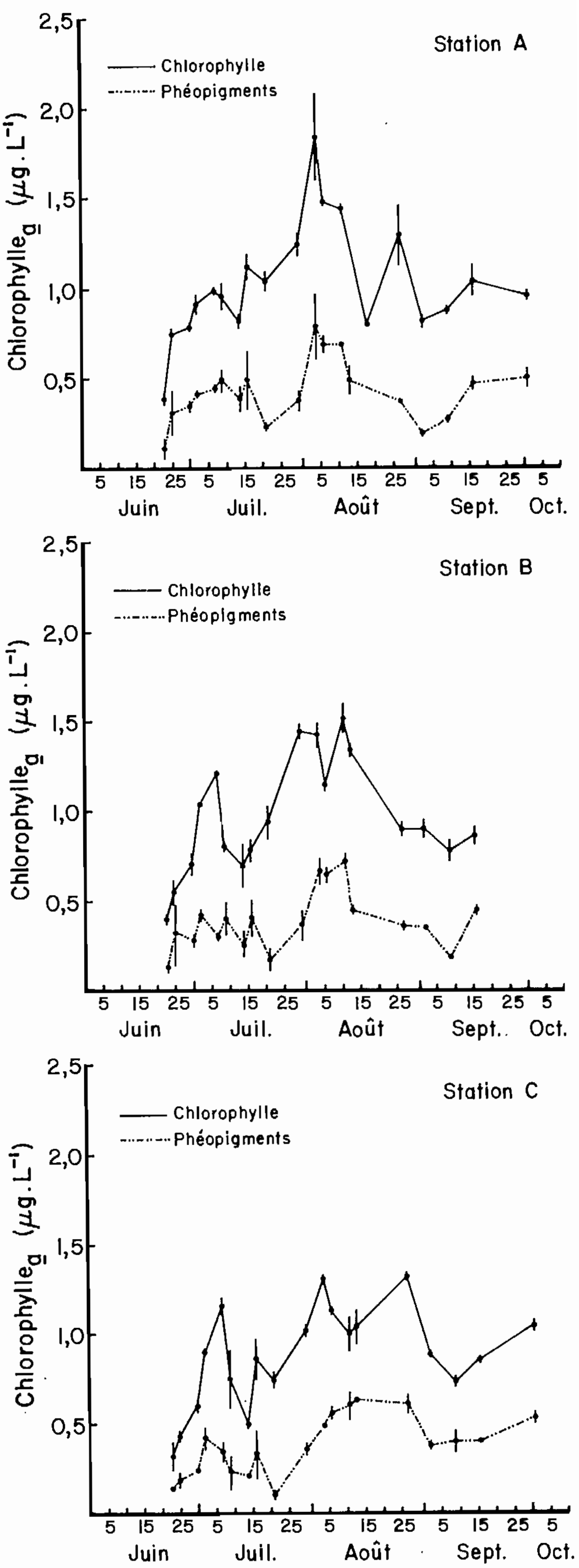

FIG. 3. Profil saisonnier de la chlorophylle *a* et des phéopigments (en équivalents de chlorophylle *a*), exprimé en μg • L^{-1}, pour les trois stations. Les traits verticaux sur cette figure et les suivantes indiquent l'écart-type des valeurs.

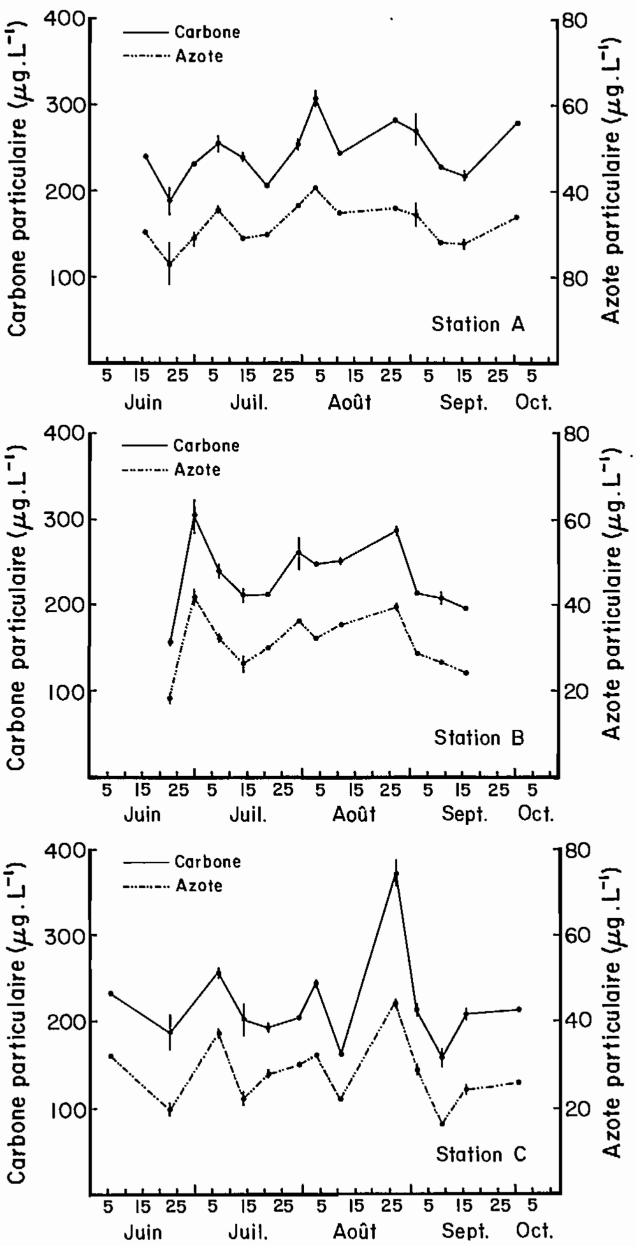

FIG. 4. Profil saisonnier du carbone et de l'azote particulaire ($\mu g \cdot L^{-1}$) pour les trois stations.

alors qu'aux autres stations, ce maximum est moins prononcé et il est accompagné de maxima secondaires les 7 juillet et 27 août. La concentration en phéopigments représente 30 à 50% de la concentration en chlorophylle *a* et son évolution temporelle suit celle de la chlorophylle (fig. 3). Dans le cas du carbone et de l'azote particulaires, les variations temporelles les plus prononcées se présentent à la station C, près du chenal (fig. 4). Le maximum estival y est observé le 4 août 1987. Le rapport atomique C/N varie très peu au cours de l'été. La station A présente une moyenne de 7,7 ± 0,6, la station B, 8,9 ± 0,5 et la station C, 8,0 ± 1,0.

Composition biochimique

Les protéines, lipides et sucres totaux (fig. 5) présentent généralement des valeurs typiques pour le phytoplancton marin (Mayzaud et Martin 1975), avec de fortes proportions de protéines et de sucres (rapport moyen de protéines : sucres totaux : lipides, calculé pour la station A = 13,0:10,6:1).

Comme précédemment, les deux profondeurs étudiées ne montrent pas de différence significative entre elles pour les variables décrivant la composition biochimique (tableau 1b). Les concentrations de sucres totaux et de protéines diffèrent cependant selon la station, les concentrations les plus fortes se retrouvant au site de moulière (tableau 1b et test de Kolmogorov–Smirnov, $P < 0{,}05$).

L'évolution temporelle des protéines montre des valeurs relativement plus fortes en été qu'en début d'automne aux trois stations. Les fluctuations sont plus prononcées à mesure qu'on se rapproche du chenal. Les variations temporelles des lipides présentent, aux trois stations, des valeurs fortes en juin, diminuant en juillet et augmentant à nouveau en août jusqu'à un maximum le 27 août. Ces variations, plus particulièrement les fortes valeurs de juin, ne correspondent pas aux variations de protéines ou de chlorophylle *a*. Quant aux sucres totaux, leur évolution temporelle ressemble à celle des protéines aux stations B et C mais diverge à la station A à partir du début d'août (augmentation de sucres totaux, diminution de protéines).

Le rapport sucres solubles/protéines fluctue entre 0,1 et 0,3 aux stations A et B et entre 0,1 et 0,6 à la station C, les valeurs maximales étant atteintes à cette dernière station les 27 août et 1er octobre 1987 (respectivement 0,54 et 0,50 $\mu g \cdot L^{-1}$ sucres solubles/$\mu g \cdot L^{-1}$ protéines). Les sucres solubles représentent environ 20 à 30 % des sucres totaux en général.

Spectres de taille et composition floristique

Les spectres de taille des particules (fig. 6) montrent la dominance du nanoplancton (2–20 µm : Sieburth *et al.* 1978). La taille des particules se situe principalement entre

TABLEAU 2. Composition floristique du phytoplancton de la lagune de Grande-Entrée. Echantillons provenant de la profondeur de 1 m. Les densités cellulaires sont exprimées en 10^3 cellules par litre. Indice de diversité de Shannon (Shannon and Weaver 1963).

Station	A	C	A	C
Taxon	21 juil.	21 juil.	13 août	13 août
Bacillariophycées				
Centrales	0	0	78.2	82.7
Pennales	93.7	5.4	606.7	108.9
Dinophycées	13.4	2.7	32.4	8.1
Prymnesiophycées	42.8	0	29.7	4.0
Cryptophycées	278.5	40.2	148.3	22.2
Prasinophycées	80.3	29.5	0	2.0
Chrysophycées	0	0	2.7	2.0
Chlorophycées	26.8	0	10.8	4.0
Cyanophycées	2.7	0	431.4	135.1
Flagellés non identifiés	878.4	123.3	628.3	129.0
Total	1416.6	201.1	1968.5	502.0
Indice de diversité	1.73	1.53	2.24	2.39

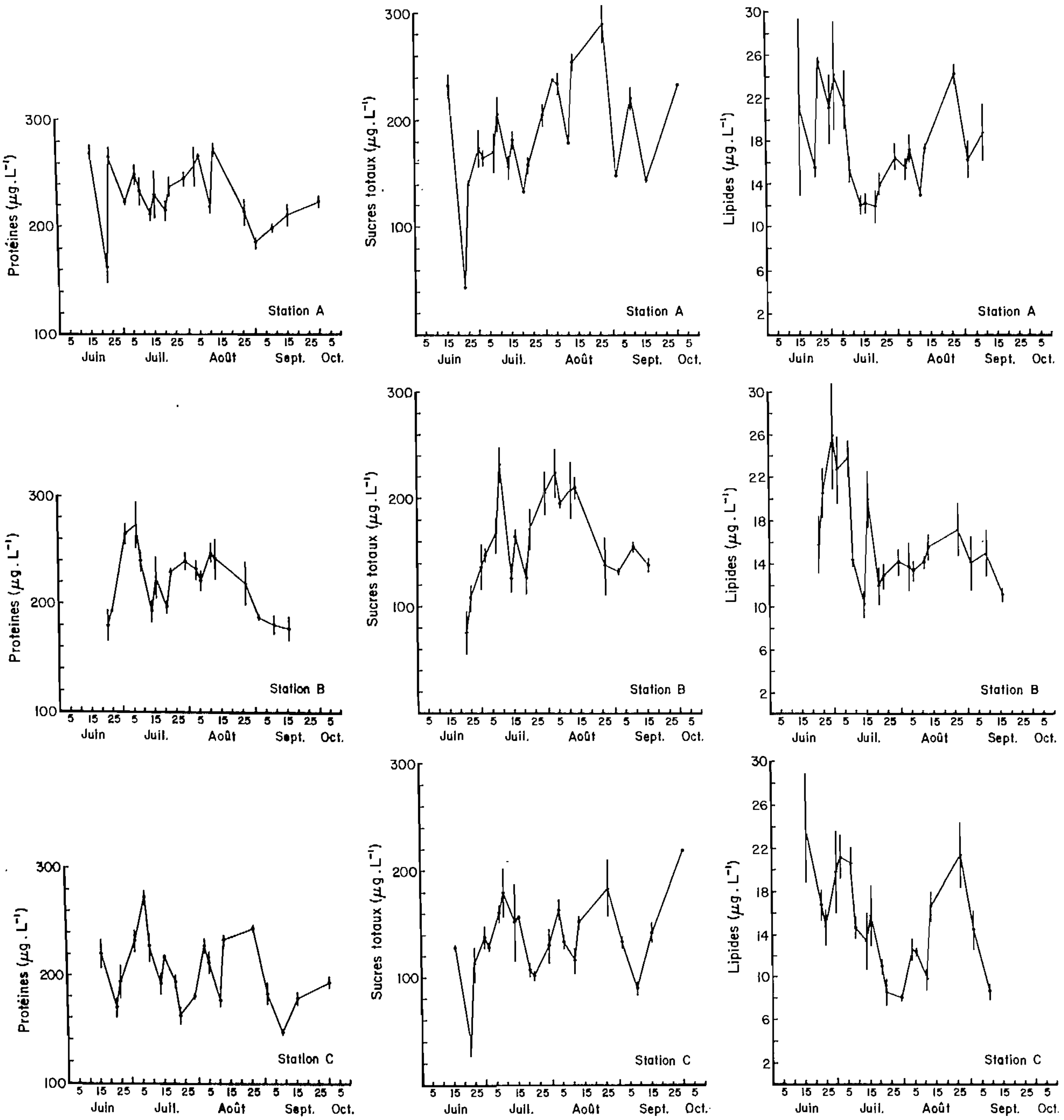

FIG. 5. Évolution saisonnière des protéines, sucres totaux et lipides (µg • L⁻¹) aux trois stations.

2 et 20 µm, avec un maximum généralement à 4–5 µm. La taille du pic principal augmente légèrement à la station A au cours de l'été. Une deuxième population, d'environ 30 µm, apparaît en début juillet, puis à 50 µm au début d'août.

La composition floristique révèle une nette prédominance des microflagellés, composés de petits flagellés (5–10 µm), cryptophycées, prasinophycées, prymnésiophycées, chrysophycées, chlorophycées et cyanophycées dont la composition détaillée n'a pas été déterminée. Pour les deux dates où une analyse taxonomique plus complète a été faite (tableau 2), la station A possède une flore plus abondante pour pratiquement tous les groupes taxonomiques considérés. Parmi les diatomées, on remarque assez souvent la présence de pennales vides ou brisées (espèces benthiques généralement) surtout à la station C; les pennales vivantes sont représentées particulièrement par trois espèces de *Nitzschia* (*N. closterium, N. longissima* et une espèce non identifiée, d'une longueur de 14 µm). Chez les diatomées centrales, les espèces dominantes sont *Skeletonema costatum* et plusieurs espèces de *Chaetoceros*, généralement de petite taille. Les dinoflagellés sont représentés par *Katodinium rotundatum* et une espèce de *Gymnodinium*. La proportion des diatomées et des cyanophycées augmente en août (tableau 2) au détriment des micro-flagellés. La diversité spécifique, mesurée au moyen de l'indice de Shannon (Shannon et Weaver 1963), montre peu de différences entre les stations A et C, mais une augmentation de la diversité entre les mois de juillet et août 1987.

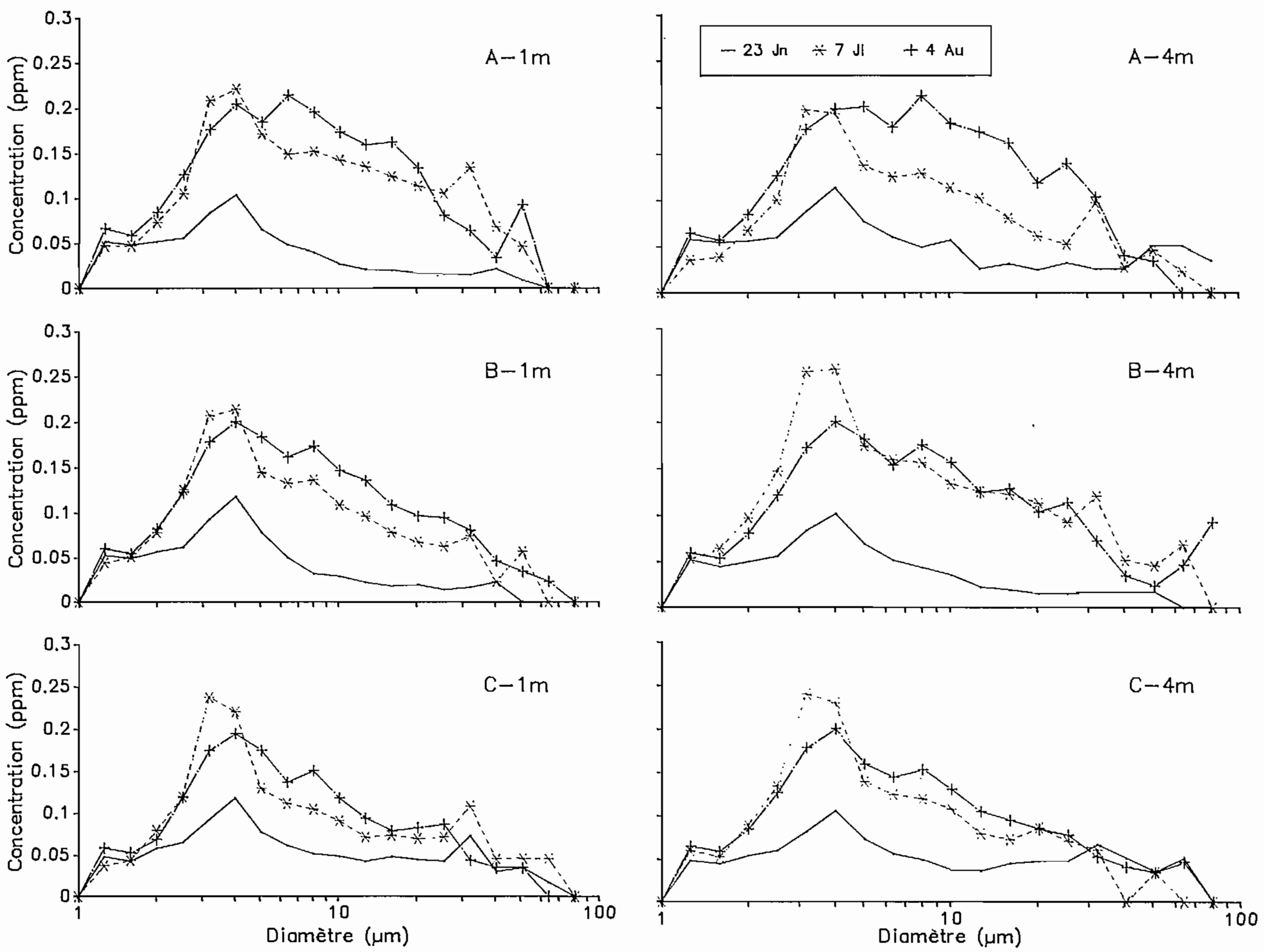

FIG. 6. Spectres de taille, obtenus au compteur Coulter, pour les dates du 23 juin, 7 juillet et 4 août 1987, aux deux profondeurs (1 m et 4 m) et aux trois stations.

Production primaire

Dans le cas de l'activité photosynthétique des algues, la profondeur à laquelle sont faites les incubations affecte significativement les résultats (tableau 1b). Par contre, le choix de la station n'entraîne aucune différence significative. Aux trois stations, le taux d'assimilation de carbone montre deux groupes de valeurs : un premier groupe se situant à environ 6–15 mg C • m^{-3} • h^{-1} de la mi-juin à la mi-août, et un deuxième groupe montrant des valeurs beaucoup plus fortes (12 à 34 mg C • m^{-3} • h^{-1}) de la mi-août au début d'octobre 1987 (fig. 7). L'augmentation observée en septembre 1987 ne se reflète pas en termes de chlorophylle ou de carbone (fig. 3 et 4), ce qui entraîne des valeurs de taux spécifique de photosynthèse (assimilation de carbone/chlorophylle *a*) anormalement élevées (>20 mg C • mg Chl a^{-1} • h^{-1}).

Discussion

Phytoplancton : composition taxonomique, biochimique et condition physiologique.

Les cellules de petite taille dominent dans la zone échantillonnée de la lagune de Grande-Entrée pendant l'été 1987 : petits flagellés, cryptophycées et autres groupes appartenant au nanoplancton (tableau 1) ainsi que les petites diatomées. Les tailles dominantes, mesurées au compteur Coulter (diamètre sphérique), sont de 4 à 6 μm (fig. 6). De petits ciliés et tintinnides sont parfois observés. La présence de ces algues minuscules, ainsi que l'absence virtuelle de nutriments minéraux azotés, suggèrent l'existence de «cycles microbiens» (Azam *et al.* 1983) qui prédominent souvent en eaux stratifiées (Cushing 1989). Dans ces réseaux trophiques microbiens, les microflagellés hétérotrophes consomment les bactéries et petits eucaryotes et sont exploités par les ciliés (microzooplancton) avant d'atteindre les chaînes trophiques traditionnelles (zooplancton-poisson). L'augmentation du nombre de transferts trophiques peut constituer une perte d'énergie pour les consommateurs supérieurs (Azam *et al.* 1983). Les eaux de la lagune, bien que fortement mélangées verticalement, s'apparentent plutôt à la zone stratifiée des eaux côtières dû à la faible profondeur. D'ailleurs, on retrouve également, en été, dans les eaux de surface du golfe du Saint-Laurent, une dominance de petits flagellés survivant grâce à la régénération des sels nutritifs (Steven 1974).

Les valeurs de chlorophylle et d'activité photosynthétique de l'été 1987 sont du même ordre de grandeur que celles mesurées à l'été 1975 par Auclair (1977 et communication personnelle) dans la même lagune, à une station

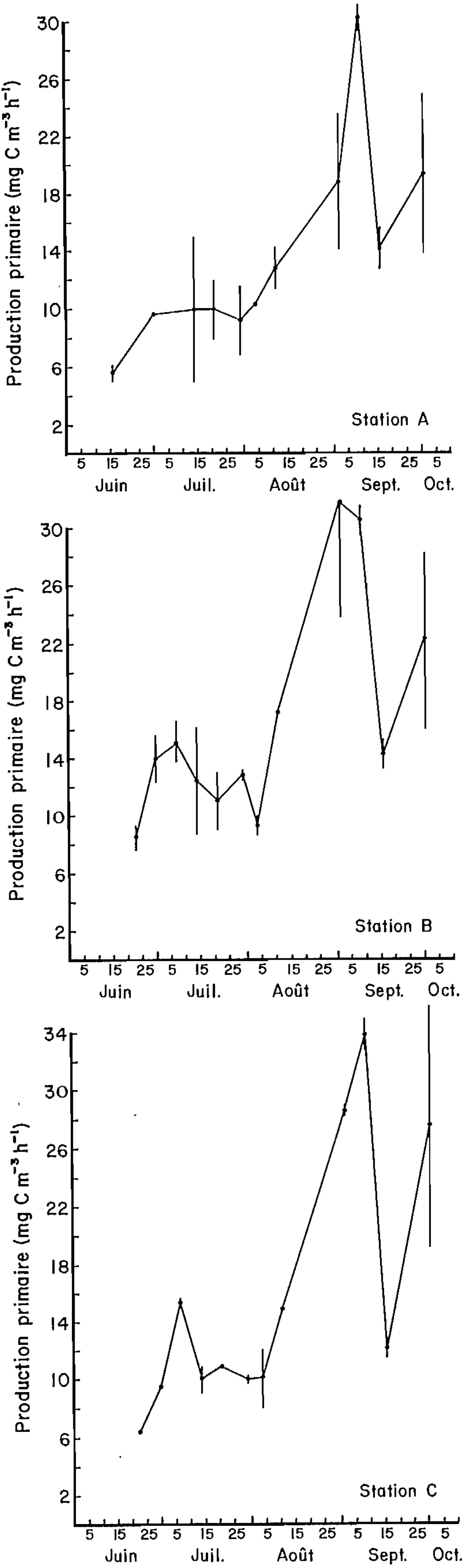

FIG. 7. Profil saisonnier de l'activité photosynthétique algale, mesurée par assimilation de carbone radioactif (mg C • m^{-3} • h^{-1}) à 1 m, aux trois stations.

située à proximité du site de moulière. Ceci suggère que l'établissement de la mytiliculture a eu peu d'effets sur ces variables. Les valeurs très fortes d'activité photosynthétique du début de l'automne semblent anormalement élevées : peut-être sont-elles dues à l'abondance d'algues de petite taille. Les données de taxonomie ne sont pas disponibles pour ces dates, cependant une augmentation du rapport sucres solubles/protéines à cette période de l'année (maximum le 1er octobre) suggère une dominance d'algues nanoplanctoniques. Le taux spécifique de photosynthèse est généralement plus élevé chez le nanoplancton, comparativement à celui des algues de plus grande taille (Malone et Chervin 1979). De fortes valeurs de production ont déjà été observées en début d'automne dans une zone voisine, située au sud du golfe du Saint-Laurent (Hargrave *et al.* 1985). Par ailleurs, la différence de porosité entre les filtres utilisés pour la mesure de la chlorophylle (porosité = 1.2 μm) et ceux utilisés pour la mesure de l'activité photosynthétique (porosité - 0.8 μm) pourrait aussi influencer les résultats en captant une fraction différente de la population algale, surtout si elle est majoritairement de petite taille.

Le rapport protéines/chlorophylle, reflet du contenu protéique des cellules algales, présente des valeurs moyennes élevées (station A = 234,9 ± 71,6, station B = 242,3 ± 75,1, station C = 255,2 ± 100,2), plus caractéristiques des cryptophycées et des dinoflagellés que des diatomées (Moal *et al.* 1987), et correspondant à la dominance des microflagellés dans l'environnement étudié. Le manque de similitude entre les profils estivaux de protéines et de chlorophylle à la station A, ainsi que la présence, à cette station, d'un maximum de concentration des particules en début juillet qui se reflète en carbone mais très peu en chlorophylle, suggèrent la présence de particules faiblement pigmentées, possiblement des flagellés hétérotrophes ou des détritus organiques en suspension. Le fort mélange vertical et des rapports C/Chl élevés (valeurs de 250 à 500 en début d'été) indiquent l'importance, dans ce milieu, des détritus, incluant les bio-dépôts résultant de la présence de la moulière. Il existe une plus grande cohérence entre les profils de particules, de carbone, de chlorophylle et de protéines aux deux autres sites étudiés, soulignant la particularité du site de moulière.

Une augmentation de la concentration en sucres totaux et en lipides parallèlement à la diminution de la concentration en protéines au mois d'août aux stations A et B suggère un changement de composition spécifique ou un changement de condition physiologique : en effet, un stress physiologique relié à de fortes intensités lumineuses ou à une carence en minéraux azotés entraîne généralement une modification dans la synthèse des macromolécules, avec une synthèse beaucoup plus prononcée de produits de réserve (sucres et lipides) au détriment des protéines (Morris 1981). Les sucres *solubles* étant plus représentatifs de ces produits de réserve que les sucres totaux, le rapport sucres solubles/protéines a été observé dans ce contexte (cf. résultats). Ce rapport n'indique pas de valeurs particulièrement élevées, surtout aux stations A et B, ce qui suggère que les changements observés dans la dynamique des sucres et des protéines en août sont plutôt dûs à des changements de composition spécifique, ce que confirment l'indice de diversité et les observations taxonomiques (tableau 2). Les fortes concentrations en lipides au mois de juin 1987 pourraient par contre être l'indication d'une période de post-floraison printanière (Parrish 1987).

Les très faibles concentrations de nutriments minéraux azotés dans cet environnement pourraient être à l'origine d'une limitation de la croissance des algues par déficience azotée ou d'une utilisation des formes organiques de l'azote ou d'ion ammonium provenant principalement de l'excrétion fluide et de la reminéralisation bactérienne. La première hypothèse est peu plausible : d'une part, la productivité des eaux de la lagune présente des valeurs moyennes normales pour une zone côtière (Parsons *et al.* 1977) et, d'autre part, une déficience *prononcée* en azote se traduirait, tel que précédemment indiqué, par une synthèse de produits de réserve (sucres et/ou lipides) plutôt que de protéines, ce qui n'est pas généralement observé (cf. les rapports sucres solubles : protéines et protéines : sucres totaux : lipides). Les valeurs relativement faibles du rapport C/N tout au cours de l'été ne supportent également pas l'hypothèse d'algues en état de déficience azotée quoique ce rapport ne soit pas toujours un très bon indice de la condition physiologique du phytoplancton (Sakshaug et Holm-Hansen 1977). L'augmentation de la diversité spécifique entre juillet et août ne supporte pas non plus cette hypothèse. Il semble donc que le phytoplancton de la lagune de Grande-Entrée utilise les formes organiques dissoutes de l'azote ou l'azote régénéré au fur et à mesure qu'il est produit.

Distribution spatiale

La distribution verticale des variables biologiques montre une grande homogénéité entre les profondeurs de 1 m et 4 m, homogénéité que partagent aussi les variables physiques et chimiques. Ceci résulte du fort mélange vertical occasionné par le vent et de la faible profondeur de la lagune. Ces résultats indiquent qu'en première approche, une seule profondeur pourrait suffire à décrire le milieu particulaire de cet environnement.

La distribution horizontale des variables étudiées indique que le site de moulières possède des concentrations plus élevées de matière particulaire que la région située près du chenal de navigation. Cependant, l'activité photosynthétique n'est pas significativement différente entre ces deux régions, indiquant que les différences inter-sites ne sont pas causées par des disparités au niveau de la production primaire. Un autre facteur biologique pouvant entraîner la différenciation des stations est la présence des moulières à la station A. Une déplétion de matière particulaire au site de moulière pourrait résulter de la nutrition des moules. Pourtant, un calcul approximatif de l'influence théorique des moules suggère qu'elles affectent peu leur milieu: en première approche, les besoins des moules se chiffrent à $2{,}7 \times 10^7$ μg Chl $a \cdot h^{-1}$ (40 000 lignes flottantes, 450 moules/ligne, taux de filtration des moules = $1{,}5\ L \cdot h^{-1} \cdot moule^{-1}$ et concentration moyenne de chlorophylle $a = 1\ \mu g \cdot L^{-1}$) et la disponibilité de la nourriture est approximativement de $2{,}6 \times 10^9$ μg Chl $a \cdot h^{-1}$ (taux photosynthétique = $10\ \mu g\ C \cdot L^{-1} \cdot h^{-1}$, C/Chl $a = 54$, volume de la zone des moulières = 14×10^9 L). Les besoins actuels des moules semblent donc représenter environ 1 % de la nourriture disponible. D'ailleurs, les observations de l'été 1987 confirment l'absence d'une diminution de la concentration des particules à proximité de la moulière (distance entre les stations = 0,75 km). Au contraire, c'est à ce site que la teneur en matériel particulaire est la plus élevée, suggérant la présence d'autres mécanismes contrôlant la distribution horizontale des particules et du phytoplancton.

Les facteurs hydrodynamiques n'ont pas été considérés en détail dans ce texte. Un modèle hydrodynamique en préparation (V.G. Koutitonsky *et al.*, INRS-Océanologie, Rimouski) indique que les vitesses de courant sont nettement plus faibles près de la moulière et qu'elles augmentent à proximité du chenal. Une température estivale moyenne légèrement supérieure à ce site (Souchu *et al.* 1991) suggère un temps de résidence de l'eau un peu plus long à cet endroit, ce qui pourrait expliquer une accumulation relative de matière dans cette zone. D'autre part, une circulation de Langmuir a été observée dans cette lagune (D. Booth, Institut Maurice-Lamontagne, Mont-Joli, communication personnelle); ces cellules de convection favoriseraient le mélange vertical et la resuspension de matériel organique s'accumulant sous les moulières et pourraient contribuer à l'explication des différences inter-sites.

Comparaison avec d'autres environnements

L'environnement particulaire de la lagune de Grande-Entrée est généralement comparable à celui du golfe du Saint-Laurent. Les valeurs de chlorophylle et de production primaire sont du même ordre de grandeur (tableau 3) que celles estimées pour différentes régions du golfe par Legendre (1971), Steven (1974), Sévigny *et al.* (1979), Citarella (1980), Hargrave *et al.* (1985), Côté *et al.* (1986) et Vandevelde *et al.* (1987). En période estivale, la composition taxonomique y est aussi dominée de façon générale par les flagellés (Steven 1974, Sévigny *et al.* 1979).

Le tableau 3 met également en parallèle la lagune de Grande Entrée avec deux autres sites de mytiliculture : Killary Harbor, en Irlande et Ria de Arosa, en Espagne. Les valeurs de chlorophylle et de production primaire observées aux Îles-de-la-Madeleine sont légèrement inférieures à celles de ces deux autres sites. La quantité de nourriture planctonique et son taux de photosynthèse dans la lagune de Grande-Entrée sont toutefois généralement dans la même gamme de valeurs. La différence la plus évidente est la composition floristique et la taille du phytoplancton : les flagellés dominent en été dans la lagune de Grande-Entrée alors que les diatomées sont plus importantes à l'année longue à Killary Harbor et à Ria de Arosa. Notre étude ne couvre que la période estivale, cependant cette période est probablement la plus importante au point de vue biologique étant donné la couverture de glace sur la lagune des mois de décembre à avril-mai. En d'autres sites de mytiliculture dans les zones tempérées, on retrouve fréquemment une dominance de diatomées, souvent de grande taille (Robert *et al.* 1982; Tenore *et al.* 1982; Roden *et al.* 1987). La moule bleue, *Mytilus edulis*, est peu efficace dans la rétention de particules de taille inférieure à 4 μm (Stuart et Klumpp 1984) et elle est capable d'un certain degré de sélection

TABLEAU 3. Teneurs moyennes en chlorophylle *a*, taux moyen d'assimilation de carbone et groupes taxonomiques dominant dans les eaux de la lagune de Grande-Entrée (Îles-de-la-Madeleine : cette étude), du golfe du Saint-Laurent et de deux autres sites mytilicoles (Killary Harbour, Irlande et Ria de Arosa, Espagne)

Site	Chlorophylle *a*		Production primaire			Phytoplancton
	$(\mu g \cdot L^{-1})$	$(mg \cdot m^{-2})$	$(mg\ C \cdot m^{-3} \cdot h^{-1})$	$(g\ C \cdot m^{-2} \cdot j^{-1})$	$(t\ C \cdot j^{-1})$	
Îles-de-la-Madeleine	1 - 2	2 - 5	10	0.3	1.4	Flagellés > Diatomées
Golfe du Saint-Laurent	0.5 - 1 (réf. 1)	10 - 20 (réf. 2)	1 - 7 (réf. 3)	0.3 (réf. 4)		Flagellés
	2 (réf. 5)		3 - 7 (réf 6)	0.9 (réf. 7)		
				0.6 - 1.0 (réf. 8)		
Killary Harbour	3 - 6 (réf. 9)				3.6 (réf. 9)	Diatomées > Dinoflagellés
Ria de Arosa		2 - 20 (réf. 10)	2 - 30 (réf. 10)			Diatomées

Réf. 1 = Vandevelde et al. 1987.
Réf. 2 = Steven 1974; Sévigny et al. 1979; Hargrave et al. 1985.
Réf. 3 = Citarella 1980.
Réf. 4 = Hargrave et al. 1985.
Réf. 5 = Côté et al. 1986.
Réf. 6 = Sévigny et al. 1979.
Réf. 7 = Steven 1974.
Réf. 8 = Legendre 1971.
Réf. 9 = Roden et al. 1987.
Réf. 10 = Tenore et al. 1982; Hanson et al. 1986.

nutritionnelle au moment de la digestion (Cucci *et al.* 1985), préférant, dans le cas de cette dernière étude, une cryptophycée aux autres espèces testées. L'importance de ces critères reste cependant difficile à déterminer. La moule bleue est généralement peu sélective, au point de vue nutritionnel, en milieu naturel (Widdows *et al.* 1979) et la présence de phytoplancton de petite taille ne devrait pas, à première vue, affecter sa nutrition si la taille des algues est supérieure à 2-4 µm (Incze *et al.* 1980). Cependant, d'autres critères que la taille peuvent avoir un effet sur la nutrition de ce bivalve, par exemple, le degré de digestibilité de la nourriture (Hitchcock 1982) et la présence d'éléments intoxicants chez certaines algues, incluant celles du nanoplancton (Tracey 1988).

Dans le cas de la lagune de Grande-Entrée, les principales caractéristiques de l'environnement trophique estival des moules montrent une abondance moyenne de phytoplancton, lequel est dominé par des algues de taille généralement inférieure à 10 µm, une croissance algale basée sur la régénération des sels nutritifs, une composition biochimique dominée par les protéines et la présence d'une composante détritique (: non phytoplanctonique) dans le matériel particulaire en suspension. L'évaluation de la compatibilité de ces caractéristiques avec une activité de culture des moules devra tenir compte de l'hydrographie du milieu; cependant, la comparaison effectuée entre les différents sites de mytiliculture suggère que le type de phytoplancton peut jouer un rôle non négligeable. Une description de l'activité nutritionnelle et métabolique des moules de cette lagune devrait permettre de relier les caractéristiques du seston à celles de la nutrition de ces bivalves.

Remerciements

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Variations de l'activité des enzymes digestives et de la ponte chez les femelles de *Calanus finmarchicus* dans le golfe du Saint-Laurent[1]

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Dans le cadre d'une étude sur la distribution et l'alimentation des larves de poissons en fonction de la productivité du copépode planctonique *Calanus finmarchicus* dans le golfe du Saint-Laurent, d'importantes variations spatiales (le long d'un transect) et temporelles (avant et après une tempête) ont été notées dans les mesures physiques, dans la chlorophylle *a*, la composition biochimique du matériel organique particulaire (glucides, protéines et lipides totaux ainsi que carbone et azote particulaires), ainsi que dans l'activité des enzymes digestives et la ponte d'oeufs des femelles *C. finmarchicus*. Les résultats obtenus montrent entre autres que le taux de ponte par femelle *C. finmarchicus* augmente considérablement après la tempête aux trois stations d'échantillonnage. Ces variations sont inversement correlées avec les concentrations de la chlorophylle dans le milieu, mais correspondent généralement à une augmentation de plusieurs des indices quantitatifs du matériel particulaire, ainsi que de l'activité de plusieurs enzymes digestives, notamment la trypsine. Nous interprétons ces résultats comme une indication d'une augmentation de la production primaire dans la couche de mélange après la tempête, peu importe la localisation de la station, ce qui implique une amélioration générale de la quantité et/ou de la qualité de la nourriture pour *C. finmarchicus*. Nos résultats ne permettent cependant pas d'éliminer la possibilité que d'autres facteurs environmementaux puissent également jouer un rôle important sur le contrôle de la ponte des copépodes en milieu naturel.

During a study of the distribution and feeding of fish larvae in relation to the productivity of the planctonic copepod *Calanus finmarchicus* in the Gulf of St. Lawrence, important spatial (along a transect) and temporal (before and after a storm) variations were observed in the physical characteristics, the chlorophyll *a* concentration, the biochemical composition of the particular organic material (total sugars, proteins and lipids, particulate carbon and nitrogen), as well as in the digestive enzyme activity and the daily production of eggs by female *C. finmarchicus*. The results obtained show, among other things, that daily egg production rate by female *C.finmarchicus* increases considerably at all three sampling stations after the storm. These variations were inversely correlated with chlorophyll concentrations, but were generally related to an increase in activity of several digestive enzymes, notably trypsin, and to several of the respective indices of particulate material. We interpret these results as indications of an increase in primary production in the mixed layer after the storm, regardless of spatial location, which provides a general increase in the quantity and/or quality of food for *C.finmarchicus*. The data do not, however, eliminate the possibility that other environmental factors may also have played an important role on the control of daily egg production by copepods in the natural environment.

Introduction

En milieu naturel les organismes, tels que les copépodes planctoniques, doivent exploiter les variations quantitatives et qualitatives du milieu nutritionnel afin d'obtenir les éléments nécessaires à leur survie et à leur reproduction.

Plusieurs auteurs ont en effet démontré qu'en milieux côtiers et en zones de remontées d'eaux profondes, il existe une relation positive entre l'activité des enzymes digestives de plusieurs espèces de copépodes et la concentration de la matière organique particulaire (Boucher et Samain 1974; Boucher *et al.* 1976; Mayzaud et Conover 1976; Mayzaud et Poulet 1978). Des résultats similaires ont été obtenus pour d'autres calanoïdes (Tande et Slagstad 1982) et des euphausiacés (Willason

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et Cox 1986) en conditions nutritionnelles limitantes, autant en milieu naturel qu'en laboratoire (Boucher *et al.* 1976; Cox 1981; Cox et Willason 1981; Hirche 1981). Cependant, il est à noter que d'autres auteurs n'ont pas pu démontrer une telle relation (Hassett et Landry 1983; 1988; Landry et Hassett 1985; Harris *et al.* 1986; Båmstedt 1988).

Il a aussi été observé chez les copépodes à tendance herbivore, que lorsque les conditions nutritionnelles sont limitantes, les taux de production d'oeufs sont positivement corrélés à la concentration de chlorophylle dans le milieu naturel (Checkley 1980b; Durbin et al. 1983; Runge 1985; Beckman et Peterson 1986; Peterson et Bellatoni 1987), ou à celle des cultures phytoplanctoniques constituant le régime alimentaire en laboratoire (Runge 1984). De plus des résultats obtenus en laboratoire indiquent que la production moyenne d'oeufs chez les femelles de *Calanus finmarchicus* (Marshall et Orr 1955) et de *Paracalanus parvae* (Checkley 1980a) varie selon les espèces phytoplanctoniques constituant le régime alimentaire (i.e. qualité de la diète). Finalement, des taux de ponte supérieurs ont également été obtenus pour *Acartia tonsa* nourris de milieu particulaire naturel en laboratoire, en comparaison avec des organismes soumis à un régime de nutrition semblable, mais en milieu naturel (Ambler 1985). Ce dernier résultat suggère que certains facteurs, autres que la quantité et/ou la qualité de la nourriture, pourraient influencer la fonction reproductrice des copépodes planctoniques.

Dans le cadre d'observations effectuées lors d'une étude plus globale sur la distribution et l'alimentation des larves de poissons en fonction de la productivité du copépode planctonique *Calanus finmarchicus* dans le golfe du Saint-Laurent, nous avons pu observer, sur un transect de quelques kilomètres, d'importantes variations spatiales (entre les stations) et temporelles (avant et après une tempête) dans l'activité des enzymes digestives et la ponte des femelles *C. finmarchicus.* Dans ce travail, nous utilisons ces données pour examiner l'hypothèse d'un lien fonctionnel entre le milieu nutritionnel et l'activité enzymatique et la ponte des femelles *C. finmarchicus* dans le golfe du Saint-Laurent. En particulier, nous avons tenté de vérifier : (1) si la réponse enzymatique des femelles *C. finmarchicus* est exclusivement liée aux variations quantitatives et/ou qualitatives du milieu nutritionnel et (2) s'il existe un lien entre l'activité enzymatique digestive et la ponte d'oeufs des copépodes.

Matériel et méthodes

Les données de cette étude proviennent de trois stations situées le long d'un transect nord-sud entre l'Île d'Anticosti et la péninsule de Gaspé dans le golfe du Saint-Laurent (fig. 1). Ce transect coupe de façon perpendiculaire le courant de Gaspé qui longe la péninsule gaspésienne (El-Sabh et Benoit 1984). La particularité principale de ces données est liée à la possibilité de comparer deux échantillonnages consécutifs effectués aux trois stations avant et après une tempête, soit respectivement du 20 au 22 juin et du 24 au 27 juin 1988 (tableau 1). Deux journées (22 et 23 juin) de vent d'ouest-nord-ouest atteignant 13 m • s^{-1} caractérisaient cet événement météorologique.

À chaque station des profiles verticaux de température et de salinité ont été réalisés à l'aide d'une sonde STD (Applied Microsystem). Les mesures des variables biologiques et biochimiques sur le matériel particulaire ont été effectuées sur des échantillons d'eau prélevés avec une pompe Little Giant aux environs de la profondeur du maximum de chlorophylle (tableau 1), lequel était déterminé à l'aide d'un fluorimètre Turner Design. A chacune des stations, l'eau pompée a d'abord été filtrée sur soie Nitex (vide de maille de 256 µm), puis des volumes de 0.5 à 1 L ont été filtrés sur Whatman GF/C (préalablement chauffés à 450°C pendant 24 h) pour les mesures de chlorophylle *a*, des phaeopigments et des paramètres

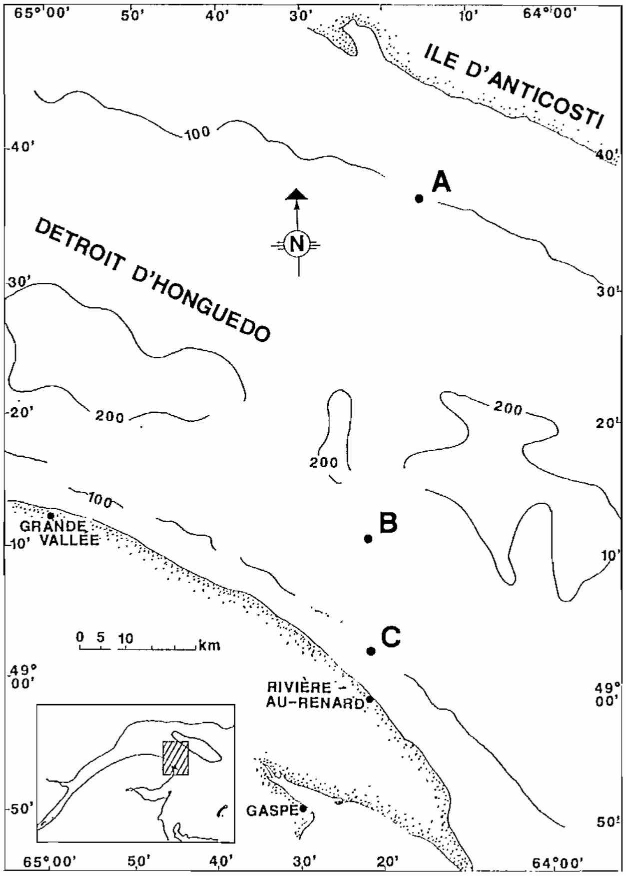

FIG. 1. Localisation des stations sur le transect d'échantillonnage dans le golfe du Saint-Laurent.

TABLEAU 1. Date, heure et profondeur (maximum de chlorophylle) auxquelles a été effectué l'échantillonnage aux Stns A, B et C avant et après la tempête.

Station		Date d'échantillonnage	Heure (h)	Profondeur (m)
A	avant	20/06/88	20:00	12
	après	25/06/88	21:40	5
B	avant	21/06/88	21:45	3
	après	24/06/88	23:15	12
C	avant	22/06/88	19:00	5
	après	27/06/88	19:00	5

biochimiques du matériel organique particulaire (protéines, glucides et lipides totaux ainsi que carbone et azote particulaires). Les filtres ont ensuite été congelés et conservés dans l'azote liquide ou à -20°C pour les mesures ultérieures en laboratoire.

Les concentrations de chlorophylle *a* et des phaeopigments ont été mesurées selon la méthode de Yentsch et Menzel (1963), telle que modifiée par Holm-Hansen *et al.* (1965). Les teneurs en protéines, glucides et lipides totaux ont été déterminées selon les techniques décrites par Mayzaud et Martin (1975). Les concentrations en carbone et en azote du matériel particulaire ont été mesurées à l'aide d'un analyseur CHN Perkin Elmer modèle 240. Tous les échantillons ont été analysés en triplicata.

Les copépodes femelles de *Calanus finmarchicus* ont été récoltés à l'aide d'un filet de 1 m de diamètre tiré verticalement de 150 m à la surface (vide de maille de 571 μm). Six groupes de 10 à 15 femelles ont été immédiatement isolés et transférés dans des béchers de 2 L contenant de l'eau de mer filtrée sur GF/C provenant du site de récolte. Après une période d'incubation de 23 à 25 h, le milieu particulaire a été filtré sur une soie Nitex de 63 μm et le matériel récolté a été transféré dans une boîte de Pétri pour l'énumération du nombre d'oeufs produits. D'autres groupes de copépodes ont également été prélevés (vingt animaux en duplicata ou triplicata) et conservés dans l'azote liquide pour les analyses ultérieures au laboratoire des mesures d'activités enzymatiques et des paramètres cinétiques V_{max} (l'activité enzymatique maximale) et K_m (la constante Michaelienne ou l'inverse de la constante d'affinité pour le substrat). Ces mesures cinétiques sont basées sur la détermination de l'activité amylasique par la méthode de Bernfeld (1951), selon laquelle l'activité enzymatique est déterminée par la production de maltose. Les activités des deux disaccharidases (cellobiase et cellulase) et de la laminarinase ont été mesurées suivant la méthode de Dahlquist (1968), telle que modifiée par Mayzaud et Mayzaud (1981). L'activité trypsique a été mesurée par hydrolyse du substrat *a*-*N*-benzoyle-*L*-arginine-*p*-nitroanilide (L. BAPNA) selon la méthode d'Erlanger *et al.* (1961). Les mesures des protéines solubles ont été faites selon la méthode de Lowry *et al.* (1951) avec l'albumine de sérum de boeuf comme standard.

Résultats et discussion

Variations du milieu physique

Les profils verticaux de température et de salinité des trois stations révèlent l'existence de variations spatio-temporelles importantes sur le transect d'échantillonnage (fig. 2). Avant la tempête, l'épaisseur de la couche de mélange de surface passe graduellement de 10 m à la Stn A, à 15 m à la Stn B, et à 20 m à la Stn C située près de la rive gaspésienne (fig. 1). Après la tempête, l'épaisseur de la couche de mélange augmente à toutes les stations, mais de façon plus prononcée aux Stns B et C. La tempête a occasionné des augmentations importantes de salinité et des diminutions correspondantes de température en surface (0–10 m) et dans les eaux sous-jacentes (< 60 m) à la Stn A, suggérant une remontée d'eaux profondes, probablement occasionnée par l'augmentation du mélange turbulent. L'effet de la tempête semble cependant avoir été différent aux Stns B et C, où une augmentation de salinité et une diminution de température ont été observées immédiatement en surface (faible cependant), alors qu'en profondeur (> 15 m), une forte diminution de salinité et une augmentation de température sont notées. La profondeur de la couche de mélange a aussi augmenté considérablement aux Stns B et C, tandis qu'elle n'a varié que de quelques mètres à la Stn A. Il semble donc que la tempête a eu pour effet d'introduire des eaux plus chaudes et saumâtres dans la couche de mélange des Stns B et C, contrairement à la Stn A où le mélange a apporté plutôt des eaux plus froides et salées dans la couche de mélange.

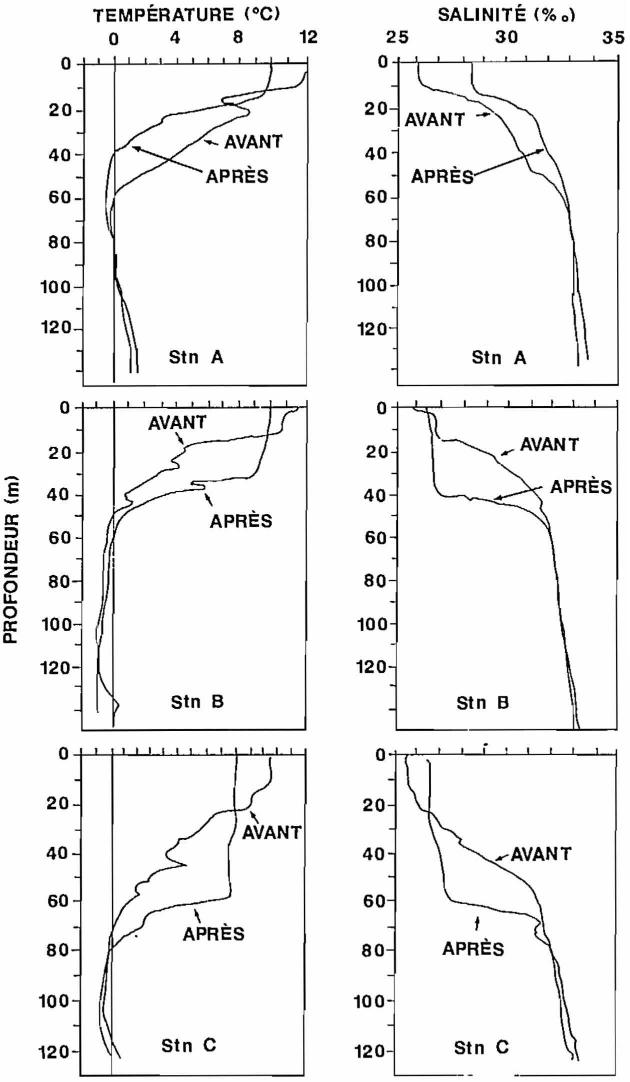

FIG. 2. Profils verticaux de température et de salinité aux stations A, B et C avant et après la tempête.

Les profils verticaux de la figure 2 suggèrent l'influence du courant de Gaspé qui a tendance à s'élargir dans la région du Golfe où notre échantillonnage a été effectué (El-Sabh et Benoît 1984; Benoît *et al.* 1985). Dans ce contexte, nos résultats peuvent s'expliquer par une hétérogénéité spatiale importante des vitesses du courant caractérisant le champ d'advection le long du transect d'échantillonnage. En effet, il a été observé que les vitesses du courant sont graduellement plus élevées à mesure que l'on s'approche de la côte de la péninsule gaspésienne (El-Sabh et Benoît 1984; Benoît *et al.* 1985). Compte tenu de l'existence d'un important gradient amont-aval des caractéristiques physiques de la masse d'eau dans le courant de Gaspé (El-Sabh et Benoît 1984), un échantillonnage quasi synoptique du champ d'advection traversant le transect d'échantillonnage aura donc inévitablement pour effet de créer des distorsions spatiales importantes, puisque les masses d'eau échantillonnées aux différentes stations proviennent de régions relativement plus amont, selon la localisation de la station dans ce champ d'advection. De telles distorsions sont susceptibles d'engendrer une hétérogénéité spatio-temporelle dans la répartition des autres variables biologiques et biochimiques mesurées à ces trois mêmes stations. Ces résultats suggèrent que de façon quasi synoptique les différences physiques observées aux Stns B et C après la tempête sont plus liées aux variations d'intensité de l'advection dans le courant de Gaspé qu'au mélange turbulent engendré par le vent. Le mélange turbulent semble par ailleurs avoir eu un effet plus ressenti que l'advection à la Stn A. Cependant, il ne faut pas oublier que la tempête a exercé la même influence sur l'ensemble du système et que les organismes biologiques y ont sans doute répondu de façon semblable. De sorte que la comparaison des stations avant et après la tempête, quoique discutable du point de vue spatial, donne vraisemblablement des résultats valables du point de vue temporel.

Variations de la biomasse et du contenu nutritionnel du milieu particulaire

Indices de biomasse — Avant la tempête, les concentrations en chlorophylle *a* sont relativement élevées et constantes aux trois stations (fig. 3a), quoique le maximum de chlorophylle ne se situe pas à la même profondeur (tableau 1). Après la tempête, la concentration de chlorophylle diminue aux trois stations et un gradient croissant est observé du large vers la côte gaspésienne. Les concentrations se situent autour de 7 à 8 $\mu g \cdot L^{-1}$ avant la tempête et autour de 5 $\mu g \cdot L^{-1}$ après la tempête. Les valeurs intégrées de chlorophylle sur les premiers 25 m de la colonne d'eau montrent également des diminutions significatives aux trois stations suite au passage de la tempête (tableau 2). Il est à souligner qu'une simple redistribution de la chlorophylle sur le plan vertical à l'intérieur de la couche de mélange

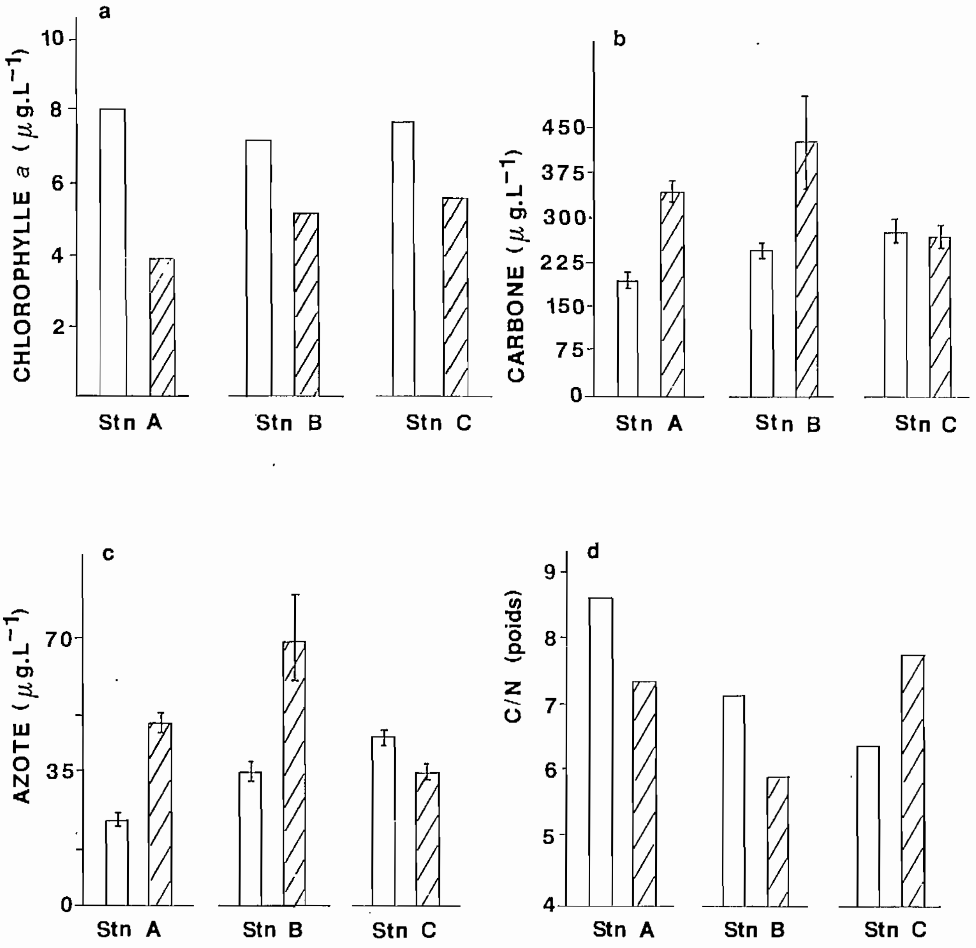

FIG. 3. Concentrations de chlorophylle *a* (a), de carbone (b) et d'azote (c) particulaires, et valeur du rapport Carbone/Azote (d) au niveau du maximum de chlorophylle des trois stations d'échantillonnage avant □ et après ▨ la tempête.

TABLEAU 2. Concentrations en chlorophylle *a* intégrées sur les 25 premiers mètres de la colonne d'eau avant et après la tempête, ainsi que les valeurs des rapports Carbone: chlorophylle (C/Chl) et Protéines: Glucides: Lipides (P/G/L) correspondants au niveau du maximum de chlorophylle pour les trois stations d'échantillonnage.

Station		Chlorophylle intégrée (mg Chl*a* • m^2)	C/Chl	P/G/L
A	avant	175	24	8/6/1
	après	74	69	4/4/1
B	avant	145	32	8/5/1
	après	91	85	9/4/1
C	avant	122	37	6/4/1
	après	176	48	6/3/1

ne devrait pas faire diminuer la valeur intégrée de chlorophylle à la Stn A puisque la couche de mélange est entièrement comprise à l'intérieur des 25 premiers mètres, avant comme après la tempête (fig. 2). Par contre, aux Stns B et C, où la couche de mélange (40–60 m) dépasse largement la profondeur d'intégration (25 m), il est possible de penser qu'un mélange de la chlorophylle du maximum profond sur une couche beaucoup plus épaisse pourrait constituer une explication valable. Toutefois, cette dilution de chlorophylle dans un volume d'eau beaucoup plus grand aux Stns B et C (couche de mélange de 40–60 m) qu'à la Stn A (≈ 15 m) aurait dû produire une diminution de chlorophylle proportionnellement plus prononcée aux deux premières stations.

Les variations spatiales du carbone et de l'azote particulaires le long du transect d'échantillonnage sont plus prononcées après qu'avant la tempête (fig. 3b, c). Contrairement aux valeurs de chlorophylle, les concentrations du carbone (C) et de l'azote (N) particulaires augmentent de façon importante aux Stns A et B après la tempête, tandis que la Stn C enregistre peu ou pas de variations significatives.

Il peut sembler étonnant que les stations du large (Stns A et B) montrent des augmentations du carbone et de l'azote particulaires alors que les concentrations de chlorophylle diminuent. D'autant plus que des valeurs du rapport C/N (en poids) se situent autour de 6 à 9 et que de telles valeurs sont généralement caractéristiques de communautés phytoplanctoniques actives ou de milieux particulaires, où la contribution de la fraction détritique est faible (Mann 1972; Eppley *et al.* 1977). En l'absence d'information sur le matériel particulaire et en particulier sur l'identification et l'énumération du phytoplancton, il est difficile d'expliquer ce résultat. Cependant, comme nous le verrons ci-après, plusieurs indices laissent croire à une croissance phytoplanctonique importante suite à la tempête, quoique cette croissance ne se soit pas reflétée par une augmentation correspondante des concentrations de chlorophylle.

En effet, des périodes de 3 à 5 jours séparant les deux échantillonnages avant et après la tempête (tableau 1) sont amplement suffisantes pour qu'une production phytoplanctonique significative ait eu lieu suivant l'introduction de nouveaux éléments nutritifs dans la couche de mélange (voir la revue de Demers *et al.* 1986). Un tel laps de temps aurait également permis la sédimentation, hors de la zone de mélange, de la matière détritique qui aurait pu être remise en suspension lors de la tempête.

Avant la tempête le phytoplancton était principalement concentré autour du maximum de chlorophylle profond, tel que normalement observé dans le Golfe en été (e.g. Sévigny *et al.* 1979; VandeVelde *et al.* 1987). Les cellules phytoplanctoniques dans ce maximum sont alors adaptées à une lumière moyenne relativement faible, ce qui se traduit généralement par une forte concentration de la chlorophylle interne des cellules (voir les revues sur la photoadaptation de Harris 1978, Falkowski 1980, Richardson *et al.* 1983, Harding *et al.* 1987). Suite à la turbulence occasionnée par la tempête, les cellules phytoplanctoniques sont soumises à une augmentation de la lumière moyenne et leur réponse photoadaptive se traduit par une diminution de la chlorophylle interne (voir références plus haut). Par ailleurs, les valeurs du rapport Carbone/chlorophylle (tableau 2) ont augmenté de 2 à 3x suite à la tempête; ceci représente des variations «normales» pour des cellules phytoplanctoniques physiologiquement actives s'adaptant à une énergie lumineuse moyenne plus élevée (Legendre 1981; Loder et Platt 1985). Ces considérations sur la photoadaptation du phytoplancton et sur les valeurs de l'indice physiologique C/Chl, ajoutées aux observations sur les variations du rapport C/N, supportent notre interprétation d'une augmentation de la production phytoplanctonique dans la couche de mélange suivant la tempête de vent, peu importe où est située la station dans le champ d'advection du courant de Gaspé. Ces résultats revêtent une grande importance car ils suggèrent qu'une croissance phytoplanctonique suivant une tempête dans un milieu stratifié ne s'accompagne pas nécessairement d'une augmentation correspondante des concentrations de chlorophylle en raison d'un épaississement significatif de la couche de mélange.

Contenu nutritionnel de la matière organique particulaire (MOP) — À l'exception de la Stn B où la concentration des glucides totaux demeure inchangée après la tempête, les variations du contenu total en glucides, protéines et lipides de la MOP sont généralement parallèles au niveau du maximum de chlorophylle (fig. 4a,b,c). Alors qu'une augmentation des concentrations caractérise les Stns A et B suivant la tempête, une diminution est enregistrée à la Stn C (fig. 4a,b,c). Ces fluctuations du contenu total en glucides, protéines et lipides correspondent généralement bien avec celles du carbone et de l'azote particulaires (fig. 3) et, par conséquent, sont inversement reliées aux variations de chlorophylle du milieu particulaire aux trois stations d'échantillonnage.

La composition biochimique du matériel particulaire récolté au cours de cette étude se caractérise par une dominance de la fraction protéique (fig. 4 et tableau 2), suggérant un métabolisme cellulaire orienté vers la synthèse des protéines (i.e. croissance exponentielle du phytoplancton) plutôt que vers celle des produits de réserve tels que les glucides (fig. 4d) ou les lipides (Haug *et al.* 1973; Ganf *et al.* 1986). Ce résultat est en accord avec notre hypothèse d'une communauté phytoplanctonique active avant comme après la tempête.

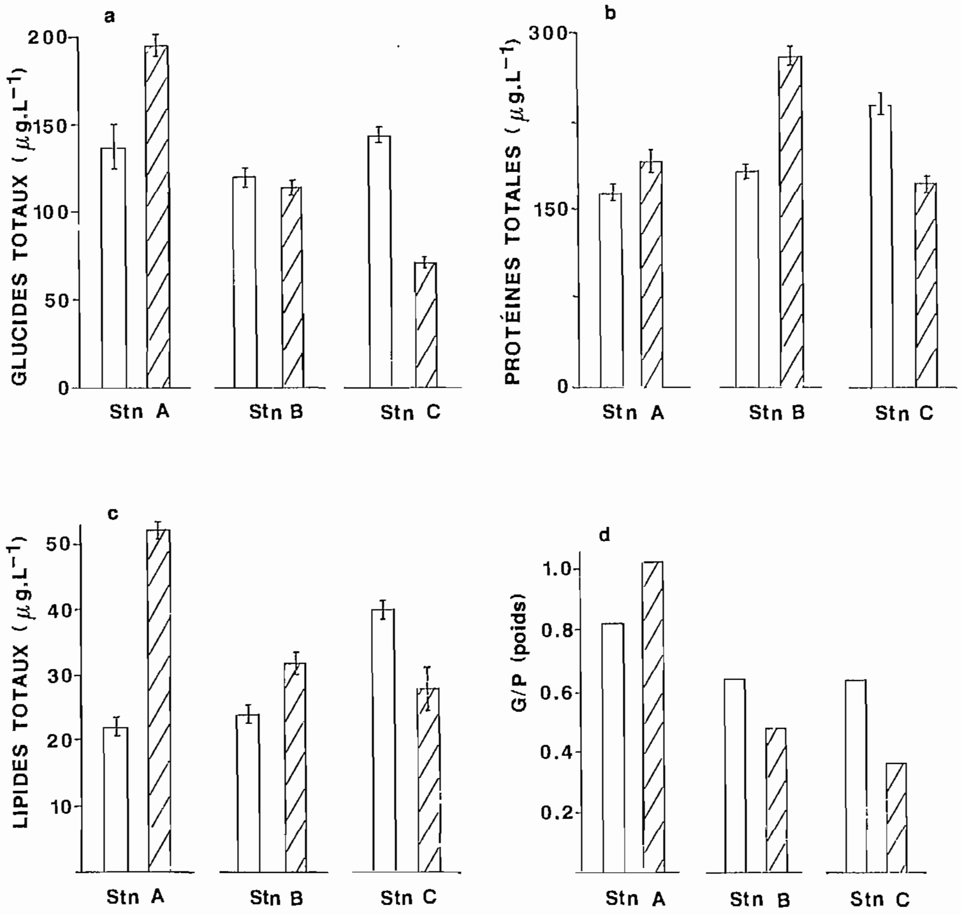

FIG. 4. Concentrations totales en glucides (a), protéines (b) et lipides (c), et valeurs des rapports Glucides/Protéines (d) au niveau du maximum de chlorophylle aux trois stations d'échantillonnage avant ☐ et après ▨ la tempête.

Les rapports protéines:glucides:lipides totaux (P/G/L) considérés comme indicateurs de la valeur nutritive du régime alimentaire des animaux sont relativement élevés aux trois stations, avant comme après la tempête, et montrent des variations notables avec la tempête seulement à la Stn A (tableau 2). Les travaux de Parsons *et al.* (1961) et de Scott (1980) sur les caractéristiques biochimiques des divers groupes de cellules phytoplanctoniques en culture ont montré que des rapports constitutifs protéines : glucides : lipides variant entre 4:3:1 et 1:1:1 favorisent la croissance des organismes zooplanctoniques sestonophages. Dans le cas présent, les rapports mesurés au niveau du maximum de chlorophylle (tableau 2) sont en général très supérieurs à ceux mentionnés par ces auteurs. Il est donc plausible de penser que les conditions trophiques aient été *qualitativement* favorables (Paffenhöfer et Van Sant 1985; Houde et Roman 1987) à la croissance et à la reproduction du zooplancton partout dans le golfe du Saint-Laurent au moment de notre échantillonnage.

Activité des enzymes digestives chez les femelles *Calanus finmarchicus*

En accord avec les résultats précédents qui suggèrent une amélioration générale de la quantité, sinon de la qualité, du milieu particulaire après la tempête, l'activité enzymatique maximale (V_{max}) de l'ensemble des enzymes digestives (à l'exception de la cellulase) a augmenté chez les femelles *C. finmarchicus* prélevées aux Stns A et C après la tempête (fig 5). Par contre, la Stn B se distingue par une diminution d'activité de la trypsine (Fig 5c) et de l'ensemble des activités des carbohydrases (laminarinase, cellobiase et cellulase : fig. 5b,d,e). Il y a également aucune modification significative de l'amylase (fig. 5a).

Les constantes cinétiques (K_m) des enzymes digestives pour l'ensemble des copépodes prélevés avant et après la tempête ne montrent pas le même patron de variations aux trois stations, selon l'enzyme considérée (fig. 6). Les variations de K_m pour l'amylase et la laminarinase ne sont généralement pas différentes pour chaque site avant et après la tempête, ni entre les stations avant ou après la tempête. Par contre, une augmentation notable du K_m pour la trypsine est observée aux Stns A et C après la tempête (fig. 6b), tandis que la Stn B montre une diminution.

Les calculs de la pente initiale des courbes de Michaelis-Menten ($\tan \alpha = V_{max} / 2K_m$) pour l'amylase, la laminarinase et la trypsine aux différents sites d'échantillonnage ont révélé une faible amplitude de variation (angle variant de 1 à 5°). Par conséquent, sauf pour la trypsine, les variations de V_{max} pour les différentes

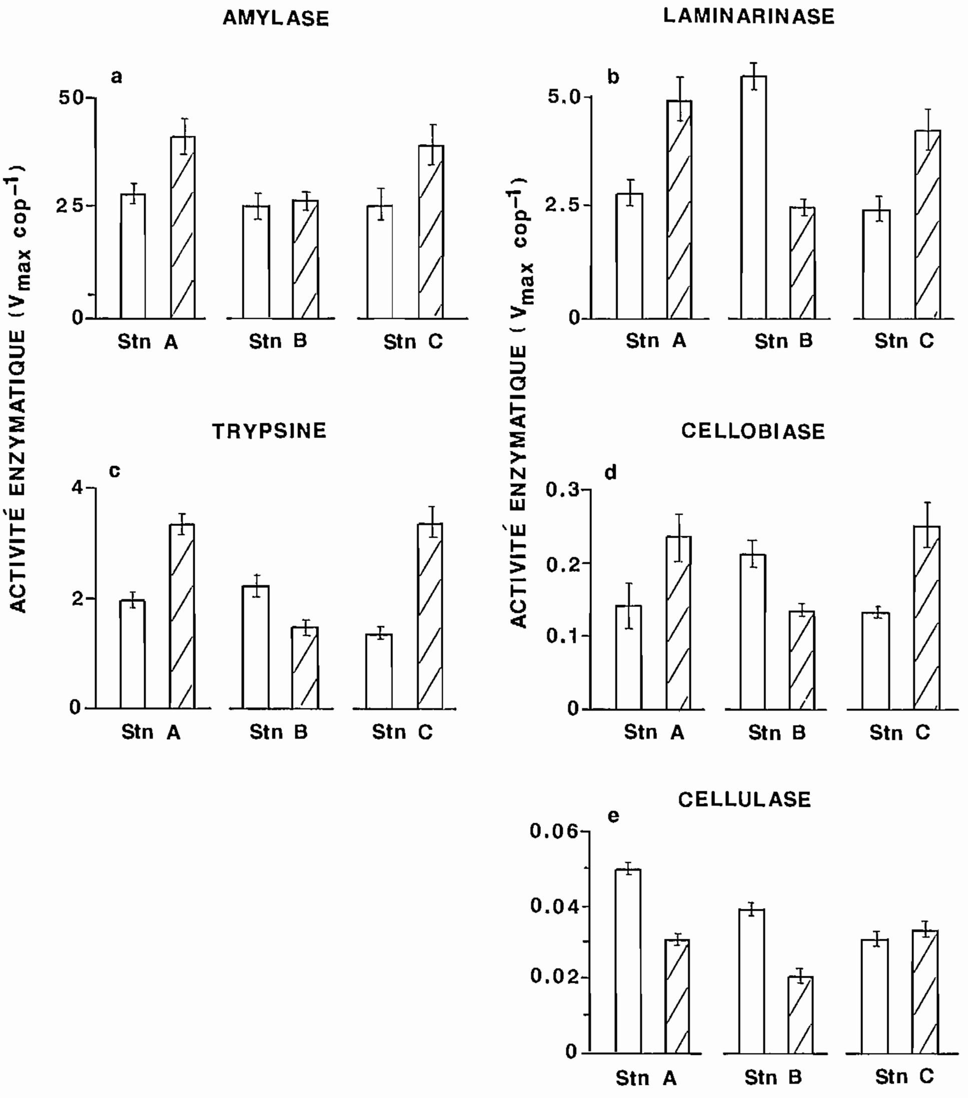

FIG. 5. Mesures de l'activité maximale (V_{max}) des enzymes digestives amylase (a), laminarinase (b), trypsine (c), cellobiase (d) et cellulase (e) de femelles *Calanus finmarchicus* récoltées aux trois stations d'échantillonnage avant □ et après ▨ la tempête.

enzymes digestives ne peuvent être attribuées aux variations dans l'affinité pour le substrat. Les résultats obtenus par Mayzaud *et al.* (1987) pour l'euphausiacé antarctique *Euphausia superba* ont montré que plus de 60% de la variance des mesures d'activité maximale des enzymes amylase et trypsine (V_{max}) pouvait être attribuée aux variations des concentrations protéiques. D'autres travaux par Mayzaud et Poulet (1978) sur les copépodes néritiques ont également montré que les variations de K_m n'influençaient pas significativement les variations de V_{max}. Les résultats obtenus pour *C. finmarchicus* dans cette étude confirment ce point puisque le K_m des enzymes étudiées n'a pas varié de façon parallèle aux changements de V_{max}. Ces observations suggèrent que durant notre étude, les capacités digestives des femelles *C. finmarchicus* étaient plus ou moins constantes et dépendaient peu des variations qualitatives ou quantitatives du régime nutritionnel.

Les protéines corporelles (données non montrées) n'ont pas varié de façon significative chez les femelles prélevées aux Stns B et C après la tempête et seule une faible augmentation de 5 μg par copépode a été mesurée chez les individus prélevés à la Stn A. Ce résultat suggère que l'augmentation générale de l'activité maximale des enzymes digestives a pu être dirigée vers des fonctions métaboliques autres que la croissance, comme par exemple la production d'oeufs.

Taux de ponte d'oeufs par les femelle *C. finmarchicus*

Le taux de ponte d'oeufs par les femelles *C. finmarchicus* augmente considérablement à chacune des stations après la tempête (fig. 7). Ces variations sont opposées à celles de la chlorophylle dans le milieu, mais correspondent globalement à celles de la quantité (carbone et azote particulaires; glucides, protéines et lipides totaux) de matériel particulaire (fig. 3 et 4), et avec celles de l'activité maximale des enzymes digestives (fig. 5). Ces résultats supportent donc l'hypothèse que la ponte d'oeufs par les femelles *C. finmarchicus* en milieu naturel est fonction

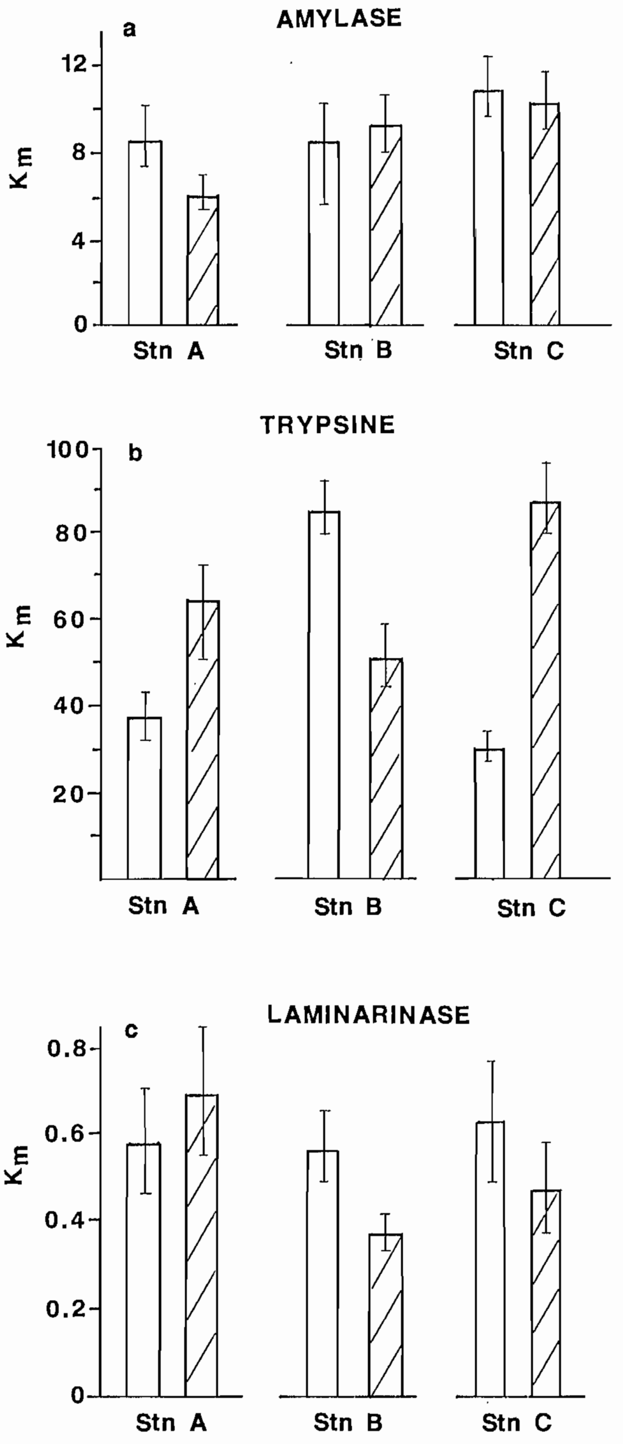

FIG. 6. Mesures de la constante Michaelienne (K_m) des enzymes digestives amylase (a), trypsine (b) et laminarinase (c) de femelles *Calanus finmarchicus* récoltées aux trois stations d'échantillonnage avant □ et après ▨ la tempête.

de la concentration et/ou de la qualité de la nourriture à court et à moyen-terme (Peterson et Bellantoni 1987).

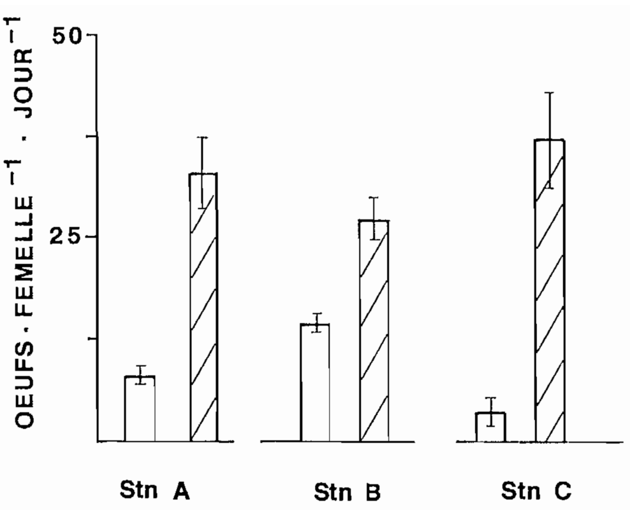

FIG. 7. Taux de ponte des femelles *Calanus finmarchicus* récoltées aux trois stations d'échantillonnage avant □ et après ▨ la tempête.

Cependant, malgré certaines tendances communes entre les 3 stations, l'importante hétérogénéité spatio-temporelle observée principalement à la Stn B permet de supposer l'existence de situations trophiques quelque peu différentes le long du transect d'échantillonnage. Il apparaît donc plus prudent d'examiner la relation ponte milieu nutritif pour chacune des stations.

À la Stn A, le passage de la tempête s'est traduit par une augmentation significative de la concentration de la nourriture (carbone et azote particulaires ainsi que glucides, protéines et lipides totaux), des activités enzymatiques à l'exception de la cellulase), de la ponte ainsi que des protéines corporelles des copépodes. L'augmentation de ces dernières suggère que l'amélioration quantitative et/ou qualitative du milieu nutritif particulaire à cette station a induit chez *C. finmarchicus* une réponse métabolique se traduisant à la fois par une croissance somatique et par une activation du processus de ponte.

À la Stn B, une augmentation de la concentration de nourriture et du taux de ponte a été observée après la tempête, mais par contre, il y a diminution de l'ensemble des activités enzymatiques et aucun changement des protéines corporelles. Ces résultats supportent les observations de Harris *et al.* (1986) indiquant une répression ou une diminution de l'activité de certaines enzymes digestives comme la laminarinase et la trypsine à des niveaux de nourriture saturants. Ces résultats suggèrent que le taux de ponte des copépodes pourrait être liée à la quantité et/ou la qualité du milieu nutritif, bien qu'une réponse enzymatique n'y soit pas nécessairement associée.

À la Stn C, la tempête a entraîné, d'une part, une diminution de la concentration de nourriture, et d'autre part, une augmentation de la réponse enzymatique et de la ponte des copépodes, et le maintien des protéines corporelles. Ces résultats suggèrent que le taux de ponte à cette station pourrait répondre autant à un changement de qualité de la nourriture qu'à une augmentation de quantité.

Les considérations qui précèdent pour chacune des stations sont intéressantes, mais il ne faut cependant pas négliger la possibilité que la tempête ait également pu faire varier d'autres facteurs environnementaux qui pourraient également avoir une influence significative sur le contrôle de la ponte des copépodes en milieu naturel.

Nos observations s'accordent donc avec celles de Kiorboe *et al.* (1988) qui montrent une augmentation du taux de ponte des femelles du copépode *Arcatia tonsa* après une tempête, même si la concentration de chlorophylle a diminué. Pour expliquer ce résultat ces auteurs ont proposé que le mélange turbulent généré par une tempête pouvait stimuler la ponte d'oeufs des copépodes planctoniques : (1) en augmentant la disponibilité d'éléments nutritifs nouveaux dans la couche de mélange, accroissant ainsi la productivité phytoplanctonique; (2) en rendant les algues phytoplanctoniques plus accessibles et nutritives pour le zooplancton (en termes de distribution et de composition chimique) et, finalement, (3) en stimulant directement l'activité de broutage du zooplancton en augmentant, par exemple, le taux de contact avec les particules tel que suggéré par Rothschild et Osborn (1988). Nous ne pouvons pas éliminer la possibilité que n'importe lequel ou tous ces facteurs puissent agir en même temps et jouer un rôle important dans notre étude.

Conclusion

Les données de cette étude, bien que préliminaires, sont en accord avec l'hypothèse d'un lien entre, d'une part, l'activité enzymatique des enzymes digestives et le taux de ponte d'oeufs des femelles *Calanus finmarchicus* et, d'autre part, la productivité (quantité et/ou qualité) du milieu particulaire nutritif dans le golfe du Saint-Laurent. Le faible nombre de stations échantillonnées et la fréquence d'échantillonnage ne permettent cependant pas d'éliminer la possibilité que d'autres facteurs environnementaux puissent également jouer un rôle important dans le contrôle de la ponte des copépodes planctoniques en milieu naturel.

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Seasonal Distribution of Demersal Fish (Osteichthyes) and Skates (Chondrichthyes) in the Southeastern Gulf of St. Lawrence[1]

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CLAY, D. 1991. Seasonal distribution of demersal fish (Osteichthyes) and skates (Chrondrichthyes) in the southeastern Gulf of St. Lawrence, p. 241–259. *In* J.-C. Therriault [ed.] The Gulf of St. Lawrence: small ocean or big estuary? Can. Spec. Publ. Fish. Aquat. Sci. 113.

Six bottom trawl surveys carried out in the southeastern Gulf of St. Lawrence between September 1986 and September 1987 indicated a marked seasonal cycle in distribution and relative abundance of demersal fish. Atlantic cod (*Gadus morhua*), white hake (*Urophycis tenuis*) and American plaice (*Hippoglossoides platessoides*) exhibited the greatest movement, migrating out of the shallow water of the southeastern Gulf in winter and returning in spring. Yellowtail flounder (*Limanda ferruginea*) and winter flounder (*Pseudopleuronectes americanus*) undertook limited movements with a portion of the population remaining in shallow water year round. Longhorn sculpin (*Myoxocephalus octodecemspinosus*) moved to slightly deeper water in winter but remained in the water shallower than 100 m where the bottom temperature reached 0°C or below. Thorny skate (*Raja radiata*) exhibited a winter migration to the warmer waters of the southern slopes of the Laurentian Channel and returned to the shallows of the southeastern Gulf in summer. There was also an indication of at least a partial movement of this species out of the Laurentian Channel to the Atlantic. Winter skate (*Raja ocellata*) moved to slightly deeper water in winter, although not as far as the Laurentian Channel, and then dispersed back to the shallows in summer. Smooth skate (*Raja senta*) exhibited no seasonal movement and remained in the relatively warm, stable, deeper water of the Laurentian Channel and Cape Breton Trough.

Six recensements au chalut de fond effectués dans le sud-est du golfe du Saint-Laurent entre septembre 1986 et septembre 1987 ont révélé un cycle saisonnier marqué dans la distribution ainsi que dans l'abondance relative des poissons démersaux. La morue franche (*Gadus morhua*), la merluche (*Urophycis tenuis*) et la plie canadienne (*Hippoglossoides platessoides*) se déplaçent le plus, quittant les eaux peu profondes du sud-est du Golfe en hiver et y retournant au printemps. La limande à queue jaune (*Limanda ferruginea*) et la plie rouge (*Pseudopleuronectes americanus*) se déplaçent assez peu puisqu'une partie de la population demeure en eaux peu profondes tout l'année. Le chaboisseau à dix-huit épines (*Myoxocephalus octodecemspinosus*) migre vers des eaux légèrement plus profondes en hiver, mais il demeure à une profondeur de moins de 100 m où la température de fond atteint 0°C ou moins. La raie radiée (*Raja radiata*) migre en hiver vers les eaux plus chaudes des pentes sud du Chenal Laurentien et revient dans les bas-fonds du sud-est du golfe du Saint-Laurent en été. Il semble aussi qu'une partie de la population de cette espèce quitte le Chenal Laurentien pour se rendre jusque dans l'Atlantique. La raie tachetée (*Raja ocellata*) migre vers des eaux légèrement plus profondes en hiver, sans toutefois se rendre jusqu'au Chenal Laurentien et elle se disperse à nouveau sur les bas-fonds en été. La raie lisse (*Raja senta*) ne montre aucun mouvement saisonnier et demeure dans les eaux plus profondes et relativement stables et chaudes du Chenal Laurentien et de la fosse du Cap-Breton.

Introduction

The Gulf of St. Lawrence is one of the most productive inland seas in the world (Dunbar 1979). Its finfish and invertebrate fisheries contribute significantly to the economy of eastern Canada. Resource surveys of demersal fish have been conducted every September since 1971 in the southern Gulf of St. Lawrence (NAFO division 4T, Fig. 1). Data from these surveys have been used in annual stock assessments as an independent index of abundance for several commercial fish species. It is important to ensure that the September survey period is not a time of active migration for these species.

Causal relationships in detailed community analysis (eg. species association) of survey data may be difficult to define due to sampling artifacts. Both the temporal (season and diel) and spatial (1 : 1.7 × 10^6 sampling

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[1] This paper forms part of the Proceedings of a Workshop/Symposium held at the Maurice Lamontagne Institute, Mont-Joli, Quebec, 14–17 March 1989.

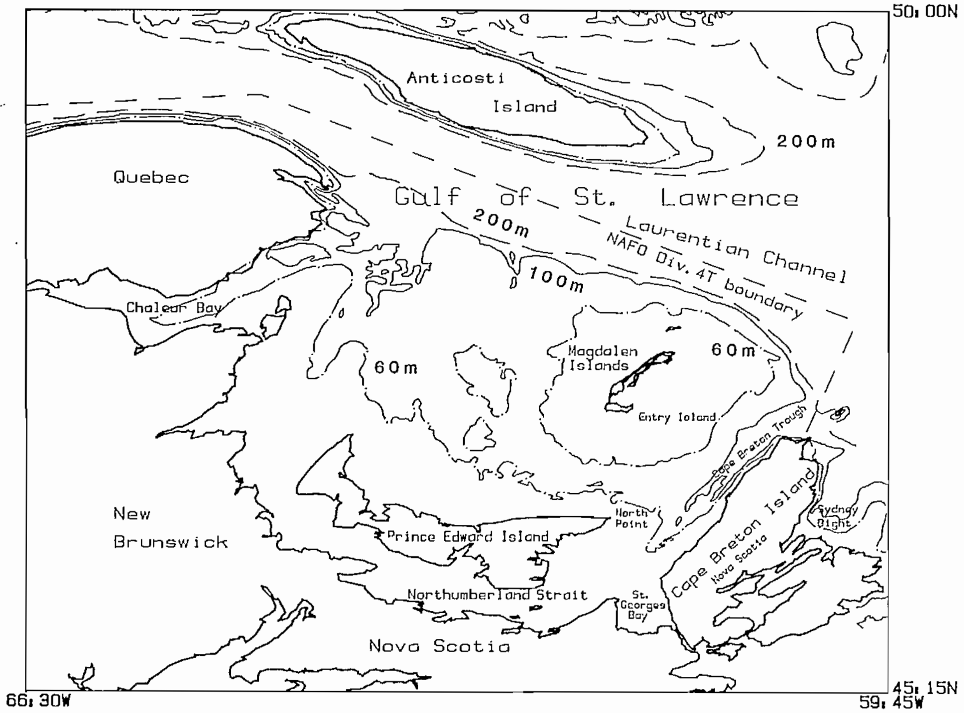


FIG. 1. Place names, bathymetry and NAFO boundary in the southern Gulf of St. Lawrence and surrounding areas.

rate) aspects of the sampling protocols are unknown. The present study aims to answer the seasonal aspect of this question and gain a better understanding of seasonal distribution and its influence on estimates of abundance from resource surveys.

This paper describes fish distribution from seasonal surveys in the southeastern Gulf during 1986 and 1987. The surveys were designed to identify seasonal movements of demersal fish and facilitate the interpretation of annual variation in relative species abundance.

Methods

Six stratified 24 h surveys were conducted in September and December, 1986 and January, May, June, and September, 1987 in the southeastern Gulf of St. Lawrence with the RV *Lady Hammond* and RV *Alfred Needler* (Table 1). Only 5 to 7 ship days were available for each of these fixed station seasonal surveys, thus weather dictated the number of successfully completed sets. September was surveyed twice, "piggy backing" on the annual resource surveys. The overall stratification scheme and method of calculating biomass was as outlined in Koeller and LeGresley (1981) for the annual southern Gulf of St. Lawrence resource surveys (1971 to 1983). However, the surveys in the present study were conducted both day and night throughout the 24 h period and sampling locations were fixed. The fixed sampling locations were the same as those used in the annual surveys from 1984 to 1987. Each sampling unit consisted of a 3.25 km tow using a Western IIA otter trawl having a wing spread of 12.6 m. Each site was identified as either a day or night set and was sampled during that time period in each survey. General cruise protocols followed Hurlbut and Clay (1990).

Data from the annual September surveys conducted in the southern Gulf were used to aid in the interpretation of seasonal movements. In the late 1960's, September was chosen for the annual survey because it was considered

TABLE 1. The research cruises, dates, and sampling frequency of the seasonal surveys conducted for this study.

Cruise[a]	Date	Number of sets[b]	Biomass estimate[c] of SE Gulf (tonnes)
H159	Sept. 3–14 1986	69	151 751
H166	Dec. 4– 9 1986	34	51 526
N073	Jan. 7–10 1987	23	5 008
H172	May 19–24 1987	43	60 097
H174	June 17–22 1987	48	70 581
H179	Sept. 3–14 1987	54	64 448

[a] H refers to the research vessel RV *Lady Hammond* (58 m LOA, stern trawler, Western IIA with 9 mm liner) N refers to the research vessel RV *Alfred Needler* (50 m LOA, stern trawler, Western IIa with 9 mm liner).

[b] Not all planned sets were completed successfully on every cruise and on some cruises some sets were repeated.

[c] The biomass estimates represent all species combined.

to be the period when the southern Gulf cod had penetrated furthest into the Gulf and were most widely distributed. These surveys were carried out by the RV *E.E. Prince* from 1971 until 1983 using a stratified random design (daylight hours only). In addition, several annual resource surveys conducted during July/August and January between 1984 and 1988, were available for analysis. These data were provided by the Quebec Region of the Department of Fisheries and Oceans. They were collected using similar cruise protocols and vessels to those mentioned above. Throughout this paper these surveys are referred to as "extended" surveys as they extend the present study coverage northwards from approximately the 200 m contour to the edge of NAFO division 4T.

The seasonal surveys covered an area that was divided into nine strata (403 and 432 to 439, Fig. 2). The stratum boundaries were selected in the late 1960's and were based upon depth, with the premise of identifying homogeneous habitats (Halliday and Kohler 1971).

Individual species catch weight, to the nearest 0.1 kg, numbers, and length frequency were recorded at each sampling site. The nine demersal species selected for this analysis represent a wide taxonomic and ecological range of the marine fish species in the southern Gulf (see Table 2 for relative abundances and sizes).

Surface and bottom temperatures during the seasonal surveys were recorded at the end of each tow, weather permitting. These data were used to provide mean temperature estimates for individual strata and a stratified survey mean (weighted by strata area). To provide long-term comparative data, an index of surface temperatures for the southeastern Gulf was obtained from the average of 20 yr of monthly mean surface temperatures from two locations, Entry Island, P.Q. and North Point, PEI (Lauzier and Hull 1969) (Fig. 1). No independent source of long-term bottom temperatures was available.

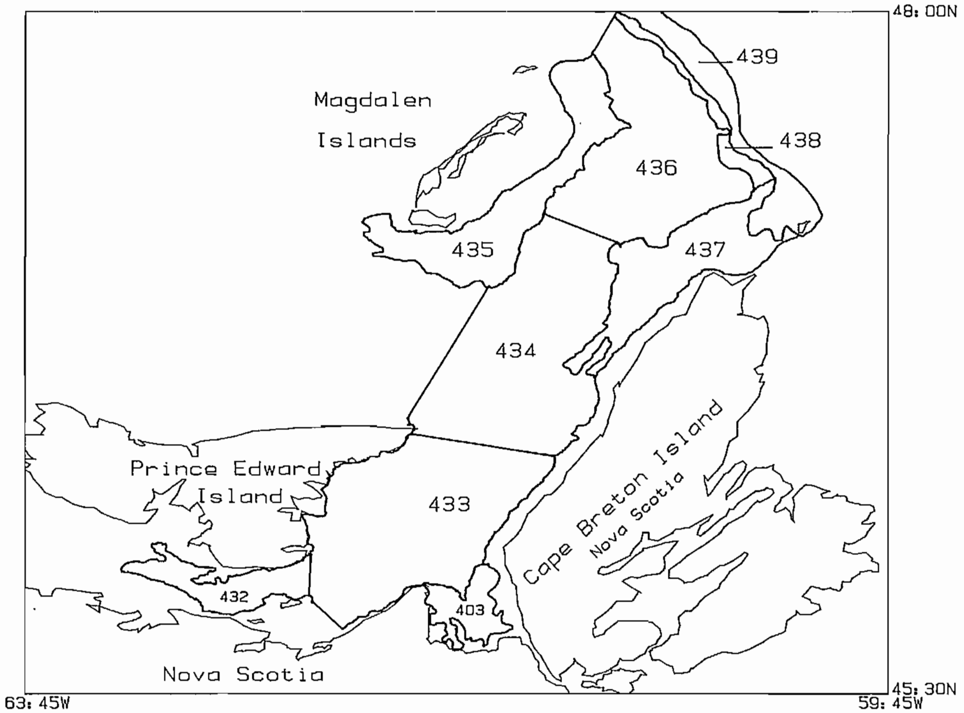


FIG. 2. Stratification of the southeastern Gulf of St. Lawrence, strata generally based on depth and the premise that they comprise a homogeneous habitat.

TABLE 2. The long-term mean biomass, numbers and average weight for the entire southern Gulf for each species investigated in this study. These data are taken from the annual September surveys (Clay and Hurlbut 1986; Koeller and LeGresley 1981) and give an indication of the relative importance of each species.

Species	Biomass tonnes	Numbers (thousands)	Mean weight (g)
Atlantic cod	175 000	208 000	840
White hake	14 500	13 000	1120
American plaice	104 000	550 000	190
Yellowtail flounder	4 100	19 000	210
Winter flounder	13 800	42 800	320
Longhorn sculpin	1 500	9 700	150
Thorny skate	4 700	6 200	1320
Winter skate	850	990	1170
Smooth skate	145	68	470

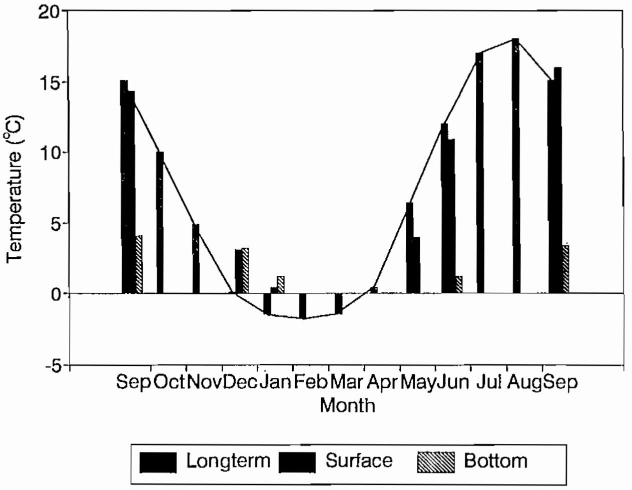


FIG. 3. Water temperatures in the southeastern Gulf of St. Lawrence. The solid line represents nearshore longterm surface temperatures from Lauzier and Hull (1969).

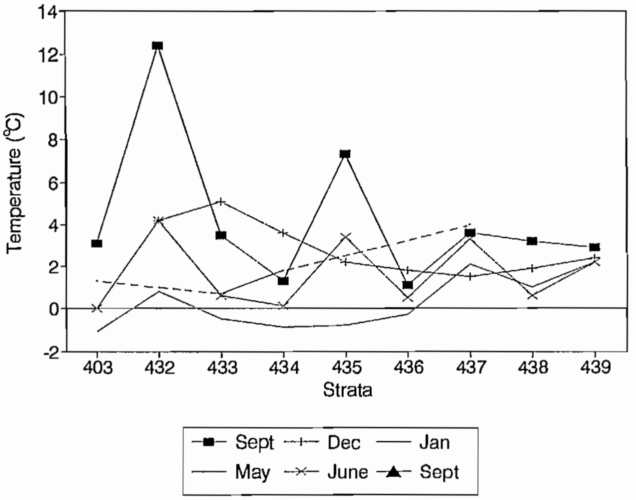


FIG. 4. Mean bottom temperature by strata for the seasonal surveys in 1986 and 1987. Broken lines indicate missing data points.

Results and Discussion

Northcote (1978) described migration as a strategy used to avoid seasonally unsuitable environments. He indicated that extreme seasonal temperature fluctuation was a key factor in the evolution of migration of many species. For this reason I have gathered the limited data available to relate the temperature of the marine environment to the general survey area and time periods.

Nearshore sites exhibit greater extremes of temperature than sites further offshore. August was the warmest (17–19°C) month as recorded from the nearshore stations, while July and September were about 3°C cooler (Fig. 3). Surface temperature from surveys followed a similar trend, although the range did not appear as extreme. Bottom temperatures did not exhibit the same range of values as surface temperatures (Fig. 4), or the same monthly pattern. The warmest mean bottom temperatures recorded for the entire survey area (about 4°C) occurred in September and December.

The shallow inshore strata (Northumberland Strait) exhibited the greatest range of seasonal temperatures with individual sites having summer surface temperatures over 19°C. These areas were often isothermal. The maximum bottom temperature observed in Northumberland Strait was 15.5°C, the highest strata mean was about 12.5°C (Fig. 4). In an overview of annual variation, Trites (1972) showed that despite large shifts in seasonal surface temperature, there were only minor seasonal variations in bottom temperatures below 60 m and no difference below 150 m in depth. The deeper water varies according to the water masses flowing into the Gulf from the Atlantic. Hjort (1919) identified a "cold layer" from 50 m to 150 m depth; in summer this layer separates the warm surface water from the water below 150 m. This cold layer, which in the shallows of the southern Gulf tends to rest on the bottom, is believed to be formed *in situ* by a process of winter cooling (Forrester 1964). The extended surveys of the Laurentian Channel (depths 150–450 m) had mean surface temperatures ranging from −0.7°C in January to 14.7°C in July/August. The mean bottom temperatures however only varied from 4.6°C in July/August to 5.6°C in January over the 4-yr period of these data.

Demersal fish living in the southern Gulf are exposed to wide annual variations in bottom temperatures in excess of 20°C (−1.0 to 20°C) in some locations. Most species appear to migrate away from the coldest water, however, fish that remain in the shallows over winter would require some antifreeze proteins to protect them against freezing (Davies et al. 1988) in the sub-zero water temperatures.

Cod, family Gadidae

Atlantic cod (*Gadus morhua,* L.)

In September (1986 and 1987) cod were found throughout the southeastern Gulf (Fig. 5), and concentrated where depth exceeded 40 m. Few fish were found in the shallow inshore waters of eastern P.E.I., St. Georges Bay and Northumberland Strait. In December, the cod moved from nearly all areas less than 60 m to depths below 100 m, both along the southern slope of the Laurentian Channel and in the Cape Breton Trough. In December cod biomass in the study area was the highest of the year (Fig. 6). This suggested some fish from the southwestern Gulf had also moved into the southeastern Gulf, probably along the southern slopes of the Channel. In January few cod remained in water less than 100 m and the concentrations along the slope of the Laurentian Channel dissipated. The January biomass in the study area was about 8 percent of the December high. The extended surveys in January in NAFO division 4T north of our survey area (Fig. 7) indicated cod were widespread in the bottom of the Laurentian Channel from Anticosti Island eastwards. Densities were higher towards Cape Breton indicating a movement out of the Gulf towards the Atlantic.

In May, cod moved off the slope back to the shallows in a pattern of distribution similar to that observed in both June and September. However, the higher estimate of biomass in the southeastern Gulf, over double that observed in the following September, indicated that some

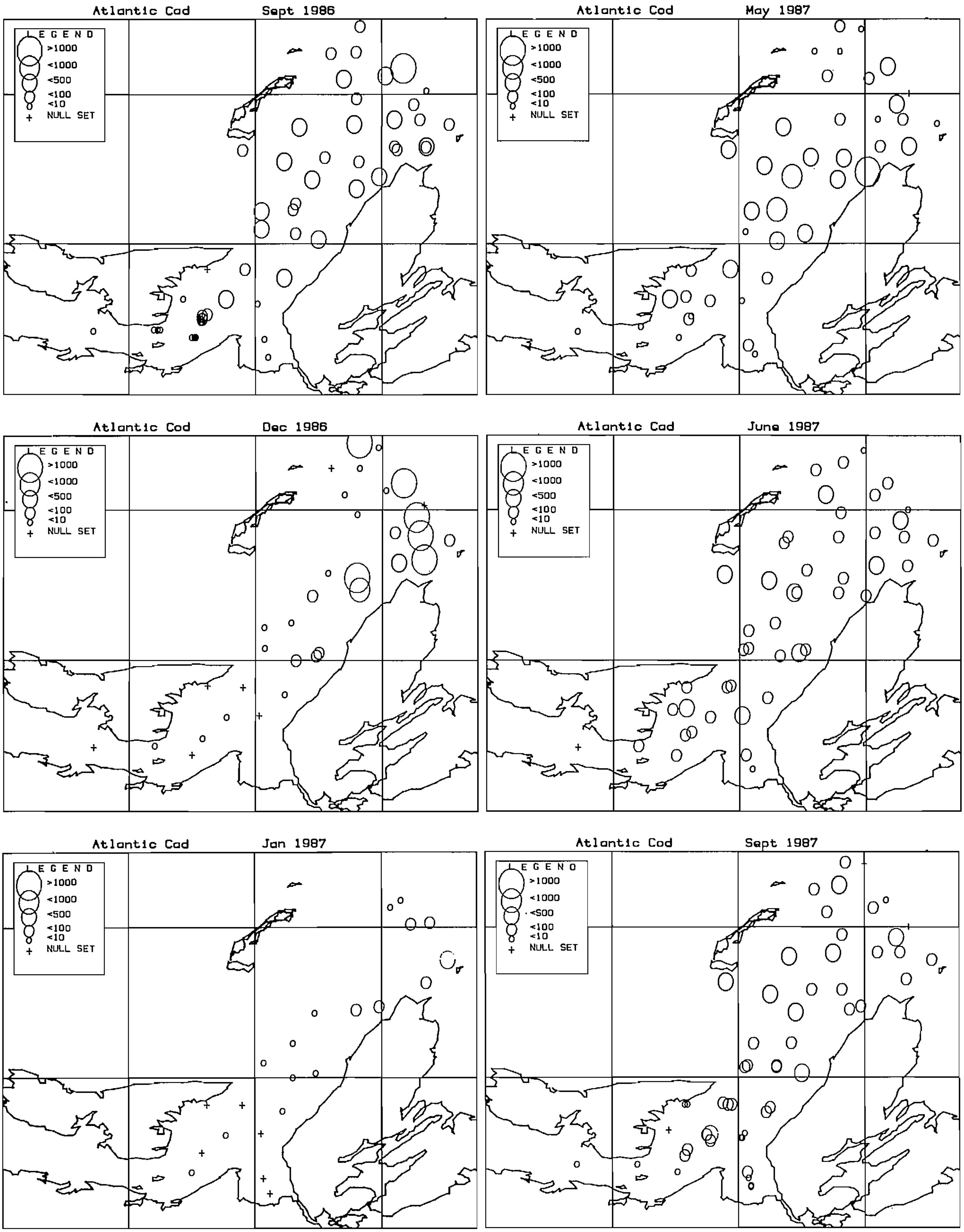


FIG. 5. Seasonal distribution of catch (kg) of Atlantic cod (*Gadus morhua*) in 1986 and 1987. Null sets are sampling sites were none of this species were caught.

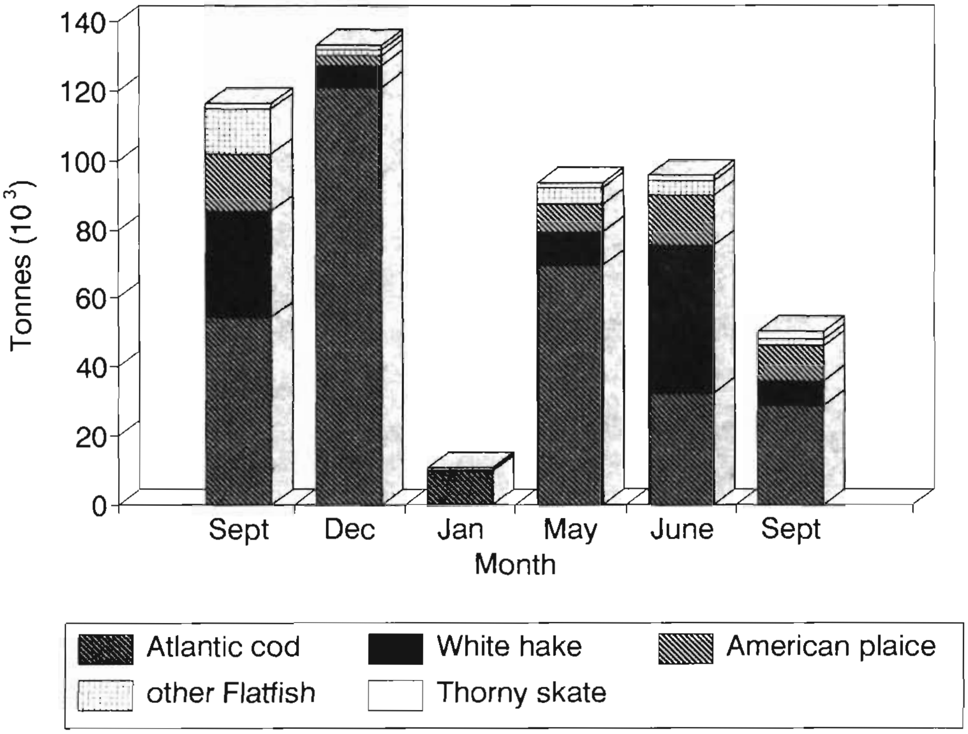


FIG. 6. Biomass estimates by species in the southeastern Gulf of St. Lawrence.

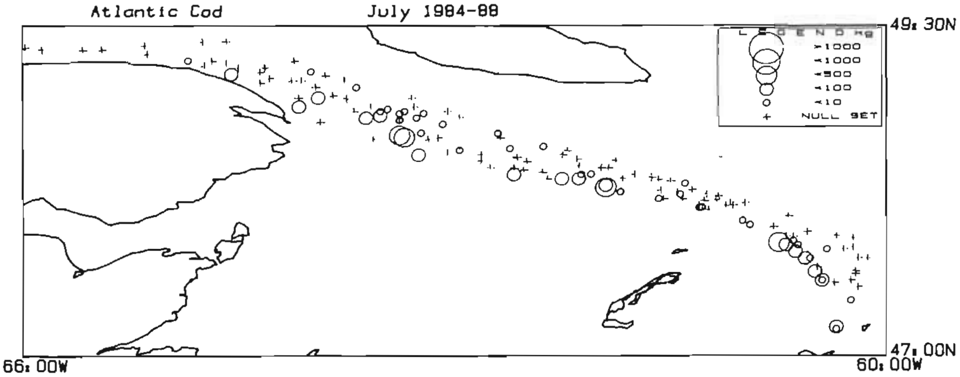


FIG. 7. January distribution of catch (kg) of Atlantic cod (*Gadus morhua*) in the area of NAFO division 4T beyond our seasonal surveys (combined data for 1984 to 1988). Null sets are sampling sites were none of this species were caught.

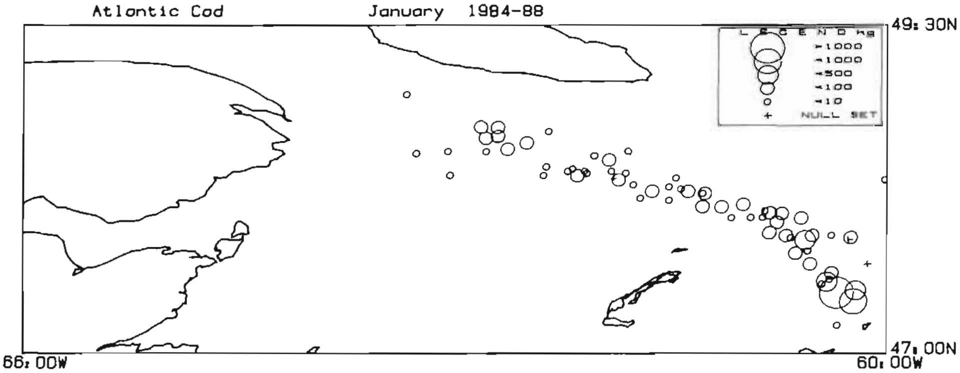


FIG. 8. July/August distribution of catch (kg) of Atlantic cod (*Gadus morhua*) in the area of NAFO division 4T beyond our seasonal surveys (combined data for 1984 to 1988). Null sets are sampling sites were none of this species were caught.

of these fish were passing through the study area, probably to the south and west of the Magdalen Islands. The extended surveys in July/August showed the presence of cod along the southern slopes of the Channel with low numbers on the sea floor of the Channel (Fig. 8).

The few fish remaining in shallow waters (strata 403, 432 to 434) in January were smaller (modal length in individual sets of 10 to 29 cm) than fish found in the same strata in September (modal length 40–59 cm). If these smaller fish do remain in the Gulf, it could reduce the fishing mortality of these juveniles from what might otherwise be expected in the January to May fishery in NAFO sub-division 4Vn (Sydney Bight). These smaller cod would be subjected to colder water (mean 1.2°C in January and −0.4°C in May) in the shallow inshore strata than would the adult fish which migrated out of the southern Gulf. Kao and Fletcher (1988) showed how juvenile cod were more resistant to freezing than adults due to higher levels of antifreeze proteins in their blood. This may account for the observed differential migratory patterns.

Cod is the dominant finfish in terms of biomass in the southeastern Gulf, thus seasonal change in total finfish biomass (all species) is largely a reflection of changes in cod abundance (Fig. 6). The biomass of Atlantic cod estimated for the entire southern Gulf from annual September surveys (1971–1985) ranged from 75 000 to 350 000 t (mean 175 000 t) (Clay 1986).

The annual September surveys indicated the main cod concentration in NAFO division 4T was the southwestern part of the Gulf. Because of their well known migration pattern, southern Gulf cod have been managed as April to December NAFO division 4T (Gulf) cod and January to May NAFO sub-division 4Vn (Sydney Bight) cod. Past tagging studies have outlined the scope of this seasonal migration (McKenzie 1941, McCracken 1959, Powles 1959 and Martin 1962). This study permits a more accurate estimate of movement timing. The cod biomass does not appear to be in a state of change during September and thus, as indicated by Koeller (1981), September appears to be the optimum time for a cod survey.

White hake (*Urophycis tenuis*, Mitchill)

The seasonal change in biomass of white hake does not follow the same trend as that of cod (Fig. 9). There was no increase in December, although a greater biomass was found in June than in May or September (Fig. 6). Both seasonal September surveys indicated that hake were found in two distinct concentrations, one in the shallow inshore area off the eastern end of PEI (Northumberland Strait), the other in the deeper waters of the Cape Breton Trough and the adjoining southern slope of the Laurentian Channel.

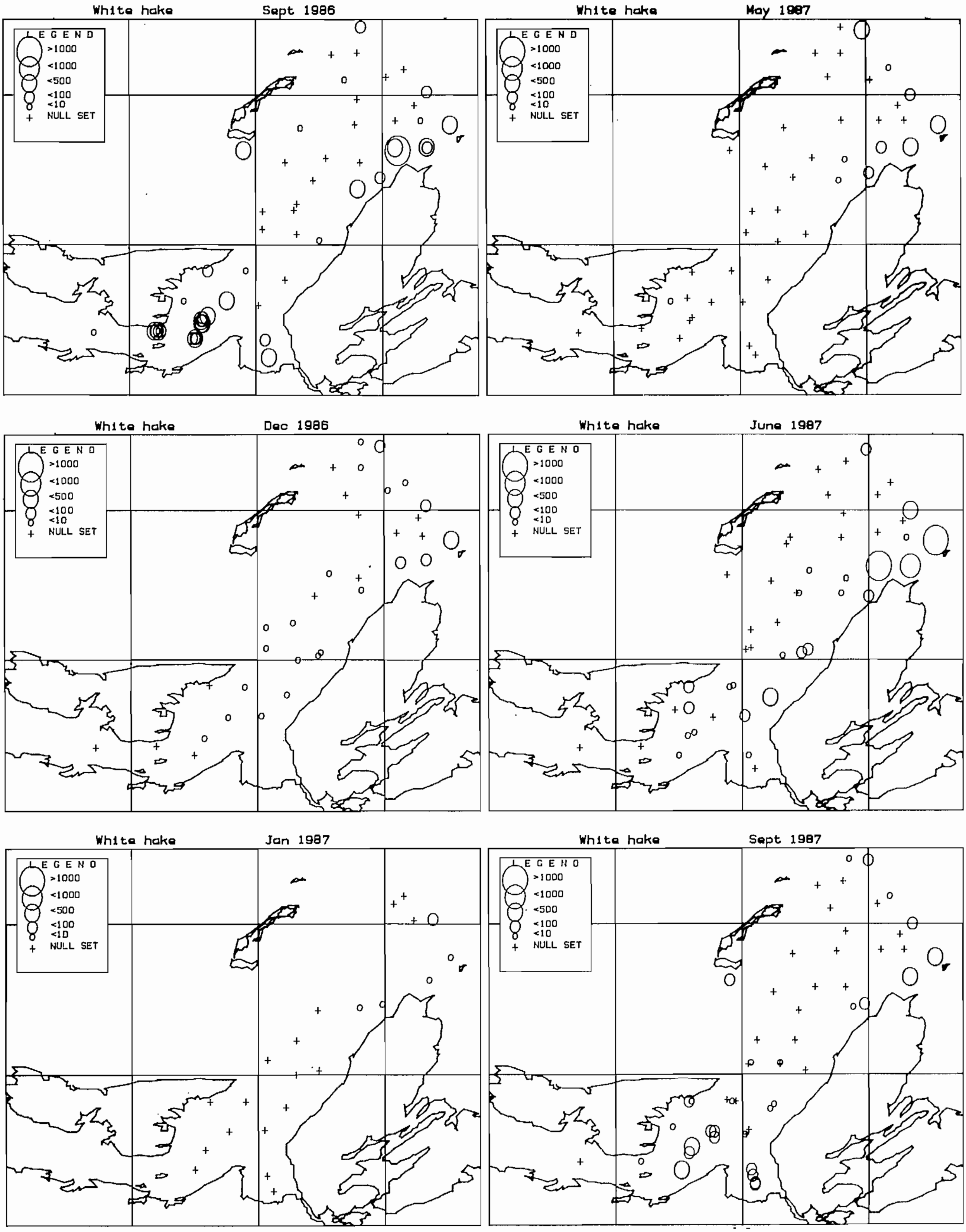
In December, the hake biomass in the study area declined to 20% of that observed in September (Fig. 6). The concentrations moved to the slope areas below 100 m depth and only a few stragglers remained in the 40–100 m depth range (Fig. 9). The few remaining hake were juveniles (modal length in individual sets of 10–29 cm) compared to the mixed size population observed in September (modal size 30–49 cm). By January, no major concentrations were found in the survey area: the few remaining fish were found in depths exceeding 100 m. Their biomass in the southeastern Gulf had declined to <1% of that in September (Fig. 6). Data from the extended surveys in January (Fig. 10) indicated that hake were found at depths over 200 m and were widespread from Anticosti Island eastward to the survey limits. This is the probable overwintering area for 3 groups of hake, the inshore and offshore components of the southern Gulf, and the northern Gulf group (NAFO divisions 4R and 4S).

The May survey indicated that the return migration began with hake massing along the slope and in the Cape Breton Trough below 100 m. One month later, in June, hake dispersed to all areas previously occupied in September, except to the shallows immediately south of the Magdalen Islands. Large concentrations still existed in the mouth of the Cape Breton Trough and in the Trough itself as they continued to move to the waters off eastern PEI and St. Georges Bay. The biomass in June exceeded that of September. The additional fish probably being transients moving south of the Magdalen Islands towards the waters of western PEI and the New Brunswick shore. Data from the extended surveys in July/August indicated that limited concentrations of hake occurred above 250 m with low numbers occurring to 300 m (Fig. 11).

White hake biomass estimates for the entire southern Gulf from the annual September surveys (1971 to 1985) ranged from 4 500 to 35 000 t (mean 14 500 t) (Clay 1986). White hake distribution observed from the annual September surveys has two geographically recognizable components (Clay and Hurlbut 1989). An inshore component occurs in Northumberland Strait and includes fish at both the east and west ends of P.E.I. The offshore component includes hake occurring along the slopes of the Laurentian Channel from Cape Breton Island to Quebec. A cross-tabulation of depth and catch for three of the annual September surveys (1985–1987) of the entire southern Gulf indicated that hake did not occur between 55 and 110 m depth, confirming the two component observation. The offshore component of southern Gulf white hake forms a continuum with the concentrations to the east along the slopes of the Laurentian Channel in NAFO division 4Vn (Scott 1981). There is also probable mixing with hake from the north in NAFO divisions 4R and 4S.

White hake from the inshore component followed a migration pattern out of the shallows in winter to the deeper slope waters as inferred by Kohler (1971), who noted that his tagging results may have been biased by the geographically and temporally limited commercial hake fishery. His data indicated that at least a portion of fish from the inshore did return, although substantial mixing could have occurred with both the offshore slope component and those hake observed in the northern Gulf of St. Lawrence (Clay and Hurlbut 1989).

A cross-tabulation of the three annual September surveys of the entire southern Gulf incorporating bottom temperature with both mean size and total hake caught, indicated that hake were found between 1 and 13°C in September with peak catches occuring at about 8°C. The largest fish were progressively more common in temperatures below 10°C with the greatest concentrations



White hake Sept 1986

White hake May 1987

White hake Dec 1986

White hake June 1987

White hake Jan 1987

White hake Sept 1987

FIG. 9. Seasonal distribution of catch (kg) of white hake (*Urophycis tenuis*) in 1986 and 1987. Null sets are sampling sites were none of this species were caught.

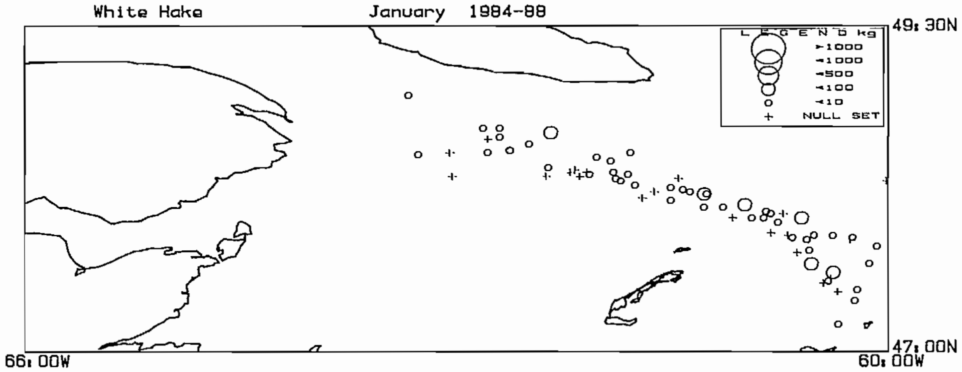


FIG. 10. January distribution of catch (kg) of white hake (*Urophycis tenuis*) in the area of NAFO division 4T beyond our seasonal surveys (combined data for 1984 to 1988). Null sets are sampling sites were none of this species were caught.

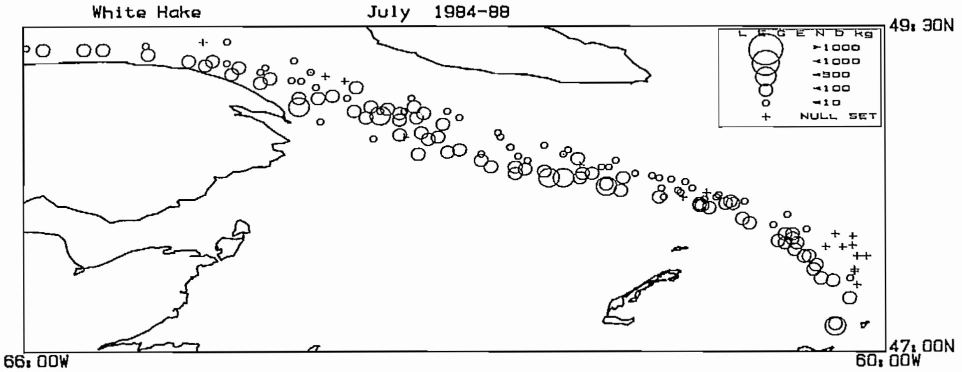


FIG. 11. July/August distribution of catch (kg) of white hake (*Urophycis tenuis*) in the area of NAFO division 4T beyond our seasonal surveys (combined data for 1984 to 1988). Null sets are sampling sites were none of this species were caught.

between 2 and 4°C. This agrees with the observations of Musick (1974) who discussed seasonal hake movements and came to the conclusion that "the adults being cool water fish, are barred from the shallows in summer by the high temperatures ...".

Flatfish, family Pleuronectidae

American plaice (*Hippoglossoides platessoides*, Fabrius)

Plaice exhibited a distribution similar to cod in both of the September seasonal surveys, except that plaice are only sparsely distributed in Northumberland Strait, off eastern PEI and at depths over 80 m along the southern slope of the Laurentian Channel (Fig. 12). In December, the concentrations moved to depths beyond 100 m along the slopes of the Channel and in the Cape Breton Trough. Only a few smaller fish (modal lengths in individual sets 10-19 cm) remained in the shallow areas (strata 403, 432 to 434) compared to the same areas in September (modal lengths of 20-39 cm). In January the low density found in the shallows in December persisted and the concentrations found in the deeper waters left the study area. These smaller plaice, similar to the small cod that remained in the shallows, would have been subjected to colder winter water temperatures than the adults. By January the plaice biomass had reached its lowest value of 3% of that observed in September (Fig. 6). Data from the extended surveys in January (Fig. 13) indicated an extensive concentration in the deep water of the Laurentian Channel between Anticosti Island and the Magdalen Islands. In the deeper waters north of the limits of our seasonal surveys lower densities with widespread distribution were observed.

In May, the plaice returned, moving in a southerly direction. By June, the spring migration appeared to be complete (Fig. 6). The plaice biomass in the study area was higher in June than in either May or September, implying additional fish passed through the southeastern Gulf to the shallows west and south of the Magdalen Islands. Data from the extended surveys in July/August indicated that no plaice remained in waters over 300 m and only small numbers were present in the remainder of the extended survey range (Fig. 14).

American plaice are considered a single management unit in NAFO division 4T despite Powles (1963) having described two ecological groups, east (present study area) and west of the Magdalen Islands. American plaice biomass estimates for the entire Gulf from the annual September surveys (1971 to 1985) ranged from 50 000 to 200 000 t (mean 104 000 t) (Clay 1986).

Powles (1963) noted that plaice in the southwestern Gulf exhibited a similar movement pattern to that observed in this study, plaice moved from the shallows to depths in excess of 185 m along the Laurentian Channel. The plaice in the southeastern Gulf moved to the warmer slope waters of the Laurentian Channel to overwinter, rather than leaving the Gulf, as did the cod. At

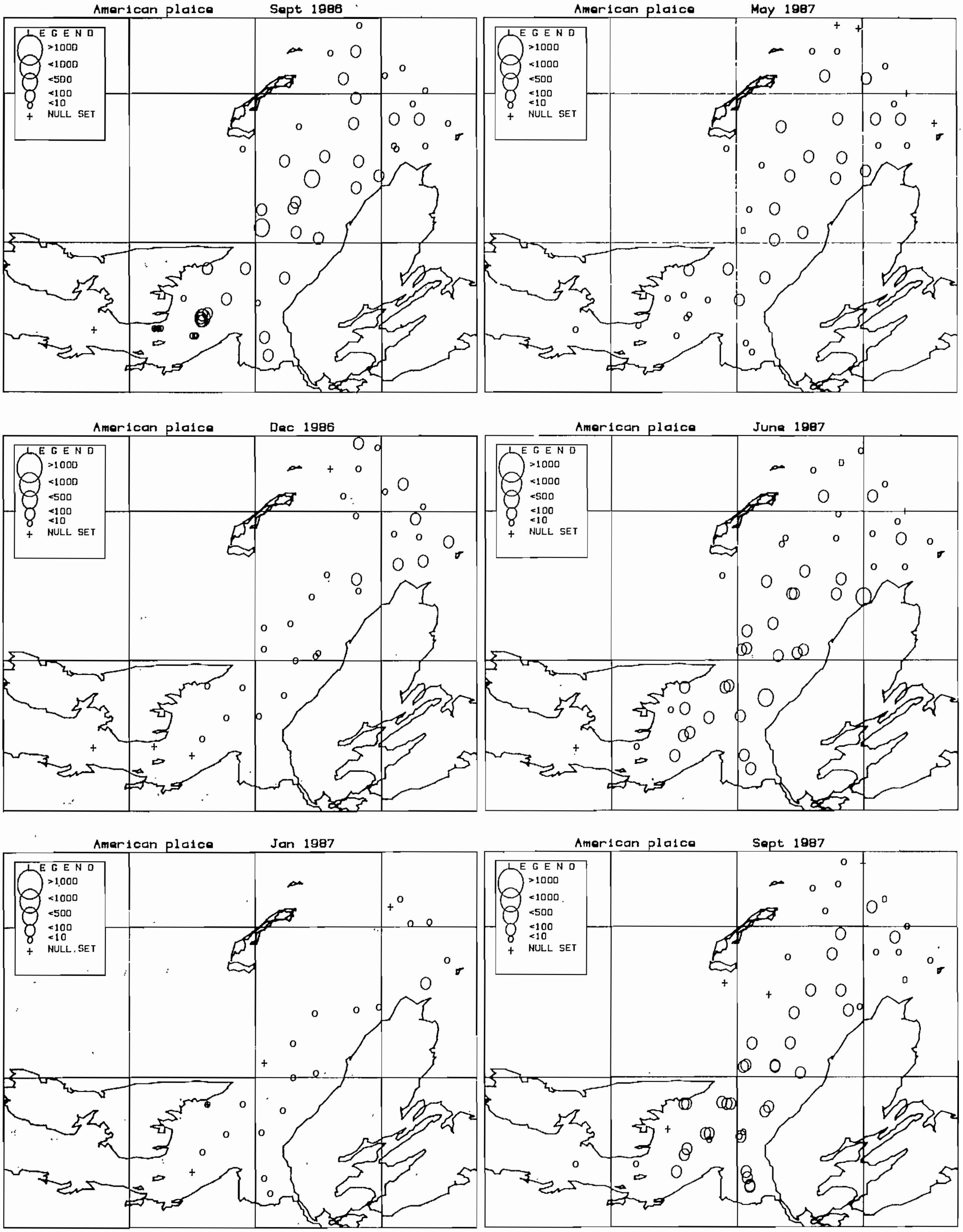


FIG. 12. Seasonal distribution of catch (kg) of American plaice (*Hippoglossoides platessoides*) in 1986 and 1987. Null sets are sampling sites were none of this species were caught.

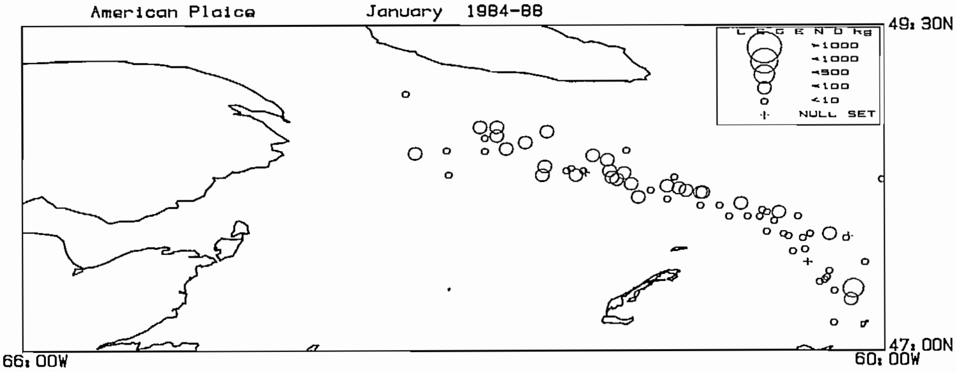


FIG. 13. January distribution of catch (kg) of American plaice (*Hippoglossoides platessoides*) in the area of NAFO division 4T beyond our seasonal surveys (combined data for 1984 to 1988). Null sets are sampling sites were none of this species were caught.

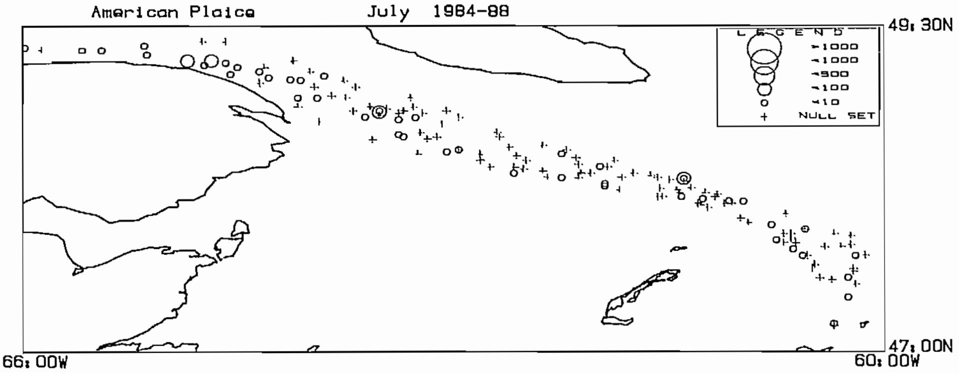


FIG. 14. July/August distribution of catch (kg) of American plaice (*Hippoglossoides platessoides*) in the area of NAFO division 4T beyond our seasonal surveys (combined data for 1984 to 1988). Null sets are sampling sites were none of this species were caught.

those depths only minor seasonal temperature changes occur (Powles 1963; Trites 1972).

Yellowtail flounder (*Limanda ferruginea*, Storer)

In the seasonal September survey of the southeastern Gulf, yellowtail appeared restricted to waters less than 60 m in depth, with two separate geographic concentrations — one north of the Magdalen Islands and the other between P.E.I. and Cape Breton Island (Fig. 15). The areas of highest abundance also had the largest fish (modal length in individual sets of 20 to 39 cm). In January, yellowtail biomass was 8 percent of that found in September, the remaining fish were dispersed over a wide range of depths. In December and January, most of the yellowtail moved to deeper waters. The group near the Laurentian Channel was observed between 40 and 100 m in December and over 100 m in January. The group nearest P.E.I. moved to water over 40 m in December. Size segregation did appear to occur in this latter area. The largest fish (mean length 36 cm) moved to the Cape Breton Trough, the intermediate fish (mean length 32 cm) remained in the 60–80 m depth range and the smallest fish (mean length 24 cm) were found in the 40–60 m depths. In January the smallest fish still remained in the 40–60 m depths, while the intermediate sized fish moved into the deeper waters of the Cape Breton Trough. In the extended survey in January only limited numbers of yellowtail occurred in 10 of the 70 sets in the Laurentian Channel. As with cod and plaice, smaller yellowtail perform more limited migrations and appeared to be more tolerant of cold water than larger yellowtail.

In May all sizes of fish were in the process of returning to the shallows, concentrations were observed off eastern P.E.I. and north of the Magdalen Islands. By June the return to the shallows (<40 m) was complete and the distribution was similar to that of September. The July/August extended surveys recorded that no yellowtail were present below 100 m.

Yellowtail biomass estimates for the entire southern Gulf from the annual September surveys (1971–1980) ranged from 1 800 to 8 100 t (mean 4 100 t) (Koeller and LeGresley 1981). Due to the low abundance of this species, there is only a limited commercial fishery. Little research has been conducted on this species in the Gulf of St. Lawrence.

Winter flounder (*Pseudopleuronectes americanus*, Walbaum)

In the September seasonal surveys of the southeastern Gulf, winter flounder were found in water less than 40 m deep (Fig. 16). Winter flounder dispersed to the deeper waters (>60 m) in December, however, unlike yellowtail they did not totally leave the shallows even in January. There was no apparent change in size composition during these months. The fish began concentrating in shallow waters in May and by June they had moved

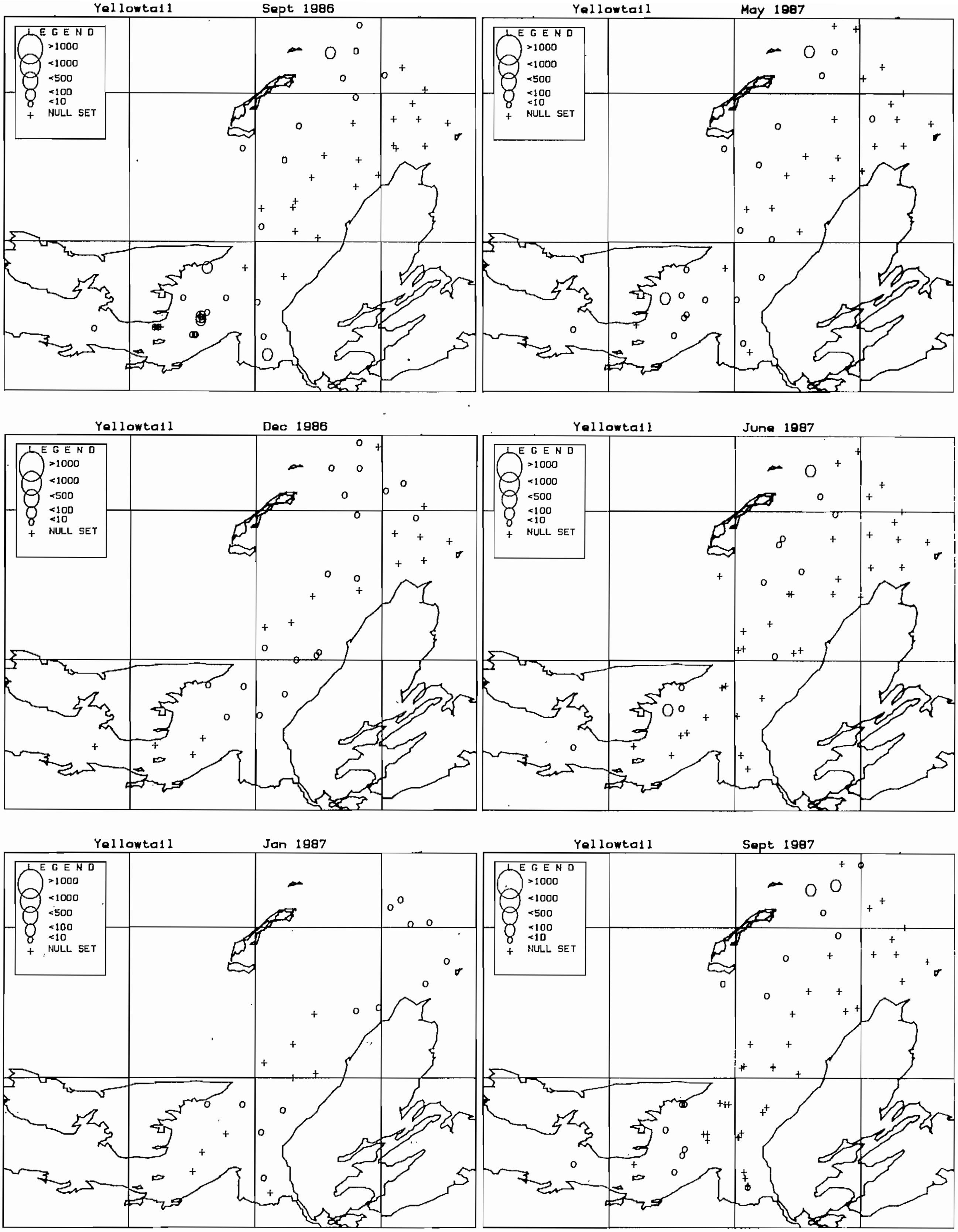


FIG. 15. Seasonal distribution of catch (kg) of yellowtail flounder (*Limanda ferruginea*) in 1986 and 1987. Null sets are sampling sites were none of this species were caught.

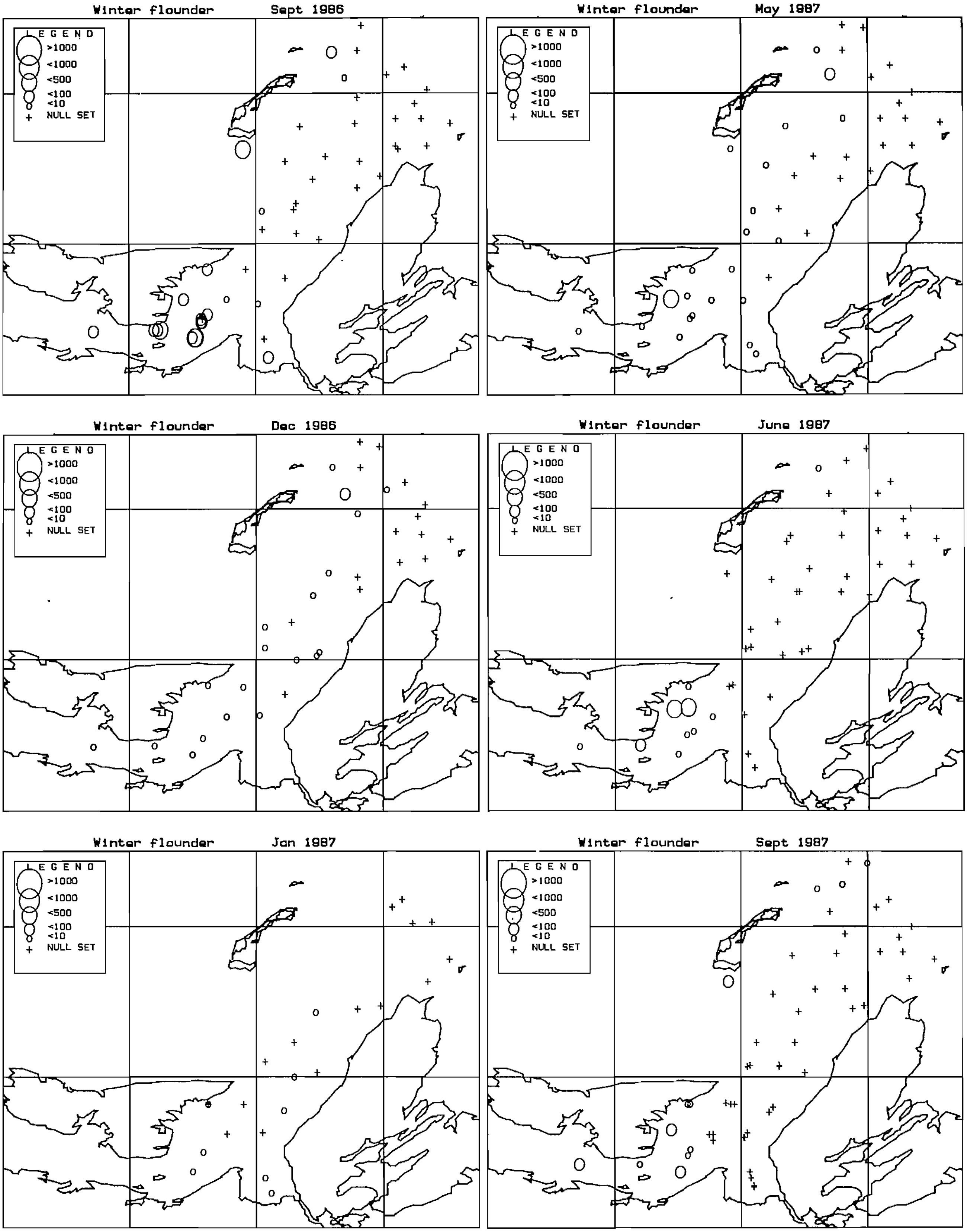


FIG. 16. Seasonal distribution of catch (kg) of winter flounder (*Pseudopleuronectes americanus*) in 1986 and 1987. Null sets are sampling sites were none of this species were caught.

away from all waters over 40 m deep. No winter flounder were recorded in either the summer or winter extended surveys conducted in the northern part of NAFO division 4T. This species appears to be able to withstand the cold water of the southern Gulf in winter. Fletcher (1977) found winter flounder to be capable of manufacturing antifreeze proteins in response to environmental cooling.

Winter flounder biomass estimates for the entire southern Gulf from the annual September surveys (1971–1980) ranged from 4 400 to 37 600 t (mean 13 800 t) (Koeller and LeGresley 1981). Like yellowtail flounder there exists only a limited commercial fishery in the southern Gulf, and little research has been conducted on migration.

Sculpins, family Cottidae

Longhorn sculpin, (*Myoxocephalus octodecemspinosus,* Mitchill)

The seasonal September surveys indicated all longhorn sculpins in the southeastern Gulf were in shallow water less than 40 m deep (Fig. 17). Substantial concentrations occurred in Northumberland Strait. In December, sculpins dispersed to the northeast of P.E.I. between 60 and 100 m. These fish appeared able to withstand the cold water of the southern Gulf. The shorthorn sculpin (*M. scorpius*) has been shown to produce antifreeze proteins (Hew et al. 1980). This, coupled with the indirect evidence of cold tolerance by longhorn sculpins, implies that they are probably able to produce an antifreeze protein similar to the shorthorn sculpin.

Distribution did not appear to change in January or May. However, by June the fish had returned to depths less than 60 m. By September they were generally distributed in depths less than 40 m. The July/August extended surveys caught no longhorn sculpins in the Laurentian Channel and in January only 4 sets of 70 had sculpins present.

Longhorn sculpin biomass estimates for the entire southern Gulf from the annual September surveys (1971–1980) ranged from 540 to 4 700 t (mean 1 500 t) (Koeller and LeGresley 1981).

Skates, family Rajidae

Thorny skate, (*Raja radiata,* Donovan)

In the September seasonal surveys of the southeastern Gulf thorny skate were widely distributed in all areas except Northumberland Strait and the shallows off eastern P.E.I. (Fig. 18). In December, most thorny skate moved deeper than 60 m, concentrating along the southern slopes of the Laurentian Channel. By January, they had moved from water less than 100 m depth, and the concentrations along the slope appeared to move to deeper water. Data from the extended surveys in January indicated that denser concentrations of thorny skate existed in the deeper waters, beyond the limits of our seasonal survey. A gradient existed with higher abundance in the more easterly portion of the Laurentian Channel towards Cape Breton Island. This implies an eastward movement along the floor and southern slopes of the Laurentian Channel during winter, possibly even out of the Gulf.

In May, thorny skate began returning to shallow water, moving up the Cape Breton Trough and the slope of the Laurentian Channel. By June the return was almost complete with only the furthest points, such as St. Georges Bay not recolonized. The extended July/August surveys indicated a patchy distribution with over half of the stations having no thorny skate and the remainder having only low numbers.

Thorny skate biomass estimates for the entire southern Gulf from the annual September surveys (1971 to 1980) ranged from 1 900 to 8 800 t (mean 4 700 t) (Koeller and LeGresley 1981).

Winter skate, (*Raja ocellata,* Mitchill)

The seasonal surveys in September indicated winter skate inhabited water less than 40 m deep around the Magdalen Islands and in the Northumberland Strait area (Fig. 19). By December they moved deeper than 40 m, with concentrations along the southern slopes of the Laurentian Channel above 100 m. In January the concentrations appeared between 100 and 200 m, although limited numbers were still found throughout much of the survey area at depths over 40 m. The January extended survey indicated that only limited numbers of winter skate occur in the Laurentian Channel, with higher densities in less than 200 m and towards Cape Breton Island.

In May this species moves up the slope and begins to recolonize waters less than 40 m in depth. By June they had left almost all areas deeper than 60 m and returned to the September distribution. The extended survey in July/August indicated no winter skate were present in the survey area of the Laurentian Channel.

Winter skate biomass estimates for the entire southern Gulf from the annual surveys (1971–1980) ranged from 500 to 1 700 t (mean 850 t) (Koeller and LeGresley 1981).

Smooth skate, (*Raja senta,* Garman)

The seasonal surveys in September indicated smooth skate occur only occasionally in the shallow water near the slopes of the Laurentian Channel and the Cape Breton Trough (Fig. 20). In other months these skates were almost always found in water over 100 m in depth and did not appear to migrate within the spatial limits of this survey. The extended surveys in July/August and January indicated a wide distribution with a relatively low but uniform abundance during both periods. The water temperature at these depths varied by only a degree over a year.

Smooth skate biomass estimates for the southern Gulf from the annual September surveys (1971–1980) ranged from 0 to 400 t (mean 145 t) (Koeller and LeGresley 1981). The limited range of distribution within our annual survey area and low sampling intensity for these surveys resulted in highly variable catches (eg. 2 yr had no occurrences).

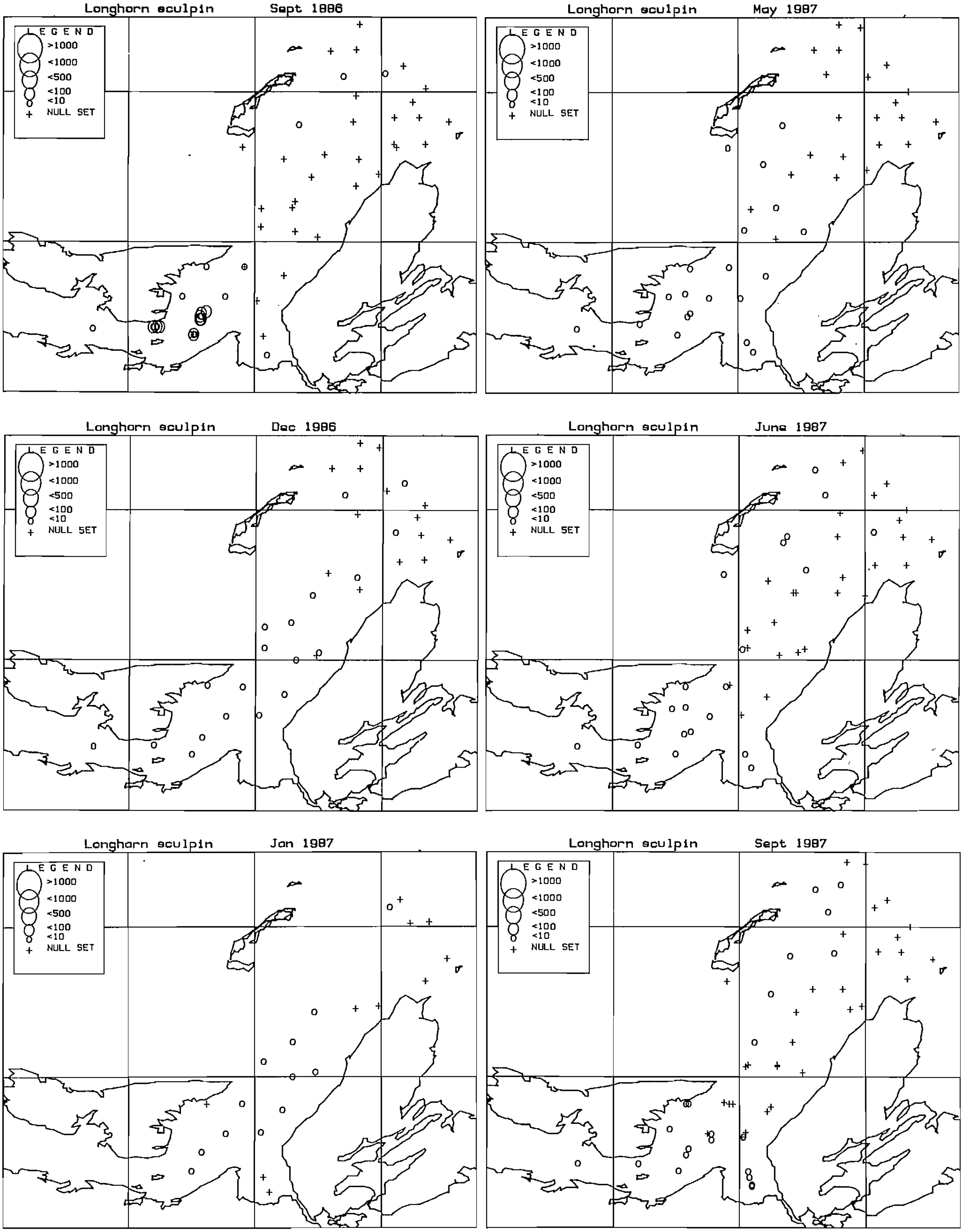


FIG. 17. Seasonal distribution of catch (kg) of longhorn sculpin (*Myoxocephalus octodecemspinosus*) in 1986 and 1987. Null sets are sampling sites were none of this species were caught.

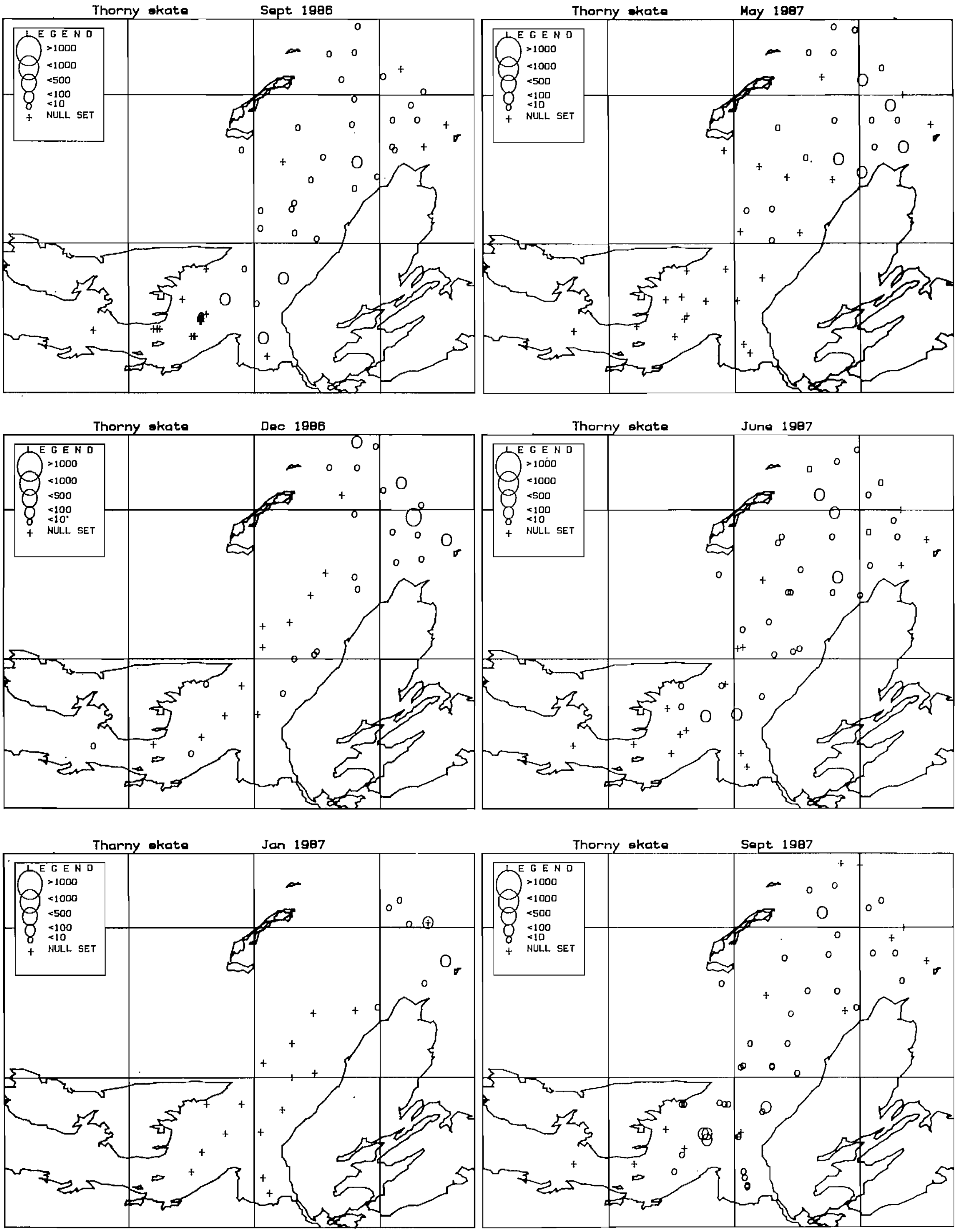


FIG. 18. Seasonal distribution of catch (kg) of thorny skate (*Raja radiata*) in 1986 and 1987. Null sets are sampling sites were none of this species were caught.

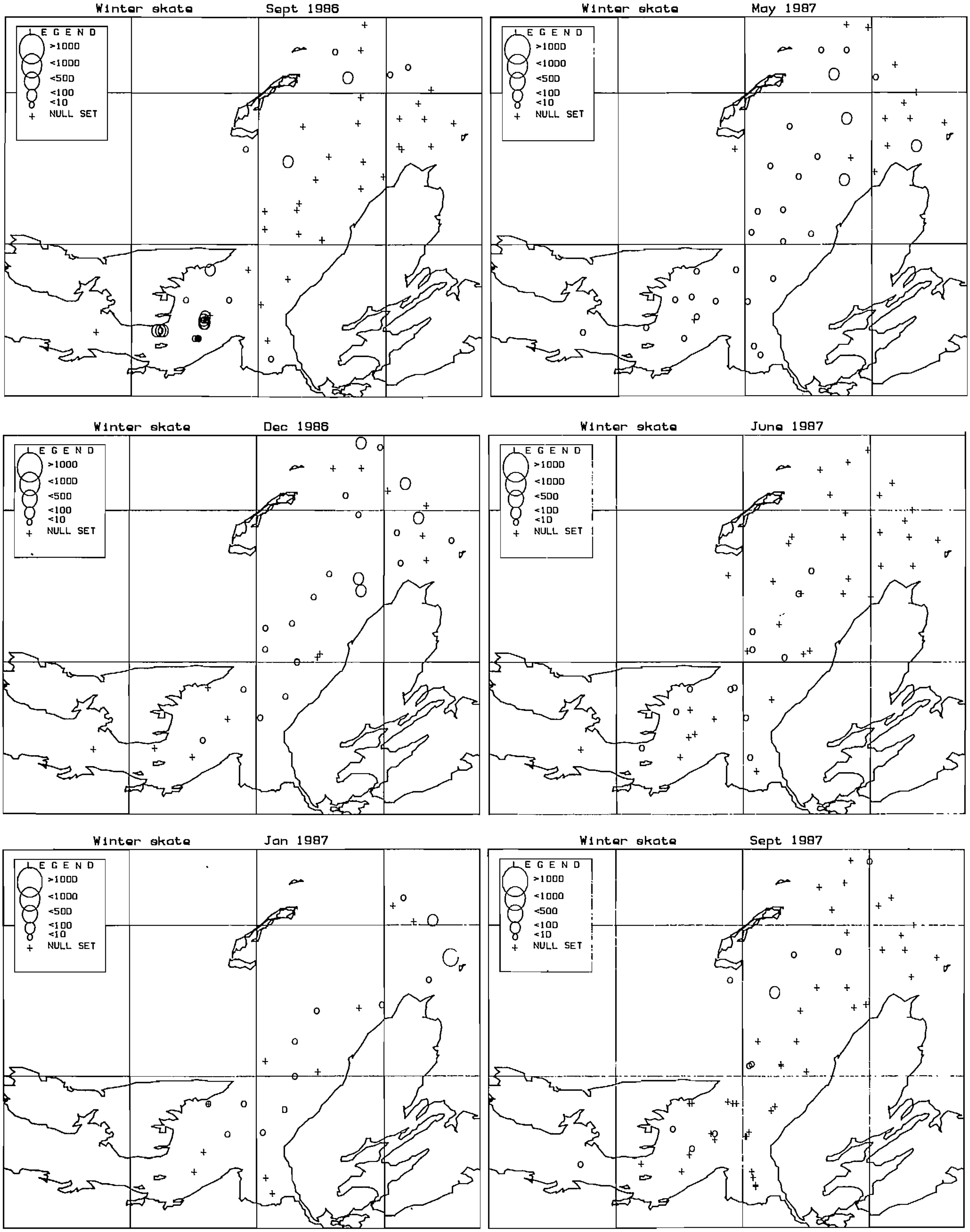
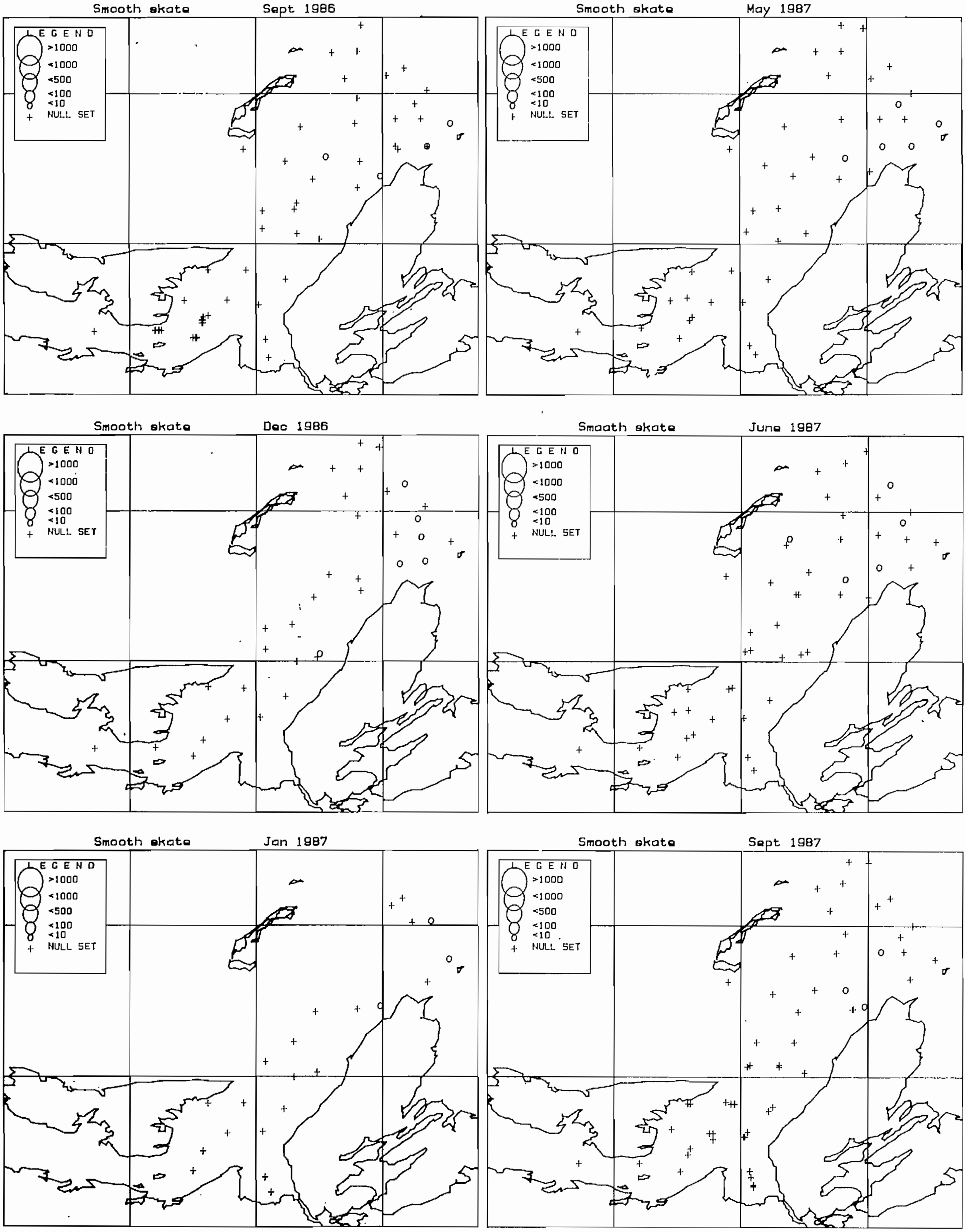


FIG. 19. Seasonal distribution of catch (kg) of winter skate (*Raja ocellata*) in 1986 and 1987. Null sets are sampling sites were none of this species were caught.



Smooth skate Sept 1986

Smooth skate May 1987

Smooth skate Dec 1986

Smooth skate June 1987

Smooth skate Jan 1987

Smooth skate Sept 1987

FIG. 20. Seasonal distribution of catch (kg) of smooth skate (*Raja senta*) in 1986 and 1987. Null sets are sampling sites were none of this species were caught.

Conclusions

The fish species investigated in this seasonal study comprised three broad groups. Cod, and possibly thorny skate, left the southern Gulf entirely in winter. Early tagging studies showed cod movement to the Atlantic side of Cape Breton Island. White hake, plaice, yellowtail, and winter skate moved from the shallow waters of the southern Gulf to deeper, warmer water in winter. Winter flounder, longhorn sculpins and smooth skate exhibited only localized movements. The latter remained in the deep water of the Laurentian Channel, and the former two species remained in shallow water throughout the year, indicating a tolerance to a great range of temperatures.

Information on species migrations allows assessment biologists to plan abundance surveys which minimize variability due to movement of the target species. The present study confirms that the annual southern Gulf survey is being conducted at the optimum time for assessing the majority of stocks, a similar conclusion to that of Koeller (1981).

Acknowledgements

Any series of surveys such as this requires much cooperation from many quarters. The crew and officers of the RV *Lady Hammond* and the RV *Alfred Needler* were extremely helpful during some very difficult situations.

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Tom Hurlbut acted as chief scientist for many of these cruises, he and Kim Skeffington were responsible for all data editing.

Estelle Leberge, Quebec Region, DFO, provided the data for that part of NAFO division 4T north of our survey area.

Data from the annual September suveys (1971 to 1982) were collected by the Maritimes Region of DFO (now reorganized into the Gulf Region and Scotia – Fundy Region).

Tom Hurlbut, Heather Clay, and Mike Chadwick provided valuable reviews and suggestions on earlier drafts of this paper.

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Comparative Growth of the Sea Scallop *(Placopecten magellanicus)* in the Southern Gulf of St. Lawrence[1]

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CHOUINARD, G.A., AND P.V. MLADENOV. 1991. Comparative growth of the sea scallop (*Placopecten magellanicus*) in the southern Gulf of St. Lawrence, p. 261-267. *In* J.-C. Therriault [ed.] The Gulf of St. Lawrence: small ocean or big estuary? Can. Spec. Publ. Fish. Aquat. Sci. 113.

Growth of the sea scallop (*Placopecten magellanicus*) from a site in Baie des Chaleurs (Nepisiguit) and two sites in Northumberland Strait (Cape Tormentine and Wood Islands) were compared. A mark-recapture study established the time of formation of the annual bands so that real age could be assigned which allowed pooling of samples from different times of the year and comparison of growth curves between sites. Growth rates were significantly different between the three sites. Scallops from Nepisiguit grew faster in terms of shell height. Wood Islands scallops had the second highest growth rate. Growth in shell weight was lowest at young ages (< 7 yr) for Nepisiguit, but highest for older animals (> 10 yr). Growth of sea scallops in Northumberland Strait is the lowest observed in the distribution range of the species. These low growth rates may have been caused by the rather limited period when temperatures are optimal for growth in this area.

La croissance du pétoncle géant (*Placopecten magellanicus*) d'un site dans la Baie des Chaleurs (Népisiguit) et de deux sites dans le Détroit de Northumberland (Cape Tormentine et Wood Islands) a été comparé. La période de formation des stries annuelles a été établie par une étude de marquage. Ceci a permis d'assigner un âge réel aux individus de sorte que les échantillons recueillis à différentes périodes de l'année ont pu être regroupés pour la comparaison des courbes de croissance. Celles-ci étaient significativement différentes entre les sites. La croissance en hauteur de la coquille était plus rapide pour les pétoncles de Népisiguit, suivi de celles de Wood Islands. La croissance en poids de coquille était moins élevée pour les jeunes pétoncles (moins de 7 ans) de Népisiguit, mais la plus élevée pour les animaux agés de plus de 10 ans. La croissance des pétoncles du Détroit de Northumberland est la moins élevée dans l'aire de distribution de cette espèce. Ces taux de croissance bas dans cette zone auraient pu être causés par la période limitée de températures optimales pour la croissance.

Introduction

The giant sea scallop (*Placopecten magellanicus* (Gmelin)) occurs only in the waters of the northwest Atlantic, ranging from Cape Hatteras (35°N) to the Strait of Belle Isle (52°N) (Posgay 1957; Squires 1962). Several growth studies have been conducted on this species in the past, but mostly on scallops from the Bay of Fundy and the Gulf of Maine (Stevenson 1936; Stevenson and Dickie 1954; Merrill et al. 1966; Posgay 1979). Studies conducted in the Gulf of St. Lawrence include one by Jamieson (1979) in Northumberland Strait, a more detailed work by Naidu (1969) in Port-au-Port Bay, Newfoundland and a study by D'Amours and Pilote (1982) on the lower north shore of Quebec. These studies showed that scallops from the Gulf of St. Lawrence generally have slower growth rates than those from the Gulf of Maine and Bay of Fundy. Differences in growth, in terms of both shell height and adductor muscle weight, have also been observed within the Gulf of St. Lawrence (Bourne et al. 1965; Jamieson 1979). In the Pectinidae, differences in growth have been ralated, in most cases, to water temperature and food availability (Mason 1957; Leighton 1979; Gruffydd 1981; Richardson et al. 1982; MacDonald and Thompson 1985).

Information on growth of a given species is particularly useful in fisheries management for the determination of optimal yield per recruit. For the sea scallop which

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is amenable to aquaculture, growth information can be an important consideration during site selection. Generally, it is desirable to conduct comparisons of growth performance between populations to determine whether a common strategy can be used or which site has better potential for aquaculture. In the southern Gulf of St. Lawrence, where scallops are fished commercially and potential for aquaculture of this species is apparent, such comparisons are of interest.

Statistical comparisons of growth rates using the von Bertalanffy equation are not easily done because of the non-linear formulation of the model and the high degree of correlation between the parameters (Moreau 1987). Several methods have been suggested (Gallucci and Quinn 1979; Misra 1980; Kimura 1980; Bernard 1981; Kirkwood 1983) to conduct the comparisons, however, in most cases the assumptions of the analyses are not fully met. In his motion for the retirement of the von Bertalanffy equation, Roff (1980) suggested that a quadratic polynomial (parabola) was a sufficient approximation of the von Bertalanffy function. This approach is particularly interesting since theory from linear models is applicable. MacDonald and Thompson (1985) used polynomial equations to compare somatic growth rates of the sea scallop.

The primary objective of this study on the growth of the sea scallop was to describe and compare statistically the shell growth of animals from three sites in the southern Gulf of St. Lawrence. Inferences as to the effect of the temperature regimes on growth were also made.

Materials and Methods

Study Sites

Scallops from three separate sites of comparable bathymetry in the southern Gulf of St. Lawrence (Fig. 1) were studied. The Cape Tormentine site was located in the center of Northumberland Strait. Depth varied between 19 and 22 m. The Nepisiguit site, located at the entrance of Bathurst Harbour, New Brunswick, had a mean depth of 19 m (range 16–21 m). The Wood Islands site was located in eastern Northumberland Strait near the Indian Rocks shoals. Depth varied from 17 to 22 m.

Sediments on the Northumberland Strait sites were composed mainly of small rocks, shells and silt. On the Nepisiguit site, sediments were a mixture of smaller rocks, gravel and shells.

Time of Formation of Annual Bands

A tagging experiment was conducted in the fall of 1983 (12–19 September and 20–21 October) at the Nepisiguit site to determine the time of formation of the annual bands on the shell of the sea scallop. This information combined with the number of annual bands and the timing of the spawning period would allow calculation of the "real" age (i.e. life duration from larval settlement to death) of the animals so that samples from the same site but taken at different times could be pooled. Scallops were collected with a scallop dredge and placed in tanks containing seawater. Each animal was measured (shell height) to ensure that shock marks would not be confused with annual bands upon recovery. They were tagged by attaching a numbered Petersen disk to the anterior auricula. Some animals were then released in the collection area ($n = 408$) while others ($n = 656$) were placed into a 25 by 25 m underwater quadrat at a depth of 15 m located approximately 19 km away near Stonehaven, N.B. (Fig. 1); a more accessible site for divers. Scallop samples were retrieved from the quadrat on 14 December 1983 ($n = 11$) and 5 April ($n = 7$), 24 May ($n = 19$), 6 June ($n = 15$) and 4 July 1984 ($n = 11$). No animals from the collection area were returned by commercial fishermen. The animals were later measured and the left valve was examined for evidence of ring formation. They were classified into three categories: (1) Ring absent: animals showing no evidence of ring formation since tagging (i.e. no evidence of new ring between the height of the shell at the time of tagging and the edge of the shell), (2) Ring forming: animals which showed evidence of new ring formation at the edge of the shell, but which did not show any "summer" growth (i.e. a light coloured band possessing more widely spaced increments) and (3) Ring complete: animals with a newly formed ring and evidence of summer growth.

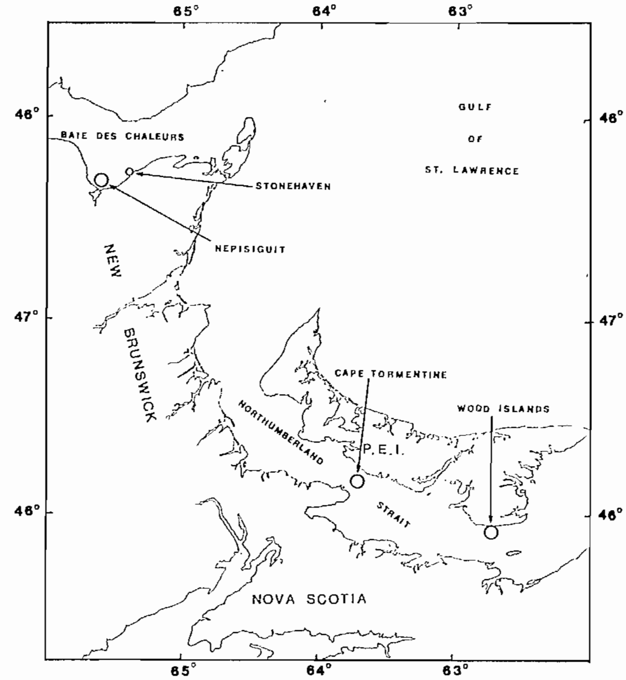

FIG. 1. The southern Gulf of St. Lawrence showing the locations of the study sites (large circles) and the Stonehaven site (small circle)

Shell Growth Rates

Random scallop samples were collected with a scallop dredge in 1982, 1983 and 1984 ($n = 1852$, Table 1). In the laboratory, the valves were cleaned of epibionts with a steel brush and dried in an oven at 70°C for 24 h and measured to the nearest mm. The shells were then weighed to the nearest 0.1 g. Annual bands were identified using the method described and validated by Stevenson and Dickie (1954) and Merrill et al. (1966). A reference collection of shells was first read to ensure consistent interpretations.

From the collection date and the information obtained on the band formation time, the "real" age was estimated assuming that peak spawning in the southern Gulf of St. Lawrence occurs around August–September. The gonadosomatic index, calculated from unpublished data for two

TABLE 1. List of samples collected for the study of shell growth rates.

Site	Date	Number of scallops
Cape Tormentine	July 7, 1983	174
Cape Tormentine	Nov. 11, 1983	202
Cape Tormentine	May 29, 1984	190
Nepisiguit	Aug. 5, 1982	47
Nepisiguit	June 30, 1983	79
Nepisiguit	Aug. 12, 1983	116
Nepisiguit	Sep. 16, 1983	110
Nepisiguit	Oct. 21, 1983	152
Wood Islands	June 4, 1982	43
Wood Islands	July 15, 1983	199
Wood Islands	Sep. 2, 1983	161
Wood Islands	Oct. 10, 1983	218
Wood Islands	July 5, 1984	161
	Total	1852

sites in the southern Gulf of St. Lawrence (J. Worms, Dept. of Fisheries and Oceans, Moncton, N.B. E1C 9B6), dropped sharply during this time period. From these observations, September 1 was arbitrarily chosen as spawning time.

Von Bertalanffy growth parameters were derived with a non-linear least squares fitting technique using a Marquardt algorithm (procedure NLIN within the Statistical Analysis System (SAS) software package, SAS Institute Inc. 1985).

Quadratic and cubic polynomial models were derived to determine the best fit of the data and the form which most closely approximated the von Bertalanffy model. In all cases, the cubic term was significant.

The independent variable (age) was first centered to reduce the effects of multicolinearity in this type of regression (Sokal and Rohlf 1981; p. 677) . It is usually suggested that the independent variable be centered around its mean (Sokal and Rohlf 1981; Neter at al. 1983). In this case, however, since it is desired to compare the curves, a common scaling factor was necessary. The rounded mean age for all sites (6) was used as scaling factor. Consequently, in all polynomial regressions, the independent variable (X) took the value of (Age – 6) for each observation. The aptness of each model was investigated through residual analysis.

Model equations were compared using an analysis of variance for testing equality of regression coefficients (Rao 1973; p. 281–284). Polynomial equations were first fitted for each site by sex and tested for difference in growth by sex. If differences were not significant, data for each site were combined and new equations derived.

Results

Formation of Annual Lines

Most of the scallops recovered ($n = 68$) during the study showed some growth since being tagged in the fall of 1983. The animals that had no apparent growth ($n = 5$) were all larger than 120 mm except for one individual of 109 mm. Animals recovered on December 14, 1983 ($n = 11$) showed an average increase in size since tagging of approximately 1.5 mm; however only 2 showed any evidence of ring formation (Table 2). Animals recovered on April 5, 1984 were all in the ring formation stage. The animals collected after April 5 were in various stages of ring completion. The results indicate that ring formation is an extended process occurring over a period of approximately 6 months (December–June). Annual bands are probably discernible by March 1 on most individuals.

Shell Growth Rates

Growth in Shell Height

A previous study (Naidu 1975) concluded that there was no significant difference in growth according to sex in this species. Comparisons of growth in shell height by sex failed to reject the null hypothesis of no difference in growth according to sex ($P > 0.05$) for each site. The power of the test was not calculated, however, sample sizes were large in all cases (> 149). In addition, there was no consistent pattern of growth by sex between sites and predicted values for the oldest age did not differ by more than 1.5 cm. Therefore, the data for the separate sexes were pooled for each site. The von Bertalanffy and the cubic polynomial models described the pooled data on growth in shell height equally well (Table 3). It should be noted that the polynomial model was not considered to provide a biological description of growth in shell height, but was used only as an approximation of the von Bertalanffy model for comparison purposes.

Comparisons of the cubic growth equations between the three sites indicated significant differences in shell growth rates ($P < 0.001$) (Table 4). The Nepisiguit site had the fastest growth rate followed by Wood Islands and Cape Tormentine (Fig. 2).

Growth in Shell Weight

From examination of residual patterns, a square root transformation was necessary to remove the heteroscedasticity in the shell weight data. Parameters of the cubic polynomial equations are presented in Table 5. Comparisons of the cubic polynomial equations (Table 6) revealed significant differences in the growth patterns between sites ($P < 0.001$). Up to about 7 yr of age, Wood Islands scallops had the fastest growth rate in terms of shell weight followed by Cape Tormentine and Nepisiguit (Fig. 3). Growth of older animals (> 10 yr) was fastest at Nepisiguit.

TABLE 2. Stage of annual band formation of tagged scallops recovered from the Stonehaven site.

Date recovered	Number recovered	Stage of band formation		
		Absent	Forming	Complete
Dec. 12, 1983	11	9	2	
Apr. 5, 1984	7		7	
May 25, 1984	19		14	5
June 6, 1984	15		5	10
July 4, 1984	11			11

TABLE 3. Summary of von Bertalanffy (a) and cubic polynomial (b) parameters of the growth curves in shell height for the three sites investigated (*L*.inf., K and t_0 are the coefficients of the von Bertalanffy growth equation; β_0, β_1, β_2 and β_3 are the coefficients of the cubic polynomial; r^2 is the coefficient of determination and n is sample size).

	Cape Tormentine	Nepisiguit	Wood Islands
a) Von Bertalanffy			
L inf.	108	141	120
K	0.3380	0.1926	0.2757
t_0	0.6646	−0.4582	0.1236
r^2	0.91	0.89	0.89
n	566	500	785
b) Cubic polynomial (where X = Age-6)			
β_0	90.1048	100.6964	96.8686
β_1	5.5475	7.8859	6.5657
β_2	−1.1763	−0.7908	−1.0566
β_3	0.1632	0.0403	0.0821
r^2	0.91	0.89	0.89
n	566	500	785

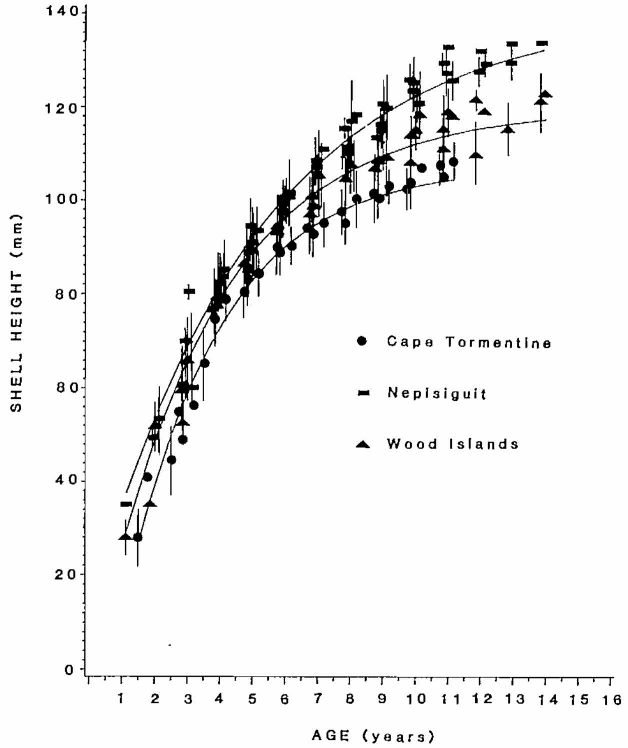

FIG. 2. Von Bertalanffy growth curves fitted to the growth in shell height for the three sites (Mean +/− 1 SD) Points with no bars have 3 observations or less.

TABLE 4. Results of the analyses of variance for the comparison of the cubic polynomial equations of growth in shell height between sites (***: $p < 0.001$).

Source	SS	DF	MS	F
a) Cape Tormentine vs Nepisiguit				
Deviation	264043.43	4	66010.86	3376.51***
Separate	20681.27	1058	19.55	
Common	284724.70	1062		
b) Cape Tormentine vs Wood Islands				
Deviation	31212.01	4	7803.00	328.27***
Separate	31952.99	1344	23.77	
Common	63165.00	1348		
c) Nepisiguit vs Wood Islands				
Deviation	8989.51	4	2247.38	60.77***
Separate	47265.89	1278	36.98	
Common	56255.40	1282		

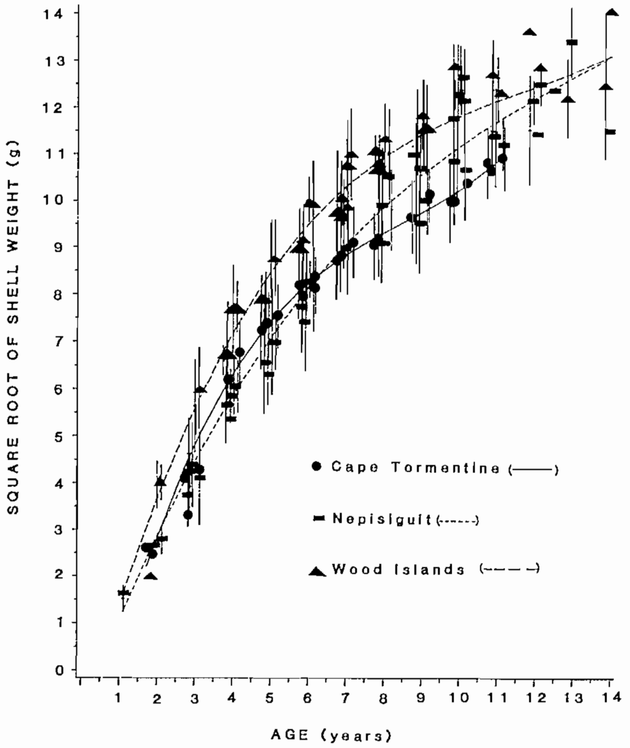

FIG. 3. Cubic polynomial curves fitted to the shell weight at age data (Mean +/− 1 SD). Points with no bars have 3 observations or less.

Discussion

The timing of the formation of the growth lines in the shells of the sea scallop in the southern Gulf of St. Lawrence is comparable to that reported for other populations. Stevenson and Dickie (1954) found that formation of the annual bands occurred between February and May in the Bay of Fundy with nearly 80% of the animals

TABLE 5. Parameters of the cubic polynomial equations describing growth in weight of shell for the three sites (where X = Age-6 and Y = square root weight (see text); β_0, β_1, β_2 and β_3 are the coefficients of the cubic polynomial; r^2 is the coefficient of determination and n is sample size).

Parameters	Cape Tormentine	Nepisiguit	Wood Islands
β_0	8.2335	8.1357	9.4898
β_1	0.6964	0.9947	0.9212
β_2	−0.1068	−0.0706	−0.1100
β_3	0.0144	0.0030	0.0064
r^2	0.77	0.86	0.89
n	566	496	786

TABLE 6. Results of the analyses of variance for the comparison of growth curves in weight between the three sites (***: $p < 0.001$).

Source	SS	DF	MS	F
a) Cape Tormentine vs Nepisiguit				
Deviation	57.76	4	14.44	23.99***
Separate	634.57	1054	0.60	
Common	692.33	1058		
b) Cape Tormentine vs Wood Islands				
Deviation	489.63	4	122.4	191.25***
Separate	870.97	1354	0.643	
Common	1360.60	1358		
c) Nepisiguit vs Wood Islands				
Deviation	443.66	4	110.91	151.66***
Separate	931.70	1274	0.7313	
Common	1375.36	1278		

showing ring formation by March 20. Naidu (1969) concluded that the formation of the annual ring for scallops in Port-au-Port Bay, Newfoundland occurs between March and May. From results of the present study, it appears that the period of ring formation is longer than in the Bay of Fundy, extending from December to June. Because the formation of the annual line is not an instantaneous process, the date of March 1 as the time of formation used in the present study is somewhat arbitrary. However, this date is consistent with observations made during the age reading. The last annual band was always near the edge in samples taken in the spring and early summer contrary to samples taken later in the year.

The overall results of the present study showed that growth in terms of shell height was fastest for the Nepisiguit site followed by Wood Islands and slowest at Cape Tormentine. Compared to the other scallop populations in the Northwest Atlantic, the Cape Tormentine population appears to have one of the lowest growth rates. Interestingly, the growth rates for Cape Tormentine and Wood Islands reported here are lower than those previously reported for the same area by Jamieson (1979) but are similar to the ones obtained by Lanteigne et al. (1987) when a half-year correction for real age is applied (i.e. compare an animal of 1.5 yr in this study to an animal of 2 yr in their study). The Nepisiguit population appears to be growing at a rate similar to the one observed for a population on the lower north shore of Quebec by D'Amours and Pilote (1982).

The pattern of growth in shell weight indicated that Wood Islands scallop had the fastest growth rate for animals less than 7 yr of age, while Cape Tormentine and Nepisiguit scallops had fairly similar growth rates for these ages (Fig. 3). For older scallops, growth rates for Wood Islands and Cape Tormentine declined while the growth rate of shell weight for Nepisiguit was maintained. These differences suggest that the utilization made of the energy available may also influences growth.

Pauly (1979, cited in Moreau 1987) proposed that the parameter K in the von Bertalanffy growth equation be considered as a "stress" factor rather than a coefficient of catabolism. A higher K for a particular population would mean that the animals are exposed to more adverse conditions for growth than a population with a lower K. Results obtained from this study are consistent with this idea. Jamieson (1979) suggested two environmental factors which make the Northumberland Strait a more stressful environment for sea scallops. Firstly the bottom sea temperatures observed are colder in winter (−2.0°C; Lauzier and Hull 1969) and warmer in summer (15–20°C; Dobson and Petrie 1982) than on other scallop beds such as Georges Bank and the Bay of Fundy. Secondly, bottom sediments on scallop beds in Northumberland Strait appear to contain more silt than areas such as Georges Bank. Within the southern Gulf of St. Lawrence, data from a long-term monitoring program indicate that bottom temperatures are generally warmer in central Northumberland Strait (Cape Tormentine) in summer while they are coldest in the Baie des Chaleurs (Dobson and Petrie 1982; 1983; 1984; 1985; Walker et al. 1987). For example, from data collected in 1983 (Dobson and Petrie 1984), the average temperature at 19 m in July and August at Shediac (near Cape Tormentine) was 17.3°C while it was 16.4°C at Pictou Island (near Wood Islands). Bottom temperatures in the Baie des Chaleurs averaged only 10.5°C in the same period in waters 7–10 m deep (Carleton and Paspebiac stations). Bottom temperature at Stonehaven (19 m) in 1986 (Walker et al. 1987) averaged 7.6°C in the same period. Winter temperatures on the bottom are comparable at the three sites. The large difference between winter and summer temperature at Cape Tormentine likely results in a shorter period with optimal temperatures for sea scallop growth (8–12°C; Posgay 1953) compared to other sites. Sediments in Northumberland Strait also contained more silt than at Nepisiguit. Consequently, Cape Tormentine would appear to have the most stressful environment of the three sites studied and Nepisiguit the least.

There is increasing evidence in the literature (Bayne and Newell 1983; MacDonald and Thompson 1985) to suggest that the simple theory of increased growth with warmer temperatures for a species in its natural habitat (Newell 1979) needs to be re-examined. While other variables also need to be considered, the number of days with optimal temperatures for growth may represent an important factor to consider. This hypothesis is consistent with results obtained by MacDonald and Thompson (1985) for sea scallops in Newfoundland.

In recent studies on the factors affecting growth rates of pectinids, growth has been found to be correlated with food abundance, in addition to temperature (Broom and Mason 1978; Leighton 1979; Posgay 1979; Wallace and Reinsnes 1984; MacDonald and Thompson 1985). In the current study, the abundance of food was not estimated. However, Citarella (1980) found values of chlorophyll-*a* in the Northwest Basin of Northumberland Strait (west from Cape Tormentine) to be high compared to other productive coastal areas. Further studies of primary productivity would be required to determine the effect of this parameter.

MacDonald and Thompson (1985) found that higher shell growth rates were generally accompanied with higher adductor muscle growth. A superior yield per recruit may thus be obtained from the Nepisiguit site as shell growth is higher on this site. The difference in growth between the areas warrants that fishery management strategies take this factor in account. As for aquaculture developments, it appears that the Nepisiguit site provides a better growing environment for sea scallops than the sites located in Northumberland Strait.

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Causes of Within-Season Decline in the Size at Age of American Plaice, *Hippoglossoides platessoides*[1]

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TALLMAN, R.F. 1991. Causes of within-season decline in the size at age of American plaice, *Hippoglossoides platessoides*, p. 269–275. *In* J.-C. Therriault [ed.] The Gulf of St. Lawrence: small ocean or big estuary? Can. Spec. Publ. Fish. Aquat. Sci. 113.

Size at age of American plaice (*Hippoglossoides platessoides*) landed by otter trawl and seine in the southern Gulf of St. Lawrence declined between the first and second halves of 1987. This apparent reversal of growth could be due (1) to depletion of larger fish early in the season, (2) to seasonal changes in the availability to gear of males compared with females, or (3) to exploitation of different populations or components of populations during different seasons of the year. Only the third of these possibilities could account for the range of age groups affected in both gear types. A dummy variable regression of length on age using predictor variables year-class, maturity, sex and statistical unit area explained 86% of the variation observed ($P < 0.0001$). The length at age of plaice in the southeastern part of the southern Gulf was significantly greater than that of the northwest. These differences, combined with the tendency of the fleet to fish more heavily during the latter part of the year in the area with smaller fish, could account for the reduction in size at age in plaice landings. Seasonal change in the sex ratio of landings may also have contributed to the decline in size at age of fish taken in trawls but this was not a factor in seine-caught fish.

La taille selon l'âge de la plie canadienne (*Hippoglossoides platessoides*) dans les débarquements provenant des chalutiers et senneurs du sud du golfe du Saint-Laurent a diminuée entre la première et la deuxième moitié de 1987. Cette décroissance apparente pourrait être dûe (1) à une diminution marquée du nombre des gros poissons tôt dans la saison, (2) à des changements saisonniers de la disponibilité aux engins de pêche selon le sexe, ou (3) à l'exploitation de populations différentes d'une saison à l'autre. Seule la troisième possibilité pourrait expliquer l'étendue des groupes d'âges affectés pour les deux types d'engins de pêche. Une régression à variable simulée de la longueur par rapport à l'âge, utilisant la classe d'âge, la maturité, le sexe et la zône de pêche comme variables indépendantes expliquent 86 % de la variation observée ($P < 0.0001$). La taille selon l'âge de la plie du sud-est du golfe dépassait significativement celle du nord-ouest. Ces différences, jointes aux tendances de la flotte à pêcher plus intensément pendant la deuxième partie de l'année et à capturer plus de petits poissons dans cette période expliqueraient la réduction de la taille selon l'âge dans les débarquements de plie. Les changements saisonniers du rapport des sexes dans les débarquements ont possiblement aussi causé une dimunition de la taille selon l'âge des poissons capturés par les chalutiers. Cependant ce n'est pas le cas pour les senneurs.

Introduction

The use of quarterly or semi-annual age-length keys in catch at age calculations accounts for the change in size of fish in an age group due to growth during the fishing season (Ricker 1975). American plaice (*Hippoglossoides platessoides*) are fished in the southern Gulf of St. Lawrence with otter trawls and Danish, Scottish, and pair seines, and samples from this fishery are used to generate semi-annual age-length keys (Tallman and Sinclair 1988). In 1987, size at age of American plaice in the southern Gulf declined from the first to the second halves of the year (Tallman and Sinclair 1988), which is contrary to the normal pattern of within-season increase in size.

This paper examines three possible explanations for this anomalous trend in size at age. First, the fleet could remove the faster-growing members of a cohort early in the year, leaving a population that was smaller at age to be fished later in the year.

Second, an increase in the male: female ratio during the fishing season could result in a smaller size at age in the second half of the year. Female plaice grow faster than males, so if the sexes are distributed so that males are proportionately more abundant in intensively fished areas later in the year, then size at age would decline in the latter part of the season.

Third, the decline in size at age might be due to the exploitation of distinct geographical populations which are fished at different times of the year (Ricker 1981). Powles (1969) suggested that there were two separate stocks of plaice in the southern Gulf: a northwest stock off the Acadian Peninsula of New Brunswick (NAFO

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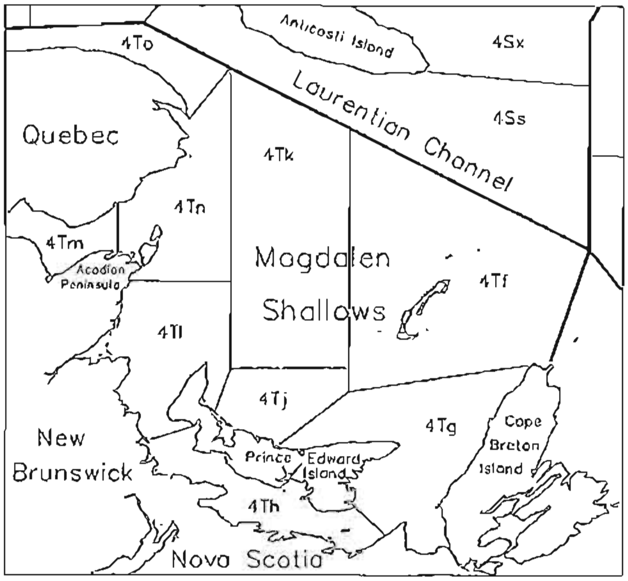

FIG. 1. NAFO Division 4T and unit areas in the southeastern Gulf of St. Lawrence.

Unit Areas 4Tn and 4Tk: Fig. 1) and a southeast stock between Cape Breton Island and Prince Edward Island (NAFO Unit Areas 4Tf and 4Tg: Fig. 1). Plaice from these areas migrate from the Magdalen Shallows to overwinter in the Laurentian Channel (Powles 1969). About 45% of American plaice landed from Northwest Atlantic Fisheries Organization (NAFO) Division 4T are taken as bycatch of mobile gear (Danish seines, Scottish seines and otter trawls) targeting Atlantic cod (*Gadus morhua*). These vessels change their fishing locations in concert with the seasonal migratory movements of cod. Thus, if size at age of plaice varies with geographic location, the fishery could be sampling from different populations.

Materials and Methods

Samples were obtained from research vessel surveys conducted each September from 1971 to 1988. Sixty or more sets were made on each survey. Detailed cruise protocols are given by Halliday and Koeller (1981). Plaice taken in trawls were sexed by direct examination of the gonads, except for juveniles which were difficult to sex in the field. For each set separate length frequency distributions were established for males, females and unsexed juveniles by measuring total length (Hubbs and Lagler 1958). In sets where more than 70 kg of plaice were captured length frequencies were derived from a 70 kg subsample.

Samples obtained from commercial catches included 200 or more fish. Length frequency distributions were created from these samples as above.

In both, survey and commercial samples, otoliths were removed from one fish per sex for each centimetre length category and stored in a glycerin–water solution. Otolith rings were read using a binocular dissecting microscope at 128 × power. Chilton and Beamish (1982) describe plaice otolith structures used in aging. To ensure consistency the age reader was tested after every 500 otoliths using the following protocol. One hundred otoliths were drawn at random from a reference collection and read, and the reader was scored for precision and bias against the historical reader. If precision was above 70% and there was no significant skewness the reader continued; otherwise the reader recalibrated until precision exceeded 70% and bias was eliminated. Landings at age were calculated by the program AGELEN (Zwanenburg and Smith 1983), which uses equations presented by Gavaris and Gavaris (1983).

To determine if fishing could be responsible for the reduction in size at age I examined the pattern of reduction in size over the age structure. For fish within a cohort to be selectively removed from the population they must reach some threshold size more rapidly than others in the cohort. If this effect occurs it will be present in the partially recruited cohorts, roughly below age 11 or 12.

To determine if an increase in the ratio of males to females in the catch had occurred, I calculated numbers in the commercial 1987 catch at age by sex. Sex ratios of total males to total females by half year period were converted to standardized frequencies by multiplying by 100. A *G*-test (Sokal and Rohlf 1981) was performed to test the hypothesis that frequencies were equal in the two halves of the year. Sex ratios were also compared within age groups. Paired *t*-tests were used to compare the first and second halves of the year in the otter trawl and seine landings. Ages 5 to 15 and 12 to 20 were used for otter trawl and Danish seine examinations, respectively.

To determine if fish in the northwest and southeast Magdalen Shallows differed in growth rate a dummy variable regression of length by age was calculated on data gathered in the 1971–88 September RV surveys. A linear modelling approach was used because it allowed partitioning of the effects of various factors such as year-class and geographical location (Neter et al. 1983). Traditional growth models, such as the von Bertallanffy growth model do not have clearly defined distributions of errors about the estimates. The parameters of the von Bertallanffy model are correlated thereby confounding statistical analysis (G. Chouinard, pers comm.). In contrast general linear models lend themselves well to statistical testing (Neter et al. 1983). The regression was allowed to flex at age 8 in slope and intercept to account for possible changes in growth rate coincident with sexual maturity. Age 8 was chosen because the spacing between the annual rings on the otolith changed at this point suggesting a reduction in average growth rate, particularly in males (unpubl. data). The predictor variables were age, year-class, maturity, sex and NAFO unit areas (Fig. 1). First order interactions between age and the indicator variables, other than year-class, were also modeled. The equation for the model using the notation of Neter et al. (1983) is as follows:

$$\begin{aligned} Y_i = {} & \beta_0 + \beta_1 X_{i1} + \beta_2 X_{i2} \ldots + \beta_{27} X_{i27} + \beta_{28} X_{i28} + \\ & + \beta_{29} X_{i29} + \beta_{30} X_{i30} \ldots + \beta_{35} X_{i35} \\ & + \beta_{36} X_{i36} + \beta_{37} X_{i37} + \beta_{38} X_{i1} X_{i28} \\ & + \beta_{39} X_{i1} X_{i29} \ldots + \beta_{48} X_{i1} X_{i38} \\ & + \beta_{50} X_{i1} X_{i39} + E_i, \end{aligned}$$

Where: Y_i = *length*, X_{i1} = age, β_0 = the overall intercept of the regression or the length when all other effects are equal to 0. X_{i2} = 1 if fish was born in 1955 of if year-class = 55, 0 otherwise; X_{i3} = 1 if year-class

= 56, 0 otherwise; X_{i4} = 1 if year-class = 57, 0 otherwise, ..., X_{i27} = 1 if year-class = 80, 0 otherwise. The coefficient β_1 represents the overall slope of the regression of length on age, the associated coefficients, β_2 to β_{27} represent the amount the length would change from the overall intercept if the fish had been born in that year. X_{i28} = 1 if unit area = 4Tf, 0 otherwise; X_{i29} = 1 if unit area = 4Tg, 0 otherwise, ..., X_{i35} = 1 if unit area = 4Tn, 0 otherwise. The associated coefficients β_{28} to β_{35}, represent the amount the length would change from the overall intercept if the fish grew in that unit area. X_{i36} = 1 if age less than 8, 0 otherwise; β_{36} is the amount the intercept would change if the fish was younger than 8 yr old. X_{i37} = 1 if sex = male, 0 otherwise; β_{37} is the amount the intercept would change if the fish was a male. The coefficients of the predictor variables represent intercepts while the coefficients of the first order interactions may be thought of as slope changes in the line. E_i = the errors about the true values assumed to be random, independent, and normally distributed about zero with a variance sigma.

Ages greater than 25 were excluded from the analysis due to their limited numbers. Other year-classes with less than 50 observations were also excluded.

The mean length, adjusted for all covariates, of the main fishing area in the northwest portion of the southern Gulf (unit areas 4Tn and 4Tk combined) was contrasted against that of the southeast portion (unit areas 4Tf and 4Tg combined) using a least squared difference technique (Sokal and Rolhf 1981).

The hypothesis that the portion of fish at each age was independent of location (northwest versus southeast) was tested using a G-test (Sokal and Rolhf 1981).

Commercial catches were tabulated by date, unit area and gear type for the 1987 fishing season from Department of Fisheries and Oceans statistical files. For each unit area and gear type within unit area a weighted mean date of capture the in terms of months and portions of month (i.e. September 15 = 9.5) Each date was weighted by the catch on that date.

Results

Mean length at age of American plaice taken by commercial trawl declined from the first to the second half of 1987 in ages 5 through 16 and age 18 (Table 1). Size at age of seined plaice decreased between the halves of 1987 for ages 12 to 20. By comparison no decline from the first half of the year to the second was observed in 1986.

The proportion of males by number in commercial trawl landings increased from the first to the second half

TABLE 1. Mean length at age (cm) by gear and time period for 1986 and 1987.

	1986				1987			
	Trawls		Seines		Trawls		Seines	
Age	Jan.–July	Aug.–Dec.	Jan.–July	Aug.–Dec.	Jan.–July	Aug.–Dec.	Jan.–July	Aug.–Dec.
1	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0
4	0	0	0	0	0	24.0	21.0	24.0
5	27.2	27.5	35.3	26.5	30.8	29.3	29.2	30.7
6	28.8	30.8	30.5	31.0	35.3	30.6	30.2	31.3
7	31.8	32.2	31.7	32.3	34.8	32.4	32.3	33.2
8	30.5	32.6	31.8	33.1	35.0	33.6	32.3	33.9
9	34.0	34.2	32.8	34.8	35.5	33.8	33.3	34.3
10	35.2	34.9	34.2	35.2	36.5	35.4	35.0	35.8
11	35.7	37.6	34.2	37.7	37.7	36.1	36.0	36.6
12	36.9	37.7	34.2	37.9	39.5	36.7	38.6	36.9
13	37.7	38.9	36.4	39.8	40.3	38.7	40.0	38.8
14	39.0	39.9	37.2	41.5	42.2	42.0	42.4	40.9
15	40.1	42.6	39.2	43.4	43.3	42.2	44.6	41.1
16	42.9	44.1	42.5	45.4	46.6	46.0	49.3	44.2
17	44.3	43.6	44.6	44.8	47.4	48.7	50.5	47.0
18	45.1	47.3	45.5	48.3	50.9	49.9	52.8	48.6
19	47.9	48.2	48.9	49.9	49.5	50.6	52.8	49.5
20	45.9	49.8	48.6	49.8	52.6	51.9	54.9	52.2
21	52.5	51.1	54.1	51.8	51.2	53.0	54.4	54.7
22	56.0	56.5	59.6	57.2	54.8	54.5	56.4	55.6
23	51.2	52.6	52.2	54.4	54.6	54.3	55.7	56.4
24	54.4	61.4	55.3	60.4	55.0	53.1	57.4	54.3
25	53.5	0	54.8	0	52.2	55.6	57.8	57.5
26	63.4	60.0	61.6	60.0	54.3	57.2	55.8	59.7
27	63.0	0	63.0	0	63.6	58.8	64.2	59.6
28	63.4	0	62.4	0	58.1	56.0	60.5	57.9
29	56.0	52.0	57.4	52.0	63.7	58.5	63.7	58.5
30	57.6	58.2	59.0	58.5	0	63.7	65.0	63.7
–[a]	36.0	38.2	34.7	39.6	42.2	39.4	44.1	38.8

[a] Overall mean.

TABLE 2. Number of male and female American plaice landed by gear and season in N.A.F.O. Division 4T during 1987.

	1st Half		2nd Half	
	Trawlers	Seines	Trawlers	Seines
Males	15 412	8 712	18 487	16 619
Females	106 754	67 013	97 675	144 056
Sex Ratio (males/females)	0.144	0.131	0.189	0.115

TABLE 3. American plaice sex ratio (male to female) in affected ages of landings in 1st and 2nd half of 1987 for trawls and seines in N.A.F.O. Division 4T.

	Trawls (Gear 11, 12, 16)		Seines (Gear 20)	
Age	Jan.-July	Aug.-Dec.	Jan.-July	Aug.-Dec.
5	0.0000	0.6858	******	******
6	0.1968	0.7849	******	******
7	0.0373	0.3552	******	******
8	0.1593	0.2971	******	******
9	0.1220	0.4014	******	******
10	0.2138	0.3802	******	******
11	0.1841	0.2136	******	******
12	0.2333	0.2104	0.2052	0.1092
13	0.1876	0.1867	0.2185	0.1073
14	0.1189	0.1081	0.0928	0.0881
15	0.1707	0.0500	0.1653	0.0605
16	******	******	0.0744	0.0582
17	******	******	0.0267	0.0191
18	******	******	0.0699	0.0440
19	******	******	0.0618	0.0016
20	******	******	0.0256	0.0038

NOTE: Trawls include side otter-trawl, stern otter-trawl and pair trawl; seines include Danish and Scottish seine.

of 1987 but the difference was not significant ($G = 1.20$, $P = 0.2733$, Table 2). In seine landings, the proportion of males declined non-significantly between the two halves of 1987 ($G = 1.0095$, $P = 0.315$, Table 2). However, age-stratified comparisons showed a significant increase in males relative to females in commercial trawl landings in the affected ages ($P = 0.035$, Table 3). Male: female ratios decreased significantly in age-stratified samples from seine landings ($P = 0.01$, Table 3).

The regression model explained 86% of the variation observed in length at age. The overall model was highly significant, as were all classes of indicator variables and interactions between indicator variables and age ($P < 0.0001$, Table 4, part A). Examination of residual plots for the entire model and for reduced models for each year class showed no evidence of heteroscedasticity. Plots of residuals for each of the unit areas 4Tf, 4Tg, 4Tn and 4Tk are shown in Fig. 2. The errors about the lengths estimated by the model appear to be random.

Interpretation of the main effects in the model was not straightforward due to the presence of significant interactions (Table 4, part B). Thus, estimable functions were calculated to test the hypothesis that growth rates differed geographically within NAFO Division 4T. Differences

TABLE 4. Analysis of variance table for dummy variable regression of length on age for American plaice in N.A.F.O. Division 4T.

Part A: Overall Model (r^2 = 0.8534)

Source	df	Sum of Squares	Mean Square	*F* Value	PR > *F*
Model	46	1854099.53	40306.52	3230.68	0.0000
Error	25094	313077.32	12.48		
Corrected Total	25114	2167176.85			

Part B: Slopes and Intercepts

Source	df	Sum of Squares	Mean Square	*F* Value	PR > *F*
AGE (intercept)	1	26678.28		2138.34	0.000
MATV (intercept)	1	54169.41		4341.83	0.000
SEX (intercept)	1	5002.01		400.93	0.000
UAREA (intercept)	8	3593.07		36.00	0.000
YRCLASS (intercept)	25	45425.36		145.64	0.000
AGE*SEX (slope)	1	20165.68		1616.33	0.000
AGE*MATV (slope)	1	50856.95		4076.32	0.000
AGE*UAREA (slope)	8	1116.62		11.19	0.0001

Part C: Northwest vs Southeast

Contrast	df	Sum of Squares	Mean Square	*F* Value	PR > *F*
NW VS SE	1	654.11		52.43	0.0001

between the northwest (unit areas 4Tk and 4Tn) and the southeast (unit areas 4Tg and 4Tf) were highly significant ($P = 0.0001$, Table 4, part C). The means with their respective confidence limits for unit areas 4Tf, 4Tg, 4Tn and 4Tk are shown in Fig. 3. Plaice were significantly larger in unit areas 4Tg ($\bar{x} = 33.55$) and 4Tf ($\bar{x} = 32.82$ cm) than in 4Tn ($\bar{x} = 32.10$ cm) and 4Tk ($\bar{x} = 31.32$ cm).

The differences observed between the northwest portion of the southern Gulf and the southeast were not due to spatial heterogeneity in the age-groups (Fig. 4).

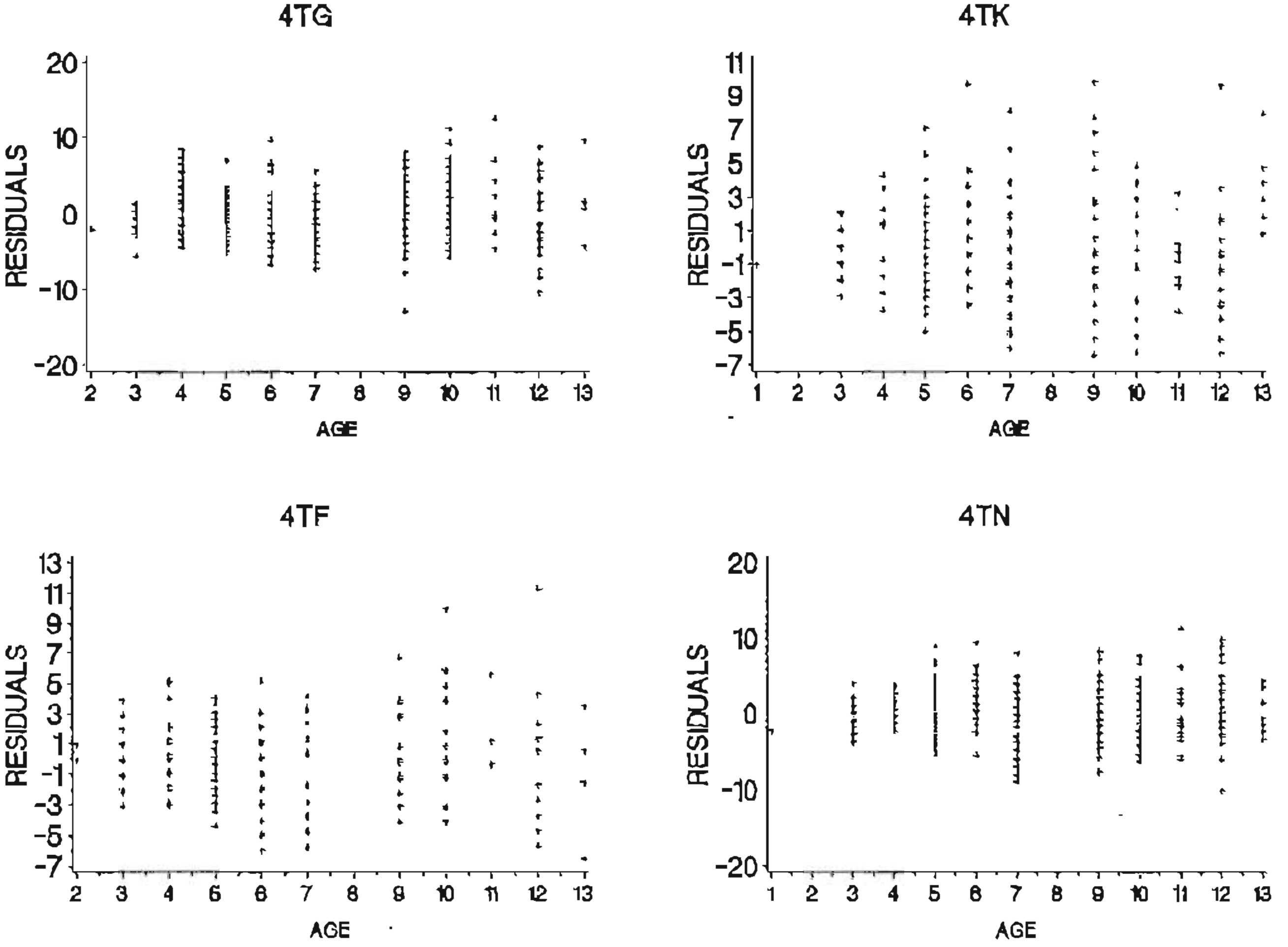

FIG. 2. Residuals of the estimated length versus age from dummy variable regression in each of the unit areas 4Tf, 4Tg, 4Tn, 4Tk.

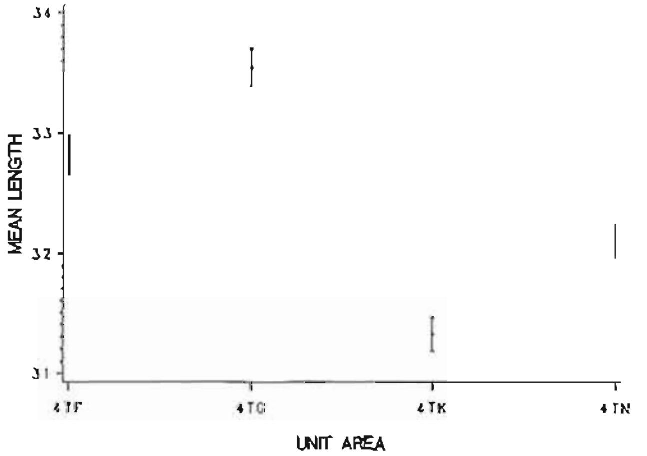

FIG. 3. Mean length, adjusted for covariates, for unit areas 4Tf, 4Tg, 4Tn and 4Tk. The vertical lines represent the 95% confidence limit about each mean.

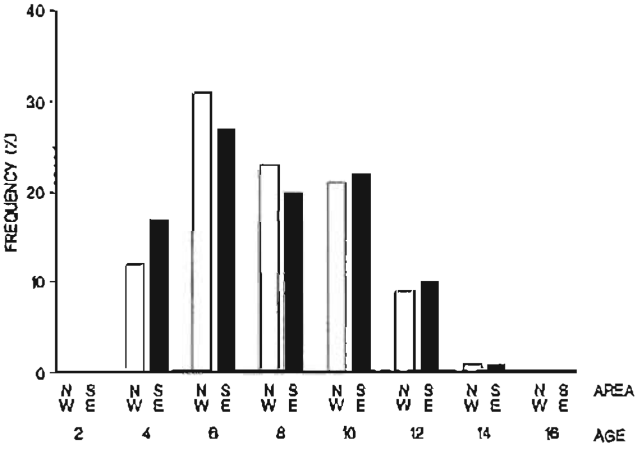

FIG. 4. The percent frequency at age for northwest (NW) and southeast (SW) portions of NAFO Division 4T. Proportion at age is independent of location ($G_{adj} = 12.462 >$ chi-square$_{.01\,(6)} = 16.812$). NW = unit areas 4Tf and 4Tg combined. SE = unit areas 4Tn and 4Tk combined.

TABLE 5. Mean month of catch and 95% confidence intervals of American plaice in N.A.F.O. Division area 4T.

	Unit Area					
GEAR[a]	4Th	4Tg	4Tf	4Tk	4Tn	4Tm
OTB-1	5.83 ± 0.427	6.00 ± 1.450	6.44 ± 1.000	8.14 ± 0.362	7.06 ± 0.254	8.91 ± 0.863
OTB-2	5.78 ± 0.100	6.78 ± 0.363	7.00 ± 1.201	7.79 ± 0.630	7.23 ± 0.256	8.32 ± 0.814
SDN	7.27 ± 0.128	6.68 ± 0.184	6.50 ± 1.412	10.20 ± 1.162	7.29 ± 0.498	8.17 ± 0.936
SSC	5.80 ± 0.592	5.96 ± 0.483	—	8.00 ± 1.018	7.61 ± 1.008	—

[a] OTB-1 = Stern Otter Trawl, OTB-2 = Side Otter Trawl, SDN = Danish Seine, SSC = Scottish Seine.

The proportions of each age were independent of geographic location.

Analysis of temporal distribution of landings showed that in May–June 1987 plaice were caught primarily in southeastern unit areas (4Tf, 4Tg) whereas in July–October the fishery shifted to the northwest (unit areas 4Tk and 4Tn) (Table 5, Fig. 1). This pattern contrasts to previous years when the late-season fishery concentrated in southeastern 4T (Chadwick and Sinclair 1991).

Discussion

This paper considers early-season depletion of large fish, changing sex ratios, and shifting fishing locations as possible explanations of the decrease in size at age in American plaice taken in the 1987 fishery. Intensive fishing early in the year could explain size at age reductions in younger fish, but this hypothesis cannot be posed as a cogent explanation for the observed decreases in older fish. Similarly, reduction in size at age due to an increase in the proportion of males in the catch of otter trawls, while not statistically significant, could contribute to the reduction in size at age of trawl-caught fish. However, this explanation could not be valid for seiners because the proportion of males decreases in that fishery. Groundfish trawlers tend to fish on rougher bottoms and further from shore than seiners in the southern Gulf of St. Lawrence. The differences in sex ratios between these gear types may reflect their different fishing locations.

Differences in relative proportions of males and females could be due to differential migration patterns. Powles (1969) and Clay (1991) have shown that the Laurentian Channel is a refugium for American plaice against the cold winter temperatures of the Magdalen Shallows. Heinke (1914) noted that North Sea plaice (*Pleuronectes platessa*) moved to deeper waters as they grew larger. If female plaice, being of larger size, distribute themselves in the deeper waters near the edge of the Shallows, then they may enter the channel earlier in the year than the males. It is possible that vessels fishing at the edge of the Shallows catch fewer females late in the year if these fish have moved off the shelf at a time when males are passing through the area on their way to the winter refugium.

Differences in growth of plaice between different areas of the southern Gulf coupled with temporal changes in the location of fishing is sufficient to explain the reduction in size at age for all age-groups and gear types. However, the effect of unit area in the model is dwarfed by the year-class effect. This suggests that growth differences may be small compared to year-to-year environmental effects or density dependent effects. The spatio-temporal pattern of fishing for plaice in 1987 is the reverse of the historical pattern described by Chadwick and Sinclair (1991). Fishing patterns in Division 4T may have changed due to restrictions on the cod fishery (Tallman and Sinclair 1988).

The American plaice fishery in the southern Gulf involves considerable discarding of fish below market size (Chouinard and Metuzals 1985; Halliday et al. 1989). Halliday et al. (1989) showed that the length and weight of plaice discarded in the southern Gulf increased in the 1970s in the course of the season but it is not clear how this would affect length at age of landings. It seems unlikely that discarding could account for the change in average size at age since fishermen would have to discard larger fish while retaining smaller ones in order to show an apparent reduction in the size of the fish over the fishing season. Even in the unlikely event that these practices were followed the effect would only be seen in the youngest age-groups caught.

The most likely explanation for the anomalous trend in size at age in the 1987 plaice fishery is that plaice grow faster in the northwest part of the Magdalen Shallows and that the timing of the fishery was such that fishing occurred in the northwest in the early part of the season and the southeast in the later part. As a result the fleet sampled different populations at different times of the year. The hypothesis that plaice populations with different characteristics exist in different parts of Division 4T is supported by the tagging experiments, which showed little exchange between northwest and southeast populations (Powles 1965, 1969). In addition, he reported distinctive patterns of annuli formation in these areas suggesting differences in growth patterns.

Distinct seasonal migrations (Powles 1969; Clay 1991) may organize the plaice stocks in the Magdalen Shallows along geographic lines perpendicular to the Laurentian Channel. Hence, separate groupings of plaice appear to have developed south of the Channel in the northwest and the southeast. Gulf of St. Lawrence cod also undergo seasonal migrations, but their routes are parallel rather than perpendicular to the Laurentian Channel (Clay 1991). As cod is the major target of the southern Gulf groundfish fleet, movements of this species may have promoted a spatio-temporal distribution of fishing effort that may be responsible for the decrease in length at age of American plaice caught from the first half to the second half of 1987. The fleet was fishing in a location where fish were smaller at age in the latter part of the year.

The possibility of geographically distinct stocks of American plaice in NAFO Division 4T has implications for fisheries management. Ideally, separate stocks should have separate management regimes. In the present case geographic variation in size at age may stem from environmental factors rather than from genetic differences. Further clarification of the genetic structure of American plaice in NAFO Division 4T is required before alternative management options can be considered. American plaice and cod in the southern Gulf are closely intertwined because cod are major predators on plaice (Powles 1965) and because plaice are a major bycatch of the cod fishery. Hence management regimes for plaice must be designed in the context of overall groundfish management in the southern Gulf.

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Prey Exploitation by Seabirds in the Gulf of St. Lawrence[1]

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CAIRNS, D.K., G. CHAPDELAINE, AND W.A. MONTEVECCHI. 1991. Prey exploitation by seabirds in the Gulf of St. Lawrence, p. 277–291. *In* J.-C. Therriault [ed.] The Gulf of St. Lawrence: small ocean or big estuary? Can. Spec. Publ. Fish. Aquat. Sci. 113.

A bioenergetics model is presented that estimates food consumption by seabirds in the Gulf of St. Lawrence. The 400 000 pairs of seabirds breeding in the Gulf and associated non-breeders are estimated to consume 80 000 t of marine prey annually. Seabird predation is most intense in the central and northern parts of the Gulf, particularly around the Gaspé Peninsula. The major prey groups are capelin (*Mallotus villosus*) and sand lance (*Ammodytes* spp.) (ca. 30 000–45 000 t) and mackerel (*Scomber scombrus*, ca. 9 000 t). Because seabirds favour small size-classes of prey and species that are not heavily fished, they do not compete directly with commercial fisheries. Seabirds remove 0.04 g $C \cdot m^{-2} \cdot yr^{-1}$ from Gulf waters. Prey exploitation in the Gulf is light compared with the nearby open Atlantic because of anthropogenic depression of bird numbers, winter ice cover, lack of non-breeding migrants, and the unsuitability of the southern Gulf to cold-water species. Seabird exploitation is presently smaller than that of commercial fisheries (ca. 325 000 t). Gulf seabird populations are increasing, and avian food consumption may exceed fisheries landings if seabird numbers return to historic levels.

On présente un modèle bioénergétique qui estime la consommation alimentaire des oiseaux marins du Golfe Saint-Laurent. Le modèle estime que les 400 000 couples d'oiseaux du golfe et les non-reproducteurs associés consomment annuellement 80 000 t de proies marines. La prédation par les oiseaux est plus intense dans les parties centrales et septentrionales du golfe, surtout aux alentours de la Péninsule gaspésienne. Les proies principales sont le capelan (*Mallotus villosus*) et le lançon (*Ammodytes* spp.) (à peu près 30 000–45 000 t) et le maquereau (*Scomber scombrus*, à peu près 9 000 t). Les oiseaux marins ne font pas présentement concurrence aux pêches commerciales du golfe parce qu'ils exploitent de préférence les petites proies et les espèces qui ne sont pas recherchées par la pêche. Les oiseaux marins prélèvent des eaux du golfe 0.04 g $C \cdot m^{-2} \cdot an^{-1}$. L'exploitation des proies par les oiseaux marins est peu intense dans le golfe comparé aux eaux Atlantiques à l'extérieur en raison de la réduction des populations par l'homme, la glace hivernale, l'absence des oiseaux non-reproducteurs migratoires, et l'habitat du sud du golfe qui n'est pas propice aux espèces adaptées à l'eau froide. L'exploitation par les oiseaux marins est présentement plus petite que celle de la pêche commerciale (à peu près 325 000 t). Les populations des oiseaux marins du golfe sont en croissance, et la consommation des oiseaux pourrait dépasser les débarquements de la pêche si leurs effectifs regagnent leur niveaux historiques.

Introduction

The vertebrate fauna of the Gulf of St. Lawrence consist of fish, birds, and mammals. Although fish, because of their commercial value, remain the pre-eminent target of marine biological research, increasing emphasis has been placed on the role of warm-blooded predators in the seas. Trophic interactions are a prime focus of this research thrust, and it is now well established that birds and mammals play major roles in marine food webs (Lavigne et al. 1985; Croxall 1987).

The principal method of evaluating prey harvest by seabirds is through bioenergetic models that calculate food

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needs from birds' daily metabolic rates. The models apply caloric requirements to diet composition to estimate total harvest of each prey taxon (Furness 1978; Wiens 1984). This approach is most successful when populations and diets are well known, because seabird metabolic rates can be predicted with reasonable accuracy from allometric equations based on direct metabolic measurements of free-living birds by the doubly-labelled water method (Nagy 1980; Birt-Friesen et al. 1989).

The Gulf of St. Lawrence provides a singular advantage in the bioenergetic modeling of seabird food consumption, because, unlike the open Atlantic coast of Canada, its waters are not frequented by large numbers of trans-oceanic and trans-equatorial migrants (Brown 1986). Thus, population estimates based on counts at breeding colonies can be used to estimate total seabird food consumption in the Gulf. In this paper we describe the population and distribution of the Gulf seabird community, and model the size, species composition, and geographical distribution of its food consumption. We also examine the question of seabird impact on fish and other organisms in the Gulf, and compare our findings with estimates of seabirds' role in other systems.

Model Structure

Seabird food consumption in the Gulf of St. Lawrence was modeled on a Lotus 1-2-3 compatible spreadsheet. Following the model structure of Furness (1978) and Wiens (1984), estimates of energy use by individual adults form the model core, and additional calculations account for needs of reproduction. A copy of the model is available on request from the senior author.

Daily energy expenditure (DEE) was taken from doubly-labelled water (DLW) measurements of free-living Leach's storm-petrels (121 kJ d^{-1}, Montevecchi et al. unpubl. data) (scientific names given in Appendix A), northern gannets (4865 kJ d^{-1}, Birt-Friesen et al. 1989), and common murres (1789 kJ d^{-1}, Cairns et al. 1991). These energy expenditures represent multiples of 2.0, 6.6, and 5.0 of BMRs (Basal Metabolic Rate) given by Ricklefs et al. (1980), Birt-Friesen et al. (1989), and Cairns et al. 1991, respectively. Expenditure of black-legged kittiwakes was estimated as 849 kJ d^{-1}, based on Gabrielsen et al.'s (1986) DLW measurements, weight-adjusted for Gulf of St. Lawrence birds. The BMR multiple for this value is 3.2 (Gabrielsen and Mehlum 1990). DEEs of other species were estimated from allometric equations for cold-water flapping ($DEE = 1737\ mass^{0.727}$; DEE in kJ d^{-1} and mass in kg) and other ($DEE = 977\ mass^{0.727}$) seabirds (Birt-Friesen et al. 1989). All adult birds were assumed to have similar energy expenditures. Non-breeding birds were not assigned lower DEEs because energetic gains due to their exemption from reproductive burdens are likely negated by lower foraging efficiencies (Gaston 1985).

DEEs were divided by assimilation efficiency (0.76 for northern gannets, Montevecchi et al. 1984; 0.80 for all other species, Furness 1978) to obtain daily energy requirements. These were converted to prey consumption using dietary data and prey caloric densities from the literature. Energy requirements for egg production were from direct measurements or the equations of Kendeigh et al. (1977) and Carey et al. (1980). Chick food needs were estimated from Kendeigh et al.'s (1977) allometric equations, or from detailed studies of food intake (e.g. Montevecchi et al. 1984; Cairns 1987a). Numbers of eggs and chicks were calculated from literature and unpublished values on clutch size, hatching success, and fledging success.

Seabird diet composition was derived from studies within the Gulf where available, or inferred from species' food habits elsewhere. Breeding populations of Quebec and Maritime colonies were taken from unpublished databases maintained by the Quebec and Atlantic Regions of the Canadian Wildlife Service, and by the Prince Edward Island Fish and Wildlife Division. Newfoundland breeding populations were taken from Cairns et al. (1986). Populations were tabulated by Northwest Atlantic Fisheries Organization (NAFO) Unit Areas. Because of incomplete census coverage of larids in Quebec and Newfoundland, breeding populations of herring and great black-backed gulls in these provinces were increased by 50% over census counts.

Seabirds have delayed reproductive maturity, and community energetics models must account for pre-breeding cohorts. To estimate numbers of pre-breeders, seabirds were classified as inshore or offshore species. Inshore and offshore seabird guilds have distinct demographic and colony dispersion patterns (Lack 1967). Using typical literature values (Lack 1967; Jouventin and Mougin 1981; Hudson 1985) we set age of first breeding at 3 and 5 yr and annual adult survivorship at 0.8 and 0.9 for inshore and offshore species, respectively. These values were used in a life table which was iterated with various values of annual pre-breeding survival until population stability was reached. The proportion of pre-breeders to adult breeding population (pairs) in the stabilized population was 0.609 and 0.678 for inshore and offshore species, respectively.

Breeders, failed breeders, and pre-breeders were assumed to attend the colony or be in its vicinity. Food consumption was modeled for pre-breeding, breeding, and post-breeding seasons. Durations of breeding seasons were taken from literature values. Pre- and post-breeding seasons were derived from Pilote (1976), Brown (1986), and personal observations of arrival and departure times of birds in the Gulf.

The model was run for each seabird species and Unit Area. Seabirds with fewer than 100 pairs in the Gulf (Caspian and roseate terns, thick-billed murres) were not modeled. Breeding parameters and diet composition were input separately for each Unit Area; values were drawn from the Area itself or from the closest available source. Model results were summarized for four regions: 4R (west coast Newfoundland), 4S (Quebec North Shore), 4Tfghjlmno (central and southern Gulf), and 4Tpq (St. Lawrence Estuary). The southern Gulf in this paper refers to Unit Areas 4Tghjl.

Results

Populations

The Gulf of St. Lawrence seabird population is estimated at 406 156 breedings pairs (Table 1). Populations

TABLE 1. Populations (breeding pairs) of seabirds in the Gulf of St. Lawrence, by NAFO Unit Area.

NAFO Unit Area	Inshore seabirds								Offshore seabirds						Total
	Great cormorant	Double-crested cormorant	Ring-billed gull	Herring gull[a,b]	Great-black-backed gull[a,b]	Common tern[a]	Arctic tern[a]	Black guillemot	Leach's storm-petrel	Northern gannet	Black-legged kittiwake	Common murre	Razorbill	Atlantic puffin	
4Ra			75	38	113	47	482	300						10	1065
4Rb			12	707	255	535	35	10							1554
4Rc	24			923	120	30		10			800				1907
4Rd	20		100	30	191	252	100								693
4R	44		187	1698	679	864	617	320			800			10	5219
4Si															0
4Ss		79			3									3	85
4Sv	73	956	2086	7683	1938	1410	342	366	41		168	13287	3195	8973	40518
4Sw			122	8460	441	712	160	5					400	8545	18845
4Sx	443		200		33	6		500		146	25681			1	27010
4Sy		1366	1308	22392	1011	5916	1369	30			1319		190	183	35084
4Sz		3339	2624	48156	5516	517	23	111	737		4265	105	331		65724
4S	516	5740	6340	86691	8942	8561	1894	1012	778	146	31433	13392	4116	17705	187266
4Tf	523	1289		2946	1679	2624	92	289		7639	3880	69	149	219	21398
4Tg	1069	735		1549	892	409	2	104					6		4766
4Th	331	1210		102	145	969		1							2758
4Tj	127	4466		1739	604	331	4	7							7278
4Tl	100		389	3881	1545	14719		5							20639
4Tm		5816	1221	7226	680	2480		464			448				18335
4Tn	16	1454	21	7234	1759	1588		1570	21	24449	39482	18302	277	1	96174
4To		576						1056			5467		40		7139
4T Gulf	2166	15546	1631	24677	7304	23120	98	3496	21	32088	49277	18371	472	220	178487
4Tp		8335	415	14039	3209			1037			299		1015		28349
4Tq		1296		5531		5		3							6835
4Tpq		9631	415	19570	3209	5		1040			299		1015		35184
Total	2726	30917	8573	132636	20134	32550	2609	5868	799	32234	81809	31763	5603	17935	406156

[a] Totals include colonies where birds were not identified to species. Counts were allocated to species according to ratios of herring:great black-backed gulls and common:Arctic terns recorded elsewhere in the NAFO Unit Area.

[b] Totals in Quebec and Newfoundland increased by 50% to account for uncensused colonies.

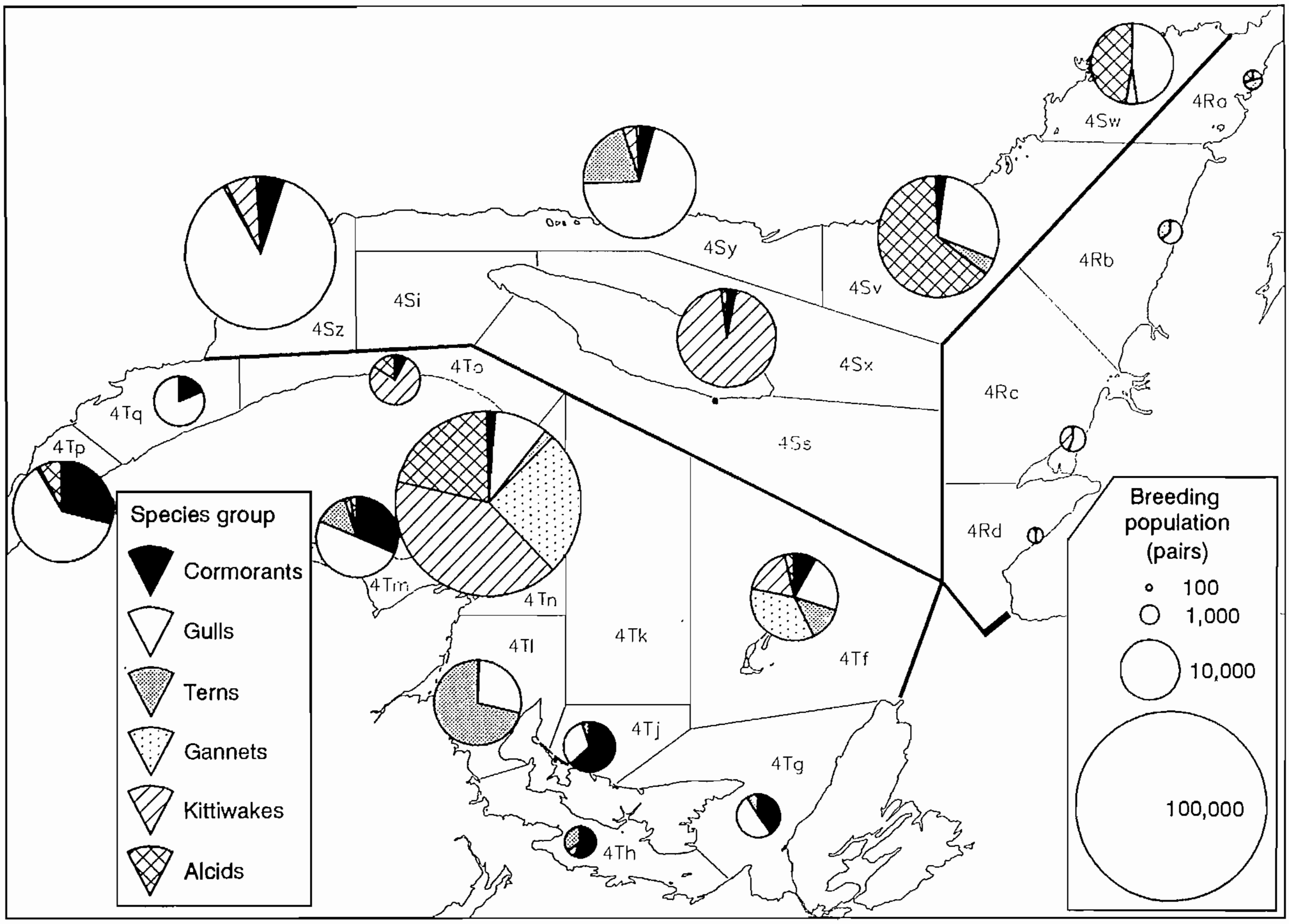

FIG. 1 Breeding populations of seabirds in the Gulf of St. Lawrence, by NAFO Unit Area. Area of symbols is proportional to populations.

are highest in the northern, central, and western Gulf (Fig. 1). The largest concentration of birds occurs off the eastern Gaspé Peninsula (Unit Area 4Tn), where about one fourth of all Gulf seabirds breed. Large numbers are also found on the Quebec North Shore and the Magdalen Islands. Seabirds numbers are lowest in the southeastern portions and the west coast of Newfoundland.

The distribution of seabird taxa is highly heterogeneous; in most Unit Areas one species group forms a simple majority of population (Fig. 1). Inshore seabirds, with 58% of the total (Table 1), are more numerous than offshore seabirds. Inshore seabirds generally breed in a large number of colonies dispersed along the coastline and offshore species breed in a small number of large colonies (Lack 1967). In the Gulf, most inshore species are represented in the majority of Unit Areas. Offshore species are absent from many Unit Areas, particularly those in the southern Gulf and western Newfoundland (Table 1).

The inshore seabird component is dominated by gulls, which comprise 68% of inshore and 40% of all species (Table 1). Gulls breed in nearly all Unit Areas (Fig. 1), and are particularly numerous in the northwestern Gulf (Unit Areas 4Syz), where breeding numbers are 50% of the Gulf total. Terns (15% of the inshore population) breed primarily in eastern New Brunswick and the Quebec North Shore; populations are low elsewhere. Cormorants (14% of the inshore population) are widespread except in western Newfoundland, but are concentrated in the southern Gulf and the St. Lawrence estuary. Because of their dispersed breeding habits, black guillemots are difficult to census, and reported numbers are only rough approximations. Guillemots are present in most regions, but are most numerous on the Quebec North Shore and the St. Lawrence Estuary.

The offshore seabird guild is dominated by black-legged kittiwakes (48% of offshore total, Table 1). Large colonies in the Magdalen Islands (Unit Area 4Tf), the Gaspé (4Tn), and Anticosti Island (4Sx) account for most breeders in the Gulf. Kittiwakes are absent from the southern Gulf and breed in low numbers elsewhere. Common murres, razorbills, and Atlantic puffins comprise 33% of offshore feeders. These alcids breed in large numbers in the Gaspé Peninsula (4Tn) and the northeastern Gulf (4Svw). Like kittiwakes, they are absent or nearly so from the southern Gulf. Gannets (19% of the offshore total) breed in only three colonies. The Gaspé Peninsula (4Tn) contains most Gulf gannets; there are smaller numbers on the Magdalen Islands (4Tf) and a few on Anticosti Island (4Sx). Only a small number of Leach's storm-petrels breed in the Gulf; their population is centred in Unit Area 4Sz.

Diets

Results of diet studies on great and double-crested cormorants, black guillemots and northern gannets in the Gulf of St. Lawrence are presented in Table 2. Meals regurgitated by great cormorants on the Magdalen Islands contained mostly benthic fish, primarily flatfish (winter flounder, yellowtail, windowpane) and cunners (Table 2). Sand lance were also important.

Five studies of double-crested cormorant, based on regurgitated meals, are available for the Gulf of St. Lawrence (Table 2). Flatfish and sculpins were major dietary components in all regions, and cunners were important in central and southern areas. On the Quebec North Shore (Unit Area 4Sv), birds preyed heavily on rock gunnels and sand lance. Pelagic fish were commonly taken in the Magdalen Islands (4Tf, herring and sand lance) and the western Gulf (4Tmno, herring and capelin). In the southern Gulf (4Tgj), white hake and a variety of estuarine species were major prey.

TABLE 2. Percent diet composition of cormorants, black guillemots, and northern gannets in the Gulf of St. Lawrence.

Prey	Great cormorant	Double-crested cormorant					Black guillemot		Northern gannet
Source of diet data[a]	4	3	4	2	2	3	1	1	5
Method[b]	1	2	1	1	1	3	4	5	1
Location of study	4Tf	4Sv	4Tf	4Tg	4Tj	4Tmno	4Sv	4Tp	4Tf
Scope[c]	All	4RS	4Tf	4Tgh	4Tjl	4Tmnopq	4RST[d]	4Tpq	4ST
Benthic fish									
Winter flounder				35.4	13.8				
Unidentified flatfish	34.1	5.4	14.0			19.6			
Cunner	25.5		22.7	17.2	30.7				
Sculpins									
Arctic staghorn sculpin								8	
Grubby			7.4	8.9	14.9	26.7		8	
Longhorn sculpin	3.6					3.5			
Shorthorn sculpin		32.4							
Moustache sculpin								8	
Unidentified sculpins	0.5		1.0						
Atlantic cod		0.9				3.5			
White hake				37.1					
Blennioidea									
Polar eelpout								8	
Ocean pout	5.5							23	
Arctic shanny							33.7		
Rock gunnel		32.6	1.8		1.7		21.6	15	
White perch					1.4				
Estuarine fish									
Alewife					5.6				
Brook trout		0.8							
Banded killifish					18.3				
Mummichog			0.3						
Atlantic silverside					4.5				
Atlantic tomcod						8.1	35.1	8	
Threespine stickleback			0.1		3.3				
Ninespine stickleback					0.4				
Unidentified sticklebacks						4.7			
American eel		0.5	0.1	1.4	5.1	3.5			
Pelagic fish and squid									
Atlantic mackerel			1.1						52.4
Atlantic herring	0.3	3.4	13.3			21.7			0.9
Capelin		7.8				6.9		15	
Sand Lance	30.6	15.0	38.1				8.5	8	37.5
Atlantic saury									8.1
Squid		0.2							1.1
Crustaceans		0.3	0.1		0.7	1.7	1.1		

[a] 1. Cairns 1981. 2. Gallant 1988. 3. Lewis 1929. 4. Pilon et al. 1983. 5. Diet averaged from regurgitation samples collected by Burton (1980) and by Cairns (unpubl.; $n=34$, September 1987; $n=18$, September 1988).

[b] 1. Percentage of regurgitations by mass. 2. Percentage of regurgitations by meals dominated by taxon. 3. Method of diet analysis not specified. 4. Percentage of chick meals by number of items. 5. Percentage of prey found near nests.

[c] NAFO Unit Areas in which diet composition is used in model.

[d] Except 4Tpq.

On both the Quebec North Shore (4Sv) and the St. Lawrence Estuary, black guillemots fed their chicks primarily benthic fish, particularly sculpins, blennies, and tomcod (Table 2). The dietary composition from this study must be taken as only a general indication of adult diet, because adult guillemots may consume substantial quantities of crustaceans (Cairns 1987b) which are rarely fed to chicks. In addition, chick diets based on counts of individual prey items may be biased because species contributions are not standardized by mass. Because no adult data are available for the Gulf, we used 4Tp chick diets to model guillemot food consumption in Unit Areas 4Tpq, and 4Sv chick diets elsewhere in the Gulf.

The northern gannet diet presented in Table 2 is the mean of weighed regurgitation samples collected on Bird Rocks, Magdalen Islands, in June–July 1978 (Burton 1980) and September 1987–88 (Cairns unpubl. data). Diet was dominated by mackerel (52%), followed by sand lance and Atlantic saury. Herring and squid were minor dietary components.

Table 3 presents estimated diet compositions for gulls, terns, storm-petrels, kittiwakes, and offshore alcids in the Gulf of St. Lawrence. With the exception of common and Arctic terns, quantitative dietary data from the Gulf are lacking for these species, and diet compositions are inferred from studies elsewhere. Gulls are omnivores, and consume fish, marine invertebrates, fish offal, and terrestrial food (Threlfall 1968; Haycock and Threlfall 1975; Lagrenade and Mousseau 1981; Pierotti 1983). We estimate that herring and great black-backed gull diets are 50% fish, 30% non-marine food, and 10% each of benthic invertebrates and fish offal (Table 3). Ring-billed gulls are less marine than other gulls (personal observations), so we estimate their diet to include 40% non-marine food.

The diets of common and Arctic tern chicks, recorded on the Quebec North Shore (4Sy, Chapdelaine et al. 1985), consisted mostly of capelin, sand lance, and pelagic invertebrates. We modeled tern food consumption in the northern and central Gulf using these dietary compositions (Table 3), although the caveats indicated for black guillemots also apply. In eastern New Brunswick (4Tl) common tern diets include a wide variety of fish, including Atlantic silversides, rainbow smelts and sticklebacks (Dufresne et al. 1974). We assume that fish: invertebrate ratios in the southern Gulf are similar to those in 4Sy, and we estimate that fish comprise 65% of tern diets in the southern Gulf, with the remainder being pelagic invertebrates.

Linton (1979) found fish, particularly lanternfish (Myctophidae), to be the dominant prey of Leach's storm-petrel on the south coasts of Newfoundland and Nova Scotia. We are uncertain as to the availability of myctophids in the Gulf, so we ascribe storm-petrel diets in the Gulf to unclassified fish (76%) and pelagic crustaceans (24%) (Table 3).

On the basis of studies in eastern Newfoundland (Threlfall 1968; Maunder and Threlfall 1972) we infer that capelin and sand lance are the major foods of kittiwakes where these prey are available, but that pelagic crustaceans and fish offal are also taken. For Gulf kittiwakes we estimate that diet composition is 70% small pelagic fish, primarily lance and capelin, 25% crustaceans, and 5% offal (Table 3).

Studies in Labrador and eastern Newfoundland suggest that lance and capelin are also preferred prey of common murres, razorbills, and Atlantic puffins (Bradstreet 1983; Birkhead and Nettleship 1987; Piatt 1987). Based on observations of prey delivered to young, these species also seem to be important in the Gulf (Bédard 1969, personal observations). We consider that 90% of murre, razorbill, and puffin prey in the Gulf is small pelagics, mostly lance and capelin (Table 3). On the basis of stomach content data (Bradstreet 1983; R.D. Elliot, Canadian Wildlife Service, Ottawa K1A 0H3, pers. comm.) we assign 10% of diet to pelagic crustaceans.

Prey Consumption

The bioenergetics model estimates that seabirds annually remove about 80 000 t of living prey from the Gulf of St. Lawrence (Table 4). About 90% of this is fish and squid, with the remainder divided between benthic and pelagic invertebrates. Most fish prey are pelagics and the model estimates a harvest of 42 263 t of this group. Many fish in the unclassified group are likely pelagic as well. Consumption of benthic and estuarine fish is estimated as 13 527 t.

Total prey removal amounts to 0.04 g $C \cdot m^{-2} \cdot yr^{-1}$, based on 72.6% water content of prey (Dunn 1975), 0.4 g $C\ g^{-1}$ dry weight (Schneider and Hunt 1982) and a Gulf surface area of 214 000 km^2 (Steven 1974).

In general, the distribution of seabird harvest follows the pattern of breeding numbers, with exploitation greatest in the northern, central, and western Gulf (Fig. 2). However the correspondence between seabird populations and prey harvest fails where the seabird community is dominated by terns (e.g. 4Tl), which eat little per capita because of their small size. Likewise, large-bodied cormorants and gannets increase total consumption in areas where they are numerous (e.g. 4Tj, 4Tn).

Benthic and estuarine fish are taken in most Unit Areas (Fig. 2). Consumption estimates for this group are highest in areas with large cormorant populations (e.g. 4Tj, 2 425 t; 4Tp, 2 698 t). The only important avian predator on mackerel is the northern gannet. The model estimates than 2079 and 6636 t of mackerel are taken in Unit Areas 4Tf and 4Tn, respectively (Table 4). Consumption of capelin and sand lance is greatest in the central and northern parts of the Gulf, where kittiwakes and alcids are numerous. The model estimate of 28 752 t for capelin and lance is probably low because many unclassified fish likely belong to these species. Because of the poorly known diets of gulls, unclassified fish are most important in model estimates where gulls are dominant (e.g. 4Sz). Invertebrates are taken by most seabird species and are consumed in moderate quantities in most Unit Areas.

Discussion

Limitations of Model Estimates

Two main factors constrain the accuracy of food consumption estimates presented in this paper. First, the

TABLE 3. Percent diet composition of gulls, terns, storm-petrels, kittiwakes, murres, razorbills, and puffins in the Gulf of St. Lawrence.

Prey	Ring-billed gull	Herring and Great black-backed gulls	Common tern	Arctic tern	Common and Arctic tern	Leach's storm-petrel	Black-legged kittiwake	Common murre	Razorbill	Atlantic puffin
Source of diet data[a]	4	3,8,9	2	2	2	5	6,9	7	1	7
Method[b]	2,3	2,4,5	1,6	1,6	2	2,7	2,4,8	2,7	2,6	2,7
Location of study	Montreal	E. Nfld	4Sy	4Sy	4Sy	S. Nova Scotia, S. Nfld	E. Nfld	E. Nfld	4Sv	E. Nfld
Scope	All	All	4RSTfn	4RSTfn	4Tghjlmq	All	All	All	All	All
Capelin			22	8						
Sand Lance			42	51						
Small pelagic fishes, mostly capelin and sand lance							70	90	90	90
Unclassified fish	35	50			65	76				
Crustaceans			36	41	35	24	25	10	10	10
Benthic invertebrates	15	10								
Fish offal	10	10					5			
Non-marine food	40	30								

[a] 1. Bédard 1969. 2. Chapdelaine et al. 1985. 3. Haycock and Threlfall 1975. 4. Lagrenade and Mousseau 1981. 5. Linton 1979. 6. Maunder and Threlfall 1972. 7. Piatt 1987. 8. Pierotti 1983. 9. Threlfall 1968.

[b] 1. Diet composition taken directly from literature source. 2. Literature source used as guide to estimate diet composition. 3. Percentage of chick regurgitations by volume. 4. Percentage of stomach contents or regurgitations by number of items. 5. Percentage of pellets or regurgitations dominated by taxon. 6. Percentage of chick meals by number of items. 7. Percentage of stomach contents by volume or mass. 8. Visual observations of feeding.

TABLE 4. Estimated prey harvest by seabirds and commercial fishery landings (tonnes) in the Gulf of St. Lawrence, by NAFO Unit Area.

NAFO Unit Area	Benthic and estuarine fish									Pelagic fish and squid								Fish, unclassified	Total fish and squid	Benthic invertebrates	Pelagic crustaceans	Total living prey	Fish offal	Non-marine food	Total food	Commercial fishery landings, 1987[b]
	Flatfish	Cunner	Sculpins	White Hake	Atlantic Cod	Blennies	Alewife	Other estuarines	Total	Mackerel	Herring	Capelin	Sand Lance	Atlantic Saury	Squid	Small Pelagics[a]	Total									
4Ra						35		22	57			1	12			1	15	22	94	5	6	105	5	14	124	11026
4Rb						1		1	2			3	7				10	104	116	21	6	143	21	63	226	9813
4Rc	6	5	1			2		1	14				6			77	83	108	205	21	27	254	26	64	344	11613
4Rd	5	4	1			1			10			2	9				10	32	52	8	4	64	7	21	92	14725
4R	11	8	1			39		24	84			7	34			78	119	265	467	55	43	565	59	163	787	74513
4Si																										6711
4Ss	2		12			12		1	28		1	3	6				10		38			39			39	11989
4Sv	43	14	151		4	195		33	440		16	45	112			4947	5120	1098	6658	237	571	7466	227	702	8395	2793
4Sw						1			1			5	10			1203	1218	902	2121	182	140	2442	181	543	3166	2985
4Sx	111	83	13			76		37	320	31	3		135	8	1	2470	2648	12	2981	4	883	3868	179	11	4059	5212
4Sy	35		212		6	220		12	485		22	90	185			186	483	2404	3373	492	127	3992	494	1469	5955	4786
4Sz	87		519		14	535		29	1184		55	128	248			496	927	5611	7722	1143	171	9036	1158	3415	13609	6383
4S	278	96	908		25	1039		113	2458	31	97	271	697	8	1	9303	10407	10027	22892	2059	1892	26843	2239	6141	35223	41513
4Tf	207	221	61			65		24	577	2079	174	16	2149	517	71	445	5451	512	6540	102	169	6811	129	307	7247	23806
4Tg	404	266	67	144		55		13	949		2		241			1	245	279	1473	54	4	1532	54	162	1748	29616
4Th	309	172	67	237		13		9	806		1		74				75	158	1039	28	10	1077	28	83	1188	18846
4Tj	360	753	358			46	133	775	2425				29				29	258	2712	50	3	2765	50	151	2965	3073
4Tk																										7419
4Tl	25	19	3			5			52				23				23	887	961	124	153	1238	122	370	1730	24073
4Tm	519		799		93	54		466	1931		574	183	8			43	808	901	3640	181	87	3908	177	538	4623	16604
4Tn	134	3	200		23	185		225	769	6636	469	55	5773	1654	228	8198	23013	949	24731	190	1876	26797	460	569	27826	46955
4To	51		79		9	124		121	385		57	18	19			534	628		1013		196	1209	38		1247	5101
4T Gulf	2008	1434	1634	381	125	547	133	1633	7894	8715	1278	272	8316	2171	299	9221	30272	3943	42109	729	2498	45336	1059	2180	48574	200929
4Tp	712		1149		127	100		609	2698		788	283	17			215	1304	1735	5737	351	92	6180	351	1050	7581	1871
4Tq	111		171		20			92	394		123	39					162	511	1067	102	10	1178	102	307	1587	4279
4Tpq	823		1320		147	100		702	3091		911	322	18			215	1466	2247	6803	453	101	7358	453	1357	9168	6150
4RST	3119	1538	3863	381	297	1726	133	2471	13527	8746	2285	871	9064	2179	300	18817	42263	16482	72272	3296	4534	80102	3809	9841	93752	323105
% of living prey	3.9	1.9	4.8	0.5	0.4	2.2	0.2	3.1	16.9	10.9	2.9	1.1	11.3	2.7	0.4	23.5	52.8	20.6	90.2	4.1	5.7	100.0				

[a] Mostly capelin and sand lance.

[b] Landings are from Department of Fisheries and Oceans Zonal Interchange (ZIF) summary files, for landings at Canadian ports of all marine finfish and invertebrates. Unit Area entries do not necessarily sum to Division totals because area of capture is unknown for some landings.

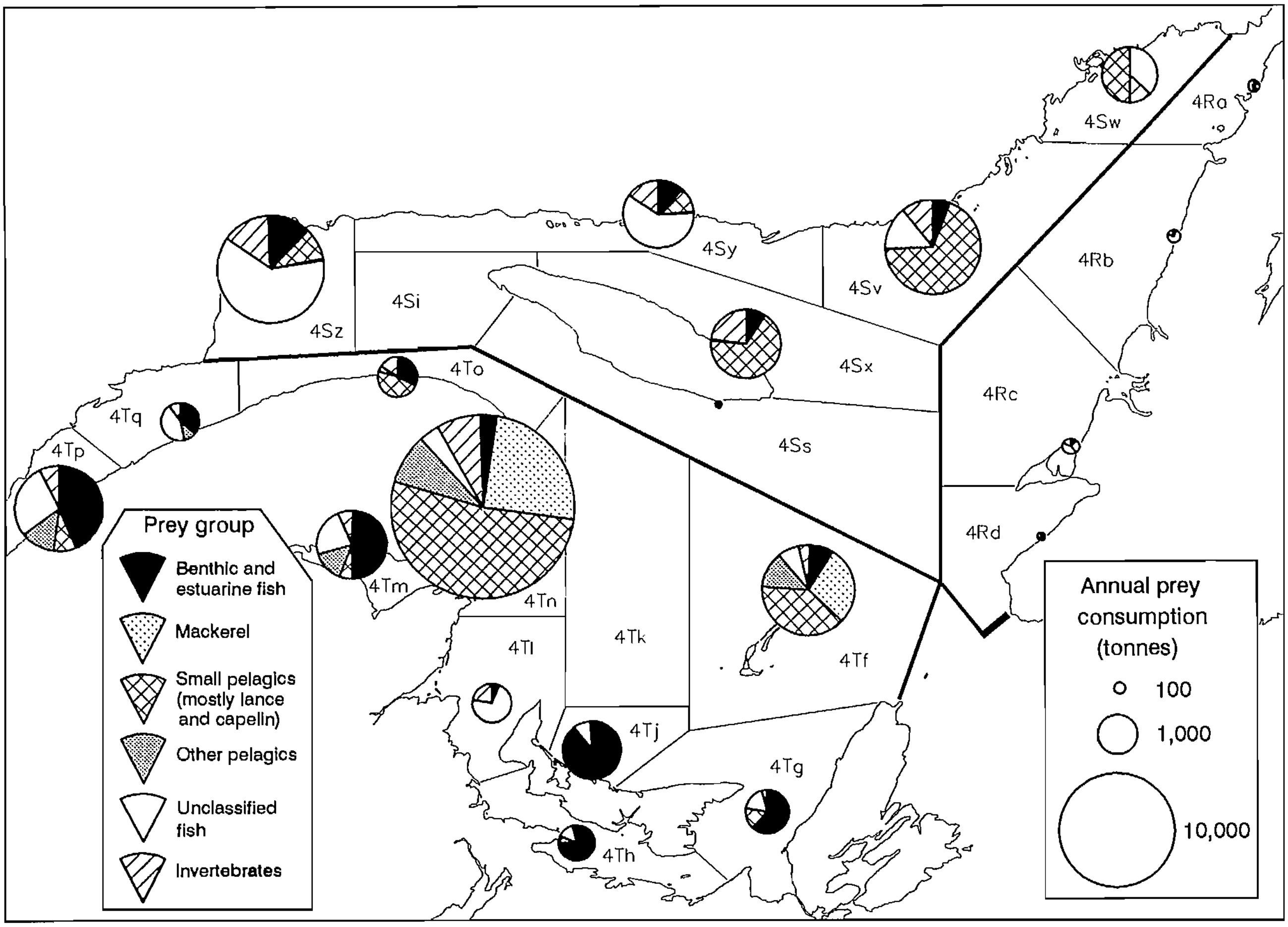

FIG. 2. Estimated prey harvest of seabirds in the Gulf of St. Lawrence, by NAFO Unit Area. Area of symbols is proportional to mass of prey consumed.

model accounts only for seabirds associated with breeding colonies, and does not include waterfowl. Large numbers of sea ducks inhabit Quebec waters of the Gulf in both summer (30 000 breeding pairs, Canadian Wildlife Service database) and winter (162 000 birds, Reed and Bourget 1977). Benthic invertebrates are the major prey of sea ducks (Goudie and Ankney 1986), and total avian consumption of invertebrates is therefore underestimated in model results. The model also excludes non-breeding migrant seabirds, most of which remain outside Gulf waters. There are nevertheless exceptions; substantial numbers of greater and sooty sheawaters penetrate the Strait of Belle Isle in summer, and many Iceland and glaucous gulls winter in the Gulf (Pilote 1976).

Secondly, model estimates are constrained by the accuracy of input data. In general, error accumulates with each step in a bioenergetics model. Thus estimates are most reliable when total energy expenditure for breeding birds during the breeding season is modeled; accuracy diminishes when one calculates in turn food requirements in kilojoules, food consumption in tonnes, and consumption of particular prey groups. Accuracy further diminishes when the model is extended to pre-, non-, and post-breeders, and food consumption for specific areas of sea surface.

Although all input values are subject to some error, most breeding or colony-based parameters are relatively well measured. Cormorant, gannet, kittiwake, and alcid populations are generally accurately censused, but gull and tern populations are poorly known, especially in Quebec and Newfoundland. Duration of pre- and post-breeding residence by seabirds in the Gulf is a major uncertainty in the model. Our estimates of non-breeding residency times are based on spotty colony-based, coastal, and shipboard observations (Pilote 1976; Brown 1986; personal observations) which give only a general guide to arrival and departure times in the Gulf. The magnitude of potential error due to incorrect non-breeding residence times varies with species. Murres and razorbills have short breeding seasons and long non-breeding residence time; the model estimates that 45–46% of their food consumption in the Gulf occurs during non-breeding periods. If non-breeding residency is incorrectly estimated, substantial error could occur in model output. In contrast, gannets have a lengthy breeding season and spend little time in the Gulf before and after breeding. The model estimates that only 6% of their food consumption occurs during non-breeding. Residency times of most other species, and therefore potential error from their incorrect estimation, are intermediate between gannets and murres/razorbills.

Reliability of estimates is decreased when consumption is categorized by prey taxon. Only cormorants and gannets have been subject to diet studies in the Gulf which measured mass contribution of prey taxa. For gannets, sampling occurred at only one of the two main Gulf colonies, and may be inadequate because the species' pelagic prey varies widely among regions (Montevecchi and Barrett 1987) and within and among years (Poulin 1968; Montevecchi et al. 1988). Diet compositions of guillemots and terns are derived from counts of chick feeds, which may not accurately reflect adult diet. For other species, diet within the Gulf is a matter of educated guesses. We therefore caution that model estimates provide only a general guide to consumption of individual prey taxa, and that reliability declines as one proceeds to narrower taxonomic units.

The model assumes that breeding and non-breeding birds derive food from within the NAFO Unit Areas where their colonies are located. This assumption is likely true during breeding for most species. Although offshore seabirds are capable of traveling long distances to feed, feeding intensity is usually greatest close to the colony (Kirkham et al. 1985; Cairns et al. 1987). Nevertheless some exceptions doubtlessly occur. For example, gannets in breeding plumage, presumably from the Magdalen and Gaspé colonies, are often seen during the breeding season in Unit Areas 4Tg, 4Tl, and 4Tm (personal observations).

The assumption that pre- and post-breeding birds forage only within their Unit Areas cannot be tested, but it is probably violated by a substantial number of birds, especially those with long periods of non-breeding residency in the Gulf (i.e. murres and razorbills).

The most reliable model output presented in this paper is total food consumption by seabirds in the Gulf. Our figure for total consumption (80 000 t of living marine prey) is a realistic estimate for seabirds, but if waterfowl were included, the tonnage would rise substantially. At finer taxonomic and geographic scales, most estimates are probably reasonable approximations of reality. There are undoubtedly some fine-scale estimates that contain substantial error in the amount, species, or location of harvest.

Seabird consumption in the Gulf is dominated by fish. Sand lance and capelin are almost certainly the major fish prey, and it is reasonable to conclude that total avian harvest of these species exceeds 25 000 t, and may lie in the range of 30 000–45 000 t. Cormorant and guillemot diets ubiquitously lean toward benthic or inshore fishes, so the estimate of about 14 000 t for benthic and estuarine species seems relatively robust. Mackerel harvest by gannets is likely substantial but may change from year to year. When mackerel are scarce a calorically equivalent tonnage of other pelagic species (herring, capelin, sand lance, Atlantic saury, squid) are likely taken.

With respect to the distribution of exploitation, the overall pattern shown in Fig. 2 is likely valid, although there may be substantial spillover of harvest from sectors with large breeding populations to neighbouring Unit Areas.

The Distribution of Seabird Harvest in Relation to Oceanographic features

Primary productivity in the Gulf of St. Lawrence tends to be highest in a broad region of the western Gulf centred on NAFO Unit Area 4Tn (Steven 1974). This zone of high primary productivity coincides with intense seabird exploitation; Unit Area 4Tn accounts for 33% of all seabird consumption in the Gulf (Table 4). Steven (1974) reported high primary productivity in the St. Lawrence estuary and the Jacques Cartier Passage north of Anticosti Island. These areas are also sites of intense seabird exploitation (Fig. 2).

The northeastern portion of the Quebec North Shore was reported by Steven (1974) to be the least productive part of the Gulf. However, recent data suggest this characterization is erroneous, and that the area is as productive as any other in the Gulf (P. Ouellet, Ministère des Pêches et des Océans, C.P. 1000, Mont-Joli, Québec G5H 3Z4, pers. comm.). The large seabird populations and prey harvests on the eastern Quebec North Shore (Fig. 1 and 2) may reflect this productivity.

Although primary productivity in the southern Gulf (Unit Areas 4Tghjl) is similar to other parts of the Gulf (Steven 1974), seabird populations there are low, and food consumption is weighted towards benthic species (Fig. 1 and 2). The low bird populations in the southern Gulf are due to the absence of gannets, kittiwakes, and alcids, offshore species which are abundant in central and northern parts of the Gulf. These are cold-water birds which do not breed in substantial numbers south of Newfoundland. Three factors may constrain their breeding in the southern Gulf.

The first factor applies primarily to murres, razorbills, and puffins, which pursue pelagic prey in open water. Burst speeds of fish more than double between 5 and 15°C (Wardle 1980). Southern Gulf waters approach 20°C in summer (Lauzier et al. 1957), which may increase fish escape speeds to the point where birds cannot effectively forage for fish in the water column. Cormorants, abundant in the southern Gulf, also pursuit-dive for fish but water temperature probably has little impact on their predation success because they prefer benthic prey which depend on camouflage for predator avoidance (Cairns 1986, personal observations).

The second factor relates to the bathymetry of the southern Gulf. Offshore seabirds typically concentrate feeding efforts at specific locations, usually oceanographic features (e.g. fronts) that serve to concentrate prey (Hunt and Schneider 1987). The southern Gulf is bathymetrically monotonous. The absence of bottom relief that concentrates prey may constrain foraging success by birds which are adapted to feeding at high prey densities (Piatt 1987).

Finally, some offshore seabirds may be prevented from breeding in the southern Gulf because of lack of nesting habitat. Offshore seabirds are generally more tightly constrained in colony site selection than inshore birds (Lack 1967). The southern Gulf has fewer cliffs and rocky islands than the central and northern Gulf. Scarce or low-quality breeding habitat may discourage offshore seabirds from breeding in the southern Gulf. This factor may also explain the paucity of breeding seabirds in western Newfoundland, which has few islands and inaccessible cliffs.

Trophic Roles and Fisheries Interactions of Gulf Seabirds

Because seabirds have high metabolic rates and are numerous in many marine systems, their communities

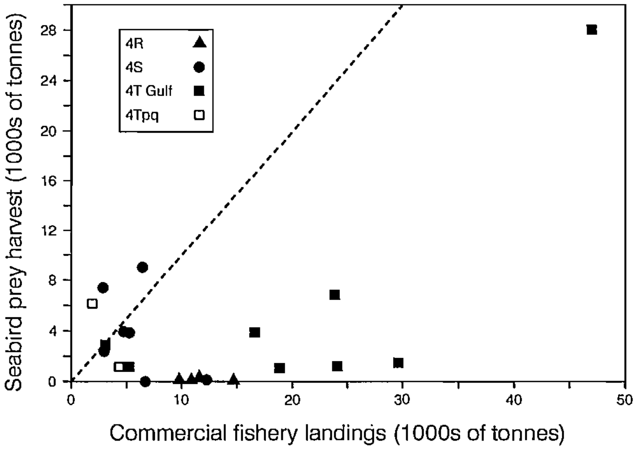

FIG. 3. The relation between estimated seabird prey harvest and reported commercial landings (1987) in the Gulf of St. Lawrence. Each symbol is a NAFO Unit Area. The dashed line represents equal avian and fishery consumption.

may consume very large amounts of food. For example, Antarctic penguins are estimated to take 30 million t of prey annually (Nemoto and Harrison 1981). Estimates that seabirds take 20–30% of local fish production (Wiens and Scott 1975; Furness 1978; Furness and Cooper 1982) suggest that seabird predation may influence the availability of fish to commercial fisheries and vice versa. However, the notion that seabirds have an important influence on fish populations remains controversial (Bourne 1983; Bailey 1986; Duffy and Siegfried 1987), largely because of difficulties in determining fish production and the number of birds in an area.

In the Gulf of St. Lawrence, bird numbers can be estimated with relative accuracy because most seabirds there are associated with colonies where breeders can be readily counted, and because non-Gulf waters are generally beyond the foraging range of major Gulf colonies (except Magdalen Islands gannets; Thomas 1981).

As a first attempt to evaluate the importance of seabirds to the Gulf ecosystem, we compared estimated seabird harvests with 1987 commercial fishery landings (Table 4). In making these comparisons it must be borne in mind that landings statistics may contain substantial errors (cf. McQuinn 1987). Reported commercial landings are larger than estimates of seabird harvest of living marine prey (323 000 vs. 80 000 t), and fishermen outconsume seabirds in most Unit Areas (Fig. 3). However, estimated seabird harvests on the Quebec North Shore (4Svwxyz) are similar in size or larger than commercial landings. Estimated seabird consumption also exceeds commercial landings in 4Tp (St. Lawrence estuary). Most commercial landings are of groundfish that are too large for seabirds to take. Mean annual landings of pelagic species in the Gulf for 1978–87 were 67 000 t (data from Chadwick et al. 1989; Castonguay and Grégoire 1989; Lambert and Bernier 1989; McQuinn 1989), which is less than total estimated seabird consumption.

Seabird-fisheries competition exists only if one or both consumers takes a substantial fraction of prey production. The major seabird prey on the Quebec North Shore appears to be sand lance, which is not commercially fished, and capelin. The capelin fishery in the Gulf is market-limited and landings in 4S averaged only eight tonnes per annum in the years 1978–87 (Lambert and Bernier 1989). Thus seabirds in the northern Gulf of St. Lawrence do not compete with the fishery, despite their sizable consumption of commercial species. However, competition could arise if recent efforts to develop the 4S capelin fishery (Lambert and Bernier 1989) are successful.

In 4Tj and 4Tp, the major avian consumers are cormorants, most of whose prey is non-commercial fish (Table 2). One prey group for which competition could occur is flatfish. Total Gulf flatfish landings for 1985 were 17 664 t (NAFO 1987), which compares to an estimated avian harvest of 3119 t (Table 2). Mean winter flounder landings in 1978–87 were 1863 t (Tallman and Sinclair 1989). Bird consumption of winter flounder may have exceeded fishery landings since winter flounder is the dominant flatfish in cormorant diets (Pilon et al. 1983; Gallant 1988).

Birt et al. (1987) showed by SCUBA transects that two Prince Edward Island bays close to large cormorant colonies were nearly devoid of flatfish, whereas flounders and other benthic fish were abundant in physiographically similar bays that were distant from cormorant colonies. It thus seems likely that cormorants depress flatfish populations near some colonies in the Gulf. However, cormorants choose much smaller size-classes than commercial fishermen, which would lessen the impact of their predation.

The model estimates that Gulf seabirds consume 8 746 t of mackerel annually, which exceeds recent commercial landings (mean 1978–87 landings were 6894 t, Castonguay and Grégoire 1989). However, the northwest Atlantic mackerel stock is very large and landings are market-limited (Castonguay and Grégoire 1989). Competition between seabirds and fishermen for mackerel is therefore unlikely at present fishing intensities.

Seabirds share the upper trophic ranks of the Gulf of St. Lawrence with marine mammals and large fish, whose diets show considerable overlap with those of birds (Powles 1958; Boulva and McLaren 1979; Waiwood and Majkowski 1984; Bowen 1985; Tables 2 and 3). Annual consumption in the Gulf of St. Lawrence has been estimated as 388 000 t for seals (Royal Commission 1986) and 727 000 t for Atlantic cod (Division 4T only, Majkowski and Waiwood 1981). Although large uncertainties attend these estimates, it appears that fish and marine mammals presently play a greater trophic role in the Gulf than do seabirds.

In the Southern Ocean, where baleen whales, seals, and penguins share a common prey, penguins and seals have increased following reduction of whale populations by whaling. This has fueled suggestions that predators exploiting a common prey form a compensatory system in which the reduction of one predator allows the increase of another (May et al. 1979). Such suggestions presuppose that predation is sufficiently intense to absorb the surplus production of the prey, and that alternate prey are unavailable. In the Gulf of St. Lawrence production estimates for major prey species (capelin, sand lance) are lacking, and harvest estimates are unavailable for cetaceans and predatory fish other than cod. In the absence of full data on predator pressure and prey availability, no clear prediction can be made on the effects of the various predatory components (seabirds, marine mammals, predatory fish, commercial fisheries) on the availability of prey to other exploiters (Harwood 1983; Bowen 1985).

Comparisons with Other Systems

Carbon flux to seabirds in the Gulf of St. Lawrence ($0.04\ g\ C \bullet m^{-2} \bullet yr^{-1}$) is generally low compared to other areas of the world for which flux estimates are available (Schneider and Hunt 1982; Abrams 1985; Briggs and Chu 1987; Schneider et al. 1987). Seabirds breed much more abundantly in the open Atlantic waters of eastern Canada than in the Gulf of St. Lawrence (5.4 million vs. 400 000 breeding pairs). Annual harvest by the breeding seabird community of eastern Canada totals about 600 000 t (Cairns et al. 1989). However, the numerically dominant avian consumers in the open Atlantic are migrants from the Arctic and South Atlantic. Total consumption by all birds in eastern Canadian waters likely exceeds the region's commercial fishery landings (ca. 1.6 million t) (Cairns et al. 1989).

Avian consumption in the Gulf is a small fraction (ca. 5%) of total eastern Canadian harvest. Why is the Gulf so lightly exploited compared with the open Atlantic? The Gulf is not unproductive, as its commercial fishery supplies about 25% of eastern Canadian landings (NAFO 1987). We propose several reasons below.

First, current Gulf seabird populations are probably well below carrying capacity. Populations of gannets and alcids in the Gulf have been greatly reduced from earlier centuries by persecution and egging. Based in part on Cartier's description from the 16th century, Fisher and Vevers (1943–44) estimated that 125 000 pairs of gannets bred on the Magdalen Bird Rocks. Early descriptions of egging on the Quebec North Shore (Fortin 1866; Frazar 1887) allow rough calculations of annual take of commercial eggers. From these we surmise that original 4S populations of murres, razorbills and puffins were in the order of 600 000, 100 000, and 100 000 pairs, respectively. If these figures are substituted for present populations in the model, avian harvest estimates rise from 80 000 to 355 000 t. This value exceeds current fishery landings (Table 4). Clearly, the anthropogenic reduction of seabird populations has greatly decreased the energy flux to seabirds in the Gulf of St. Lawrence.

Second, sea ice limits seabird exploitation in winter. The Gulf of St. Lawrence is largely ice-covered for 3–4 mo per year, forcing most seabirds to leave the Gulf, and reducing their annual harvest there.

Thirdly, trans-oceanic and trans-equatorial migrants, abundant on the Scotian Shelf and Grand Banks, do not enter the Gulf in appreciable numbers (Brown 1986, personal observations). The absence of these birds from the Gulf markedly decreases avian consumption compared to the open Atlantic. We are uncertain why these migrants shun the Gulf, except to note that some species (northern fulmar, Wilson's storm-petrel) tend to avoid sight of land when not breeding, and might find the Gulf too confining.

Fourthly, the southern Gulf is inhospitable to offshore seabirds, which closes a substantial area to important predator species (see preceding section).

Of the factors which reduce the importance of seabirds in the Gulf, the most important is the artificial depression of populations. Gulf seabird populations are now rising following a cessation of persecution in most areas (e.g. annual increases of 2.9% for gannets and 4.6% for kittiwakes; Chapdelaine and Brousseau 1989; Chapdelaine unpubl. data). If Gulf colonies follow the pattern of eastern Newfoundland where populations have rebounded to form enormous colonies (Cairns et al. 1986), we can expect that avian food consumption in the Gulf will increase to levels typical of seabird communities elsewhere, and eventually approach or surpass commercial fishery landings.

Conclusions

Seabirds presently absorb a modest energy flux from Gulf of St. Lawrence trophic pathways. The role of seabirds was much greater in the past, and will be so in the future if their populations continue to increase towards historic levels. The Gulf of St. Lawrence is an excellent place to investigate the role of seabirds in the marine community because the scarcity of non-breeding migrants simplifies the estimation of avian prey harvest. Homoiothermic predators may play significant roles in marine trophic processes, including those that lead to commercial fishes, and bioenergetic modeling of prey harvest can make an important contribution to understanding these systems. The value of such contributions will increase as better input data become available, particularly on diet composition.

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Appendix A. Scientific Names

Common name	Scientific name
Birds:	
Northern fulmar	*Fulmarus glacialis*
Greater shearwater	*Puffinus gravis*
Sooty shearwater	*Puffinus griseus*
Wilson's storm-petrel	*Oceanites oceanicus*
Leach's storm-petrel	*Oceanodroma leucorhoa*
Northern gannet	*Sula bassanus*
Great cormorant	*Phalacrocorax carbo*
Double-crested cormorant	*Phalacrocorax auritus*
Ring-billed gull	*Larus delawarensis*
Herring gull	*Larus argentatus*
Iceland gull	*Larus glaucoides*
Glaucous gull	*Larus hyperboreus*
Great black-backed gull	*Larus marinus*
Black-legged kittiwake	*Rissa tridactyla*
Caspian tern	*Sterna caspia*
Roseate tern	*Sterna dougallii*
Common tern	*Sterna hirundo*
Arctic tern	*Sterna paradisaea*
Common murre	*Uria aalge*
Thick-billed murre	*Uria lomvia*
Razorbill	*Alca torda*
Black guillemot	*Cepphus grylle*
Atlantic puffin	*Fratercula arctica*
Fish:	
American eel	*Anguilla rostrata*
Alewife	*Alosa pseudoharengus*
Atlantic herring	*Clupea harengus*
Brook trout	*Salvelinus fontinalis*
Capelin	*Mallotus villosus*
Rainbow smelt	*Osmerus mordax*
Atlantic cod	*Gadus morhua*
Atlantic tomcod	*Microgadus tomcod*
White hake	*Urophycis tenuis*
Atlantic saury	*Scomberesox saurus*
Banded killifish	*Fundulus diaphanus*
Mummichog	*Fundulus heteroclitus*
Atlantic silverside	*Menidia menidia*
Threespine stickleback	*Gasterosteus aculeatus*
Ninespine stickleback	*Pungitius pungitius*
White perch	*Morone americana*
Cunner	*Tautogolabrus adspersus*
Polar eelpout	*Lycodes polaris*
Ocean pout	*Macrozoarces americanus*
Arctic shanny	*Stichaeus punctatus*
Rock gunnel	*Pholis gunnellus*
Sand lance	*Ammodytes* spp.
Atlantic mackerel	*Scomber scombrus*
Arctic staghorn sculpin	*Gymnocanthus tricuspis*
Grubby	*Myoxocephalus aenaeus*
Longhorn sculpin	*Myoxocephalus octodecemspinosus*
Shorthorn sculpin	*Myoxocephalus scorpius*
Moustache sculpin	*Triglops murrayi*
Windowpane	*Scophthalmus aquosus*
Yellowtail flounder	*Limanda ferruginea*
Winter flounder	*Pseudopleuronectes americanus*

Les pêches commerciales de poissons dans les baies, estuaires et rivières du sud-ouest du golfe du Saint-Laurent[1]

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CHAPUT, G.J. ET C.H. LEBLANC. 1991. Les pêches commerciales de poissons dans les baies, estuaires et rivières du sud-ouest du golfe du Saint-Laurent, p. 293–301. *Dans* J.-C. Therriault [éd.] Le golfe du Saint-Laurent : petit océan ou grand estuaire? Publ. spéc. can. sci. halieut. aquat. 113.

Les pêches commerciales de poissons dans les baies, les estuaires et les rivières du sud-ouest du golfe du Saint-Laurent exploitent, par ordre d'importance des débarquements, le gaspareau (*Alosa aestivalis* et *A. pseudoharengus*), l'éperlan arc-en-ciel (*Osmerus mordax*), l'anguille d'Amérique (*Anguilla rostrata*), le poulamon atlantique (*Microgadus tomcod*), la capucette (*Menidia menidia*), l'alose savoureuse (*Alosa sapidissima*), et le bar rayé (*Morone saxatilis*). Dans le golfe, plusieurs de ces espèces sont à la limite nord de leur distribution et la plupart passent l'hiver à l'extérieur du golfe dans des eaux plus profondes et moins froides. La plus grande diversité d'espèces pêchées ainsi que les débarquements les plus élevés proviennent du Nouveau-Brunswick, suivi de l'Île-du-Prince-Édouard. Seule la pêche au gaspareau est d'une importance significative dans les districts de la Nouvelle-Écosse. Durant les deux dernières décennies, les prises sont demeurées relativement stables, malgré des fluctuations interannuelles importantes. Les pêcheries s'effectuent à différentes saisons de l'année selon l'espèce concernée.

The rivers, estuaries and bays of the southwest Gulf of St. Lawrence are sites of commercial fisheries which exploit in decreasing quantity landed gaspereau (*Alosa aestivalis* and *A. pseudoharengus*), rainbow smelt (*Osmerus mordax*), American eel (*Anguilla rostrata*), Atlantic tomcod (*Microgadus tomcod*), silverside (*Menidia menidia*), Atlantic shad (*Alosa sapidissima*), and striped bass (*Morone saxatilis*). For many of these species, the Gulf of St. Lawrence represents the northern limit of their distribution in the western Atlantic and most overwinter outside the gulf in deeper, warmer waters. The greatest variety of species and the largest quantities are landed from the New Brunswick coast, followed by Prince Edward Island. The only species landed in any quantity from Nova Scotia is gaspereau. During the last 20 years, landings have fluctuated annually but overall have remained stable. The fisheries occur during all seasons but exploit different species at differing times of the year.

Introduction

Le golfe du Saint-Laurent est une zone de pêche commerciale particulièrement importante pour les espèces de poissons marins (Rivard *et al.* 1988; Chadwick et Sinclair 1991). De plus, au delà de 100 rivières autour du golfe du Saint-Laurent sont des lieux importants de frai et de croissance pour le saumon de l'Atlantique (*Salmon salar*) : les rivières Miramichi et Restigouche sont les deux plus importantes rivières de l'est du Canada en terme de nombre de saumons capturés par la pêche sportive (Marshall 1988). Il s'avère qu'une gamme d'espèces de poissons moins connues et beaucoup moins étudiées utilisent les affluents du golfe. Au-delà de 78 espèces de poissons ont été recensées dans la rivière et l'estuaire de la Miramichi (McKenzie 1959), tandis que 32 espèces ont été identifiées dans la baie de Malpèque à l'Île-du-Prince-Édouard (Needler 1940). Parmi celles-ci, quelques-unes font l'objet de pêches commerciales lorsqu'elles sont présentes dans les estuaires, les baies et les rivières, même si les débarquements sont faibles comparativement aux prises des espèces exclusivement marines du golfe.

Dans cet exposé, nous dressons un bilan des prises commerciales de huit espèces de poissons pour les années 1968 à 1987 : l'anguille d'Amérique (*Anguilla rostrata*), le gaspareau (*Alosa aestivalis* et *A. pseudoharengus*), l'alose savoureuse (*Alosa sapidissima*), l'éperlan arc-en-ciel (*Osmerus mordax*), le poulamon atlantique (*Microgadus tomcod*), le bar rayé (*Morone saxatilis*) et la capucette (*Menidia menidia*). Cette présentation est limitée au nord-ouest de l'Atlantique et au sud-ouest du golfe du Saint-Laurent. Les études antérieures qui décrivent la distribution et l'abondance de ces espèces dans le golfe du Saint-Laurent sont peu nombreuses et quelques-unes datent d'une trentaine d'année. McKenzie (1964) a décrit les pêches commerciales de l'éperlan de la rivière et de la baie Miramichi de 1931 à 1963, tandis que la pêche à l'anguille a été décrite par Eales (1972) et Loftus (1982). La pêche à l'alose savoureuse au Québec de 1917 à 1981 a été décrite par Provost *et al.* (1984).

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[1] Cet article fait partie des Compte rendus d'un atelier/symposium tenu à l'Institut Maurice-Lamontagne, Mont-Joli (Québec) du 14 au 17 mars 1989.

Autrement, les études réalisées sont plutôt spécifiques, traitant d'une espèce particulière dans un cadre spatio-temporel restreint [Chaput et LeBlanc (1989a et b) ainsi que Crawford et Tully (1989) pour le gaspareau; Jessop et Morantz (1982) pour la capucette; Hogans et Melvin (1984) pour le bar rayé]. Andersen et Gagnon (1980) ont présenté un survol des pêches des espèces fréquentant l'estuaire du fleuve Saint-Laurent.

L'analyse des prises commerciales de ces huit espèces décrit leurs distributions dans le nord-ouest de l'Atlantique. Pour le sud-ouest du golfe du Saint-Laurent, le suivit des tendances spatio-temporelles de ces débarquements illustre les variations dans l'abondance, d'une part, et d'autre part, dans les niveaux d'exploitation de ces espèces. L'ensemble de cette recherche fait ressortir le rôle primordial du sud-ouest du golfe du Saint-Laurent comme habitat, du moins pour une période de leur cycle vital, pour de nombreuses espèces qui utilisent ses rivières, estuaires et baies.

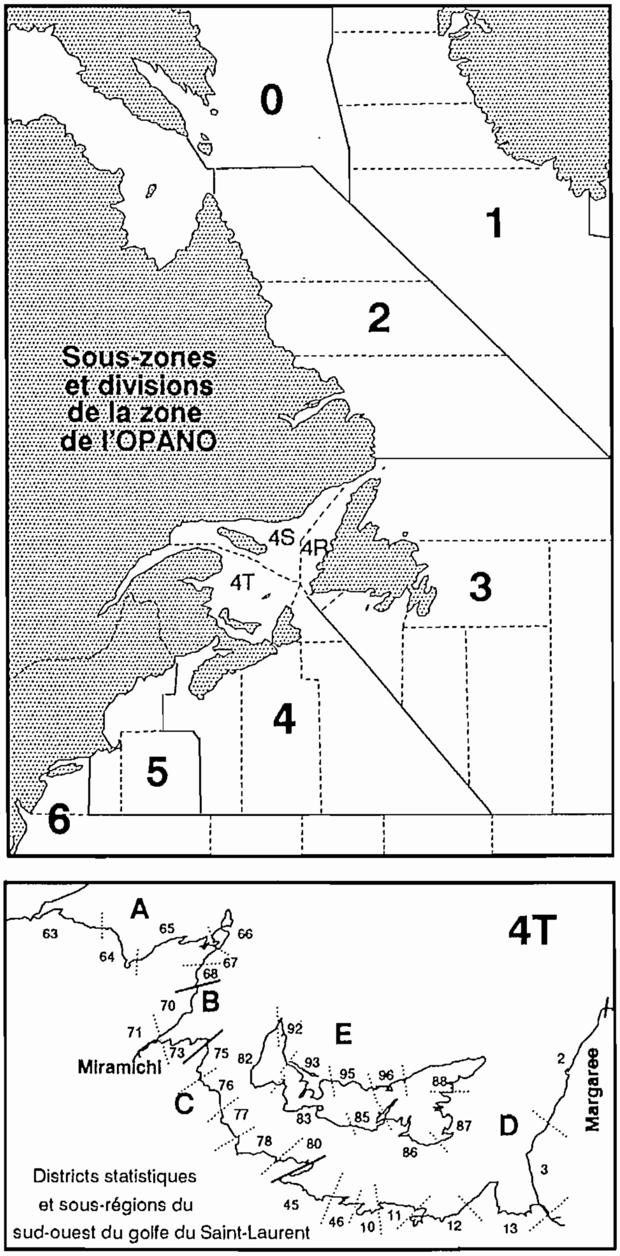

FIG. 1. Sous-zones et divisions statistiques de l'Organisation des Pêches de l'Atlantique Nord-Ouest (OPANO) et sous-régions avec districts statistiques du sud-ouest du golfe du Saint-Laurent.

Matériel et méthodes

Les données proviennent de deux sources. La première source est l'Organisation des Pêches de l'Atlantique Nord-Ouest (l'OPANO) qui publie des bulletins sur les statistiques des débarquements des pêches commerciales du nord-ouest de l'Atlantique (fig. 1). Nous avons analysé ces statistiques pour la période de 1954 à 1985. Ces données sont compilés par division et les débarquements du golfe du Saint-Laurent sont constitués de la somme des débarquements des divisions 4R, 4S et 4T. La division 4T n'inclue pas la partie de la côte nord du fleuve Saint-Laurent à l'est de Pointe Des Monts au Québec. D'ailleurs, les débarquements provenant du Québec sont absents ou incomplets dans les bulletins statistiques de l'OPANO, ce qui fausse les statistiques des divisions 4S et 4T.

La deuxième source est constituée de données compilées par le service des statistiques du Ministère des Pêches et des Océans pour les années 1968 à 1987. Ces débarquements sont compilés par district statistique et concernent uniquement les régions des provinces maritimes adjacentes au golfe. Pour les années 1968 à 1977, seulement les sommes mensuelles des débarquements par espèce et par district sont disponibles. Depuis 1978, les débarquements enrégistrés sont plus détaillés et proviennent de trois formulaires d'inscription :

1) des bordereaux d'achats sur lesquels figurent les débarquements quotidiens par pêcheur, par espèce et par lieu de débarquement,

2) des sommaires mensuels, appelés «supplémentaires B», de prises par espèce et par communauté, complétés par les agents de pêche.

3) des bordereaux, appelés «supplémentaires A», provenant d'acheteurs de l'extérieur du district et qui ne donnent que le total acheté par espèce, la date et le lieu d'achat.

La région du sud-ouest du golfe du Saint-Laurent est délimitée par les districts des trois provinces maritimes attenantes au golfe (fig. 1). Pour cette région, les débarquements sont regroupés en cinq sous-régions qui se résument ainsi :

A — côte nord-est du Nouveau-Brunswick, districts 63–68
B — baie et rivière Miramichi, districts 70–73
C — côte sud-est du Nouveau-Brunswick, districts 75–78 et 80
D — côte de Nouvelle-Écosse, districts 2, 3, 10–13, 45 et 46
E — l'Île-du-Prince-Édouard, districts 82–96

Nous avons comparé les prises annuelles (période janvier à décembre) d'anguille de l'Île-du-Prince-Édouard pour les années 1920 à 1987; les statistiques pour les années 1920 à 1965 proviennent de Eales (1972). Dans le cas de l'éperlan, l'analyse porte sur les débarquements des années 1931 à 1987 (période d'avril à mars) pour la rivière et la baie Miramichi (districts 70 à 73); les débarments annuels par espèce, par sous-région et par décennie. Les données brutes ont été transformées (logarithme). Les débarquements moyens par région et par intervalles d'années ont été analysés à l'aide de la procédure GLM (option PDIFF) du logiciel SAS (1985).

Les tendances temporelles dans les prises entre 1978 et 1987 sont présentées sous forme de courbes cumulatives permettant de démontrer la progression quotidienne des prises. Seules les données provenant de bordereaux d'achats ont été utilisées pour cette compilation.

La proportion des débarquements, par région et par espèce, provenant de bordereaux d'achats est incluse pour les années 1978 à 1987, permettant de juger de la fiabilité des données servant aux comparaisons spatiales et temporelles. Les données disponibles avant 1978 ne permettent pas de faire une telle distinction.

Dans ce travail, les débarquements sont exprimés en unité de tonne métrique.

Résultats

Aucune des espèces retenues pour notre analyse n'est mentionnée dans les statistiques des débarquements des sous-zones 0 à 3 de l'OPANO, sauf pour l'anguille qui est pêchée en faibles quantités dans la péninsule d'Avalon à Terre-Neuve. Conséquemment, les débarquements du nord-ouest de l'Atlantique proviennent essentiellement des sous-zones 4 à 6 de l'OPANO.

Dans ces sous-zones, les prises des espèces étudiées révèlent de grandes fluctuations interannuelles depuis 1954 (fig. 2). Parmi ces espèces, les débarquements annuels de gaspareau sont les plus élevés et de beaucoup supérieurs à ceux du bar, de l'alose savoureuse, de l'anguille et de l'éperlan, dont les prises se situent tous dans un même ordre de grandeur. Les débarquements annuels de poulamon restent inférieurs à 750 t et ceux de la capucette inférieurs à 350 t (fig. 2).

Plus de la moitié des débarquements d'anguille du nord-ouest de l'Atlantique proviennent du golfe du Saint-Laurent. C'est aussi le seul lieu de pêche pour le poulamon et la principale région en débarquements pour l'éperlan et la capucette (fig. 2). Par contre, les prises de bar et d'alose savoureuse provenant du golfe sont minimes dans l'ensemble des débarquements du nord-ouest de l'Atlantique. La proportion de gaspareau en provenance de ces régions a, quant à elle, augmenté durant les 20 dernières années, passant de moins de 2% en 1969 pour se situer à plus de 70% en 1985 (fig. 2).

Depuis 1954, la tendance à la baisse dans les débarquements de gaspareau et de bar notée pour l'ensemble du nord-ouest de l'Atlantique ne se reflète pas dans les débarquements du golfe du Saint-Laurent. Au contraire, ces pêcheries sont demeurées stables ou ont même augmenté depuis le début des années 70 (fig. 2). Aucune tendance d'augmentation ou de diminution n'est discernable dans les débarquements de l'anguille ou de l'alose savoureuse. Il en est de même pour les débarquements d'éperlan et de capucette malgré les grandes fluctuations interannuelles. Cependant, les débarquements de poulamon sont en décroissance depuis les années 50 (fig. 2).

Dans le golfe du Saint-Laurent, le secteur sud-ouest est le lieu prédominant pour la pêche de gaspareau, d'alose savoureuse, de poulamon, de bar et de capucette; cette dernière étant pêchée exclusivement à l'Île-du-Prince-Édouard. Une grande proportion d'anguilles et d'éperlans est aussi débarquée dans le sud-ouest du golfe (fig. 2).

De 1968 à 1987, l'importance des diverses espèces dans les débarquements du sud-ouest du golfe a varié selon les zones géographiques (fig. 1). Les prises de la région de la rivière Miramichi (région B) sont généralement au moins égales sinon supérieures à celles des autres régions pour toutes les espèces concernées, sauf l'anguille (tableau 1). Sur la côte sud-est du Nouveau-Brunswick (région C), on exploite des quantités plus importantes d'anguille, de gaspareau et d'éperlan que sur la côte nord-est (région A). Les pêcheries de l'Île-du-Prince-Édouard (région E) exploitent surtout l'anguille, l'éperlan et le poulamon tandis qu'en Nouvelle-Écosse (région D), le gaspareau est la seule espèce débarquée en grande quantité (tableau 1).

Durant les 20 dernières années, les variations annuelles dans les prises de ces espèces ne permettent pas de discerner de tendances générales d'augmentation ou de diminution. Cependant, des changements régionaux ressortent. Les prises d'anguille ont diminué en Nouvelle-Écosse (D) et sur la côte nord-est du Nouveau-Brunswick (A) depuis 1978 (tableau 1). Cependant, à l'Île-du-Prince-Édouard, les débarquements d'anguille n'ont pas changé significativement depuis 1948 (tableau 2; fig. 3). Les prises de gaspareau ont augmenté pour toutes les régions sauf la région A, mais les augmentations sont surtout significatives pour la Miramichi (B) et l'Île-du-Prince-Édouard (E) (tableau 1). Les prises d'éperlan restent relativement constantes depuis 1968, sauf en Nouvelle-Écosse où les prises ont chuté depuis 1978 (tableau 1). Dans la zone de la rivière Miramichi, les débarquements d'éperlan sont demeurés assez stables depuis 1953, mais sont de beaucoup inférieurs au rendement des années 1931 à 1942 (tableau 2; fig. 3). Les prises de poulamon ont diminué dans toutes les régions, surtout à l'Île-du-Prince-Édouard et sur la côte nord-est du Nouveau-Brunswick, tandis que celles de l'alose savoureuse restent faibles dans toutes les régions sauf pour une augmentation significative dans la région A (tableau 1).

Deux espèces d'aloses, débarquées sous le nom commun gaspareau, sont exploitées en proportions d'abondance variables selon les régions du sud-ouest du golfe. En Nouvelle-Écosse, *Alosa pseudoharengus* domine largement dans les prises de gaspareau tandis que dans la rivière Miramichi, *Alosa aestivalis* est généralement l'espèce la plus abondante (tableau 3). Depuis 1982, les proportions respectives de chacune de ces espèces dans les prises de la Miramichi fluctuent annuellement; *Alosa pseudoharengus* représentant de 24% à 71% des débarquements de gaspareau. On attribue ces variations partiellement au fait que *Alosa pseudoharengus* remonte la Miramichi approximativement 2 semaines avant *Alosa aestivalis* (fig. 4), et la pêche se terminant le 15 juin (Chaput et LeBlanc 1989a), des proportions différentes de ces deux espèces sont exploitées selon les variations annuelles dans leur synchronisme de remontée. En outre, des différences interrégionales de synchronisme ont été notées pour *Alosa pseudoharengus*; ceux de la rivière Margaree, en Nouvelle-Écosse, remontent la rivière environ 2 semaines avant ceux de la Miramichi (fig. 4).

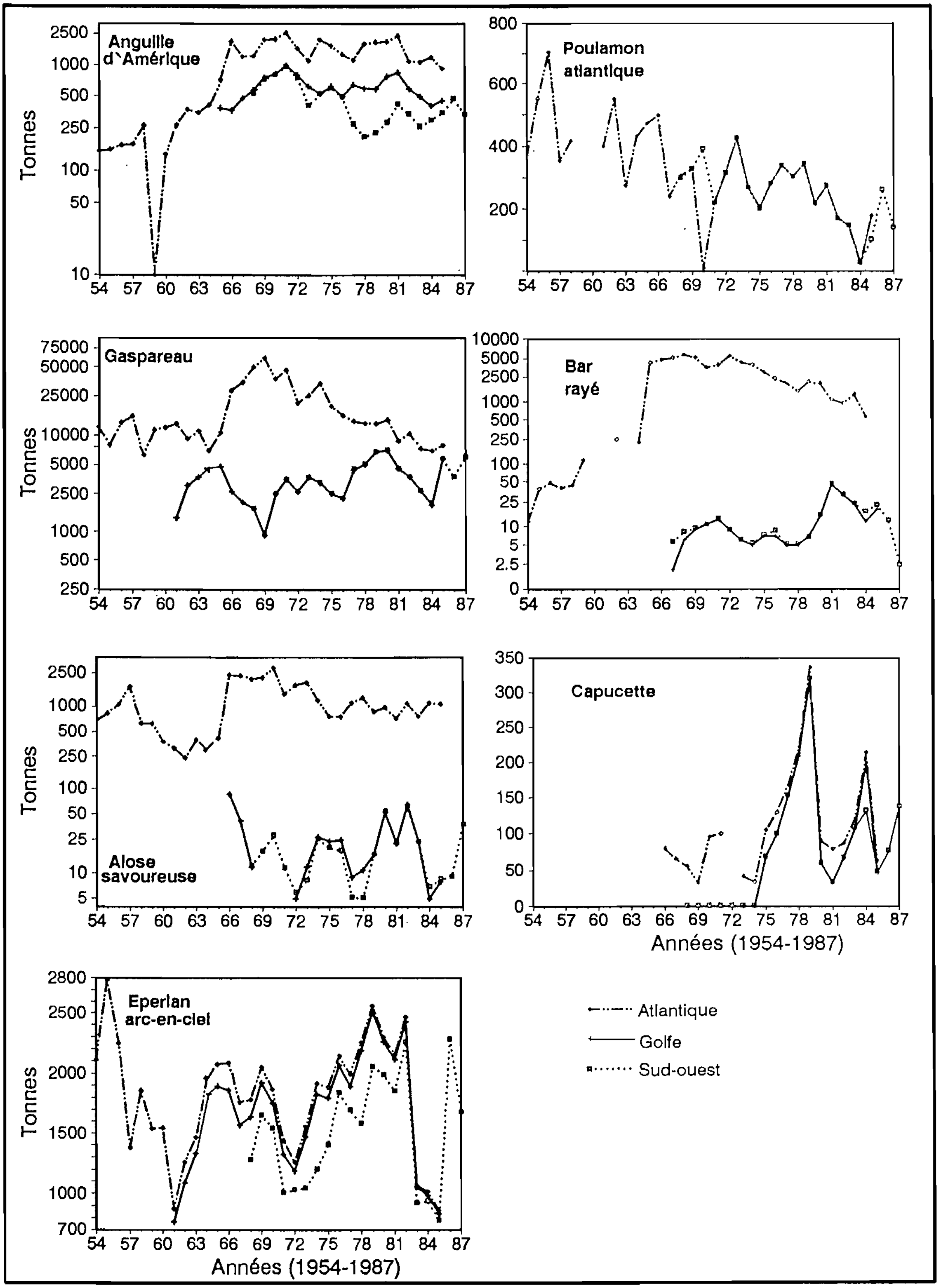

FIG. 2. Débarquements annuels des diverses espèces de l'Atlantique nord-ouest, du golfe du Saint-Laurent et du sud-ouest du golfe, 1954 à 1987.

TABLEAU 1. Comparaisons des débarquements annuels en tonnes par décennie et par sous-région du sud-ouest du golfe du Saint-Laurent. Les sous-régions rejointes par une lettre minuscule commune ne sont pas significativement différentes pour cette décennie (SAS PDIFF deux-à-deux; $P > 0.05$). Pour les sous-régions marqués par un asterix, les débarquements diffèrent significativement entre les deux décennies (SAS PDIFF deux-à-deux; $P < 0.05$). Les sous-régions A à E sont décrites dans le texte.

	Décennie 1968–1977			Décennie 1978–1987		
Espèce	Sous-région	moyenne	écart	Sous-région	moyenne	écart
Anguille d'Amérique	a B	46.6	21.1	D	11.8	5.4
	a C	78.0	36.5	a B	21.4	8.9
	a A*	78.3	33.6	a A	38.3	24.6
	b E	172.9	88.0	C	91.5	56.5
	b D*	227.2	117.4	E	156.1	39.0
Gaspareau	E*	54.5	50.5	a E	234.5	144.3
	a C	463.5	177.4	a A	392.0	201.5
	a A	577.3	399.5	b C	786.7	461.2
	a B*	742.9	633.6	c b D	1476.0	640.2
	a D	942.9	520.2	c B	1895.1	1070.0
Alose savoureuse	E	—	—	a E	1.8	2.4
	A*	0.5	0.9	a D	3.1	3.0
	a D	2.3	2.2	a A	4.3	4.5
	b a C	3.1	3.6	b a C	8.0	11.7
	b B	10.6	5.9	b B	9.3	5.0
Éperlan arc-en-ciel	D*	127.0	77.6	D	34.7	23.5
	a A	244.9	46.8	a A	238.4	111.8
	a C	317.4	107.0	b a E	340.6	145.8
	a B	358.7	142.5	b B	424.0	263.7
	a E	361.2	126.6	b C	527.8	314.6
Poulamon atlantique	D*	0.3	0.4	a D	1.6	1.6
	a C	36.8	14.1	b a A	10.4	16.7
	b a A*	40.5	20.3	b C	35.3	28.0
	c b B	106.7	39.4	b E	50.2	56.0
	c E*	123.0	37.9	B	91.8	64.3

TABLEAU 2. Comparaisons des débarquements annuels de l'anguille d'Amérique pour l'Île-du-Prince-Édouard et de l'éperlan arc-en-ciel pour la région Miramichi (districts 70–73). Les intervales d'années rejoints par une lettre minuscule commune ne sont pas significativement différents (SAS PDIFF deux-à-deux; $P > 0.05$).

		Débarquement (t)	
Intervale		moyenne	écart
Prises de l'anguille d'Amérique de l'Île-du-Prince-Édouard (districts 82–96) [Données pour 1920 à 1965 de Eales (1972)]			
1928 à 1937	a	79.3	39.4
1938 à 1947	b a	103.3	48.7
1920 à 1927	b a	154.3	132.9
1978 à 1987	c b a	156.3	40.4
1968 à 1977	c b	184.6	101.3
1948 à 1957	c b	195.9	76.3
1958 à 1965	c	259.1	118.5
Prises de l'éperlan arc-en-ciel de la Miramichi (districts 70–73) [Données pour 1931 à 1962 de McKenzie (1964)]			
1968 à 1977	a	358.7	142.6
1953 à 1962	a	385.4	233.1
1978 à 1987	b a	424.0	263.8
1943 à 1952	b	722.5	252.8
1931 à 1942		1021.1	270.2

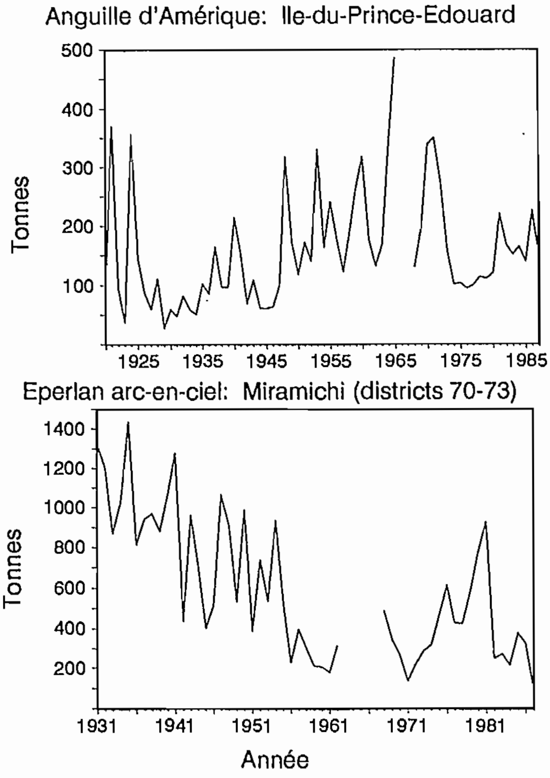

FIG. 3. Débarquements d'anguille de l'Île-du-Prince-Édouard et d'éperlan de la région de la Miramichi.

TABLEAU 3. Proportions de *Alosa pseudoharengus* dans les échantillons de gaspareau prélevés des rivières du sud-ouest du golfe du Saint-Laurent[a]. Sources d'information : Margaree (Chaput et LeBlanc 1989b), South (Chaput et Alexander 1989), Pictou (Crawford et Tully 1989), Miramichi (Chaput et LeBlanc 1989a).

		Année						
Rivière	Méthode de capture	1982	1983	1984	1985	1986	1987	1988
Margaree[a]	pêche commerciale		99.4	99.7	99.3	99.8	99.9	99.5
South[a]	barrière d'énumération		98.2	99.9	99.1	99.9	99.9	
Pictou	passe à poisson	34.8	43.0	55.8	78.7	82.0	84.0	85.0
Miramichi[a]	pêche commerciale	46.6	46.1	71.1	23.9	62.4	45.5	32.6
	filet-trappe indice de Millbank (MPO)	29.6	34.1	33.4	16.1	33.8	34.5	19.8

[a] Les proportions sont calculées par rapport aux échantillons pondérés par les débarquements ou comptes totaux.

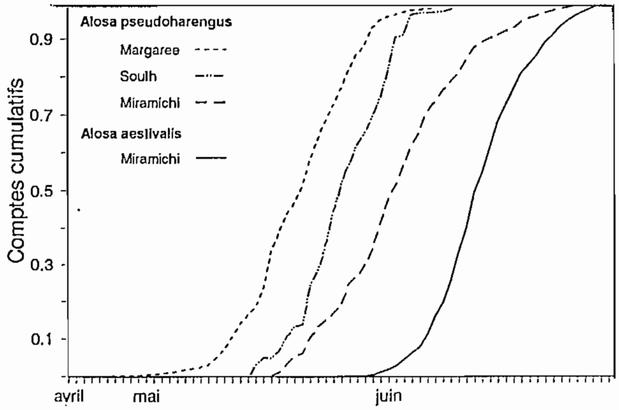

FIG. 3. Débarquements d'anguille de l'Île-du-Prince-Édouard et d'éperlan de la région de la Miramichi.

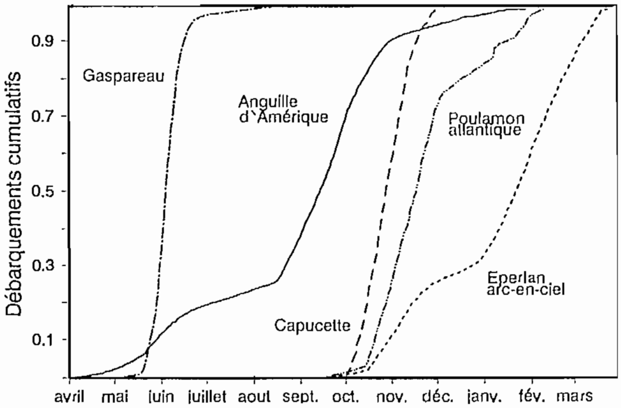

FIG. 4. Synchronisme de la remontée de gaspareau dans diverses rivières du sud-ouest du golfe du Saint-Laurent.

Les pêcheries s'effectuent à différentes périodes de l'année; cette périodicité reflète la disponibilité des espèces sur les lieux de pêche. La pêche à l'anguille s'effectue pendant toute l'année, mais la majorité des prises se font à l'automne (fig. 5). La capucette et le poulamon sont débarquées presque exclusivement en automne tandis que la pêche d'hiver sous la glace exploite surtout l'éperlan avec une quantité moindre de poulamon et d'anguille. La pêche au gaspareau est de courte durée, soit de la mi-mai à la fin de juin (fig. 5). Le bar et l'alose savoureuse sont essentiellement des prises accessoires à celle-ci.

La proportion des débarquements annuels par région et par espèce enrégistrée par l'entremise des bordereaux d'achats de 1978 à 1987 se situe généralement au-dessus de 60% (tableau 4), sauf pour quelques espèces, notamment en Nouvelle-Écosse. On a remarqué que les débarquements de gaspareau d'une région de cette province ne sont pas inscrits sur les bordereaux d'achats car le poisson est transformé sur les lieux de pêche et seulement vendu plus tard dans l'année. Cependant, les débarquements de l'alose savoureuse et du bar, quoique faibles, proviennent presque exclusivement des bordereaux d'achats et reflèteraient les prises réelles (tableau 4).

Discussion

Le golfe du Saint-Laurent représente la limite nord de distribution de certaines espèces présentes dans le nord-ouest de l'Atlantique, notamment les deux espèces nommées gaspareau, l'alose savoureuse, le bar et la capucette. Les débarquements de ces espèces dans le golfe sont faibles comparativement à l'ensemble du nord-ouest de l'Atlantique, exception faite de la capucette. D'ailleurs, les débarquements du golfe proviennent presque exclusivement du sud-ouest. Les prises de capucette ne sont cependant pas indicatives de l'abondance de cette espèce dans le nord-ouest de l'Atlantique (Scott et Scott 1988), mais reflètent plutôt des conditions de marché qui limitent les prises ailleurs; la région de l'Île-du-Prince-Édouard ayant réussi à combler la demande du marché actuel.

Le gaspareau, dont le golfe représente la limite nord de distribution, est surtout abondant dans le sud-ouest : on a retrouvé quelques individus seulement au large de Terre-Neuve (Winters *et al.* 1973) et aucune exploitation commerciale ne s'éffectue dans l'estuaire du Saint-Laurent (Andersen et Gagnon 1980; Roy 1968). Les pêcheries du sud-ouest exploitent les deux espèces en grande quantité durant la migration des reproducteurs dans les rivières au printemps. Cependant, le gaspareau n'hiverne pas dans le golfe. Des études de marquage démontrent que ces espèces peuvent migrer hors du golfe à l'automne (Crawford et Tully 1989). Au printemps, *Alosa pseudoharengus* remonte les rivières de la Nouvelle-Écosse, tributaires du golfe, environ une à deux semaines avant la remontée de la rivière Miramichi au Nouveau-Brunswick. Ce décalage dans la période de remontée progresse suivant la localisation géographique des rivières

TABLEAU 4. Pourcentage des débarquements annuels provenant de bordereaux d'achats par espèce et par sous-région géographique du sud-ouest du golfe du Saint-Laurent pour les années 1978 à 1987. Les sous-régions A à E sont décrites dans le texte.

		Pourcentage provenant de bordereaux d'achats			Débarquement annuel total (tonne)		
Espèce	S-région	moyenne	écart	*n*	moyenne	écart	*n*
Anguille d'Amérique	A	60.0	29.7	9	38.3	24.6	10
	B	73.1	21.9	9	21.4	8.9	10
	C	72.0	16.2	10	91.5	56.5	10
	D	25.1	17.2	9	11.8	5.4	10
	E	88.3	8.8	10	156.1	39.0	10
Gaspareau	A	92.2	7.3	10	392.0	201.5	10
	B	88.4	15.8	10	1895.1	1070.0	10
	C	71.6	20.1	10	786.7	461.2	10
	D	27.5	24.6	10	1476.0	640.2	10
	E	12.9	9.3	10	234.5	144.3	10
Alose savoureuse	A	81.6	36.9	10	4.3	4.5	10
	B	50.8	32.1	10	9.3	5.0	10
	C	93.4	16.8	10	8.0	11.7	10
	D	97.8	5.8	7	3.1	3.0	7
	E	98.8	2.8	5	1.8	2.4	5
Eperlan arc-en-ciel	A	69.3	14.7	10	238.4	111.8	10
	B	76.9	21.9	10	424.0	263.7	10
	C	68.1	24.9	10	527.8	314.6	10
	D	22.1	25.3	10	34.7	23.5	10
	E	76.5	26	10	340.6	145.8	10
Poulamon atlantique	A	63.3	19.2	8	10.4	16.7	10
	B	89.4	17.1	10	91.8	64.3	10
	C	91.8	12.9	10	35.3	28.0	10
	D	98.5	2.1	2	1.6	1.6	2
	E	78.3	33	10	50.2	56.0	10
Bar rayé	A	93.6	18.2	8	1.3	1.1	8
	B	56.9	36.7	10	7.0	4.5	10
	C	75.8	33.2	7	10.1	11.9	10
	D	100.0	0.0	2	0.2	0.2	2
	E	100.0	—	1	0.5	—	1
Capucette	C	100.0	—	1	4.2	—	1
	E	91.0	19.2	10	118.3	90.4	10

de l'est vers l'ouest. De telles différences sont à prévoir si le gaspareau doit contourner l'île du Cap-Breton au printemps, après avoir hiverné à l'extérieur du golfe.

Tout comme dans le cas du gaspareau, le golfe du Saint-Laurent est la limite nord de distribution de l'alose savoureuse : seulement quelques individus ont été recueillis au large du Labrador (Dempson *et al.* 1983). Dans le sud-ouest du golfe, l'alose savoureuse est débarquée comme prise accessoire durant la pêche au gaspareau. Les débarquements dans le fleuve Saint-Laurent ont atteint plus de 400 t en 1954 pour chuter à moins de 25 t depuis 1970 (Provost *et al.* 1984). Des populations distinctes de celles de la côte nord-ouest de l'Atlantique fraient dans les rivières du golfe et passent l'hiver à l'extérieur, au large de la Nouvelle-Écosse et possiblement plus au sud (Dadswell *et al.* 1987).

Le bar est plus abondant dans le nord-ouest de l'Atlantique que dans le golfe du Saint-Laurent, mais des populations distinctes ont été identifiés dans le golfe (Magnin et Beaulieu 1967). On reconnaît aussi, d'après des études de marquage, que certains bars, originaires des rivières de l'est des États-Unis, migrent dans le golfe et s'alimentent dans les rivières et estuaires (Hogans et Melvin 1984).

L'éperlan et le poulamon ont une distribution centrée dans le golfe du Saint-Laurent. Ces deux espèces habitent les eaux côtières peu profondes pendant l'hiver, grâce à des protéines antigel dans le sang qui leurs permettent de survivre à basses températures (Reisman *et al.* 1987; K.V. Ewart et G.L. Fletcher, OSC, Memorial Univ. of Newfoundland, St. John's (Terre-Neuve) comm. pers). L'éperlan ne migre pas très loin de sa rivière natale et reste dans les estuaires et baies peu profondes en automne et hiver (McKenzie 1964; Fréchet *et al.* 1983). On le retrouve dans les baies plus profondes durant l'été (Pêches et Océans, Division des poissons marins et anadromes, Moncton (N.-B.) données inédites; McKenzie 1964). Le poulamon n'effectue pas de grandes migrations marines et les affluents importants du golfe soutiennent des populations distinctes (Vladykov 1955).

D'une part, les disparités régionales dans les débarquements représentent des différences dans la quantité d'habitat propice pour les diverses espèces concernées. La rivière, l'estuaire et la baie de Miramichi sont des hauts lieux de production et des sites de frai privilégiés pour les espèces anadromes telles que le gaspareau, l'alose savoureuse, et l'éperlan. Les deux espèces de gaspareau ont chacune des lieux de frai bien distincts. *Alosa pseudoharengus* préfère frayer dans les lacs et rivières avec peu de courant (Loesch 1987); elle est l'espèce dominante de la rivière Margaree en Nouvelle-Écosse (Chaput et LeBlanc 1989b) où le frai s'éffectue dans les eaux du lac Ainslie, d'une superficie de 57,4 km carrés (O'Neil 1980). Par contre, *Alosa aestivalis* préfère frayer en rivière (Loesch 1987), et est l'espèce prédominante de la rivière Miramichi, quoique l'on y retrouve *A. pseudoharengus* (Chaput et LeBlanc 1989a). La côte du sud-est du Nouveau-Brunswick, avec de nombreux estuaires formant des bassins allongés et peu profonds, est un habitat propice pour les populations de gaspareau, d'éperlan et d'anguille.

D'autre part, les différences régionales dans les prises de chaque espèce sont partiellement attribuables à des variations de l'effort de la pêche. Dans les régions de la Miramichi et du sud-est du Nouveau-Brunswick, par exemple, on retrouve le plus grand nombre de détenteurs de permis de pêche à l'éperlan du golfe. En outre, ces pêcheurs utilisent une plus grande quantité de filets (Cairns 1989).

Enfin, on doit s'interroger sur la fiabilité des données qui ont servi à l'examen de variations temporelles et spatiales. Il s'avère que ces données ne représentent pas la totalité des prises de ces espèces, principalement dû à des lacunes dans la précision des débarquements réels et dans l'enregistrement des produits transformés. Ceci peut s'expliquer par les caractéristiques variables de ces pêches et les multiples utilisations de la ressource. Par exemple, les formulaires «supplémentaire B» sont des estimés, fournis par les agents de pêche, des prises non-vendues qui servent comme appât ou à la consommation locale. Or, le niveau de cette utilisation locale varie selon l'espèce et la région et est parfois difficile à estimer. D'ailleurs, pour les années 1978 à 1987, la grande proportion des débarquements proviennent de bordereaux d'achats qui fournissent des informations plus détaillées que les formulaires «supplémentaire B», permettant ainsi un suivi spatio-temporel fiable. Une étude de la pêche à la capucette en 1979 a démontré une concordance rapprochée entre les débarquements, compilés par la division des statistiques, et les prises enrégistrées dans les journaux quotidiens de prises et de l'effort de pêche; la différence étant de l'ordre de 1,6% (Jessop et Morantz 1982). Des données brutes de débarquements commerciaux ont également servi à l'examen de la concordance entre les changements dans les prises de nombreuses espèces du nord-ouest de l'Atlantique et les cycles de marées à long terme (Cabilio *et al.* 1987).

Les pêcheries des affluents du golfe ont surtout une importance locale. Elles se pratiquent pendant différentes périodes de l'année dans toutes les régions du golfe. D'ailleurs, une quantité non-négligeable de poissons est débarquée en automne comme en hiver; période de l'année qui autrement présente peu d'occasions de pêche. Ces pêches sont pratiquées par de nombreux individus utilisant une variété d'engins de pêche peu dispendieux, ce qui rend ces pêches rentables (Cairns 1989; Eales 1972; McKenzie 1964).

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Caractéristiques de trois populations de saumon atlantique *(Salmo salar)* du golfe du Saint-Laurent et leurs impacts sur la gestion des stocks[1]

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L'examen des caractéristiques de trois populations de saumon atlantique (*Salmo salar*) du golfe du Saint-Laurent, fait sur plusieurs années, démontre à la fois des similitudes et des différences. Les madeleineaux (un an de mer) sont presque toujours des mâles alors que les saumonneaux (smolt), les saumons dibermarins (deux ans de mer) et les saumons tribermarins (trois ans de mer) sont majoritairement des femelles. Les dibermarins dominent très largement le groupe des saumons rédibermarins (plus d'un an de mer). La proportion de madeleineaux varie considérablement d'une rivière à l'autre. Plus la proportion de madeleineaux est importante, plus le pourcentage de femelles est élevé chez les dibermarins. Les saumonneaux de la rivière Saint-Jean sont habituellement plus âgés et plus petits que ceux des rivières de la Trinité et Bec-Scie. Toutefois, après leur migration en mer, ils sont plus grands que ceux de la rivière de la Trinité, ces derniers étant plus grands que ceux de la Bec-Scie. La taille moyenne des saumonneaux, madeleineaux et dibermarins d'une rivière donnée peut varier d'une année à l'autre. On ne perçoit pas de synchronisme dans la variation de la taille moyenne des saumonneaux alors que chez les madeleineaux et les dibermarins, les années où la taille est inférieure à la moyenne (1984 et 1985) coïncident avec les années où les populations de saumons furent faibles. Nous concluons que les différences entre les trois populations sont suffisantes pour justifier une approche différente de gestion d'un stock à l'autre.

The analysis of characteristics of three populations of Atlantic salmon (*Salmo salar*) of the Gulf of St. Lawrence for several years shows similarities and differences. Grilse (one sea-winter salmon) are almost always males, while smolts and multi-sea-winter salmon show female biased sex-ratios. Multi-sea-winter salmon are predominently two-sea-winter individuals. The proportion of grilse is largely variable between rivers. The more the grilse proportion is important, the more the two sea-year run is female biased. Smolts of the Saint-Jean river are usually older and smaller than those of the de la Trinité and Bec-Scie rivers; however returning adults are larger than salmon of the Trinité river, which are in turn larger than those of the Bec-Scie river. Mean length of smolts, one sea-winter and two sea-winter salmon vary between years. We did not find any synchronism in the variation of the mean length of smolts, however for one sea-winter and two sea-winter salmon, years of lower mean length (1984 and 1985) are also years of small returning populations. We conclude that the differences between the three populations justify implementing management programs appropriate for each river.

Introduction

Plusieurs auteurs ont présenté des données concernant les caractéristiques de certains stocks de saumon atlantique (*Salmo salar*) des rivières du Québec méridional. Certains travaux ont permis de décrire des populations de saumons (Gibson et Côté 1982; Power 1981; Shooner 1967), d'autres ont permis de mettre en lumière la variabilité des stocks d'une rivière à l'autre (Bielak et Power 1985; Schiefer 1971) et l'effet des variables environnementales sur celles-ci (Power 1981; Saunders 1981) ou encore de décrire les variations qui se seraient produites sur une longue période (Bielak 1984; Bielak et Power 1986). Il est important de bien connaître les caractéristiques d'une population, de même que leur évolution dans le temps, si on veut faire une gestion adéquate des stocks. Bien qu'il soit difficile de suivre et de gérer les différents stocks en mer (Saunders 1981), la gestion au niveau local demeure tout de même un facteur d'importance pour le maintien des populations.

Au cours des dernières années, nous avons effectué des travaux principalement sur trois rivières situées dans des

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zones salmonicoles différentes: la rivière Saint-Jean près de Gaspé, la rivière de la Trinité sur la Haute Côte-Nord et la rivière Bec-Scie sur l'île d'Anticosti (fig. 1). Le but de cette étude est de décrire, pour quelques années consécutives, les caractéristiques des populations de saumon qui nous paraissent importantes pour la gestion des stocks.

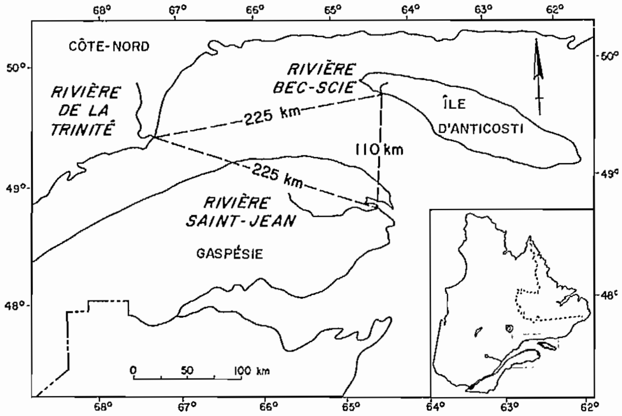

FIG. 1. Localisation des rivières Saint-Jean, de la Trinité et Bec-Scie.

Matériel et méthodes

Description des rivières

Les trois rivières possèdent des caractéristiques qui les distinguent (tableau 1). La rivière Saint-Jean est la plus importante des trois rivières; située à l'extrémité est de la Gaspésie, elle draine une superficie de 1 134 km^2 et s'étend sur 102 km de longueur. Le saumon fréquente les 92 premiers kilomètres, soit une superficie totale de 23 308 unités de 100 m^2 lorsque l'on exclut l'estuaire (Boudreault 1988). Environ 97 % de cette superficie est classifié comme un habitat très favorable au saumon juvénile, 1 % favorable et 2 % peu favorable selon la classification des habitats proposés par Côté *et al.* (1986). La pente est régulière et le saumon ne rencontre aucun obstacle sur tout son cours si ce n'est quelques barrages de castor en tête de bassin. Le monitoring des migrations des saumons a permis de constater que la dévalaison des saumonneaux a lieu en mai et juin. On atteint généralement 50 % de la dévalaison (date médiane) entre le 23 mai et le 3 juin. La date médiane du retour à la rivière des saumons adultes, calculée par les captures enregistrées au poste de marquage en estuaire, varie du 24 juin au 5 juillet.

La rivière de la Trinité est située sur la Haute Côte-Nord du Saint-Laurent et draine un bassin de 562 km^2. Elle s'étend sur 60 km et est fréquentée sur tout son long par le saumon. L'assise rocheuse est granitique et l'écoulement est caractérisé par une alternance de rapides et de seuils avec des eaux plus lentes dans les bassins et les chenaux. L'habitat des juvéniles totalise 21 129 unités de 100 m^2 dont 12,3 % d'habitat très favorable, 40,3 % d'habitat favorable et de 47,4 % d'habitat peu favorable au saumon juvénile. La pêche commerciale a cours aux environs immédiats de la rivière et il s'y capture presque essentiellement des rédibermarins (Caron et Mercier 1988). La date médiane de la dévalaison des saumonneaux se situe entre le 16 et le 26 juin de chaque année. D'autre part, on y a généralement enregistré à la passe migratoire la moitié des saumons adultes de retour à la rivière entre le 8 et le 12 juillet.

La rivière Bec-Scie est de loin la plus petite rivière des trois. Située sur l'île d'Anticosti, elle draine un bassin de 131 km^2. La pente est faible et régulière, l'assise

TABLEAU 1. Caractéristiques des rivières Saint-Jean, de la Trinité et Bec-Scie.

	Saint-Jean	de la Trinité	Bec-Scie
Bassin de drainage (km^2)	1 134	562	131
Longueur (km)			
totale	102	60	14
fréquentée	92	60	14
Latitude nord	48°46′	49°25′	49°43′
Longitude ouest	64°26′	67°18′	64°03′
Assise rocheuse	Calcaire	Granite	Calcaire
Habitat (100 m^2)			
Très favorable	22 502	2 602	614
Favorable	304	8 511	362
Peu favorable	502	10 016	670
Date médiane de la dévalaison des des saumonneaux	23 mai–3 juin	16–26 juin	29 mai–11 juin
Date médiane de la montaison des adultes	24 juin–5 juillet	8–12 juillet	9–23 juillet
Montaison annuelle moyenne (1980–1988)	1 200	2 300	200
Capture annuelle moyenne (1980–1988)	500	700	60

rocheuse est formée de roche calcaire; on rencontre deux lacs sur le parcours de la rivière et deux autres lacs en tête des deux principaux embranchements. Le saumon utilise toute la rivière, soit 14 km plus un embranchement important. Les habitats fluviatiles de juvéniles totalisent 1 646 unités de 100 m^2 dont 37 % sont très favorables, 22 % favorables et 41 % peu favorables au saumon. La date médiane de dévalaison des saumonneaux varie du 29 mai au 11 juin et celle du retour des saumons adultes se situe généralement entre le 9 et le 23 juillet. Toutefois, il est à noter que la montaison peut être retardée significativement sur cette rivière quand les étés sont secs.

Les embouchures de ces rivières sont distancées par moins de 1 degré de latitude et la distance maximale qui les sépare est de 225 km (fig. 1).

Cueillette de données

Sur les rivières de la Trinité et Bec-Scie, les saumons adultes en montaison doivent franchir un système de piège où ils sont dénombrés et mesurés (longueur totale) à l'aide d'une échelle graduée au 10 cm placée sur le plancher du piège. L'évaluation grossière de la taille permet de distinguer deux catégories, soit les madeleineaux et les rédibermarins. En effet, la taille des saumons nous permet de distinguer les madeleineaux des rédibermarins avec une très grande précision, les données ayant été validées par des lectures d'âge. La longueur à la fourche minimale à partir de laquelle on peut classer les rédibermarins est très voisine sur les rivières Saint-Jean et de la Trinité mais de beaucoup inférieure sur la rivière Bec-Scie (tableau 2).

En l'absence de piège permettant un dénombrement complet de la montaison sur la rivière Saint-Jean, les captures faites par la pêche sportive sont considérées représentatives de la population de saumons. En effet, si l'échantillonnage effectué par les pêcheurs de la rivière Saint-Jean est similaire à celui des pêcheurs de la rivière de la Trinité, il est justifié de considérer celui-ci comme représentatif de la population puisque, sur la rivière de la Trinité, nous n'observons aucune différence entre la structure de population calculée à partir des retours à la rivière et celle calculée à partir des captures à la pêche sportive (ANOVA, $N = 6$, $F = 0{,}38$, $p > 0{,}05$).

Les données morphologiques des saumons adultes sont recueillies lors de l'enregistrement des captures faites par les pêcheurs sportifs. Les poissons frais sont habituellement pesés, mesurés (longueur totale et longueur à la fourche), des écailles sont récoltées et le sexe inscrit lorsque l'on procède à l'examen des gonades. L'âge des spécimens est déterminé par la lecture des écailles en laboratoire faite par du personnel expérimenté selon les normes reconnues. Lorsqu'aucune des écailles récoltées ne correspond aux exigences de la détermination de l'âge, le spécimen est rejeté.

Des données sont disponibles pour les années 1980–1988 pour la rivière de la Trinité, 1981–1988 pour la rivière Saint-Jean et 1983–1988 pour la rivière Bec-Scie.

Pour les saumonneaux, on procède à la mesure totale d'un certain nombre de spécimens vivants à tous les jours durant la période de dévalaison; ce nombre a été d'un maximum de 50 par jour sur chaque rivière depuis 1985 et a varié dans les années antérieures. Ces mesures permettent de comparer les longueurs des saumonneaux entre les rivières et entre les années. Chaque jour ou presque, quelques spécimens sont récoltés, de façon aléatoire sur les rivières de la Trinité et Bec-Scie de même que sur la rivière Saint-Jean en 1988, et par strate de taille (petit, moyen, grand, déterminé de façon subjective) sur la rivière Saint-Jean avant 1988. Ces poissons ont été préservés de diverses façons (alcool, formol, congélation ou mis sur la glace) pour des périodes variables allant de quelques heures à plusieurs mois avant d'être examinés en laboratoire. Les mesures de poids, longueur totale, longueur à la fourche et détermination du sexe par examen des gonades sont alors faites. Cette variation dans la méthode de préservation interdit l'utilisation de ces spécimens pour un certain nombre de comparaisons d'une année à l'autre et d'une rivière à l'autre.

Toutes les comparaisons de longueurs sont faites par la longueur à la fourche pour les saumons adultes et la longueur totale chez les saumonneaux. Lorsque la longueur à la fourche des saumons adultes était inconnue mais que nous possédions la longueur totale, nous avons calculé la longueur à la fourche à l'aide de la régression établie à partir des 3 172 spécimens pour lesquels nous avions ces deux mesures :

$$\text{Longueur à la fourche} = -1{,}0802 + 0{,}9706(\text{longueur totale}) \quad (R^2 = 0{,}99)$$

Pour la comparaison des longueurs moyennes entre mâle et femelle, nous avons utilisé un test de t. La comparaison des longueurs moyennes annuelles pour une même population et la comparaison des longueurs moyennes entre les populations sont faites par analyse de variance suivi d'un test de comparaison multiple (Tukey-Kramer). Les tests statistiques ont été faits à l'aide du progiciel SAS version 6.03.

Dans ce texte, nous utilisons les noms : saumonneau, madeleineau, dibermarin, tribermarin, saumon à frai antérieur et rédibermarin pour décrire le saumon à un stade précis de sa vie; les définitions sont présentées dans le glossaire. Les madeleineaux, dibermarins et tribermarins sont des poissons de premier frai et chaque groupe

TABLEAU 2. Classification des saumons en madeleineaux et rédibermarins en fonction de la longueur à la fourche (cm).

	N	Longueur à la fourche (cm)	Erreur de classification (%)		
			Madeleineau	Rédibermarin	Total
Saint-Jean	2 223	63,0	0,27	0,76	1,03
De la Trinité	4 168	62,5	1,20	0,20	1,40
Bec-Scie	116	58,0	0,00	0,00	0,00

provient d'une même cohorte de saumoneaux. Les saumons à frai antérieur et les saumons rédibermarins sont formés d'un regroupement de saumons appartenant à des cohortes différentes.

Résultats

Les saumons adultes

La proportion de madeleineaux diffère beaucoup d'une rivière à l'autre, ce qui permet de caractériser les populations (tableau 3). Les madeleineaux représentent en moyenne 25 % des saumons qui remontent la rivière Saint-Jean, comparativement à 75 % et 51 % pour les rivières de la Trinité et Bec-Scie respectivement. Les rédibermarins sont très nettement dominés par les dibermarins qui représentent 89 % ou plus de ce groupe sur les trois rivières (tableau 4). Les tribermarins sont rares sur la rivière Saint-Jean et pratiquement absents sur les deux autres rivières. Les saumons à frai antérieur forment également une faible portion des rédibermarins. Notons que, sur la rivière Bec-Scie, un seul des saumons ayant remonté la rivière au cours des saisons 1985 à 1988 et dont nous avons une lecture d'écailles était un saumon à frai antérieur; il s'agissait d'un mâle.

Les madeleineaux sont rarement des femelles si ce n'est sur la rivière Bec-Scie où elles représentent 15 % des madeleineaux (tableau 3). Les dibermarins sont au contraire majoritairement des femelles tandis que la population de tribermarins est formée presqu'exclusivement de femelles. Par contre, les mâles à frai antérieur sont plus nombreux sur les rivières de la Trinité et Bec-Scie (54 % et 100 % respectivement) mais ne représentent que 14 % de ce groupe sur la Saint-Jean (tableau 4).

La comparaison des longueurs à la fourche moyennes des mâles et des femelles a été faite là où les nombres le permettaient, soit sur les dibermarins de la rivière Saint-Jean et sur les madeleineaux et dibermarins de la rivière de la Trinité. Étant donné qu'il n'y a pas de différence significative dans 21 cas sur 24, nous avons regroupé les données indépendamment du sexe pour la suite des analyses. On observe des variations de la longueur à la fourche des madeleineaux et des dibermarins d'une même rivière d'une année à l'autre. Toutefois, en comparant la moyenne annuelle à la moyenne interannuelle pour chaque rivière ($X = X_i - \overline{X}$, i = année), on note que les variations annuelles sont relativement faibles en termes absolus (fig. 2 et 3). Il est à noter que les patrons de variations de la longueur des madeleineaux et des dibermarins se ressemblent pour les trois populations.

Étant donné la présence d'un effet d'interaction rivière-année, nous avons dû effectuer une analyse de comparaison de la longueur à la fourche moyenne des saumons entre les rivières pour chacune des années (tableau 5 et 6).

TABLEAU 3. Caractéristiques (moyenne ± écart-type) des saumons adultes des rivières Saint-Jean, de la Trinité et Bec-Scie.

	Saint-Jean	de la Trinité	Bec-Scie
Madeleineau (%)	24,7 ± 19,9 (8)^{a}	74,7 ± 5,9 (7)^{b}	51,0 ± 9,9 (6)^{c}
% de femelles	2,3 ± 3,3 (6)^{a}	5,7 ± 3,2 (9)^{a}	14,9 ± 8,4 (5)^{b}
Longueur à la fourche (cm)	54,43 ± 3,71 (407)	51,96 ± 3,28 (3 685)	50,14 ± 2,92 (81)
Rédibermarin (%)	75,3 ± 19,8 (8)^{a}	25,3 ± 5,9 (7)^{b}	49,0 ± 9,9 (6)^{c}
% de femelles	61,6 ± 5,3 (6)^{a}	82,5 ± 7,8 (9)^{b}	56,7 ± 23,0 (6)^{a}
Longueur à la fourche (cm)	76,54 ± 6,89 (1 852)	72,01 ± 5,70 (489)	68,10 ± 4,05 (89)
TOTAL	731 ± 336 (7)	2 166 ± 651 (10)	137 ± 75 (6)
% de femelles	50,3 ± 6,5 (6)^{a}	26,1 ± 13,9 (9)^{b}	42,2 ± 21,6 (6)^{ab}

NOTE : Les moyennes ont été comparées à l'aide d'un ANOVA suivit d'un test de comparaisons multiples *a posteriori* de Tukey-Kramer ($\alpha = 0{,}05$). Les moyennes ayant une lettre différente sont significativement différentes. La taille des échantillons est donnée entre parenthèses.

TABLEAU 4. Répartition (moyenne ± écart-type) des rédibermarins sur les rivières Saint-Jean, de la Trinité et Bec-Scie.

	Saint-Jean	de la Trinité	Bec-Scie
Dibermarin (%)	89,6 ± 6,3 (8)^{a}	89,4 ± 5,8 (9)^{a}	98,8 ± 2,4 (4)^{b}
% de femelles	93,0 ± 6,2 (8)	89,6 ± 6,7 (9)	72,4 ± 16,8 (4)
Longueur à la fourche (cm)	75,11 ± 4,51 (1 640)	71,49 ± 4,31 (918)	67,76 ± 4,28 (49)
Tribermarin (%)	4,2 ± 2,9 (7)	0,6 ± 0,2 (2)	0.0 ± 0.0 (4)
% de femelles	98,9 ± 2,9 (7)	100 ± 0,0 (2)	—
Longueur à la fourche (cm)	90,23 ± 5,40 (63)	84,93 ± 3,90 (3)	—
Frai antérieur (%)	7,8 ± 4,2 (7)	10,4 ± 5,9 (9)	1,2 ± 2,4 (4)
% de femelles	85,5 ± 13,6 (7)	45,9 ± 8,0 (9)	0,0 ± 0
Longueur à la fourche (cm)	87,84 ± 13,20 (121	74,08 ± 12,60 (97)	84,0 (1)

NOTE : Les moyennes ont été comparées à l'aide d'un ANOVA suivit d'un test de comparaisons multiples *a posteriori* de Tukey-Kramer ($\alpha = 0{,}05$). Les moyennes ayant une lettre différente sont significativement différentes. La taille des échantillons est donnée entre parenthèses.

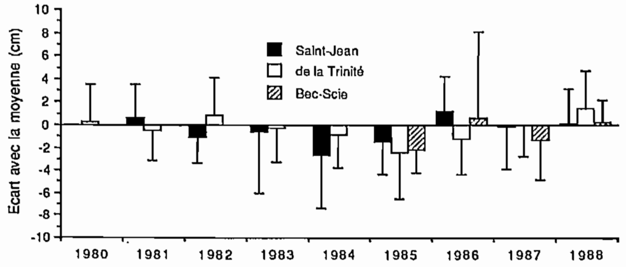

FIG. 2. Écart annuel entre la longueur à la fourche moyenne et la moyenne générale des madeleineaux pour chacune des rivières.

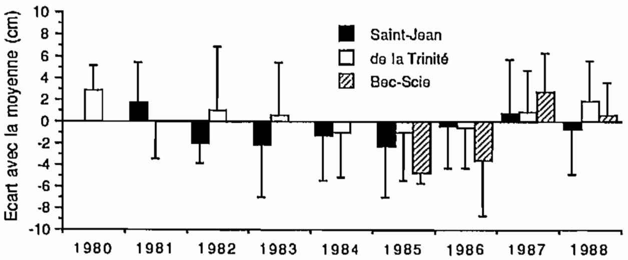

FIG. 3. Écart annuel entre la longueur à la fourche moyenne et la moyenne générale des dibermarins pour chacune des trois rivières.

TABLEAU 5. Variations inter-annuelles (moyenne ± écart-type) de la longueur à la fourche (en cm) des madeleineaux des rivières Saint-Jean, de la Trinité et Bec-Scie.

Année	Saint-Jean	de la Trinité	Bec-Scie
1980		52,21 ± 3,19 (372)	
1981	55,04 ± 2,88 (24)^{a}	51,42 ± 2,56 (317)^{b}	
1982	53,33 ± 2,28 (8)	52,81 ± 3,30 (674)	
1983	53,77 ± 5,43 (41)^{a}	51,68 ± 2,94 (123)^{b}	
1984	51,72 ± 4,68 (19)	51,12 ± 2,95 (418)	
1985	53,00 ± 2,90 (13)^{a}	49,57 ± 4,16 (161)^{ab}	48,94 ± 2,03^{b} (18)
1986	55,58 ± 3,04 (76)^{a}	50,77 ± 3,12 (504)^{b}	51,67 ± 7,57^{ab} (3)
1987	54,29 ± 3,80 (108)^{a}	51,94 ± 2,80 (520)^{b}	49,81 ± 3,53^{c} (26)
1988	54,51 ± 3,08 (117)^{a}	53,46 ± 3,23 (594)^{a}	51,32 ± 1,92^{b} (20)
Total	54,40 ± 3,70 (403)	51,96 ± 3,28 (3 683)	50,11 ± 3,09 (67)

NOTE : Les moyennes ont été comparées à l'aide d'un ANOVA suivit d'un test de comparaisons multiples *a posteriori* de Tukey-Kramer (α = 0,011). Les moyennes ayant une lettre différente sont significativement différentes.

TABLEAU 6. Variations inter-annuelles (moyenne ± écart-type) de la longueur à la fourche (en cm) des dibermarins des rivières Saint-Jean, de la Trinité et Bec-Scie.

Année	Saint-Jean	de la Trinité	Bec-Scie
1980		74,37 ± 2,30 (30)	
1981	77,84 ± 3,64 (38)	71,44 ± 3,33 (21)	
1982	74,15 ± 1,86 (4)	72,52 ± 5,81 (62)	
1983	73,92 ± 4,79 (242)	72,08 ± 4,89 (73)	
1984	74,79 ± 4,05 (278)	70,47 ± 4,18 (112)	
1985	73,89 ± 4,79 (260)^{a}	70,49 ± 4,46 (230)^{a}	63,12 ± 1,11 (6)^{b}
1986	75,73 ± 3,85 (184)^{a}	70,92 ± 3,65 (193)^{b}	64,21 ± 5,10 (7)^{c}
1987	76,89 ± 4,91 (206)^{a}	72,39 ± 3,75 (116)^{b}	70,42 ± 3,60 (16)^{b}
1988	75,37 ± 4,16 (428)^{a}	73,41 ± 3,64 (81)^{a}	68,28 ± 3,12 (20)^{b}
Total	76,11 ± 4,51 (1 640)	71,49 ± 4,31 (918)	67,77 ± 4,28 (49)

NOTE : Les moyennes ont été comparées à l'aide d'un ANOVA suivit d'un test de comparaisons multiples *a posteriori* de Tukey-Kramer (α = 0,011). Les moyennes ayant une lettre différente sont significativement différentes.

Les saumons de la rivière Saint-Jean sont toujours plus grands ou égaux à ceux de la rivière de la Trinité, ceux-ci étant plus grand ou égaux à ceux de la rivière Bec-Scie.

Les droites de régression poids-longueur à la fourche sont significativement différentes d'une rivière à l'autre (ANCOVA, $P < 0{,}0001$). On constate que pour une longueur donnée les saumons de la rivière Saint-Jean(1) sont les plus lourds, suivit de ceux de la Bec-Scie(3) et que les saumons de la Trinité(2) sont les plus légers.

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(1) Ln (poids) = − 10,7957 + 2,8237 * Ln (longueur à la fourche) ($R^2 = 0{,}8488$)

(2) Ln (poids) = − 10,7173 + 2,8186 * Ln (longueur à la fourche) ($R^2 = 0{,}9108$)

(3) Ln (poids) = − 10,4095 + 2,7483 * Ln (longueur à la fourche) ($R^2 = 0{,}9262$)

Les saumonneaux

Les principales caractéristiques des saumonneaux sont présentées au tableau 7. Les saumonneaux de la rivière Bec-Scie sont de taille plus grande que ceux des autres rivières et ceux de la rivière de la Trinité sont généralement plus grands (sauf en 1983) que les saumonneaux de la rivière Saint-Jean (tableau 8). Par contre, ces derniers demeurent habituellement plus longtemps en rivière (excepté en 1987) que les saumoneaux des rivières de la Trinité et Bec-Scie (tableau 9). La structure de population des saumonneaux des trois rivières a été comparé à

TABLEAU 7. Caractéristiques des saumonneaux (moyenne ± écart-type) des rivières Saint-Jean, de la Trinité et Bec-Scie.

	Saint-Jean	de la Trinité	Bec-Scie
Longueur totale (mm)	131,4 ± 12,1 (6 765)	132,0 ± 11,9 (17 838)	148,8 ± 16,6 (4 656)
Âge à la smoltification (%)			
+1	1,6 ± 4,3 (8)		0,7 ± 0,9 (5)
+2	14,2 ± 23,3 (8)	22,3 ± 18,4 (6)	20,6 ± 11,7 (5)
+3	41,2 ± 24,3 (8)	70,4 ± 15,7 (6)	72,9 ± 12,3 (5)
+4	39,8 ± 29,6 (8)	7,2 ± 5,9 (6)	5,8 ± 5,5 (5)
+5	2,9 ± 3,1 (8)	0,1 ± 0,1 (6)	
+6	0,3 ± 0,7 (8)		
Âge à la smoltification (années)	3,33 ± 0,79 (1 729)	2,88 ± 0,51 (1 121)	2,77 ± 0,52 (764)
% de femelles	63,4 ± 4,0 (7)^{ab}	56,6 ± 3,9 (6)^{b}	66,1 ± 8,0 (5)^{a}

NOTE : Les moyennes ont été comparées à l'aide d'un ANOVA suivit d'un test de comparaisons multiples *a posteriori* de Tukey-Kramer (α = 0,05). Les moyennes ayant une lettre différente sont significativement différentes. La taille des échantillons est donnée entre parenthèses.

TABLEAU 8. Variations inter-annuelles (moyenne ± écart-type) de la longueur totale (mm) des saumonneaux des rivières Saint-Jean, de la Trinité et Bec-Scie.

Année	Saint-Jean	de la Trinité	Bec-Scie
1982	137,8 ± 12,5 (559)		
1983	136,3 ± 10,0 (815)^{a}	135,5 ± 13,5 (578)^{b}	152,1 ± 16,7 (1 203)^{c}
1984	124,1 ± 12,3 (510)^{a}	130,8 ± 11,2 (11 010)^{b}	148,4 ± 17,8 (856)^{c}
1985	129,4 ± 10,0 (984)^{a}	135,5 ± 11,2 (1 703)^{b}	
1986	131,5 ± 12,0 (1 597)^{a}	131,2 ± 13,0 (1 511)^{a}	148,5 ± 16,6 (1 063)^{b}
1987	132,1 ± 12,3 (955)^{a}	136,6 ± 12,9 (1 390)^{b}	149,9 ± 16,5 (619)^{c}
1988	129,4 ± 11,9 (1 345)^{a}	123,4 ± 13,3 (1 643)^{b}	144,3 ± 14,2 (915)^{c}
Total	131,4 ± 12,1 (6 735)	132,0 ± 11,9 (17 838)	148,8 ± 16,6 (4 656)

NOTE : Les moyennes ont été comparées à l'aide d'un ANOVA suivit d'un test de comparaisons multiples *a posteriori* de Tukey-Kramer (α = 0,011). Les moyennes ayant une lettre différente sont significativement différentes. La taille des échantillons est donnée entre parenthèses.

TABLEAU 9. Variations inter-annuelles (moyenne ± écart-type) de l'âge à la smoltification (an) des saumonneaux des rivières Saint-Jean, de la Trinité et Bec-Scie.

Année	Saint-Jean	de la Trinité	Bec-Scie
1981	3,41 ± 0,50 (37)		
1982	3,85 ± 0,46 (182)		
1983	2,86 ± 0,42 (293)^{a}	2,48 ± 0,50 (94)^{b}	2,62 ± 0,53 (353)^{b}
1984	3,67 ± 0,88 (236)^{a}	2,88 ± 0,39 (283)^{b}	2,89 ± 0,38 (177)^{b}
1985	3,65 ± 0,56 (316)^{a}	2,90 ± 0,49 (86)^{b}	2,77 ± 0,56 (47)^{a}
1986	3,76 ± 0,53 (250)^{a}	3,01 ± 0,42 (207)^{b}	2,98 ± 0,39 (80)^{b}
1987	2,07 ± 0,56 (148)^{a}	3,10 ± 0,45 (221)^{b}	
1988	3,06 ± 0,65 (267)^{a}	2,73 ± 0,63 (230)^{b}	2,93 ± 0,60 (107)^{a}
Total	3,33 ± 0,79 (1 729)	2,88 ± 0,51 (1121)	2,77 ± 0,52 (764)

NOTE : Les moyennes ont été comparées à l'aide d'un ANOVA suivit d'un test de comparaisons multiples *a posteriori* de Tukey-Kramer (α = 0,0125). Les moyennes ayant une lettre différente sont significativement différentes. La taille des échantillons est donnée entre parenthèses.

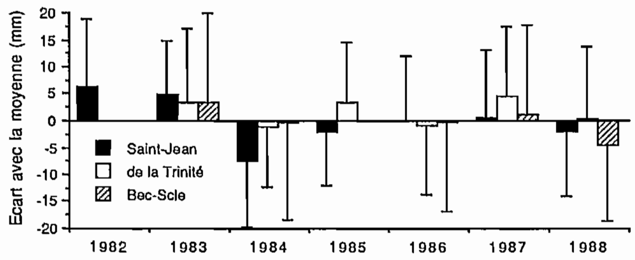

FIG. 4. Écart annuel entre la longueur totale moyenne et la moyenne générale des saumonneaux pour chacune des trois rivières.

l'aide d'un test G (Sokal et Rohlf 1981). Il apparaît que les populations des rivières de la Trinité et Bec-Scie sont semblables ($G_H = -279.2$) mais que celle de la rivière Saint-Jean est différente des deux autres ($G_H = 60.62$).

Tout comme chez les saumons adultes, les tests ne révèlent pas de différences significatives des longueurs en fonction du sexe. La taille moyenne varie d'une année à l'autre (fig. 4) sans toutefois s'écarter de façon importante de leur moyenne respective ($X = X_i - \bar{X}$, i = année). Toutefois, la taille moyenne varie de façon significative en fonction de l'âge à la smoltification selon les données de 1988, seule année où la récolte des spécimens et les mesures ont été prises de façon homogène sur des spécimens frais pour les trois rivières (tableau 10). L'étendue de la taille à un âge donné est toutefois trop grand pour nous permettre une distinction fiable de l'âge en fonction de la taille.

Les saumonneaux sont majoritairement des femelles dans les trois cas (tableau 7). Celles-ci forment 63 % de la population sur la rivière Saint-Jean, 57 % sur la rivière de la Trinité et 66 % sur la rivière Bec-Scie.

Discussion

Les caractéristiques des stocks de saumons des trois rivières sont différentes sur plusieurs points. La grande variabilité observée dans la composition des stocks (madeleineaux vs rédibermarins) ainsi que la variation importante du sexe ratio à l'intérieur d'une même classe d'âge d'une rivière à l'autre font en sorte que l'estimation du nombre d'oeufs déposés dans chacune des rivières peut être très différente. Il est intéressant de noter que, contrairement aux résultats publiés par Power (1981) et par Schaffer et Elson (1975), le pourcentage de madeleineaux ne semble pas être inversement proportionnel au débit ou à la longueur de la rivière. En effet, la rivière de la Trinité est celle des trois rivières étudiées ayant la plus grande proportion de madeleineaux bien que sa longueur accessible et son débit soient supérieurs à ceux de la rivière Bec-Scie.

Tout comme l'avait observé Power (1981), les madeleineaux sont principalement de sexe mâle tandis que les rédibermarins ont un sexe-ratio biaisé en faveur des femelles. Ceci peut s'expliquer par le fait que plus il y a de mâles qui reviennent comme madeleineaux, moins il en reste pour revenir l'année suivante de telle sorte qu'ils sont peu nombreux parmi les dibermarins. Ceci explique également pourquoi le rapport des sexes favorisant les femelles au stade saumonneau est disparu voir même, dans certains cas, largement renversé en faveur des mâles lors du retour des saumons adultes.

Sur une rivière comme la rivière Saint-Jean, le nombre de reproducteurs laissés en rivière est assez représentatif du nombre d'oeufs qui doivent y être déposés puisque 75 % est constitué de rédibermarins dont 61,6 % sont des femelles (tableau 3). Sur la rivière de la Trinité, la très forte proportion de madeleineaux (75 %) dont 94 % sont des mâles, peut conduire à de très mauvaises estimations de la déposition d'oeufs si on se fie uniquement sur le nombre de reproducteurs; on devra donc procéder à l'évaluation de la composition du stock sous cet aspect sur une base annuelle. Toutefois, la très nette dominance des saumons dibermarins dans le groupe des rédibermarins et la stabilité relative des caractéristiques observées d'une année à l'autre dans chaque groupe en ce qui concerne le rapport des sexes et la taille des spécimens ne semblent pas justifier, dans ces cas du moins, de procéder plus en détail à la caractérisation des groupes sur une base annuelle.

Pour la rivière Saint-Jean, les madeleineaux, bien que numériquement faibles, contribuent à maintenir un sexe ratio mâle/femelle de 50:50; sans vouloir présumer de l'importance de ce phénomène, on peut tout de même

TABLEAU 10. Caractéristiques des saumonneaux (moyenne ± écart-type) des rivières Saint-Jean, de la Trinité et Bec-Scie, 1988.

Âge (année)	Saint-Jean	de la Trinité	Bec-Scie
2+			
Longueur totale (mm)	116,7 ± 25,1 (43)^a	124,9 ± 18,5 (85)^{ab}	131,5 ± 9,0 (23)^b
Poids (g)	11,7 ± 7,2 (43)^a	15,6 ± 4,1 (85)^b	20,1 ± 4,6 (23)^c
3+			
Longueur totale (mm)	125,2 ± 23,6 (170)^a	132,0 ± 16,6 (123)^b	144,3 ± 12,1 (68)^c
Poids (g)	14,0 ± 7,1 (170)^a	16,9 ± 4,7 (123)^b	24,9 ± 6,3 (68)^c
4+			
Longueur totale (mm)	140,9 ± 26,3 (49)^a	141,5 ± 13,5 (22)^a	155,6 ± 11,1 (16)^a
Poids (g)	20,1 ± 8,0 (49)^a	20,2 ± 6,0 (22)^a	29,3 ± 5,0 (16)^b

NOTE : Les moyennes ont été comparées à l'aide d'un ANOVA suivit d'un test de comparaisons multiples *a posteriori* de Tukey-Kramer ($\alpha = 0{,}05$). Les moyennes ayant une lettre différente sont significativement différentes. La taille des échantillons est donnée entre parenthèses.

noter qu'une plus grande exploitation des madeleineaux conduirait à un débalancement des sexes. Sur la rivière de la Trinité, le sexe ratio est de 74:26 en faveur des mâles; étant donné le petit pourcentage de femelles parmi les madeleineaux, on pourrait accentuer l'exploitation de ce segment de la population sans compromettre la déposition d'oeufs ni déséquilibrer défavorablement les sexes. Sur la rivière Bec-Scie, la situation est mitoyenne (58:42) mais permettrait tout de même une exploitation dirigée vers les madeleineaux sans compromettre ni l'équilibre des sexes ni la déposition d'oeufs. Bien que les 19 % de madeleineaux femelles ne soient pas négligeables au point de vue numérique, elles ne contribuent que très peu à la déposition d'oeufs étant donné la faible fécondité absolue observée chez les poissons de cette classe d'âge (Thorpe *et al.* 1984).

Les distinctions observées entre ces trois populations soulèvent un nombre important de questions. Nous ne pouvons pas expliquer pour l'instant les raisons pour lesquelles la croissance des saumonneaux est plus lente sur la rivière Saint-Jean que sur les deux autres rivières. Les inventaires de juvéniles (données non publiées) ne laissent pas croire à première vue qu'il puisse s'agir d'un phénomène relié à la densité. Dans le cas de la rivière Bec-Scie, une partie de l'explication pourrait venir du fait de la présence de lacs en tête et sur le parcours de la rivière est de nature à favoriser une plus grande productivité du milieu (Gibson et Côté 1982). Les variations interannuelles de la taille moyenne des saumonneaux (fig. 4) et de l'âge moyen à la smoltification (tableau 9) ne présentent pas, à première vue du moins, un patron similaire d'une rivière à l'autre indiquant ainsi que ces variations ne sont pas dues à des causes communes. Nous n'observons pas, comparativement à Bielak et Power (1985), de tendance à la baisse pour l'âge à la smoltification des saumonneaux.

La croissance en longueur plus grande en mer des saumons de la rivière Saint-Jean et de la Trinité par rapport à ceux de la rivière Bec-Scie peut être partiellement expliquée par des stratégies différentes adoptées par les saumons. En effet, les saumons de la Bec-Scie semblent investir plus dans le poids que dans la longueur. Quant à la croissance légèrement supérieure des saumons de la Saint-Jean sur ceux de la Trinité, on pourrait l'expliquer partiellement par le fait que les saumonneaux de la Saint-Jean amorcent leur migration potamique environ deux semaines avant ceux de la Trinité (tableau 1). Toutefois, il n'est pas exclus que la qualité des pâturages marins soit différente pour ces trois populations.

Le fait que la variation inter-annuelle de la taille des saumons présente un patron semblable d'une rivière à l'autre soulève un point d'intérêt majeur; il est plausible de croire que ces saumons subissent en mer un stress commun, stress relié à la température, à l'abondance de nourriture ou à tout autre facteur susceptible d'affecter leur croissance (fig. 2 et 3). Le fait en particulier que la taille moyenne des madeleineaux de 1983, 1984 et 1985 ainsi que celle des dibermarins de 1984 et 1985 ait toujours été sous leur moyenne respective pourrait être mis en relation avec les faibles retours de saumons observés durant ces trois années au Québec (Caron et Mercier 1989), au Canada et dans les pêches du Groenland (International Council for the Exploration of the Sea 1988).

Pour conclure, nous croyons que ces données démontrent clairement qu'il est justifié d'utiliser des approches de gestion variant d'un stock à l'autre en fonction des caractéristiques propres à chacun.

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Glossaire

Madeleineau : saumon qui revient en rivière pour frayer après avoir passé un seul hiver en mer.

Dibermarin : saumon qui revient en rivière pour frayer après avoir passé deux hivers consécutifs en mer.

Tribermarin : saumon qui revient en rivière pour frayer après avoir passé trois hivers consécutifs en mer.

Saumon à frai antérieur : saumon qui a déjà frayé au cours des années antérieures une ou plusieurs fois.

Rédibermarin ou grand saumon : tout saumon revenant à la rivière à l'exclusion des madeleineaux.

Reproducteurs : ensemble des saumons revenus à la rivière et présents au moment de la fraye.

Saumonneau : saumon juvénile qui amorce sa première migration vers la mer.

Unité de production : superficie de 100 m^2 qualifiée de favorable ou très favorable au saumon juvénile.

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Une procédure d'identification de la rivière d'origine de saumons de l'estuaire du Saint-Laurent par l'analyse discriminante de mesures scalimétriques[1]

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Des analyses discriminantes ont été effectuées afin de déterminer les caractères scalimétriques les plus explicatifs qui permettraient de distinguer les groupes de saumons provenant de rivières différentes. La première analyse est basée sur un ensemble de 13 variables lues sur les écailles de saumons 3,2+ (en 1986) provenant de trois rivières de l'estuaire du Saint-Laurent (Québec, Canada) dont les embouchures sont distantes de 65 à 265 km. Le nombre de saumons retenu de chaque rivière varie entre 22 et 24 individus, pour un total de 69 saumons. Deux fonctions discriminantes sont nécessaires pour différencier les trois groupes de saumons, avec une contribution significative de neuf des 13 variables et un taux d'erreur de classification de 5,8 % (quatre saumons mal classés sur 69). Deux séries de 10 rééchantillonnages de 10 saumons et de 15 saumons par rivière, respectivement, ont été effectués afin de tester la capacité discriminante de ces fonctions dans des conditions plus restrictives. Les résultats montrent que le pourcentage de classification des saumons se maintient en moyenne à 94 % ± 4 % et que sept des 13 variables sont prépondérantes. L'analyse discriminante basée sur ces sept variables scalimétriques montre un taux de classification de 89,9 % des 69 saumons du lot initial. Une série de 10 rééchantillonnages de 15 saumons par rivière, analysés dans les mêmes conditions indique un taux de classification moyen de 92 %, avec un écart type de 3,4 %. Ces résultats confirment la possibilité d'utiliser un nombre restreint de caractères scalimétriques pour discriminer les stocks de saumons provenant de l'estuaire du Saint-Laurent.

Discriminant analysis were performed to determine the most reliable scale characters for distinguishing groups of salmon taken from different rivers. The analysis was based on 13 scale characters on a group of 3,2+ salmons originating from three rivers of the St-Lawrence estuary (Québec, Canada) separated by 65 km to 265 km. Between 22 and 24 individuals were taken from each river for a total of 69 salmon. Two discriminant functions are necessary to differentiate the three groups of salmons with a significant contribution of nine out of the 13 variables and a classification error rate of 5.8% (four salmon misclassified). Two series of 10 resamplings of 10 and 15 salmon per river were analyzed, respectively, in order to verify the classification ability of these functions under more restricted conditions. The results indicated that the classification level is maintained to an average of 94% ± 4% and that seven of the 13 characters were highly involved in the discrimination. The discriminant analysis based on these seven selected scale characters provided a classification rate of 89.9% on the initial set of 69 salmon, and 92% on a series of 10 resampling of 15 salmon per river, with a standard error of 3.4%. These results confirm the possibility to use a reduced number of scale characters for discriminating salmon stocks encountered in the St-Lawrence estuary.

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Introduction

Trois utilisateurs compétitionnent dans le partage des captures de saumons de l'Atlantique soit : les pêches commerciales, les pêcheurs sportifs et, plus récemment, les pêches de subsistance des peuples autochtones (Indiens et Inuits). La politique de gestion actuelle consiste à répartir la ressource parmi les utilisateurs tout en priorisant la conservation des stocks (Ritter *et al.* 1980; Saunders 1981). Le problème majeur vient du fait que les pêches commerciales de saumons sont situées sur les sites d'engraissement ou sur les principales voies de migration, là où les stocks sont mélangés et où les engins de pêches sont les plus efficaces. Ainsi, si la priorité est donnée à la conservation des stocks, l'identification de ces stocks hors du site de reproduction représente la clef de l'application de cette politique.

Konovalov (1971) avait soulevé l'hypothèse selon laquelle le taux de développement des écailles et des marques périodiques qui y sont laissées (circuli, annuli, checks, etc.) sont reliés aux conditions environnementales auxquelles sont soumis les saumons de l'Atlantique. Considérant que les conditions environnementales sont probablement différentes d'une rivière à l'autre, certaines informations accumulées sur les écailles devraient être également différentes, au point de permettre l'identification de la rivière d'origine d'un saumon capturé en mer. De nombreux auteurs ont déjà exploré cette approche : Lear (1972), Lear et Misra (1978), Reddin et Misra (1978, 1985), Lear et Sandeman (1980), Cook et Lord (1978), Cook (1982), Reddin *et al.* (1984), De Pontual et Prouzet (1986a, b), Claytor *et al.* (1987), Prévost (1987). Dans la plupart de ces études, le choix et le nombre de variables sont très limités. La région investie est parfois très vaste (Lear et Sandeman 1980) ou très restreinte (ex. : limitée à l'estuaire d'une seule rivière, Reddin et Misra 1985).

Dans la présente étude, nous effectuons une discrimination de stocks de saumons de l'Atlantique à partir de 13 variables scalimétriques, sur un territoire de dimension intermédiaire, soit de quelques centaines de kilomètres. La méthode est appliquée sur un lot de saumons provenant de trois rivières de l'estuaire du Saint-Laurent dont les embouchures sont distantes de 65 à 265 km l'une de l'autre. Ceci permet d'évaluer la limite de résolution de cette approche par rapport à une échelle spatiale de l'ordre des dizaines ou des centaines de kilomètres.

Par cette approche, nous souhaitons fournir des informations supplémentaires qui pourraient aider au processus d'élaboration de stratégies de gestion et d'allocation des stocks de saumons de l'est canadien. Cette méthode, testée ailleurs et généralisée, devrait aider à évaluer la contribution relative des différentes rivières ou systèmes de rivières aux stocks mixtes impliqués dans les pêches commerciales de petite ou de grande envergure du saumon de l'Atlantique.

Matériel

L'échantillonnage d'écailles de saumons provenant de la pêche sportive de 1986 dans les rivières Matane (rive sud du Saint-Laurent), de la Trinité (rive nord du Saint-Laurent) et Anse Saint-Jean (Saguenay) a été mis à notre disposition. Aucune de ces rivières n'a reçu d'ensemencements préjudiciables à notre recherche, ou n'a subi de stress particulier pendant les 5 années précédant 1986. Les écailles ont été prélevées selon la méthode proposée par Anonyme (1984). Seules ont été retenues pour fin d'analyse, les écailles qui respectaient les critères suivants : (1) âge : 3,2+ ans; (2) sans érosion évidente à l'extrémité de l'axe principal; (3) sans marque de fraie; (4) écailles les plus grosses possibles et de forme standard au site habituel de prélèvement; (5) écailles avec le plus petit foyer possible, circulaire de préférence ou légèrement ovale. Une seule écaille par saumon a été retenue pour fin de lecture : Prévost (1987) mentionne que, même si c'est une pratique souhaitable de définir chaque saumon à partir d'au moins deux écailles au lieu d'une seule, cette pratique ne permet pas d'augmenter considérablement la cohésion interne de chaque groupe d'individus à discriminer. Ainsi, 23 saumons de la rivière Anse Saint-Jean, 24 de la rivière de la Trinité et 22 de la rivière Matane ont été retenus pour les analyses.

Méthode

Les 13 variables mesurées sont : LR1 (distance en millimètre entre le centre du foyer de l'écaille et le premier annulus de rivière); LR2 (distance entre le premier et le deuxième annulus de rivière; LR3 (distance entre le deuxième et le troisième annulus de rivière); LM1 (distance entre le troisième annulus de rivière et le premier annulus de mer); LM2 (distance entre le premier et le deuxième annulus de mer); LR19 (mesure de LR1 mais à 90° à la droite de l'axe principal); LR29 (mesure de LR2 mais à 90° à la droite de l'axe principal); LR39 (mesure de LR3 mais à 90° à la droite de l'axe principal); CR1 (nombre de circuli de la première année de rivière); CR2 (nombre de circuli de la deuxième année de rivière); CR3 (nombre de circuli de la troisième année de rivière); CM1 (nombre de circuli de la première année de mer); CM2 (nombre de circuli de la deuxième année de mer).

Les mesures et comptages ont été effectués avec le logiciel « Optical Pattern Recognition System », (BioSonics 1986). Vers la fin de la période de smoltification, quelques circuli apparaissaient de façon évidente en dehors de la plage d'observation de 5° de part et d'autre de l'axe principal, mais étaient inexistants ou mal définis à l'intérieur de cette plage. Dans ces quelques rares cas, le circuli manquant était alors ajouté sur la radiale, à l'endroit où il aurait dû la couper. De plus, dans les quelques cas où les annuli marins étaient difficiles à discerner des marques d'hiver (« winter check »), le recours au rétrocalcul linéaire, à titre de guide, a permis de préciser leur position. Enfin, la croissance de l'année en cours (le « + ») a été exclue de la variable CM2, mais a été mesurée pour les besoins éventuels du rétrocalcul.

Toutes les analyses statistiques ont été effectuées à l'aide du logiciel SPSS/PC+ Advanced Statistics^{TM} (Norusis 1986). Précisons que 16 mesures sur un total de 897 (13 variables mesurées sur 69 saumons) étaient hors-distribution (« outliers ») ou extrêmes (à plus de deux inter-quartiles par rapport à la médiane) et ont été considérées comme aberrantes. Ces valeurs aberrantes ont été remplacées par la valeur moyenne du groupe pour la variable en question. Jackson (1968) mentionne que cette pratique est légitime quand les valeurs aberrantes sont réparties au hasard dans l'ensemble des données et que leur pourcentage est faible. Chan et Dunn (1972) indiquent que cette méthode ainsi que la méthode des composantes principales sont supérieures aux autres méthodes. De plus, elle permet de conserver toutes les autres mesures effectuées sur l'écaille. Ainsi, deux saumons ont fait l'objet de deux corrections et 12 autres n'ont subi qu'une seule correction.

L'homogénéité des matrices de variances-covariances des différents groupes a été testée au moyen de la statistique « M » de Box, disponible dans la procédure « Manova » de SPSS/PC+ (Norusis 1986).

L'analyse discriminante dite « pas-à-pas » (*stepwise*) à été effectuée dans un premier temps sur l'ensemble des 13 variables. Le critère de sélection des variables était en fonction de la distance de Mahalanobis, avec un niveau d'inclusion des variables fixé à 1,0 pour la statistique F partielle associée à chacune d'elles et un niveau de tolérance de 0,001. La classification subséquente des saumons a été effectuée par la méthode du « leaving-one-out » et la règle de Bayes.

Par la suite, deux séries de 10 analyses discriminantes chacune ont été effectuées avec 10, puis 15 saumons par rivière, respectivement, chaque groupe de saumons étant tiré au hasard parmi l'ensemble des 69 saumons. Cette étape a permis de vérifier si la capacité discriminante se maintenait toujours malgré une réduction du nombre de saumons impliqués dans chaque analyse et d'établir le pourcentage d'erreur qui lui est associé. Elle a aussi permis d'identifier les variables les plus importantes dans la discrimination de ces trois rivières et le nombre d'observations nécessaires à la constitution des équations discriminantes.

L'analyse discriminante a été reprise avec sept variables et les 69 saumons des trois rivières pour vérifier les conséquences sur le taux de classification des saumons de cette réduction du nombre de variables.

Une dernière série de 10 rééchantillonnages de 15 saumons par rivière a permis d'estimer un écart type applicable au taux de classification résultant de l'étape précédente.

Résultats

Le tableau 1 présente les valeurs moyennes et les écarts types des 13 variables selon leur rivière. Le test de sphéricité de Bartlett (527,3 avec 78 ddl et $p < 0{,}0005$) montre que la matrice des corrélations n'est pas une matrice unité et justifie l'emploi de l'analyse de variance multivariée « Manova ». Celle-ci a permis de confirmer l'homogénéité des matrices de variance-covariance intragroupe (M de Box = 273,46, F (182, 11433 ddl) = 1,07 avec $p = 0{,}247$), qu'il existe une différence significative entre les groupes (rivières) de saumons (Pillais = 1,24 ($S = 2, M = 5, N = 26$), $p < 0{,}0005$ et Wilks = 0,141, $P < 0{,}0005$), ainsi que la contribution significative de certaines variables à la variation totale.

Analyse discriminante et rééchantillonnages (13 variables)

L'analyse discriminante sur les 13 variables pour les trois rivières indique que la première fonction discriminante est constituée des variables LR2, CR2, LR29 et LR39 (tableau 2a), et explique 59,3 % de la variance totale. La deuxième fonction discriminante est constituée des variables LR1, LR19, LM1, CM1 et LM2, et explique les derniers 40,7 % de la variance. Les variables CR1, CR3, LR3 et LM2 sont rejetées. Le pourcentage de classification de ces deux fonctions impliquant neuf variables est de 94,2 %, ce qui correspond à un taux d'erreur de 5,8 %, soit quatre saumons mal classés sur 69.

Une première série de dix analyses discriminantes considérant 10 saumons tirés au hasard par rivière a été exécutée et indique que les variables de rivière LR2, LR29, CR2 et LR39 sont sollicitées 9, 7, 9 et 7 fois sur 10, respectivement. Pour leur part, les variables de mer LM1

TABLEAU 1. Moyennes (*x*) et écarts types (EcT) des longueurs (en millimètre) et du nombre de circuli, mesurés sur les écailles de saumons provenant des rivières Anse Saint-Jean, de la Trinité et Matane en 1986.

Variables	Rivières							
	Anse Saint-Jean		de la Trinité		Matane		Groupées	
	(n=23)		(n=24)		(n=22)		(n=69)	
	($\bar{x}$)	(EcT)	($\bar{x}$)	(EcT)	($\bar{x}$)	(EcT)	($\bar{x}$)	(EcT)
LR1	0,215	(0,035)	0,193	(0,044)	0,250	(0,041)	0,219	(0,046)
LR2	0,277	(0,057)	0,245	(0,051)	0,244	(0,057)	0,256	(0,056)
LR3	0,316	(0,074)	0,233	(0,045)	0,243	(0,052)	0,264	(0,068)
LM1	1,743	(0,214)	1,693	(0,210)	1,948	(0,248)	1,791	(0,247)
LM2	1,519	(0,162)	1,355	(0,211)	1,463	(0,241)	1,444	(0,215)
LR19	0,167	(0,026)	0,150	(0,026)	0,180	(0,025)	0,165	(0,028)
LR29	0,170	(0,024)	0,139	(0,030)	0,140	(0,034)	0,150	(0,032)
LR39	0,181	(0,030)	0,135	(0,029)	0,134	(0,032)	0,150	(0,037)
CR1	9,478	(1,810)	7,875	(1,360)	9,364	(1,529)	8,884	(1,720)
CR2	13,174	(2,367)	10,208	(1,911)	9,864	(1,320)	11,087	(2,412)
CR3	12,435	(2,761)	9,792	(1,668)	9,364	(1,255)	10,536	(2,398)
CM1	32,565	(3,906)	32,500	(3,452)	31,773	(4,093)	32,290	(3,777)
CM2	27,304	(3,573)	24,875	(3,261)	24,773	(3,545)	25,652	(3,605)

TABLEAU 2. Coefficients non-standardisés des fonctions discriminantes pour les rivières Anse Saint-Jean ($n = 23$), de la Trinité ($n = 24$) et Matane ($n = 22$), 69 saumons, en 1986. a) 13 variables. b) sept variables.

a)

Variables	LR1	LR2	LM1	LM2	LR19	LR29	LR39	CR2	CM1	Cste[b]
fonction 1 :	-8,81	-16,65[a]	-2,26	1,60	10,87	9,736[a]	20,44[a]	0,49[a]	0,225	-11,15
fonction 2 :	6,53[a]	-24,27	6,69[a]	-0,325[a]	15,3[a]	23,04	-0,044	0,44	-0,31[a]	-7,63

b)

Variables	LR1	LR2	LM1	LR29	LR39	CR2	CM1	Cste[b]
fonction 1 :	-5,48	-13,03[a]	-2,323	9,38[a]	20,36[a]	0,448[a]	0,198[a]	-7,144
fonction 2 :	13,39[a]	-24,13	6,21[a]	24,58	2,85	0,44	-0,26	-8,49

[a] Variable significative ($p < 0,05$) sur cette fonction.
[b] Constante.

et CM1 sont aussi sollicitées 9 fois sur 10. Les autres variables ne sont sollicitées que quatre fois ou moins chacune. De plus, le pourcentage moyen de classification de ces dix analyses est de 94 % avec un écart type de 5,4 % ($n = 10$). Les variables dominantes correspondent globalement à celles de la deuxième année de rivière (R2) et celles de la première année de mer (M1).

Une deuxième série d'analyses discriminantes avec 15 saumons par rivière, toujours tirés au hasard, montre que les variables de la deuxième année de rivière CR2, LR2 et LR29 et celles de la première année de mer LM1 et CM1, ainsi que LR39, sont impliquées dans chacune des 10 analyses. De plus, la variable LR1 s'impose dans 9 cas sur 10. Ces résultats ressemblent globalement à ceux obtenus dans la série de rééchantillonnages précédents avec 10 saumons par rivière. Les variables dominantes, qui sont ici plus nettes, sont les mêmes mais avec LR1 en plus. Le pourcentage moyen de classification est de 93,8 % avec un écart type de 3,4 % ($n = 10$).

Analyse discriminante et rééchantillonnages (7 variables)

À la lumière de ces deux séries de rééchantillonnages, une analyse discriminante a été reprise avec les 69 saumons des rivières Anse Saint-Jean, de la Trinité et Matane et les sept variables dominantes tirées des analyses précédentes, soit LR1, CR2, LR2, LR29, LR39, LM1 et CM1, afin d'évaluer le pouvoir discriminant de ce sous-ensemble de prédicteurs. Les résultats indiquent que toutes les variables sont impliquées dans toutes les analyses. Les variables CR2, LR2, LR29, LR39 et CM1, qui constituent la première fonction discriminante, expliquent 58 % de la variance totale. Les variables LR1 et LM1, qui constituent la deuxième fonction, expliquent le reste de la variance. De plus, le taux de classification perd 4,3 % par rapport à l'analyse avec les 13 variables et passe à 89,9 %. Notons que de ces sept variables, cinq sont des longueurs, deux seulement sont des circuli et cinq sont des variables de rivière.

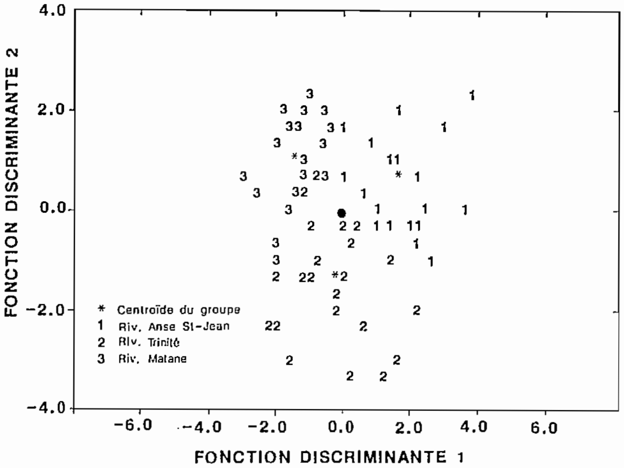

FIG. 1. Position des 69 saumons et des centroïdes des rivières Anse Saint-Jean, de la Trinité, et Matane résultant de l'analyse discriminante sur les 7 variables dominantes.

La figure 1 représente la position des centroïdes des trois rivières et la position des 69 saumons considérés dans l'analyse discriminante avec sept variables. La position d'un saumon est calculée linéairement à l'aide de la valeur des coefficients non-standardisés des fonctions discriminantes du tableau 2(b) et de la valeur que prend sa variable correspondante. De la même façon, la position des centroïdes est calculée à l'aide de ces mêmes coefficients et des valeurs moyennes des variables correspondantes du tableau 1.

Une dernière série de 10 analyses discriminantes effectuées avec 15 saumons par rivière, tirés au hasard, et appliquées aux sept variables mises en évidence précédemment, montrent que ces sept variables sont toujours sollicitées et mènent à un taux moyen de classification de 92 %, avec un écart type de 3,4 % ($n = 10$).

Discussion

Nous avons proposé une technique d'identification de l'origine de saumons de l'Atlantique et mis en évidence les variables scalimétriques les plus susceptibles de répondre à un tel objectif. Cette procédure a impliqué trois rivières à saumons dont les embouchures sont distantes de 65 à 265 km l'unes à l'autre et, originalement, 13 caractères scalimétriques qui étaient susceptibles d'exprimer les différences environnementales et/ou génétiques des populations de saumons de la région de l'estuaire du Saint-Laurent.

La réalisation des deux premières séries de rééchantillonnages atteint les deux objectifs visés : le taux de classification des saumons s'est maintenu à 94 % avec un écart type de près de 4 %, et sept variables sur les 13 disponibles sont régulièrement sollicitées. Le rééchantillonnage a été limité à 15 et 10 saumons par rivière car une réduction plus poussée du nombre d'individus aurait introduit une plus grande instabilité dans la détermination des fonctions discriminantes et un risque de classification erronée plus élevé. En effet, les groupes bien séparés nécessitent un plus petit nombre d'échantillon pour les discriminer que les groupes qui sont près les uns des autres (Lachenbruch 1968), mais ceci jusqu'à une certaine limite.

L'analyse discriminante demeure donc la façon la plus rapide de classer des saumons d'origine inconnue. Par contre, la contrainte majeure vient du fait que, pour un groupe donné de variables, toutes les rivières doivent démontrer des profils moyens significativement différents.

À partir de nos résultats et des variables que nous avons mis en évidence, tout saumon d'origine inconnue de 3,2+ ans en 1986 pourrait être testé par rapport aux trois rivières qui font l'objet de cette présente recherche. Si ces trois rivières étaient considérées comme représentatives de leur région respective, des analyses discriminantes pourraient aider à préciser les conséquences des pêcheries commerciales, qui ont toujours court sur la rive nord de l'estuaire du fleuve Saint-Laurent, sur les rivières à saumons de cette région. Le désavantage de cette approche est que tous les groupes (rivières) impliqués doivent être représentés dans la règle de décision (équation de classification) parce que chaque individu sera assigné à un des groupes, qu'il en soit membre ou non (Marshall *et al.* 1987). En effet, l'équation de classification n'identifie pas, ni ne rejette l'individu qui est anormalement éloigné des centroïdes.

Par contre, rien n'indique dans nos résultats que les équations discriminantes décrites au tableau 2 seraient applicables à des saumons d'une autre année d'échantillonnage ou d'une autre classe d'âge. Cette application est encore à vérifier.

Le nombre de rivières impliquées dans de telles analyses doit être appuyé par des variables de qualité et un nombre suffisant d'individus. De nos résultats, on peut déduire qu'il existe certaines limites en-deçà ou au-delà desquelles les analyses discriminantes deviennent inefficaces. Actuellement, ces limites doivent être constamment ajustées parce qu'on ne peut établir des différences strictes entre les profils des saumons de toutes les rivières (voir Claytor *et al.* 1987).

Reddin et Misra (1985) mentionnent que, selon leur approche, quatre variables devraient suffire pour discriminer des stocks. Mais dans le cas de plusieurs rivières ou de rivières rapprochées, ces quatre variables seraient probablement insuffisantes pour obtenir une capacité discriminante et un taux de classification intéressants, à moins que celles-ci ne définissent clairement des différences entre les groupes impliqués.

Lachenbruch (1977) de même que Habbema et Hermans (1977) mentionnent que si l'objectif est d'étudier les différences entre les groupes et de mettre en évidence des variables discriminantes, et que les conditions d'égalité des covariances, de normalité et d'échantillonnage au hasard sont respectées, alors l'emploi de la statistique F est approprié, même si le taux d'erreur est optimiste. Ils ajoutent qu'avec un objectif subséquent d'allocation des individus (classification), il est important de valider le taux d'erreur, parce qu'une estimation trop optimiste peut mener à l'usage d'une règle non satisfaisante. Ainsi, dans notre cas, l'emploi de la statistique F lors de nos analyses discriminantes est justifié.

Dans le même sens, Turlot (1989) mentionne que la pertinence d'un critère dépend de la structure même des données. En pratique, la sélection d'un sous-ensemble de prédicteurs effectuée sur la base de connaissances a priori (variables forcées), puis la sélection d'un petit nombre de prédicteurs parmi les variables exploratoires, constituent une protection contre une sélection en partie artificielle, et le biais de sélection s'en trouve réduit. Mais, de fait, l'estimation par rééchantillonnages des taux d'erreur de classement présente un plus faible biais (Turlot 1989). Ainsi, notre validation des taux d'erreur de classification par des rééchantillonnages est aussi pertinente.

Les résultats qui viennent d'être présentés sont à la fois intermédiaires et complémentaires à ceux obtenus par les auteurs qui ont déjà appliqué l'analyse discriminante sur des mesures scalimétriques de saumons. Intermédiaires, en ce sens qu'ils ne visent pas à solutionner des problèmes relatifs aux continents américain et européen, comme les travaux de Lear et Sandeman (1980), ni à une rivière en particulier, comme ceux de Reddin et Misra (1985). Et complémentaires, en ce sens que nos résultats démontrent qu'il est possible de discriminer trois rivières rapprochées de 65 à 265 km, avec un faible nombre d'individus et sept variables bien définies. Ces sept variables mises en évidence sont LR1, LR2, LR29, CR2, LR39, LM1 et CM1, soit majoritairement celles de la deuxième année de rivière et celles de la première année de mer.

Par ces sept variables, la séparation des stocks (fig. 1) est aussi nette entre les rivières Matane (groupe #3) et de la Trinité (groupe #2), distantes de seulement 65 km, qu'entre les rivières Matane et Anse St-Jean (groupe #1) ou les rivières de la Trinité et Anse St-Jean qui sont éloignées d'environ 265 km.

Plusieurs facteurs pourraient expliquer cette séparation des groupes. Mais nous ne pouvons qu'émettre des hypothèses puisqu'aucun auteur, à notre connaissance, n'a pu ou n'a cherché à comprendre en quoi ce sont les variables de la deuxième année de rivière et celles de la première année de mer qui différencient les saumons de ces trois rivières. La géologie des sols des bassins versants respectifs, soit de type granitique sur la rive nord (rivières Anse St-Jean et de la Trinité), et sédimentaire sur la rive sud (rivière Matane), les conséquences de l'acidification des plans d'eau (Watt *et al.* 1983), l'amplitude de la réponse de l'effet tampon des sols sur les pluies acides (Haines, 1981), le régime des températures d'eau, les variations saisonnières du débit, la compétition intra et interspécifique, sont tous des facteurs susceptibles d'expliquer en partie cette différenciation. Conséquemment, les aptitudes (ou limites) déjà acquises génétiquement, ou développées en fonction des conditions environnementales de la rivière où ces saumons vivent, pourraient se répercuter sur leur taux de croissance (et sur le développement conséquent de leurs écailles), sur leur capacité de survie en rivière et lors de leur voyage en mer. Mais il reste à comprendre en quoi ces facteurs, ou d'autres, sont impliqués dans les différences observées dans la deuxième année de rivière et la première année de mer.

Ces avenues doivent être explorées pour découvrir d'autres variables encore plus spécifiques qui pourront éventuellement être appliquées à des systèmes plus complexes de rivières (tel que présenté par Marshall *et al.* 1987) ou à des stocks mixtes à très grande échelle comme ceux du Groenland.

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Diving Observations of Subtidal Communities in the Northern Gulf of St. Lawrence[1]

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A SCUBA survey was made to examine the organization of subtidal communities in the northern Gulf of St. Lawrence. In a narrow zone in shallow water, where urchins are rare, rock surfaces are dominated by macroalgae and mussels. Below this is an abrupt transition to a vast urchin-dominated zone, where the only conspicuous organisms other than urchins are crustose coralline algae and a few fleshy grazing-resistant algae. At greater depths, there is an increase in ophiuroids and other suspension feeders. On sediment bottoms, below the rocky zone, the predominant macoorganisms are bivalves and sand dollars. Four types of mobile subtidal predators are present: (1) the gastropod *Buccinum undatum*, (2) four seastars, *Leptasterias polaris*, *Asterias vulgaris*, *Crossaster papposus* and *Solaster endeca*, (3) two crabs, *Hyas araneus* and *Cancer irroratus*, and (4) a number of fishes. *Buccinum* and *Leptasterias* are the most abundant predators. This contrasts with more southern communities, where fishes and decapod crustaceans are the predominant predators, and suggests differences in community organization. All of the major predators in the northern Gulf show broad habitat preferences, being common on both rocky and sediment bottoms. The four seastar predators feed on a large variety of benthic invertebrates and probably strongly limit the abundance of a number of their prey.

Un inventaire fut effectué en scaphandre autonome pour examiner l'organization des communautés de l'étage infralittoral de l'archipel de Mingan, au nord du golfe du Saint-Laurent. La plupart des espèces d'algues y sont confinées à une étroite bande sur les substrats rocheux en eau peu profonde. La zone d'algues se termine abruptement pour laisser place à une vaste zone dominée par les oursins verts. Les principaux macroorganismes, autre que l'oursin, sont les algues calcaires et quelques autres algues résistantes au broutage. Plus en profondeur, une augmentation du nombre d'ophiures et d'autres animaux suspensivores se produit. Sur le fond de sédiment, en dessous de la zone rocheuse, les organismes prédominants sont les bivalves et les oursins plats. Quatre principaux types de prédateurs se retrouvent dans l'étage infralittoral : (1) le gastéropode *Buccinum undatum*, (2) quatre étoiles de mer, *Leptasterias polaris*, *Asterias vulgaris*, *Crossaster papposus* et *Solaster endeca*, (3) deux crabes, *Hyas araneus* et *Cancer irroratus*, et (4) un certain nombre de poissons. *Buccinum* et *Leptasterias* sont les prédateurs les plus abondants. Le homard, la tanche-tautogue et le loup atlantique, des prédateurs importants du nord-ouest de l'Atlantique, sont pratiquement absents. Tous les principaux prédateurs au nord du golfe montrent peu de préférence pour un habitat en particulier: ils se retrouvent aussi bien en milieu rocheux que sur les sédiments. La guilde des étoiles de mer s'alimente de la plupart des espèces non-prédatrices et limite probablement l'abondance de plusieurs de ses proies.

Introduction

During the past 10–15 yr SCUBA diving has been used extensively to study the structure of subtidal communities. In the western North Atlantic region, the majority of such work has been done in the Canadian Maritime Provinces (MacFarlane 1966; Edelstein et al. 1969; Miller et al. 1971; Mann 1972, 1982; Chapman 1981; Logan et al. 1983; Scheibling 1984; Miller 1985), and a number of studies have been done in Newfoundland (Himmelman 1969, 1985; Hooper 1980, Fletcher et al. 1974; Keats et al. 1982, 1985), the St. Lawrence Estuary (Himmelman et al. 1983a,b; Himmelman and Lavergne 1985) and New England (Sears and Wilce 1975; Witman 1985). However, for the extensive region along the north shore of the Gulf of St. Lawrence (Fig. 1) there is virtually no information on the structure of subtidal communities. Our knowledge of this region is limited to a few distributional records based on samples collected by drag or grab and on fisheries data for some species (Dunbar et al. 1980).

In the present study a rapid technique using SCUBA is used to evaluate the structure of subtidal communities in a section of the northern Gulf, the Mingan Islands. I restrict my attention to relatively large benthic organisms and focus on patterns of distribution and abundance, the size structure of certain predator populations, and on trophic interactions. The observation

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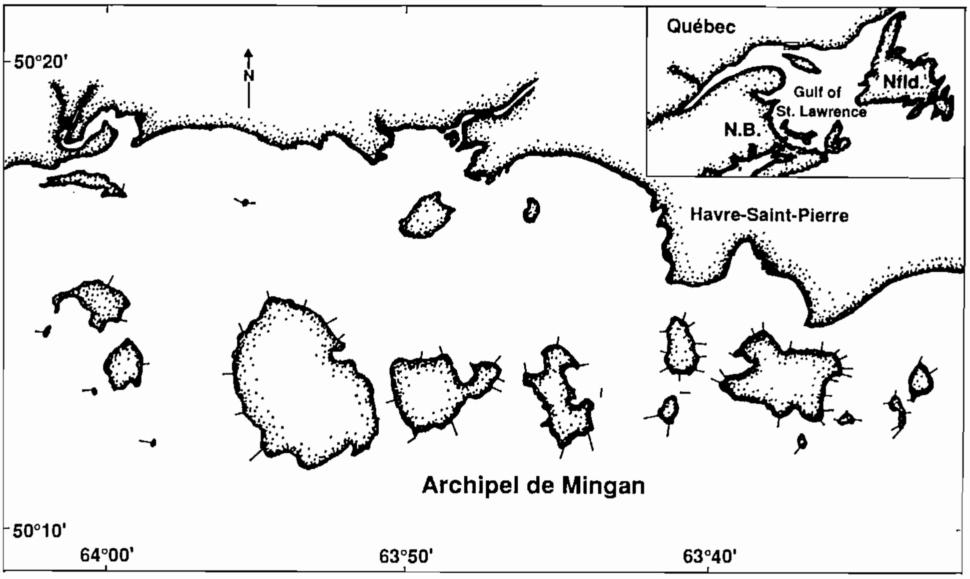

FIG. 1. The Mingan Islands in the northern Gulf of St. Lawrence, showing the sites where the 71 rapid transects were made.

period was limited to 2 months in each of two summers. We qualitatively noted utilization of primary space by conspicuous algae and invertebrates, and paid particular attention to the location of distinct zones of certain species. Since predation potentially affects the organization of subtidal communities (eg. Breen and Mann 1976; Duggins 1980), we estimated the abundance of predators and carefully described all observed predation.

Methods

The Mingan Islands (Fig. 1) were chosen for study because they were accessible by road, and because the islands provided a large diversity of habitats within a relatively short distance. The evaluation of subtidal communities was made by pairs of divers assisted by one person in a boat. Each diver was equipped with a plexiglass writing pad with an attached ruler and depth meter. The divers swam in a line perpendicular to the shore, starting in the intertidal region and continuing to a depth of 20–30 m. Most transects covered a horizontal distance of 100–300 m, but several in gently sloped areas may have covered 500 m.

In developing the notational procedure I wanted to maintain a balance between observations on algae and non-predatory invertebrates and those on predators, and at the same time keep the dives brief enough to permit completion of a transect during one dive. Each dive lasted 40–75 min and a pair of divers usually made two successive dives. Initially, the type of substratum (bedrock, boulders, cobbles, gravel, sand, mud) was recorded. The abundance of conspicuous algae and non-predatory invertebrates was noted using ranks: abundant (A), common (C), scattered (S) and rare (R). Attention was given to describing the limits (depth, substratum) of visually striking zones such as mussel or algal beds, urchin aggregations or dense populations of filter feeders. For most of the large predator species, we noted the size of each individual encountered. The diameter of seastars, shell length of predatory gastropods, maximum carapace dimension of crabs and estimated length of large fish species were recorded. In transects where the gastropod *Buccinum undatum* was too abundant to permit measuring each individual an abundance rank was noted. Only the general abundance of the small fishes, the Arctic shanny *Stichaeus punctatus* and the radiated shanny *Ulvaria subbifurcata*, was recorded. When predation was noted the size of the predator and prey was recorded. To facilitate taking notes underwater, abbreviations were used extensively for indicating species names, predation and abundance and size notes. For example, $\text{L}_{38} > \text{Clino}_{6.5}$ indicates the observation of the seastar *Leptasterias polaris* measuring 38 cm in diameter preying on a clam *Clinocardium ciliatum* measuring 6.5 cm in shell length.

As soon as possible after diving the two divers made a schematic sketch of the shore indicating the substratum type, depth and predominant zones of organisms. All notes taken underwater were transcribed onto this sketch at the appropriate position along the shore profile. A total of 39 transects were made in 1981 by a group of four divers, and 32 transects were made in 1982, 24 of which were made by the same two divers. In evaluating the relative abundance of predators and the size-structure of seastar populations, I used only the transects made by experienced persons. Thus I retained 15 of the transects made in 1981, and 24 of those made in 1982.

Results and Discussion

Subtidal Zonation Pattern

The majority of species and their distributional pattern generally corresponded to that previously reported for the northwestern Atlantic region, particularly for Newfoundland and the St. Lawrence Estuary (Himmelman 1969, 1985; Hooper 1980; Himmelman and Lavergne 1985; Keats et al. 1985). Thus, rocky areas were characterized by two major zones, one in shallow water dominated by macroalgae and one in deeper water dominated by urchins. Himmelman and Lavergne (1985) describe three subzones for the algal zone, (1) the intertidal zone where fucoid algae and mussels predominate, (2) the algal fringe which is dominated by *Alaria esculenta*, and (3) a subzone of grazing-resistant algae; and two subzones for the urchin-dominated zone, (1) a barrens with high numbers of urchins and a scarcity of organisms other than crustose coralline algae, and (2) filter feeders at greater depths where urchin grazing is reduced yet sufficient to limit algal abundance. These zones were readily recognized in the Mingan Islands. In the present study most transects were continued beyond the limit of rocky substrates and thus sediment bottom organisms such as clams and sand dollars were also encountered. The relative importance of the different zones varied greatly depending on the substratum, slope of the shore, wave exposure and the strength of tidal currents. To describe the zonation pattern in the subtidal region of the Mingan Islands, I will present four contrasting situations which encompass most of the variations observed.

1) **Moderately exposed, medium-sloped bottoms** (Fig. 2, 3). Medium-sloped bottoms were most common on the east and west side of the islands although they sometimes occurred on the northern sides. The transition between zones was abrupt. In the intertidal region, primary space was dominated by *Fucus* spp. and *Mytilus edulis*, except in the low intertidal region usually occupied by a narrow zone of the green alga *Spongomorpha arcta*. At more exposed sites the red alga *Devaleraea ramentacea* was also common near low tide level. The frequent occurrence of opportunistic algae, such as *Chordaria flagelliformis*, *Scytosiphon lomentaria*, *Dictyosiphon foeniculaceus* and *Ulvaria obscura*, in the low intertidal to upper subtidal region suggested denudation by ice during the winter.

An *Alaria* fringe, which usually included scattered *Saccorhiza dermatodea*, *Laminaria digitata* and *Laminaria longicruris*, began near low water level and extended to at most 2 m in depth. The width of this zone increased with exposure. Its lower limit was abrupt and coincided with an abundance of urchins *Strongylocentrotus droebachiensis*. Aggregations of large urchins were often observed foraging at the lower edge of the fringe. Below the *Alaria* fringe was an urchin-dominated barren zone covering a depth range of 2–3 m. Fleshy macroalgae, other than scattered *Desmarestia viridis* and *Agarum cribrosum*, were absent.

Beginning at 4–6 m in depth (coinciding with a decrease in urchin abundance) and continuing to the end of the rocky zone, filter feeding species, notably the ophiuroid *Ophiopholis aculeata*, the tunicate *Halocynthia pyriformis*, the frilled anemone *Metridium senile*, and the sea cucumbers *Psolus fabricii* and *Cucumaria frondosa*, were abundant. The predatory northern red anemone *Tealia felina* was common in the lower part of rocky slopes. Scattered *Agarum* and other grazing-resistant algae were present on rocky substrates below the *Alaria* fringe but did not form distinct zones.

On sediment bottoms below the rocky slopes, sand dollars *Echinarachnius parma* and a variety of clams (eg. *Clinocardium ciliatum*, *Serripes groenlandicus* and *Spisula polynyma*) were the predominant animals. There was a gradual change in the size of the sediments, from gravel to sand and eventually to mud. Urchins were always present in the sediment zone, but their numbers and size decreased with distance from the shore.

2) **Exposed, gently sloping bedrock platform** (Fig. 4). In the southern part of the islands, most exposed to waves, the calcareous rock formed extensive gently sloped platforms on which biotic zones were very broad and the transitions between zones gradual. In the lower intertidal region there was a distinct green zone composed of a dense growth of *Spongomorpha arcta*, and at a slightly lower level a red zone composed of *Devaleraea ramentacea* with an undergrowth of *Spongomorpha*.

The *Alaria* fringe was broad and included patches of *Saccorhiza dermatodea* and *Laminaria digitata*. In the upper part of the fringe, *Spongomorpha* and *Devaleraea* were present as understory species, but in the mid- to lower fringe most of the bedrock surfaces between kelp holdfasts were covered with the crustose coralline algae, *Clathromorphum* spp. The algae *Ulvaria obscura* and *Porphyra miniata* occurred sporadically on the bedrock, and *Palmaria palmata* was sometimes epiphytic on *Alaria*. The small gastropod grazers, *Margarites* spp. and *Lacuna vincta*, were common on algal fronds.

Urchins were absent in the upper part of the fringe but progressively increased in abundance with depth. They first appeared individually, then in groups, and then in dense patches in clearings in the *Alaria* bed. Clearings with high densities of urchins increased in frequency with depth and eventually merged, marking the end of the algal fringe. Mussel beds were abundant in the lower intertidal and upper subtidal regions (where seastars were absent) but ended abruptly within the algal fringe zone at about the depth where the seastars, *Leptasterias polaris* and *Asterias vulgaris* (individuals <15–20 cm in diameter) became abundant. The majority of seastars encountered in the fringe zone were foraging on mussels.

Grazing-resistant algae (Himmelman 1985) covered extensive surfaces, but the cover was not continuous. It was reduced in depressions and increased on rocky prominences. Just below the *Alaria* fringe was a zone of *Agarum cribrosum* with a sparse understory of mostly *Ptilota serrata*. At greater depths grazing-resistant red algae (mainly *Ptilota* and secondarily *Callophyllis cristata* and *Phycodrys rubens*) often predominated and *Agarum* could be absent. Urchins were always present among the grazing-resistant algae but their numbers and size decreased with the distance from the *Alaria* fringe. On the exposed southern platforms there was often no distinct urchin-dominated barrens, rather there was a transition from the zone of grazing-resistant algae to a zone of filter feeders. *Ophiopholis aculeata* and *Cucumaria frondosa* were the most common. The grazing-resistant foliose red alga *Turnerella pennyi* often occurred with filter feeders in deeper water.

3) **Rocky faces** (Fig. 5). Vertical rocky faces occurred at a number of locations along deep channels separating the islands. On these faces the algal zone was <1 m in width, mainly in the lower intertidal region, and the zone of filter feeders was very extensive. Immediately below a narrow band of *Fucus* and *Alaria* in the intertidal

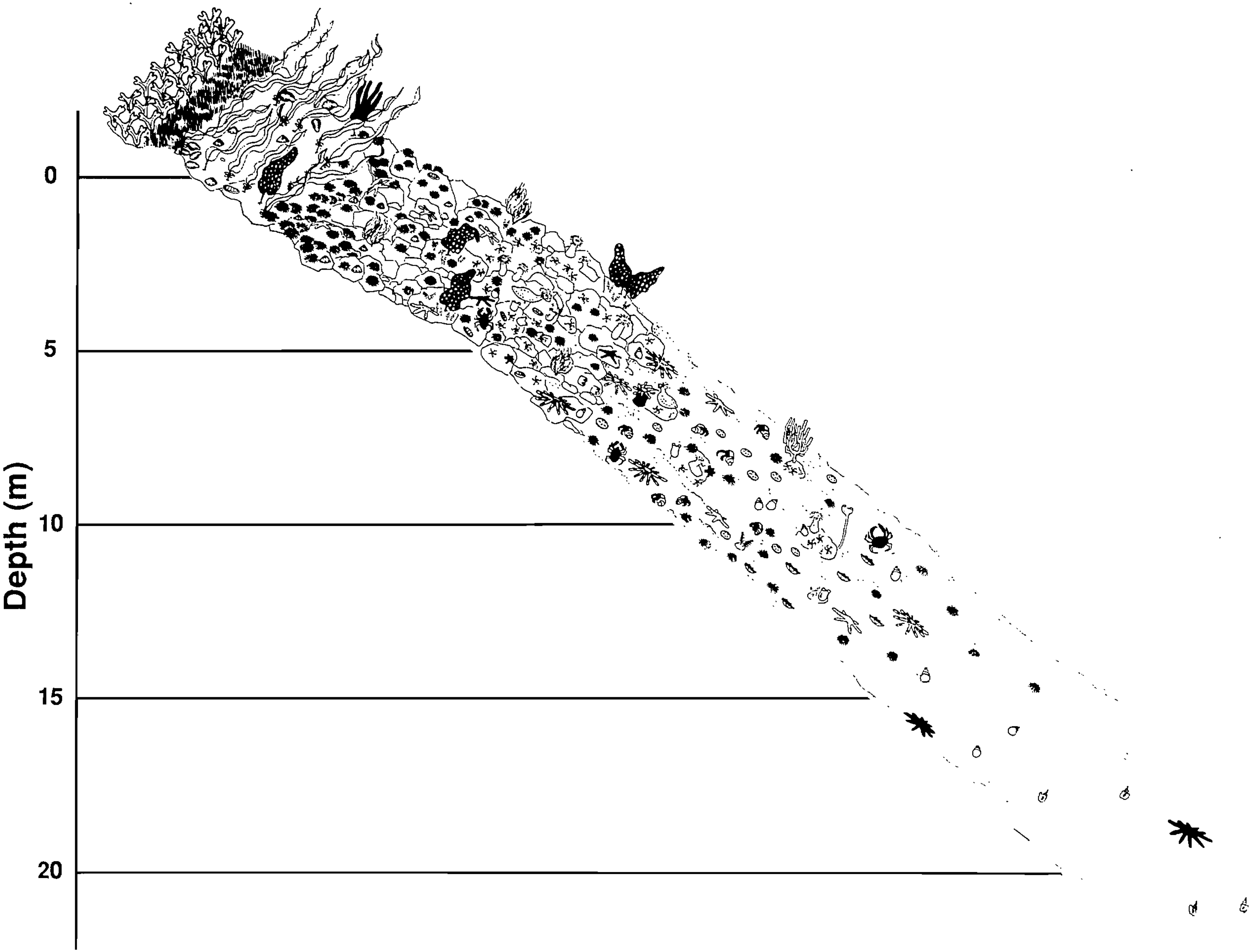

FIG. 2. Sketch of the distribution of macroorganisms on moderately exposed, medium-sloped bottoms. The symbols for the macroorganisms are defined in Fig. 3.

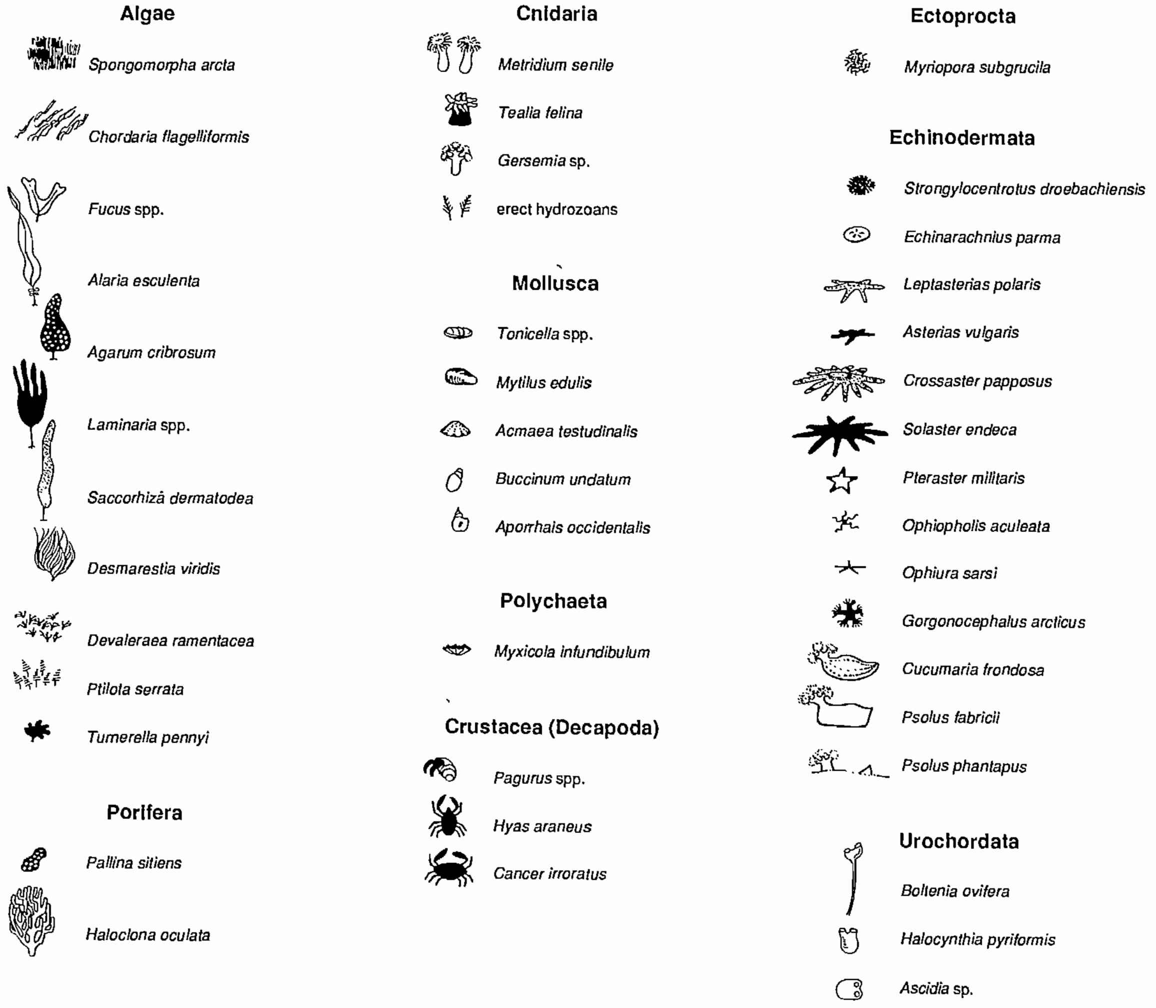

FIG. 3 List of symbols for the different macroorganisms shown in Fig. 2, 4, 5 and 6.

region, an urchin barrens covered a depth range of 2–3 m and was succeeded by a zone of filter feeders. The filter feeders increased in abundance and diversity with depth to a maximum at 15–20 m. Densities of *Ophiopholis aculeata*, *Halocynthia pyriformis* and *Metridium senile* were extremely high, and often large colonies of the branched ectoproct *Myriopora subgrucila* and the soft globular-shaped sponge *Pallina sitiens* were present. The anemone *Tealia felina*, which was observed feeding on dislodged urchins, was abundant in the lower part of rocky faces as well as on talus slopes just beneath vertical faces. Grazing-resistant algae were rare on rocky faces.

4) **Gently sloping sediment bottoms in areas of strong tidal current** (Fig. 6). Sediment bottoms associated with strong tidal currents predominated on the northern side of many of the islands. Usually the intertidal and upper subtidal regions were gently sloped, but a short distance from shore (and associated with a sharp increase in current) the slope increased and the sediments became coarser. This slope eventually gave way to a gently sloped bottom.

When there was rock in the intertidal and upper subtidal regions, algae such as *Fucus*, *Chordaria*, *Dictyosiphon*, *Spongomorpha* and *Ulvaria* and sometimes a few *Alaria* were present. In shallow water the abundance of urchins and other macroinvertebrates was low. This was probably due to the abrasion of ice carried by currents since coralline algal cover was very low. At greater depths the first filter feeders encountered were ophiuroids. *Gersemia* sp. and *Cucumaria frondosa* were often found on rocks, particularly where there was an increase in slope and the presence of cobbles and small boulders.

On the gentle slope at greater depths a sand bottom often predominated and supported populations of *Echinarachnius parma* or clams. Whenever cobbles and boulders were present filter feeders were abundant, the most common being *Gersemia* and ophiuroids. *Cucumaria frondosa*, *Psolus fabricii*, *Boltenia ovifera* (stalked tunicate), *Halocynthia pyriformis*, *Metridium senile*, *Lurcernaria quadricornis* (stauromedusa), *Chlamys islandica* (scallop) and *Tealia felina* varied in abundance from rare to common, and the basket star *Gorgonocephalis arcticus* was found at several sites. When the bottom was muddy, the ophiuroid *Ophiura sarsi*, *Buccinum undatum* and *Aporrhais occidentalis* were the most conspicuous macroorganisms. On current-swept sediment bottoms, *Agarum* sometimes occurred on boulders, and at greater depths some smaller grazing-resistant red algae, such as *Ptilota*, were common when rocky material was present.

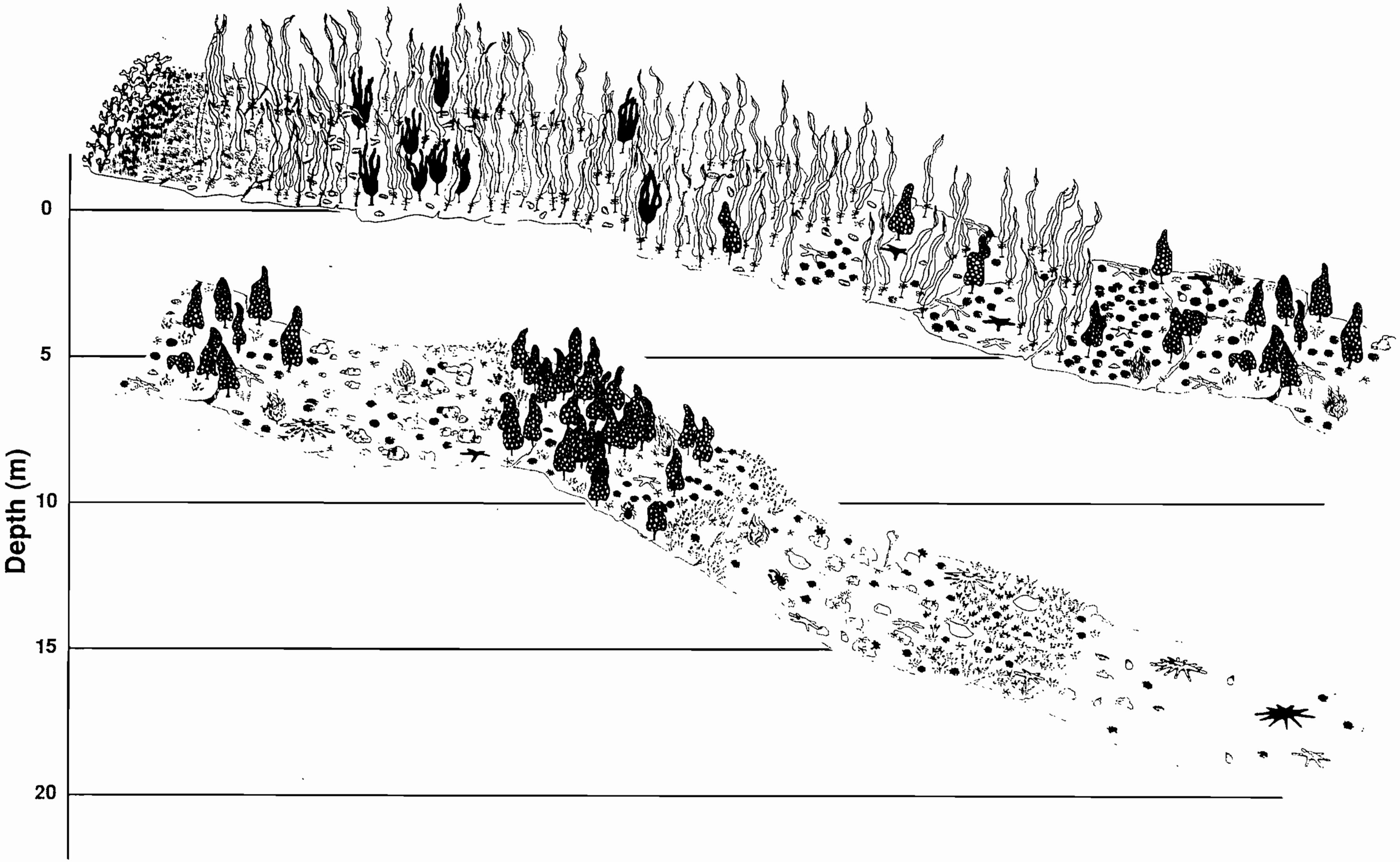

FIG. 4. Sketch of the distribution of macroorganisms on exposed, gently-sloped bedrock platforms. The symbols for the macroorganisms are defined in Fig. 3.

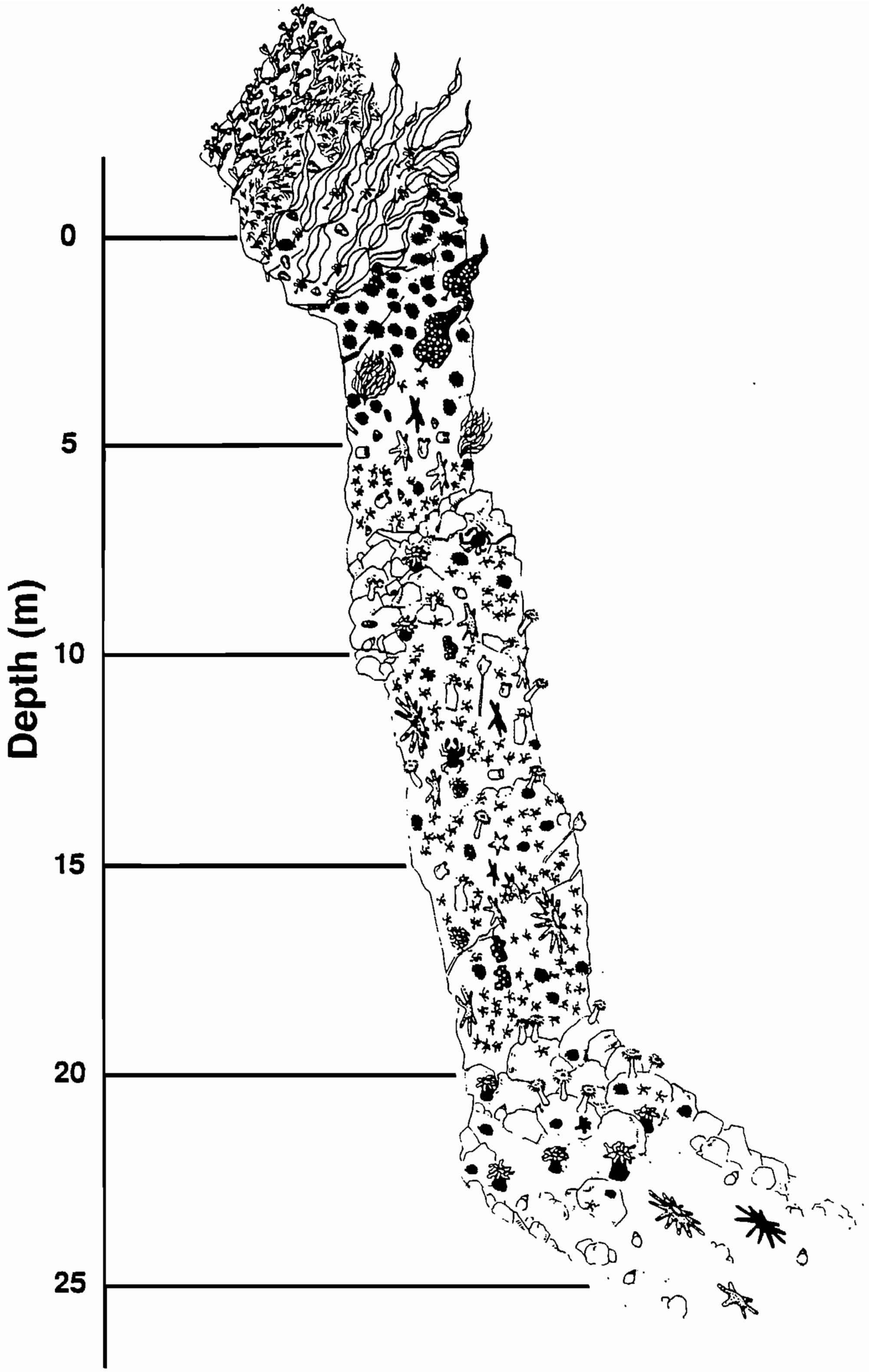

FIG. 5. Sketch of the distribution of macroorganisms on rocky faces. The symbols for the macroorganisms are defined in Fig. 3.

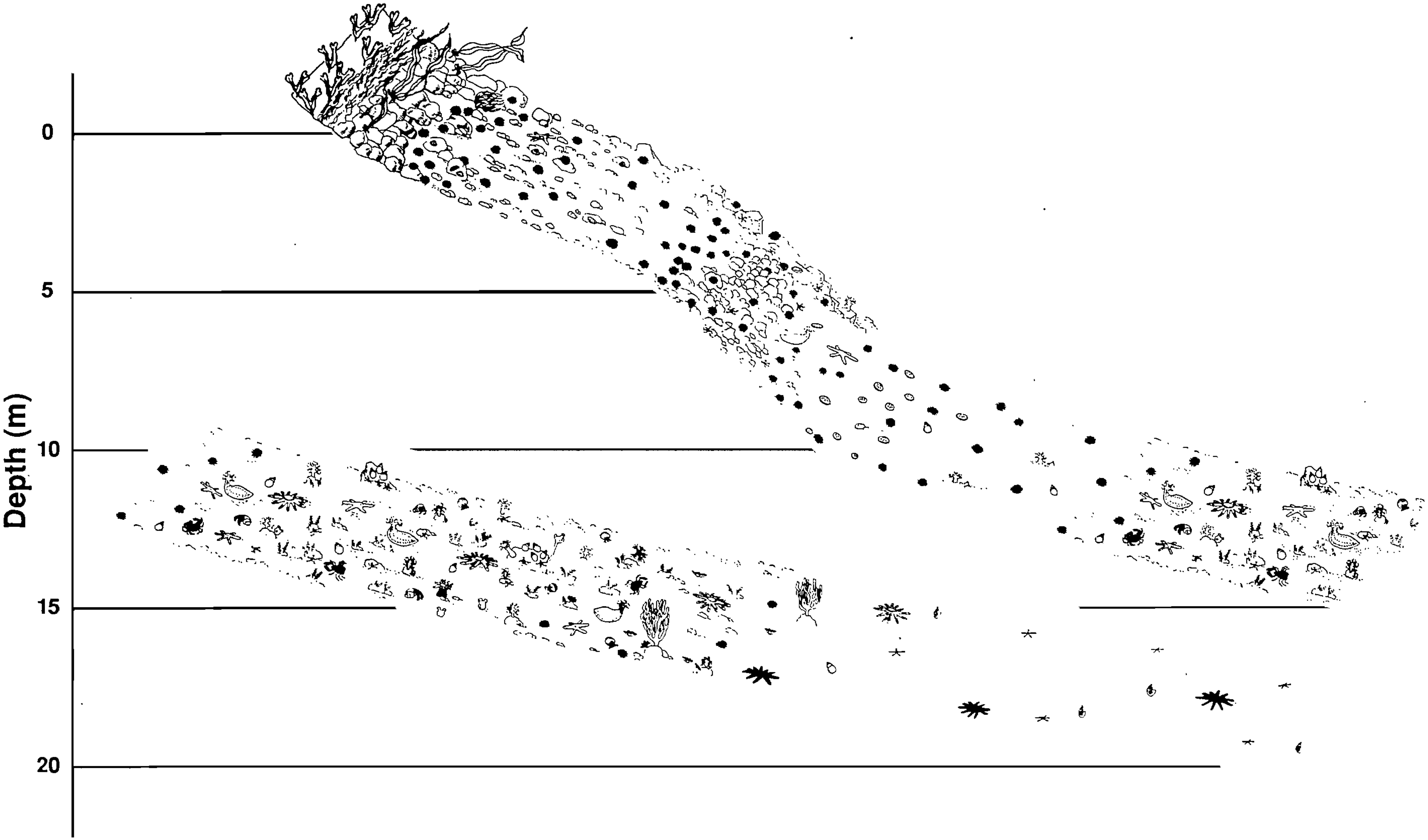

FIG. 6. Sketch of the distribution of macroorganisms on gently sloped sediment bottoms in areas of strong tidal current. The symbols for the macroorganisms are defined in Fig. 3.

TABLE 1. Abundance of various predators in the Mingan Islands, expressed as the mean number of individuals observed • h^{-1} during 39 rapid transects, and as the mean number of individuals • m^{-2} as estimated from quadrat sampling (Jalbert 1986). In the quadrat sampling, the mean density is based on 1317 quadrats of 1 m^2 for the crabs and on 1772 quadrats of 1 m^2 for the other species. Only larger individuals (as indicated in parenthesis after the name of each predator group) were retained for these calculations. For each value, the mean plus and minus the value in parenthesis gives the 95% confidence interval.

	Rapid Transects (individuals observed • h^{-1}	**Quadrat Sampling** Density • m^2
	Gastropods (>5 cm in shell length)	
Buccinum undatum	>35.	0.417 (0.045)
Neptunea despecta tornata	0.10 (0.16)	0.006 (0.007)
	Seastars (>10 cm in diameter)	
Leptasterias polaris	26.2 (4.47)	0.150 (0.022)
Asterias vulgaris	4.9 (2.17)	0.027 (0.009)
Crossaster papposus	8.2 (1.77)	0.010 (0.005)
Solaster endeca	1.9 (0.88)	0.002 (0.003)
	Crabs (>3 cm in maximum carapace dimension)	
Hyas araneus	4.4 (1.23)	0.055 (0.016)
Cancer irroratus	3.5 (1.34)	0.053 (0.012)
	Fishes (>10 cm in length)	
Myoxocephalus scorpius	3.15 (0.73)	
Pseudopleuronectes americanus	0.22 (0.22)	
Macrozoarces americanus	0.14 (0.11)	
Hemitripterus americanus	0.11 (0.09)	
Cyclopterus americanus	0.10 (0.10)	

Predators

We recorded the number of large mobile predators observed per hour by two divers during each transect and then calculated the mean for the 39 transects in which the notational technique was standardized (Table 1). It is important to keep in mind that these predators were observed as we slowly passed from 0 to 20–30 m in depth noting distributional patterns as well as predators. If we had looked only for predators, the incidence of predators observed would have been greater. Small individuals of most predators were underestimated due to their low visibility. During another project, 1772 quadrats of 1 m^2 along 24 transects in various regions of the Mingan Islands were observed and the abundance and size of all invertebrate predators recorded (Jalbert 1986). These data provided a measure of the validity of our semiquantitative data (Table 1).

Four types of large active predators were present: (1) the common northern whelk *Buccinum undatum*, (2) four sea stars, *Leptasterias polaris*, *Asterias vulgaris*, *Crossaster papposus* and *Solaster endeca*, (3) two crabs, *Hyas araneus* and *Cancer irroratus*, and (4) a number of fishes (Table 1). Since it was not practical to record the numbers of whelks when they were abundant, I can only indicate that >35 individuals measuring >5 cm in length were observed per hour. In the quadrat sampling, the density of whelks >5 cm in length was 42 individuals • 100 m^{-2}. Both techniques indicated that *Buccinum* was the most abundant invertebrate predator. Another large gastropod *Neptunea despecta tornata* was present in far lower numbers (Table 1) and mainly on sediment bottoms in deeper water. The Atlantic dog whelk *Nucella* (*Thais*) *lapillus* was not encountered in the subtidal transects; however, I have observed it in low numbers in the intertidal zone (pers. observations).

Seastars were a striking group of predators due to their abundance, large size, and because they were frequently feeding. The six-armed seastar *Leptasterias polaris* was the most abundant, with 26 individuals >10 cm in diameter being observed • h^{-1} (Table 1). This compared with 15 individuals • 100 m^{-2} in the quadrat sampling (Table 1). The rapid transects indicated that the purple seastar *Asterias vulgaris* and spiny sunstar *Crossaster papposus* were 3–5 times less abundant than *Leptasterias*, and the purple sunstar *Solaster endeca* was 14 times less abundant than *Leptasterias*. The quadrat sampling showed that the rapid transect technique overestimated the abundance of *Crossaster* and *Solaster*. This was probably because of their striking form, generaly large size, and non-cryptic behaviour compared to *Leptasterias* and *Asterias*.

The two sampling techniques indicated that the rock crab *Cancer irroratus* and toad crab *Hyas araneus*, were approximately as dense as *Asterias* and *Crossaster*. Our technique did not permit us to quantify the abundance of hermit crabs *Pagurus* spp., since most were small; however, they were clearly very abundant on sediment bottoms. Fish were generally not abundant in the Mingan Islands. Whereas our technique did not permit a quantitative estimation of Arctic and radiated shannies, *Stichaeus punctatus* and *Ulvaria subbifurcata*, respectively, due to their small size, they were without doubt many times more abundant than other fish. The most common of the larger fishes, the shorthorn sculpin *Myoxocephalus scorpius*, was observed at a rate of about 3 • h^{-1}, whereas the next four species, the winter flounder *Pseudopleuronectes americanus*, ocean pout

Macrozoarces americanus, sea raven *Hemitripterus americanus* and lumpfish *Cyclopterus americanus*, were much less abundant. The last species only comes to the shallow water zone to reproduce (Goulet et al. 1988).

Size-structure of Seastar Populations

The rapid transect method gave little information on the abundance of small individuals, but demonstrated the differences in the size structure of adult seastars (Fig. 7). Furthermore, it provided a better indication of the maximum size attained, as well as size-structure data for the rarest species *Solaster endeca*, which would be difficult to obtain using quadrat sampling. The most frequent diameters of both *Leptasterias polaris* and *Asterias vulgaris* were 10–15 cm. The size-structure of *Leptasterias* was strongly skewed towards the large sizes whereas that of *Asterias* was relatively symmetric. Since small individuals were not as visible as larger individuals, an underestimate of their relative abundance was expected. In fact, size distributions based on the quadrat sampling (Fig. 7) revealed that 0–5 cm individuals were the most frequent group for both *Asterias* and *Leptasterias*. The semiquantitative data indicated that *Crossaster papposus* had a relatively symmetrical size-structure, as for *Asterias*, but the mean size was larger. The quadrat data confirmed the size difference and also that small individuals were infrequent. Finally, the semiquantitative data for *Solaster endeca* showed a symmetric size structure pattern centered at an even greater size than for *Crossaster*. The quadrat sampling of Jalbert (1986) provided no information on the size-structure of *Solaster* since only one individual was encountered in the 1772 m^2 examined.

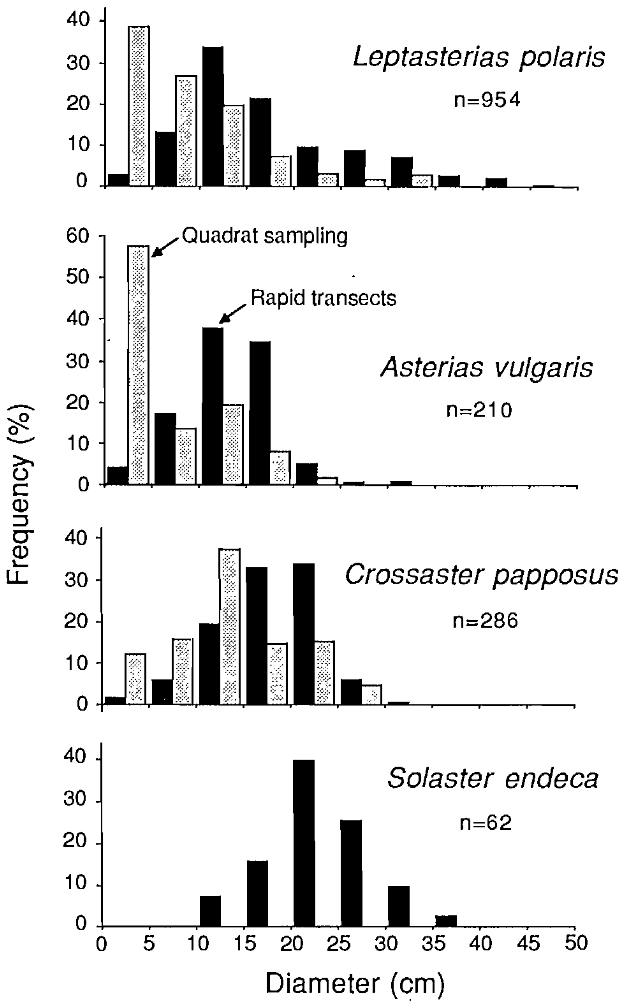

FIG. 7. Size-distributions of the predatory seastars, *Leptasterias polaris*, *Asterias vulgaris*, *Crossaster papposus* and *Solaster endeca*, based on the data from (1) rapid transects (sample sizes are given under the names of the seastar) and (2) from the quantitative sampling of Jalbert (1986).

TABLE 2. Relative frequency (%) of prey in the diets of five size groups of *Leptasterias polaris*. Individual with their stomach eviscerated into crevices were considered to be feeding, although the prey could not be identified.

	Diameter (cm)				
	0–10	10–20	20–30	30–40	40–50
	Leptasterias polaris				
Mollusca					
Mytilis edulis	33.3	28.0	23.0	0	0
Musculus sp.	0	5.9	0	0	0
Modiolus modiolus	0	0.5	2.3	0	0
Hiatella arctica	36.1	36.0	2.3	0	0
Spisula polynyma	0	0.5	7.0	4.3	20.0
Clinocardium ciliatum	0	0	2.3	13.0	20.0
Serripes groenlandicus	0	0	2.3	13.0	0
Ensis directus	0	0	0	4.3	0
Mya arenaria	0	0.5	4.7	4.3	0
Mya truncata	0	2.0	16.0	39.0	40.0
Macoma sp.	0	2.5	0	0	0
Astarte sp.	0	0.5	2.3	0	0
Cyrtodaria siliqua	0	0.5	0	4.3	0
Chlamys islandica	0	0.5	2.3	8.7	0
Tonicella marmorea	0	0.5	0	0	0
Acmaea testudinalis	8.3	3.0	0	0	0
Puncturella noachina	0	0.5	0	0	0
Littorina sp.	0	1.0	0	0	0
Lacuna vincta	0	1.0	0	0	0
Margarites spp.	2.8	2.0	2.3	0	0
Buccinum undatum	2.8	3.0	16.0	8.7	20.0
Aporrhais occidentalis	0	1.0	2.3	0	0
Echinodermata					
Strongylocentrotus droebachiensis	0	0.5	2.3	0	0
Echinarachnius parma	0	1.0	2.3	0	0
Ophiopholis aculeata	0	0.5	0	0	0
Urochordata					
Halocynthia pyriformis	0	1.0	2.3	0	0
Boltenia ovifera	0	0	4.7	0	0
Ascidia sp.	2.8	0	0	0	0
Annelida					
Harmothoe sp	0	0.5	0	0	0
Pectinaria granulata	5.6	2.0	0	0	0
Potamilla reniformis	0	0.5	0	0	0
Crustacea, Arthropoda					
Balanus sp.	0	1.5	0	0	0
Stomach eviscerated	8.3	3.9	2.3	0	0
Number of individuals feeding	36	203	43	23	5
Number of individuals observed	163	578	187	98	24
Percentage feeding	22.1	35.1	23.0	23.5	20.8

Prey of the Seastars and Whelks

There were notable differences in the diets of the four main seastar species. *Leptasterias polaris* had a broad diet, which included a large number of molluscs, several echinoderms and ascidians, and a few polychaetes and barnacles (Table 2). A distinct change in diet with size was evident. Individuals measuring <20 cm in diameter feed mainly on rocky bottom species, particularly *Mytilus edulis* and *Hiatella arctica*, whereas larger individuals feed on whelks and a variety of large bivalves associated with the deeper sediment zone. *Asterias* had a similar diet except that it fed more frequently on the ophiuroid *Ophiopholis aculeata* and that it was not seen feeding on ascidians or polychaetes (Table 3). In contrast to *Leptaterias* and *Asterias*, *Crossaster papposus* ate mainly echinoderms, particularly urchins, and occasionally *Leptasterias* and sand dollars (Table 3). *Crossaster* was the only seastar observed to be a predator of Cnidaria (hydroids, anemones and soft corals) and to be cannibalistic. Finally, *Solaster endeca* had the most specific diet (Table 3). It was only observed preying on echinoderms, and mostly on sea cucumbers. For *Leptasterias*, *Asterias* and *Crossaster*, 35–38% of individuals 10–20 cm in diameter were feeding. Larger *Crossaster* showed a similar rate of feeding, whereas there was a significant (*G* test; $P<0.05$) drop in percentage feeding for *Leptasterias* and *Asterias* measuring >20 cm in diameter. For *Solaster* the maximum feeding rate was 16% for individuals measuring 20–30 cm in diameter.

TABLE 3. Relative frequency (%) of prey in the diets of four size groups of *Asterias vulgaris*, *Crossaster papposus* and *Solaster endeca.* Individuals with their stomach eviscerated into crevices were considered to be feeding, although the prey could not be identified.

	Diameter(cm)			
	0–10	**10–20**	**20–30**	**30–40**
		Asterias vulgaris		
Mollusca				
Mytilis edulis	28.6	29.0	0	0
Musculus sp.	0	1.4	0	0
Hiatella arctica	28.6	15.0	0	0
Mya truncata	14.3	2.8	0	0
Chlamys islandica	0	0	50.0	0
Tonicella marmorea	0	1.4	0	0
Acmaea testudinalis	0	1.4	0	0
Margarites sp.	0	1.4	0	0
Buccinum undatum	0	2.8	50.0	0
Echinodermata				
Echinarachnius parma	0	1.4	0	0
Ophiopholis aculeata	14.3	33.0	0	0
Leptasterias polaris	0	2.8	0	0
Stomach eviscerated	14.3	6.9	0	0
Number of individuals feeding	7	72	2	0
Number of individuals observed	58	199	15	4
Percentage feeding	12.1	36.2	13.3	0
		Crossaster papposus		
Mollusca				
Mytilis edulis	0	1.7	0	0
Hiatella arctica	0	1.7	0	0
Clinocardium ciliatum	0	3.3	4.5	0
Mya truncata	0	0	2.3	0
Chlamys islandica	0	3.3	2.3	0
Buccinum undatum	0	0	2.3	0
Echinodermata				
Strongylocentrotus droebachiensis	33.3	47.0	30.0	0
Echinarachnius parma	0	6.7	9.1	0
Ophiopholis aculeata	33.3	5.0	0	0
Asterias vulgaris	33.3	0	2.3	0
Leptasterias polaris	0	6.7	11.0	100.0
Crossaster papposus	0	0	6.8	0
Cnidaria				
Hydroids	0	10.0	4.5	0
Metridium senile	0	1.7	2.3	0
Gersemia rubiformis	0	1.7	11.0	0
Urochordata				
Ascidia sp.	0	1.7	0	0
Didemnum albidum	0	3.3	0	0
	0	6.7	11.0	0
Stomach eviscerated				
Number of individuals feeding	3	60	44	1
Number of individuals observed	22	156	119	2
Percentage feeding	13.6	38.5	36.9	50.0
		Solaster endeca		
Echinodermata				
Cucumaria frondosa	0	0	18.0	0
Psolus fabricii	0	50.0	36.0	100.0
Psolus phantapus	0	0	9.1	0
Chiridota laevis	0	0	9.1	0
Echinarachnius parma	0	50.0	9.1	0
Leptasterias polaris	0	0	9.1	0
Stomach eviscerated	0	0	9.1	0
Number of individuals feeding	0	2	11	1
Number of individuals observed	0	32	67	10
Percentage feeding	0	6.3	16.4	10.0

Our survey technique provided little information on the prey of other benthic predators. The most abundant invertebrate predator species, *Buccinum undatum*, was only observed feeding on 16 occasions and in all but one instance a number of whelks (3–15) were feeding on a single prey. 12 of the attacks were on clams (*Mya truncata*, *Clinocardium ciliatum*, *Serripes groenlandicus* and *Spisula polynyma*) at the sediment surface, and 4 were on *Hyas araneus* (probably not killed by whelks). In contrast to seastars, whelks have a remarkable ability to detect and locate carcasses of dead animals on the bottom (Himmelman 1988). This suggests that scavenging is an important means of obtaining food; however, since we rarely encountered dead animals on the bottom (except during a few weeks in June when capelin *Mallotus villosus* were spawning), it is doubtful that such food resources are sufficient to support the dense whelk populations observed in the Mingan Islands. Predation by crabs and fish was not observed.

Comparison with Other Benthic Communities in the Northwestern Atlantic

Whereas I cannot compare other regions using exactly the same type of data, examination of literature indicates a number of differences compared with other regions in the northwestern Atlantic. Observations I have made in Newfoundland and Nova Scotia and discussions with other workers permitted additional comparisons.

Decapod crustaceans and fishes, which are abundant and indicated to be instrumental in determining community structure in the Maritime Provinces (Breen and Mann 1976; Bernstein et al. 1983), do not appear to be the major predators in the Mingan Islands. The lobster *Homarus americanus*, Jonah crab *Cancer borealis*, and cunner *Tautogolabrus adspersus* were absent and the Atlantic wolffish *Anarhichas lupus* was rare. The wolffish was not observed during this study but was observed a few times during more recent studies (pers. observations). The absence of these predators may be due to low temperatures. Temperatures in the Mingan Islands exceed 5°C for only 3-4 wk annually. Low temperatures reduce activity levels for some species, particularly fishes (most large fish species could be captured by hand) and may reduce larval success for such species as *Homarus americanus*, *Cancer* spp. and *Asterias vulgaris*. The northern Gulf is the limit of the geographic distribution of the latter species.

In the Mingan Islands, in contrast to the Maritime provinces, *Buccinum undatum* and *Leptasterias polaris* are the most abundant predators. The geographic distribution of *Buccinum* extends to New Jersey; however, fisheries data suggest that it attains high numbers only in the St. Lawrence Estuary and northern Gulf of St. Lawrence (Caddy et al. 1974; Villemure and Lamoureux 1975). *Leptasterias* is rare in the southern Gulf of St. Lawrence and does not occur further south. *Buccinum* does not appear adversely affected by low temperatures and Martel et al. (1986) indicate that *Buccinum* feeds mainly in the winter. Reduced feeding during the summer associated with breeding would explain why few *Buccinum* were observed feeding in this study. Nielsen (1975) indicates that *Buccinum* feeds on bivalves and describes its behavioural technique for attacking them. Thus, it may interact with *Leptasterias* and *Asterias* which also feed on bivalves. A part of *Buccinum*'s success in the northern Gulf may be due to the absence of southern predators. For example, the lobster can probably easily break open the thin-shelled *Buccinum* typical of the Mingan Islands (Martin and Himmelman 1988) and is absent there and in the St. Lawrence Estuary where whelks are abundant.

The abundance of *Leptasterias polaris* and other seastars, and their frequent predation, indicates that they are potentially important in determining community structure. As a group, seastars are diversified in their feeding, to the extent that there are few slow moving or sessile species which they do not consume. *Leptasterias* and *Asterias vulgaris* may limit the distribution of animals such as mussels, barnacles, ascidians and scallops (*Chlamys*), which are generally present in low numbers in the zone inhabited by seastars. The dense beds of *Mytilus edulis* in shallow water disappeared abruptly at the depth where seastars became abundant, and aggregations of *Leptasterias* and *Asterias* were often observed feeding at the lower limit of the mussel zone. In the deeper, sediment zone the density of seastars is reduced; nevertheless they attain a large size (20-50 cm) and could limit abundance of the clams *Clinocardium ciliatum* and *Spisula polynyma*.

A number of algae are notably less abundant in the Mingan Islands than in more southern communities. *Laminaria* spp., which frequently forms extensive subtidal beds in the Maritimes (Miller 1985; Moore et al. 1986), was limited to a few small beds in the Mingan Islands. Irish moss, *Chondrus crispus*, which in the Maritimes forms a zone near low water level and is often sufficiently abundant for commercial harvesting (MacFarlane 1966; Michanek 1975), was not encountered during the present study. The articulated coralline alga, *Corallina officinalis*, which is common in Newfoundland and in the Maritimes (Himmelman 1969; D.W. Keats and R. J. Miller, pers. comm.), was rare and at most formed very small growths in the Mingan Islands.

Some non-predatory invertebrates also showed changes in abundance compared to the Maritimes, Newfoundland and New England. Whereas the horse mussel, *Modiolus modiolus*, often forms large patches in the latter locations (pers. observations; Witman 1985), only scattered large individuals are found in the Mingan Islands. Similarly, the giant scallop, *Placopecten magellanicus*, which is common in the subtidal zone of the Maritimes (personal observations) was not observed in this study (2 large individuals were found below 20 m in depth during other studies). Inversely, the Iceland scallop *Chlamys islandica* is more abundant in the Mingan Islands. It was scattered throughout rocky and sediment bottoms and in some locations (particularly where there are strong tidal currents) formed extensive beds. *Chlamys* is absent in shallow water along the Atlantic shore of Nova Scotia (R. J. Miller, pers. comm.). The ophiuroid *Ophiopholis aculeata* was strikingly abundant in the Mingan Islands (particularly on steep rocky slopes) and even occurred in high densities on the exposed surfaces of rocks. In Newfoundland, it is more cryptic and when exposed by overturning rocks is rapidly eaten by cunners *Tautogolabrus adspersus* (pers. observations). The absence of the cunner may thus contribute to the high abundance of *Ophiopholis aculeata* in the Mingan Islands.

The general character of the subtidal zone, rocky areas supporting high densities of urchins and large fleshy algae being limited to a narrow shallow water zone, resembles that in the St. Lawrence Estuary (Himmelman and Lavergne 1985) and on the Newfoundland and Labrabor coasts (Himmelman 1969, 1985; Fletcher et al. 1974; Hooper 1980). Breen and Mann (1976), Himmelman et al. (1983a) and Keats et al. (1985) demonstrate the importance of urchins in limiting the distribution and abundance of algae in such communities. Most algae exist in the subtidal zone only where urchin numbers or their feeding activities are limited by physical factors such as waves, low salinities, and ice action (Himmelman and Lavergne 1985). For example, the progressive increase in the size of the subtidal algal fringe with increasing exposure, as previously described by Himmelman (1985), was clearly evident going from the sheltered north to the exposed south sides of the islands. Furthermore, the urchin-dominated zone extended to shallower water when the slope of the shore was steeper. The virtual absence of several urchin predators (lobster, *Cancer borealis*, cunner and wolffish) should add to the persistence of the urchin-dominated community in the northern Gulf.

The semiquantitative method used in the present study demonstrated striking differences between the subtidal community in the northern Gulf and those described in Newfoundland, the southern Gulf, and Maritime Provinces. The increased importance of whelks and seastars and decreased importance of fishes and decapod crustaceans in the Mingan Islands suggest differences in community organization. One predator guild not considered in the present study was marine birds. The most common species in the Mingan Islands are the common eider, herring and great black backed gulls, the double-crested cormorant, common and Arctic terns, and several species of sandpipers (M. Guillemette, pers. comm.). These predators undoubtedly feed mainly on macrobenthic organisms, but we did not examine their abundance or feeding and therefore cannot indicate their impact on benthic communities.

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CHAPITRE V

RECUEIL DE RÉFÉRENCES CHOISIES

CHAPTER V

SELECTED REFERENCES

Bibliography of the Biological Oceanography for the Gulf of St. Lawrence[1]

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ST-PIERRE, J.-F., AND Y. DE LAFONTAINE. 1991. Bibliography of the biological oceanography for the Gulf of St. Lawrence, p. 335–359. *In* J.-C. Therriault [ed.] The Gulf of St. Lawrence: small ocean or big estuary? Can. Spec. Publ. Fish. Aquat. Sci. 113.

An index of bibliographical references on the biological oceanography of the Gulf of St. Lawrence has been compiled on a popular software. The evolution of the biological research from the last century until today, shows, except for a temporary decline during the Second World War, a constant increase in the number of scientific publications especially after 1950. This index of 636 references represents a useful tool for scientists working in the Gulf, and copies of the original file can be made available on floppy disk upon request.

Une banque de références bibliographiques, montée à partir d'un logiciel populaire, rassemble toutes les publications traitant de l'océanographie biologique dans le Golfe du Saint-Laurent, depuis les débuts de la recherche dans cette région. La compilation de ces références démontre, mis à part la période correspondant à la deuxième guerre mondiale, une augmentation constante du nombre de publications scientifiques spécialement à partir des années 1950. Ce document, constitué de 636 références, s'avère un outil de recherche intéressant pour les intervenants du Golfe du Saint-Laurent et une copie du fichier informatisé est disponible sur demande auprès des auteurs.

Introduction

The exploitation and economic importance of fisheries resources in the Gulf of St. Lawrence has promoted the development and the support of biological and oceanographic research in the area.

Despite the fact that two symposia on the Gulf of St. Lawrence were held in the past, no effort has been made to highlight the general trend of biological research realized since its beginning during the second half of the nineteenth century. A bibliographic index on the physical oceanography for the Gulf (El-Sabh et al. 1969), and a bibliography (up to 1970) for fishes in the Gulf (Srivastava 1971), are the only two indexes of references for the area of interest. No bibliographic reference list has been produced for biological oceanographic research to date.

The third symposium on the Gulf of St. Lawrence, held in spring 1989, gave us the opportunity to provide the scientific community with an efficient tool for bibliographic research. Our objective was the gathering, as exhaustive as possible, of the biological literature that brings worthwhile information published on the Gulf of St. Lawrence to date. In addition, this would permit the visualisation of the evolution and the major orientations of biological oceanographic research conducted in the Gulf thoughout the century and before.

Methods

The physical support chosen for the data bank is the IBM compatible software Q&A (TM). This program provides great flexibility for bibliographic consultation and is of easy use, including interactive capabilities.

To gather all the references on the Gulf we, in a first step, interrogated, by means of key words, the various bibliographic data bases accessible by computers. All the titles that pertain to the Gulf of St. Lawrence were extracted. Because these data bases do not date very far back in time, we performed a job of cross referencing in order to cover all the work published since the very first days of biological oceanography in the Gulf.

In a second step, we consulted the references that did not mention explicitly the Gulf, or a region inside the Gulf, and checked the pertinence of the published content. This explains why some publications in the data bank cover larger areas than the Gulf itself.

Once all references were filed on computer, we allocated key words that describe the field of activity of each publication. Six basic subjects were defined: primary production, zooplankton, benthos, fishes including ichthyoplankton, commercial macroinvertebrates and general reviews. Topics on primary production include works on nutrients, productivity and phytoplankton. Commercial macroinvertebrates are composed principally of lobster, snowcrab, pink shrimp and mollusc. General reviews deal with general ecosystems and fisheries or pollution problems.

Results are presented in seven tables. Tables 1 to 6 present the chronological list of authors of publications

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[1] This paper forms part of the Proceedings of a Workshop/Symposium held at the Maurice Lamontagne Institute, Mont-Joli, Quebec, 14–17 March 1989.

pertinent to each subject. Table 7 gives the alphabetical list of all the references found for the Gulf.

To achieve this laborious work, we set aside some publications, notably the annual Canadian Atlantic Fisheries Scientific Advisory Committee (CAFSAC) research documents dealing with stock assessements of marine fish stocks and M.Sc. and Ph.D. theses works. Biological subjects like marine mammals, birds and most of anadromous fishes (principally salmon) were also excluded.

Although every effort was made to search for and include the largest number of references, some errors or omissions may occur. We, therefore, encourage readers to forward omissions and corrections to the authors in order to update the data bank.

Copies of the data file including all the references of the bank can be made available upon request from the authors. Files can be provided in ASCII files or Q&A (TM) files formats.

Results and Discussion

The evolution of biological research in the Gulf of St. Lawrence since the first publication found and until 1989, shows, except for the period corresponding to the Second World War, a constant increase in the amount of scientific publications (Fig. 1). The large increase, after 1950, corresponds to the implantation of marine science laboratories in the early sixties (Bedford Institute of Oceanography 1986), and a growing interest in fisheries research. This is illustrated in Fig. 2 where research on fish represents almost half of all the scientific work realized in the Gulf.

The decline observed in the eighties corresponds to the fact that some of the work, conducted during these years, has not yet been issued. This fact may mask the recent trend that would indicate a stagnation in the amount of publications. However, it should be remembered that, since 1976, much of the research activities conducted by two main federal laboratories, i.e. St. Andrews and Bedford Institute of Oceanography, has been redirected toward the 200-mile limit zone outside the Gulf. This might have resulted in a slight decrease in Gulf related papers.

Interestingly, plankton research in the Gulf has focused first, in the early sixties, on the zooplankton and subsequently, during the seventies, on primary production (Fig. 3). But this may not be representative of a general trend in biological science because, as shown in Table 2, most of the research on zooplankton during the sixties was undertaken mostly by two scientists, P. Brunel and G. Lacroix, who were very active in the Baie-des-Chaleurs.

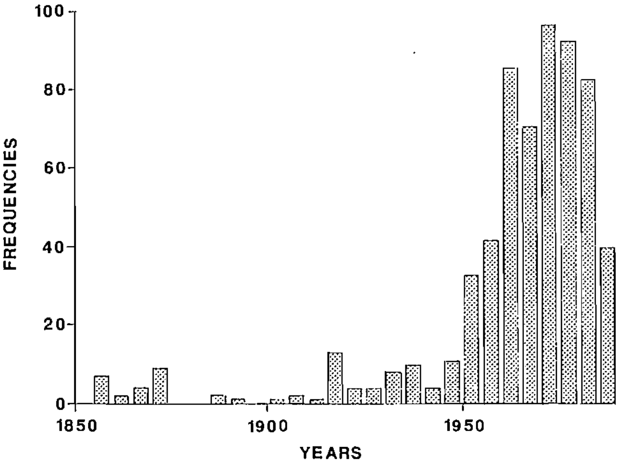

FIG. 1. Number of publications on biological oceanography for the Gulf of St. Lawrence, from 1850 to 1989.

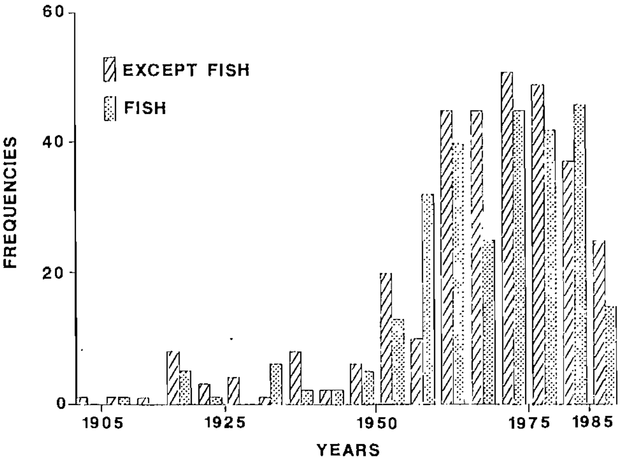

FIG. 2. Comparison of the number of publications on fishes and other than fishes for the Gulf of St. Lawrence since 1900.

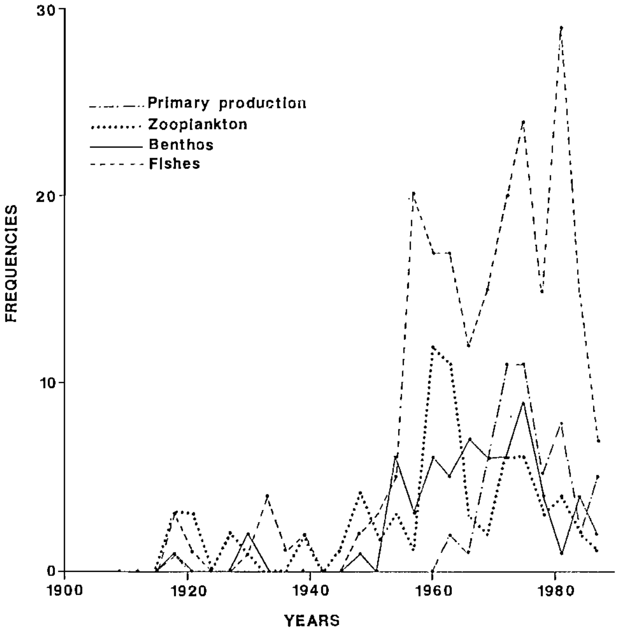

FIG. 3. Number of publications dealing with four biological oceanographic disciplines for the Gulf of St. Lawrence since 1900.

In conclusion, studies on the biological oceanography in the Gulf have developed in a counterway to the natural continuum of the food chain. Fishes were first studied, while zooplankton and finally primary production gradually received more scientific interest (Fig. 3). Although we do not intend to give any advice on further research, it is hoped that the slight decline in publications observed during the 1980's is only temporary.

Acknowledgements

We wish to thank Mr. André Ducharme for his excellent help and guidance in the use of the Q&A software and also Miss Nicole Beaudry for her help in literature search.

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SRIVASTAVA, V.M. 1971. Fish of the Gulf of St. Lawrence. Fish. Res. Board Can. Tech. Rep. 261: 141 p.

TABLE 1. Chronological list of authors for studies on primary production of the Gulf of St. Lawrence.

Years	Authors
1919	Gran, H. H.
1954	Hunstman, A. G., et al.
1962	Brunel, J.
1968	Legendre, L.
1969	Legendre, L.
	Moseley, C. M., and C. I. MacFarlane.
1970	Legendre, L., and W.D. Watt.
1971	Legendre, L.
1972	Bullied, E. R., and D. M. Steven.
	Herring, F., and C. MacBeth.
	Platt, T.
	Platt, T.
	Sutcliffe, W. H. Jr.
1973	Dunbar, M. J.
	Legendre, L.
	Steven, D. M., et al.
	Steven, D. M., et al.
	Steven, D. M., et al.
1974	Spence, C., and D. M. Steven.
	Steven, D. M.
1975	Bélanger, C., and A. Cardinal.
	Coote, A. R., and R. S. Hiltz.
	Steven, D. M.
	Taylor, A. R. A.
1976	Sinclair, M., et al.
1977	Prouse, N. J., and B. T. Hargrave.
1978	Dunbar, M. J.
1979	Coote, A. R., and P. A. Yeats.
	De Sève, M. A., et al.
	Drinkwater, K. F.
	Hargrave, B. T.
	Sévigny, J. M., et al.
	Tan, F. C., and P. M. Strain.
1980	Citarella, G.
	Dunbar, M. J.
	Dunbar, M. J., and J. C. Acreman.
	Marine Ecology Laboratory.
1981	de Lafontaine, Y., et al.
	Hargrave, B. T., and N. J. Prouse.
	Pringle, J. D.
	Pringle, J. D., et al.
1982	Bugden, G. L., et al.
1983	Bird, C. J., et al.
	Gendron, L.
	Pringle, J. D., and R. E. Semple.
1984	de Lafontaine, Y., et al.
	Lavoie, A., et al.
	Pringle, J. D., and R. E. Semple.
	Sinclair, M., et al.
1985	Gendron, L.
	Hargrave, B.T., et al.
	Pocklington, R.
	Pocklington, R.
1986	Pocklington, R.
	Sinclair, M., et al.
1987	Legendre, L.
	Novaczek, I.
	Pocklington, R.
	Vandevelde, T., et al.
1988	Chopin, T., et al.

TABLE 2. Chronological list of authors for studies on zooplankton of the Gulf St. Lawrence.

Years	Authors
1895	Rodger, A.
1907	Scott, T.
1919	Gran, H. H.
	Huntsman, A. G.
	Willey, A.
1921	Huntsman, A. G.
	Huntsman, A. G.
	Huntsman, A. G., and M. E. Reid.
1926	Pinhey, K. F.
1927	Pinhey, K. F.
1930	Johansen, F.
1940	Kerswill, C. J.
	Rogers, H. M.
1946	Filteau, G.
1947	Filteau, G.
1948	Filteau, G.
	Sullivan, C. M.
1949	Filteau, G.
1951	Bousfield, E. L.
1952	Bousfield, E. L.
1953	Filteau, G., and J.-L. Tremblay.
1954	Hunstman, A. G., et al.
	Udvardy, M. D. F.
1955	Bousfield, E. L.
1956	Bousfield, E. L.
1959	Brunel, P.
1960	Brunel, P.
	Lacroix, G.
1961	Bousfield, E. L.
	Brunel, P.
	Brunel, P.
	Brunel, P.
	Brunel, P.
	Lacroix, G.
	Lacroix, G.
	Lacroix, G.
	Lacroix, G.
1962	Brunel, P.
	Brunel, P.
	Lacroix, G.
	Lacroix, G. and P. Morisset.
1963	Brunel, P.
	Brunel, P.
	Brunel, P.
	Lacroix, G.
	Lacroix, G., and J. Bergeron.
1964	Brunel, P.
	Lacroix, G. and L. Legendre.
1965	Brunel, P.
1967	Lacroix, G., and L. Méthot.
	Pennell, W.
1969	Lacroix, G., and G. Filteau.
1970	Lacroix, G., and G. Filteau.
1971	Lacroix, G., and G. Filteau.
	Shih, C.-T., et al.
1973	Hoar, W. S.
	Lacroix, G., and E. Bourget.
	Steven, D. M., et al.
	Steven, D. M., et al.
	Steven, D. M., et al.
	Ware, D. M., and R. F. Addison.
1974	Steven, D. M.
1975	Steven, D. M.
1976	Berkes, F.
	Berkes, F.
	Pennell, W. B.
	Sameoto, D. D.
	Sameoto, D. D.
1977	Berkes, F.
	Ware, D. M.
1978	Dunbar, M. J.
1980	Dunbar, M. J.
	Lambert, T. C.
	Sameoto, D. D.
1982	Bugden, G. L., et al.
	Lambert, T. C., et al.
1983	Sameoto, D. D.
1985	Hargrave, B. T., et al.
1986	Harding, G. C., et al.

TABLE 3. Chronological list of authors for studies on the benthos of the Gulf St. Lawrence.

Years	Authors
1858	Dawson, J.
	Dawson, J.
1860	Dawson, J.
1869	Whiteaves, J. F.
1870	Whiteaves, J. F.
1871	Whiteaves, J. F.
1872	Whiteaves, J. F.
	Whiteaves, J. F.
1873	Whiteaves, J. F.
1874	McIntosh, W. C.
	Whiteaves, J. F.
	Whiteaves, J. F.
1875	Whiteaves, J. F.
	Whiteaves, J. F.
1895	Rodger, A.
1918	Kindle, E. M., and E. J. Wittaker.
1930	Johansen, F.
	Shoemaker, C. R.
1948	Sullivan, C. M.
1953	Berkeley, C., and E. Berkeley.
1954	Bousfield, E. L.
	Corbeil, H. E.
	Stephenson, T. A.
1955	Bousfield, E. L.
	Bousfield, E. L.
1956	Bousfield, E. L.
	Brunel, P.
1960	Brunel, P.
	Brunel, P.
1961	Bousfield, E. L.
	Brunel, P.
	Brunel, P.
	Brunel, P.
	Brunel, P.
	Brunel, P.
1962	Brunel, P.
	Clarke, A. H. Jr.
1963	Brunel, P.
	Peer, D. L.
1964	Brunel, P.
1965	Brunel, P.
1966	Brunel, P.

TABLE 3. (*Continued.*)

Years	Authors
1967	Cardinal, A.
	Cardinal, A.
	Cardinal, A.
	Cardinal, A.
	Laite, P. S.
	Parker, S. L.
	Villalard, M.
1968	Cardinal, A.
	Lee, R. K. S.
1969	Ledoyer, M.
	Moseley, C. M., and C. I. MacFarlane.
1970	Brunel, P.
	Brunel, P.
	Granger, D.
	Ledoyer, M.
	South, G. R., and A. Cardinal.
1971	Hughes, R. N., and M. L. H. Thomas.
	Ledoyer, M.
	Younker, D., and K. MacWilliams.
1972	Herring, F., and C. MacBeth.
	Hoffer, S. A.
	Laycock, R. A., and D. H. Loring.
	Ledoyer, M.
1974	Lamoureux, P.
1975	Lamoureux, P.
	Lamoureux, P.
	Ledoyer, M.
	Ledoyer, M.
	Ledoyer, M.
	Ledoyer, M.
	Taylor, A. R. A.
1977	Caddy, J. F., et al.
1979	Brunel, P.
	De Sève, M. A., et al.
	Granger, D., et al.
1980	Colodey, A. G., et al.
	Fradette, P., and E. Bourget.
1981	Fradette, P., and E. Bourget.
1983	Bird, C. J., et al.
	Bourget, E., and D. Messier.
	Gendron, L.
	Sainte-Marie, B., and P. Brunel.
1984	Desrosiers, G., et al.
	Lavoie, A., et al.
	Pringle, J. D., and R. E. Semple.
1985	Able, K. W., and W. Irion.
	Cossa, D., and E. Bourget.
	Gendron, L.
	Hargrave, B. T., and G. A. Phillips.
	Sainte-Marie, B., and P. Brunel.
1986	Worms, J. M., and L. A. Davidson.
1987	Lamarche, G., and P. Brunel.
	Novaczek, I.
1988	Chopin, T., et al.
	McQuinn, I. H., et al.

TABLE 4. Chronological list of authors for studies on macroinvertebrates of the Gulf of St. Lawrence.

Years	Authors
1850	Perley, M. H.
1859	Bell, R. Jr.
1869	Whiteaves, J. F.
1890	Provancher, L.
1895	Rodger, A.
1901	Whiteaves, J. F.
1912	Cornish, G. A.
1916	Nelson, J.
1918	Kindle, E. M., and E. J. Wittaker.
1919	MacKay, D.A.
1920	MacKay, D.A.
1930	Johansen, F.
1934	Templeman, W.
1936	Needler, A. W. H.
	Templeman, W.
1937	Templeman, W.
1938	Smith, G. F. M.
	Smith, G. F. M.
1939	Templeman, W.
1941	Tremblay, J.-L., et al.
1945	Templeman, W., and S. N. Tibbo.
1948	Corrivault, G.-W., and J.-L. Tremblay.
Undated	Chiasson, L. P.
1951	Chiasson, L. P.
	Dickie, L. M.
1952	Chiasson, L. P.
	Corbeil, H. E.
1953	Montreuil, P.
	Wilder, D. G.
1954	Marcotte, A.
	Montreuil, P.
	Wilder, D. G.
1955	Medcof, J. C., and J. S. MacPhail.
1956	Wilder, D. G., and R. C. Murray.
1958	Dickie, L. M., and C. D. McInnes.
	Squires, H. J.
1961	Brunel, P.
1962	Brunel, P.
	Wilder, D. G.
1963	Brunel, P.
1964	Bourne, N.
	Scarratt, D. J.
1965	Bourne, N., and T. W. Rowell.
	Bourne, N., and T. W. Rowell.
	Bourne, N., et al.
	Carbonneau, J.
	Carbonneau, J.
	Carbonneau, J.
	Carbonneau, J.
	Chandler, R. A.
	Rowell, T. W., and E. I. Lord.
	Rowell, T. W., and E. I. Lord.
1966	Bergeron, J.
	Carbonneau, J.
	Carbonneau, J.
	Powles, H. W.
1967	Bergeron, J.
	Bergeron, J.
	Carbonneau, J.
1968	Couture, R., and P. Trudel.
	Powles, H. W.
	Scarratt, D. J.
	Thomas, M. L. H.
1969	Couture, R., and P. Trudel.

TABLE 4. (*Continued.*)

Years	Authors
1970	Couture, R.
	Naidu, K. S.
	Squires, H. J.
	Watson, J.
1971	Couture, R.
	Couture, R.
	Couture, R., and G. Filteau.
	Rycroft, J., et al.
	Younker, D., and K. MacWilliams.
1972	Boulanger, J. M., and G. Myre.
	Brunel, P.
	Watson, J., and P. G. Wells.
1973	Dunbar, M. J.
	Fréchette, J., et al.
	Fréchette, J., and J. Lamy.
	Myre, J.
	Poirier, L.
	Scarratt, D. J.
	Sutcliffe, W. H. Jr.
1974	Fréchette, J.
	Fréchette, J., and A. Dubois.
	Lamoureux, P.
	Lamy, J.
	Myre, J.
	Myre, J., and Y.-A. Beaulé.
1975	Fréchette, J., et al.
	Jobin, L., and L. Poirier.
	Lamoureux, P.
	Lamoureux, P.
	Simard, Y., et al.
	Stasko, A. B.
1976	Amaratunga, T., et al.
	Berkes, F.
	Bourget, E., and D. Cossa.
	Caddy, J. F., and R. A. Chandler.
	Haynes, E., et al.
	Messieh, D.
	Poirier, L.
	Stallworthy, W. B.
1977	Boudreault, F.-R., et al.
	Caddy, J. F., et al.
	Lamoureux, P.
	Lavoie, R. E.
	Poirier, L.
	Poirier, L.
	Stasko, A. B., et al.
	Tobey, A.
1978	Axelsen, F., and P. Dubé.
	Bailey, R. F. J.
	Boghen, A. D.
	Giguère, M., and P. Lamoureux.
1979	Bernier, L., and L. Poirier.
	Caddy, J. F.
	Dadswell, M. J.
	Dadswell, M. J.
	Harding, G. C. H., et al.
	Jamieson, G. S.
	Robinson, D. G.
	Varma, C. P.
1980	Campbell, A.
	Cossa, D., and E. Bourget.
	Dunbar, M. J.
	Stasko, A. B.
1981	Bernier, L., and L. Poirier.
	Bernier, L., and L. Poirier.
	Munro, J., and J.-C. Thérriault.
1982	Bailey, R.
	Bugden, G. L., et al.
	D'Amours, D., and S. Pilote.
	Greendale, R., and R. F. J. Bailey.
	Harding, G. C. H., et al.
	Lamoureux, P., and P. E. Lafleur.
	Waiwood, K. G., and R. N. Elner.
1983	Bailey, R. F. J.
	Campbell, A., and D. G. Robinson.
	Harding, G. C., et al.
	Munro, J., and J.-C. Thérriault.
	Portelance, B., and J. Fréchette.
1984	Brêthes, J.-C., et al.
	Chouinard, G. A.
	Lafleur, P. E., et al.
1985	Attard, J.
	Brêthes, J.-C., et al.
	Cossa, D., and E. Bourget.
	Coulombe, F., et al.
	Jamieson, G. S., and A. Campbell.
	Taylor, D., et al.
1986	Bouchard, R., et al.
	Brêthes, J.-C. F., et al.
	Elner, R. W., and R. F. J. Bailey.
	Fogarty, M. J., and J. S. Idoine.
	Gagnon M., and L. Hovington.
	Hudon, C., et al.
	Worms, J. M., and L. A. Davidson.
1987	Attard, J., and C. Hudon.
	Brêthes, J.-C. F., et al.
	Gilbert, M., and D. Gascon.
	Hudon, C.
1988	Dufour, R.
	Gendron, L.
	Hudon, C., and P. Fradette.
	McQuinn, I. H., et al.
	Portelance, B., et al.
	Sainte-Marie, B. and R. Dufour.

TABLE 5. Chronological list of authors for studies on fish in the Gulf of St. Lawrence.

Years	Authors
1850	Perley, M. H.
1859	Perley, M. H.
1864	Fortin, P.
	Fortin, P.
1866	Austin, F. W. G.
1875	Whiteaves, J. F.
1887	Goode, G. B., and J. W. Collins.
1895	Rodger, A.
1907	Cornish, G. A.
1916	Cox, P.
1917	Huntsman, A. G.
1918	Huntsman, A. G.
	Huntsman, A. G.
1919	Dannevig, A.
1921	Cox, P.
1931	Jeffers, G. W.
1932	Anon.
	Jeffers, G. W.
1933	Anon.

TABLE 5. (*Continued.*)

Years	Authors
1934	Anon.
1938	Frost, N.
1940	Needler, A. W. H.
	Rogers, H. M.
1943	McKenzie, R. A.
1944	Tremblay, J.-L.
1946	McKenzie, R. A.
1947	McCracken, F. D.
1948	Marcotte, A., and J.-L. Tremblay.
	McKenzie, R. A.
	Templeman, W.
1951	Vladykov, V. D.
1952	McKenzie, R. A.
	Vladykov, V. D.
1953	Corbeil, H. E.
	Jean, Y.
	Jean, Y.
	McKenzie, R. A.
1954	Corbeil, H. E.
	Huntsman, A. G., et al.
	Jean, Y.
1955	Jean, Y.
	Leim, A. H.
	McKenzie, R. A., and G. F. M. Smith.
1956	Jean, Y.
	Leim, A. H.
	McKenzie, R. A., and W. B. Scott.
1957	Day, L. R.
	Day, L. R.
	Day, L. R.
	Leim, A. H., et al.
	Ronald, K.
	Ronald, K.
	Scott, D. M., and R. Martin.
	Steele, D. H.
	Templeman, W., et al.
	Tibbo, S. N.
	Vladykov, V. D.
1958	Bergeron, J.
	McCracken, F. D.
	McCracken, F. D., and J. R. Clark.
	McKenzie, R. A.
	Powles, P. M.
	Ronald, K.
	Ronald, K.
	Steele, D. H.
1959	Boulanger, J. M.
	McCracken, F. D.
	McKenzie, R. A.
	Myers, B. J.
	Scott, D. M., and W. R. Martin.
	Tibbo, S. N.
1960	Bergeron, J.
	Brunel, P.
	Leim, A. H.
	Ronald, K.
	Ronald, K.
1961	Bergeron, J.
	Bergeron, J.
	Brunel, P.
	Brunel, P.
	Day, L. R.
	Lacroix, G., and A. Marcotte.
	Marcotte, A.

TABLE 5. (*Continued.*)

Years	Authors
1962	Bergeron, J.
	Brunel, P.
	Marcotte, A.
	Templeman, W.
1963	Bergeron, J. and G. Lacroix.
	Brunel, P.
	Brunel, P.
	Jean, Y.
	Jean, Y.
	Jean, Y.
	Jean, Y.
	Jean, Y.
	Jean, Y., and F. D. McCracken.
	Marcotte, A.
	McCracken, F. D.
	Pitt, T. K.
	Powles, P. M.
	Ronald, K.
	Templeman, W.
1964	Beaulieu, G., and E. Corbeil.
	Brunel, P.
	Jean, Y.
	Jean, Y.
	Kennedy, V. S., and V. S. Powles.
	Kohler, A. C.
	Lacroix, G., and J. Bergeron.
	McKenzie, R. A.
1965	Brunel, P.
	Lauzier, L., and S. N. Tibbo.
	Martin, W. R., and A. C. Kohler.
	McCracken, F. D.
	Moussette, M., et al.
	Powles, P. M.
1966	Beamish, F. W. H.
	Brunel, P.
	Pinhorn, A. T.
	Tibbo, S. N.
1967	Hourston, A. S., and R. Chaulk.
	Jean, Y.
	Lacroix, G.
	MacKay, K. T.
1968	Bergeron, J.
	Eales, J. G.
	Kohler, A. C.
	Paloheimo, J. E., and A. C. Kohler.
	Squires, H. J.
	Wiles, M.
1969	Ennis, G. P.
	Kohler, A. C., and D. N. Fitzgerald.
	MacKay, K. T., and G. Thomas.
	Messieh, S. N.
	Powles, P. M.
	Tibbo, S. N., et al.
1970	Brunel, P.
	Iles, T. D., and S. N. Tibbo.
	Powles, P. M., and A. C. Kohler.
	Scarratt, D. J., and A. J. Wilson.
	Templeman, W.
1971	Beckett, J. S.
	Brunel, P.
	Hodder, V. M., and L. S. Parsons.
	Kohler, A. C.
	Lear, W. H., and J. H. C. Pippy.
	Messieh, S. N., and S. N. Tibbo.
	Srivastava, V. M.
	Vladykov, V. D.

TABLE 5. (*Continued.*)

Years	Authors
1972	Brunel, P.
	Fletcher, G. L.
	Garside, E. T., et al.
	Halliday, R. G.
	Hodder, V. M.
	Hodder, V. M., and G. H. Winters.
	Messieh, S. N., and A. C. Kohler.
	Scarratt, D. J., and R. Lowe.
	Sutcliffe, W. H. Jr.
1973	Delisle, D. E.
	Dunbar, M. J.
	Minet, J. P.
	Sandeman, E. J.
	Scott, J. S.
	Sutcliffe, W. H. Jr.
1974	Halliday, R. G.
	Kohler, A. C., et al.
	Kohler, A. C., et al.
	Templeman, W.
1975	Beamish, F. W. H., and I. C. Potter.
	Jobin, L., and L. Poirier.
	Kohler, A. C., et al.
	Lett, P. F., et al.
	Lett, P. F., et al.
	Lussiaa-Berdou, J.-P., and G. Johnson.
	Messieh, S. N.
	Messieh, S. N.
	Moores, J. A., et al.
	Pilote, S.
	Pilote, S.
	Roy, J. M., et al.
	Scott, J. S.
	Scott, J. S.
	Scott, J. S.
	Scott, J. S.
	Ware, D. M.
	Winters, G. H., and V. M. Hodder.
1976	Able, K. W., et al.
	Caddy, J. F., and R. A. Chandler.
	Faber, D. J.
	Kohler, A. C., et al.
	Lett, P. F., and A. C. Kohler.
	Lett, P. F., and W. G. Doubleday.
	Messieh, S. N.
	Minet, J. P.
	Parent, S., and P. Brunel.
	Scott, J. S.
	Winters, G. H.
1977	Bailey, R. F. J., K. W. Able, and W. C. Leggett.
	Bailey, R. F. J., et al.
	Caddy, J. F., et al.
	Côté, G. and P. Lamoureux.
	Jacquaz, B., et al.
	Kohler, A. C., et al.
	Lussiaa-Berdou, J.-P.
	Messieh, S. N.
	Ware, D. M.
1978	Able, K. W.
	Bailey, R. F. J.
	Kott, E.
	Minet, J. P., and J. B. Perodou.
	Sharp, J. C., et al.
	Ware, D. M., and B. L. Henriksen.
	Winters, G. H., and J. S. Beckett.
1979	Dadswell, M. J.
	MacKay, K. T.
	Messieh, S. N., and D. S. Moore.
	Messieh, S. N., et al.
	Messieh, S. N.
	Mousseau, P.
	Spénard, P.
	Ware, D. M.
1980	Beacham, T. D., and S. J. Nepszy.
	Bowering, W. R.
	Côté, G., et al.
	de Lafontaine, Y.
	Dunbar, M. J.
	Greendale, R., and H. Powles.
	Kenchington, T.
	Khan, R. A., et al.
	Pottle, R. A., et al.
	Ware, D. M.
1981	de Lafontaine Y., et al.
	Fairbairn, D. J.
	Koeller, P.
	Koeller, P., and M. LeGresley.
	Messieh, S. N., et al.
	O'Boyle, R. N., and L. Cleary.
	Tremblay, C., and F. Axelsen.
	Vesin, J.-P., et al.
1982	Bailey, R.
	Beacham, T. D.
	Beacham, T. D.
	Beacham, T. D.
	Beacham, T. D.
	Bowering, W. R.
	Bugden, G. L., et al.
	Buzeta, M. I., and K. G. Waiwood.
	Doubleday, W. G., and T. Beacham.
	Halliday, R. C., and A. T. Pinhorn.
	Iles, D. T., and M. Sinclair.
	Jessop, B. M., and D. L. Morantz.
	Lafleur, P.-E., and J.-P. Lussiaa-Berdou.
	Lambert, T. C., et al.
	Markle, D. F., et al.
	Scott, J. S.
	Skud, B. E.
	Stobo, W. T., et al.
	Waiwood, K. G., and R. N. Elner.
1983	Beacham, T. D.
	Cleary, L., and B. Mercille.
	Elouard, B., et al.
	Fréchet, A., et al.
	Fréchet, A., et al.
1984	Atkinson, D. B.
	Atkinson, D. B.
	Bowering, W. R., and W. B. Brodie.
	Cleary, L.
	de Lafontaine, Y., et al.
	Hogans, W. E.
	Koslow, J. A.
	Lambert, T. C.
	Lambert, T. C., and D. M. Ware.
	Sinclair, M., and M. J. Tremblay.
	Sinclair, M., et al.
	Walsh, S. J.
1985	Able, K. W., and W. Irion.
	Hargrave, B. T., and G. A. Phillips.
	Hogans W. E.
	McClelland, G., et al.
	Messieh, S. N., et al.

Table 5. (*Continued.*)

Years	Authors
	Tremblay, M. J., and M. Sinclair.
	Ware, D. M., and T. C. Lambert.
1986	Atkinson, D. B.
	Cleary, L., and J. Hamel.
	Gagnon M., and L. Hovington.
	Messieh, S. N., and R. A. Pottle.
	Pelletier, L.
1987	Gilbert, M., and D. Gascon.
	Messieh, S. N.
	Messieh, S. N.
	Ouellet, G.
	Ouellet, P.
1988	Gagné, J., and D. Lefaivre.
	Johnston, C. E., and M. Morse.
	Rose, G. A., and W. C. Leggett.
	Rubec, L. A.

Table 6: Chronological list of authors for studies on general reviews on the Gulf of St. Lawrence

Years	Authors
1859	Bell, R. Jr.
1919	Hjort, J.
1970	Dickie, L. M.
	Dunbar, M. J.
	Keen, M. J.
	Steven, D. M.
1972	Trites, R. W.
1973	Dunbar, M. J.
1975	Steven, D. M.
	Trites, R. W., and A. Walton.
1978	Dunbar, M. J.
1980	Dunbar, M. J.
	Dunbar, M. J., et al.
1983	Dickie, L. M., and R. W. Trites.

Table 7 : Alphabetical list of all the biological oceanographic research on the Gulf of St. Lawrence.

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Able, K.W., R. Bailey, B. Jacquaz, and J.P. Vesin. 1976. Biologie du capelan (*Mallotus villosus*) de l'estuaire et du golfe St-Laurent. M. I. C. Qué., Dir. gén. Pêch. mar., Dir. Rech., Cah. Inf. 75: 24 p.

Able, K.W., and W. Irion. 1985. Distribution and reproductive seasonality of snailfishes and lumpfishes in the St. Lawrence River estuary and the Gulf of St. Lawrence. Can. J. Zool. 63: 1622–1628.

Amaratunga, T., J.F. Caddy, and A.B. Stasko. 1976. Northumberland Strait project: an interdisciplinary study of the declining shellfish resources. ICES Shellfish and Benthos Committee, C. M. 1976/k: 26: 15 p.

Anctil, M. 1968. Implications écologiques de la structure rétinienne chez quelques téléostéens marins du golfe du St-Laurent. Rapp. ann. 1967, Sta. Biol. mar. Grande-Rivière: 67–73.

Anon. 1932. First list of fishes in the Newfoundland fishing area. Ann. Rep. Nfld. Fish. Res. Comm. for 1931, 1(4): 107–110.

Table 7. (*Continued.*)

Anon. 1933. Second list of fishes in the Newfoundland fishing area. Ann. Rep. Nfld. Fish. Res. Comm. for 1932, 2: 125–127.

Anon. 1934. Third list of fishes in the Newfoundland fishing area. Ann. Rep. Nfld. Fish. Res. Comm. for 1933, 2(2): 115–117.

Atkinson, D.B. 1984. Discarding of small redfish in the shrimp fishery off Port-au-Choix, Newfoundland, 1976–80. J. Northw. Atl. Fish. Sci. 5: 99–102.

Atkinson, D.B. 1984. Distribution and abundance of beaked redfish in the Gulf of St. Lawrence, 1976–1981. J. Northw. Atl. Fish. Sci. 5: 189–197.

Atkinson, D.B. 1986. Distribution of non-commercial finfish in the Gulf of St. Lawrence, 1976–1981. Can. Tech. Rep. Fish. Aquat. Sci. 1423: 56 p.

Attard, J. 1985. Fécondité individuelle et production d'oeufs par recrues du homard (*Homarus americanus*) sur les côtes nord et sud des Îles-de-la-Madeleine, golfe du St-Laurent. Rapp. tech. can. sci. halieut. aquat. 1417: 14 p.

Attard, J., and C. Hudon. 1987. Embryonic development and energetic investment in egg production in relation to size of female lobster (*Homarus americanus*). Can. J. Fish. Aquat. Sci. 44: 1157–1164.

Austin, F.W.G. 1866. On some of the fishes of the St. Lawrence. Trans. Lit & Hist. Soc. Qué, N. S. 4: 103–120.

Axelsen, F., and P. Dubé. 1978. Étude comparative du homard (*Homarus americanus*) des différentes régions de pêche des Îles-de-la-Madeleine. M. I. C. Qué., Dir. gén. Pêch. mar., Cah. Inf. 86: 49 p.

Bailey, R.F.J. 1978. Whelks on snow crab fishing grounds in the southwestern Gulf of St. Lawrence. Fish. Mar. Ser. Ind. Rep. 104: 9 p.

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Beacham, T.D. 1982. Some aspects of growth and exploitation of yellowtail flounder (*Limanda ferruginea*) in the Canadian Maritimes area of the Northwest Atlantic Ocean. Can. Tech. Rep. Fish. Aquat. Sci. 1092: 27 p.

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