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Population Biology of Sealworm *(Pseudoterranova decipiens)* in Relation to its Intermediate and Seal Hosts

Edited by W.D. Bowen

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W.D. Bowen

Department of Fisheries and Oceans
Marine Fish Division, Biological Sciences Branch
Bedford Institute of Oceanography
Dartmouth, Nova Scotia, Canada B2Y 4A2

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The parasite (*Pseudoterranova decipiens*), commonly known as the sealworm, is found in the flesh of many fish species in the North Atlantic. Reduction in product value and the removal of this parasite costs the Canadian fishing industry alone millions of dollars annually. This volume is an attempt to bring together current information on the population biology of the sealworm, its intermediate and definitive seal hosts to better understand the complex interactions which determine it's abundance in the marine environment. At present, there is a lack of time series on trends in the abundance of sealworm in fish and seal hosts, on host population trends, and on inter-annual, geographic and seasonal variation in the diets of seals. Little is known about the transmission rates of sealworm through invertebrate and fish hosts or about the dynamics of the parasite in the gut of seals. These uncertainties make it currently impossible to discriminate between alternative hypotheses about the relative importance of various abiotic and biotic factors in determining sealworm numbers. Available data are insufficient to define models of sealworm population dynamics that are appropriate to address management issues arising from the presence of sealworm in commercial fish species.

Résumé

BOWEN, W. D. [ED.]. 1990. Population biology of sealworm (*Pseudoterranova decipiens*) in relation to its intermediate and seal hosts. Can. Bull. Fish. Aquat. Sci. 222: 306 p.

Pseudoterranova decipiens, parasite vulgairement appelé ver du phoque, est retrouvé dans la chair de nombreuses espèces de poisson de l'Atlantique nord. La baisse de la valeur du produit et l'enlèvement de ce parasite coûtent des millions de dollars à l'industrie halieutique canadienne chaque année. Le présent document se veut un regroupement des données courantes sur la biologie des populations de ver du phoque et sur son hôte intermédiaire et définitif, soit le phoque, afin de mieux comprendre les interactions complexes qui en détermine l'abondance dans le milieu marin. On dispose de peu de séries chronologiques sur les tendances de l'abondance du ver du phoque chez ses hôtes, soit le poisson et le phoque, sur les tendances démographiques des hôtes et sur les variations interannuelles, géographiques et saisonnières du régime alimentaire des phoques. On connaît mal les taux de transmission du ver du phoque par l'entremise des hôtes invertébrés et du poisson ou la dynamique du parasite dans le système digestif des phoques. Ces lacunes ne permettent pas d'établir une différence entre les hypothèses sur l'importance relative des divers facteurs biotiques et abiotiques qui influent sur les effectifs du ver du phoque. Les données disponibles ne sont pas sufisantes pour établir des modèles de la dynamique de la population du ver du phoque nécessaires à l'étude des problèmes de gestion soulevés par la présente du ver du phoque chez les espèces commerciales de poisson.

Acknowledgements

A project of this kind is truly the product of the efforts of many people. Dr. J.E. Stewart provided the initial stimulus for the project and was instrumental in securing funding to allow the Workshop to proceed. I am grateful to G. McClelland, B. Mohn, and W. Stobo for helping me to organize the structure and agenda of the Workshops. The organizational skills of Val Myra and Donna King contributed in a substantial way to the success of the meetings and I gratefully acknowledge their invaluable assistance. I would like to thank the nearly three dozen reviewers for their time and advice. Finally, I would like to thank the participants of both Workshops. In the end, it was their committment to the project that enabled this first comprehensive analysis of the population biology of sealworm to be conducted.

General Introduction

W. D. Bowen

Department of Fisheries and Oceans
Marine Fish Division, Biological Sciences Branch
Bedford Institute of Oceanography
Dartmouth, Nova Scotia, Canada B2Y 4A2

Economically, the parasite (*Pseudoterranova decipiens*), commonly known as the sealworm, is one of the most important nematodes infecting fish in North Atlantic waters (Malouf 1986). The larvae of this parasite are found in the flesh of fish, many of which are of commercial importance, making fillets unsightly and unappealing to consumers. Although sealworms can be mildly pathogenic if consumed in raw or improperly cooked fish, few cases of illness in man have been reported (Margolis 1977). However, the presence of the parasite in fish fillets reduces the market value of fish products and its detection and removal increases the cost of production (Fisheries Council of Canada 1985; Malouf 1986). Processing costs resulting from the removal of sealworm larvae from Atlantic cod (*Gadus morhua*) fillets alone were estimated to be in excess of \$29 million in 1982 in Atlantic Canada (Fisheries Council of Canada 1985) and about \$30 million for all species in Atlantic Canada in 1984 (Malouf 1986).

The presence of sealworm in valuable commercial fishes in Eastern Canada has been documented in the scientific literature for more than 30 years. According to the extensive surveys of Scott and Martin (1957) and Templeman et al. (1957), Scotian Shelf cod were lightly infected in the early 1950's, while fish in southern Gulf of St. Lawrence and around Cape Breton Island had the greatest infections and constituted the main source of the sealworm problem for the fishing industry. Studies conducted by the Canadian Department of Fisheries and Oceans since 1981 showed that a significant change had taken place since the earlier work; high levels of prevalence and abundance of this parasite now were found in a number of fish species of the Scotian Shelf, as well as in the Gulf of St. Lawrence, and along the southern coast of Newfoundland (McClelland et al. 1983a, b, 1985, 1987). Other studies showed an exponential increase in the number of grey seals being born on Sable Island over the past 25 years (Zwanenburg et al. 1985). Although it is clear that seals are an essential component of the parasite's life cycle, the relationship between the number of seals and the abundance of the parasite in fish is bound to be complex and is currently poorly understood.

It is against this background, that Dr. J. E. Stewart, then Director of Biological Sciences Branch, Scotia-Fundy Region, proposed an international meeting on the population biology of *P. decipiens* and set in motion the action necessary to bring it about. This was the culminating step in the efforts Dr. Stewart had made since 1980 to improve our understanding of the ecology of sealworm by promoting broadscale research into its distribution and abundance in fishes of commercial importance. After a number of discussions, we decided to hold a two-part workshop with the following objectives:

1) to provide a forum to integrate current information on the biology and population dynamics of the sealworm parasite,
2) to increase our understanding of the complex interactions which determine the abundance of sealworm,
3) to clarify the relationship between seal abundance and the abundance of sealworm in commercially important fishes, and
4) to identify significant gaps in our knowledge as a guide to future research.

The Workshops were held in Halifax, Nova Scotia in April 1987 and June 1988 and were attended by scientists from Canada, England, Iceland, Norway, Scotland, and the

Federal Republic of Germany (Appendix 1). The group reports reflect current understanding based on both presented papers and discussion held by four working groups throughout the two 5-day workshops. Each of the manuscripts appearing in this volume was anonymously reviewed by one or two referees.

The value of international participation was particularly evident in compiling basic information about the biology of sealworm and its intermediate and definitive hosts. Although the quality and quantity of data often exceeded expectations, the group noted the lack of time series on trends in the abundance of *P. decipiens* in fish and seal hosts, on host population trends, and on inter-annual, geographic and seasonal variation in the diet of seals. Relatively little is known about the transmission rates of sealworm through the various invertebrate and fish hosts or the dynamics of the parasite within the gut of seals. These uncertainties make it difficult to discriminate between alternative hypotheses relating to the importance of various factors, both biotic and abiotic, in determining the abundance of sealworm in the marine environment.

Those actively involved in research on the ecology of sealworm and its hosts found that the workshops clearly identified critical research questions. The value of this process cannot be overstated. The sealworm has a complex life cycle and its management poses a number of difficult and as yet largely unanswered questions. Perhaps more than anything else the workshops served to highlight and emphasize the need for long-term research programs. Only through such programs will it be possible to provide sound scientific advice on the management of *P. decipiens.*

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Historical Background to the Sealworm Problem in Eastern Canadian Waters[1]

Wilfred Templeman

Department of Fisheries and Oceans, Science Branch,
Northwest Atlantic Fisheries Centre, P.O. Box 5667,
St. John's, Nfld., Canada A1C 5X1

TEMPLEMAN, W. 1990. Historical background to the sealworm problem in eastern Canadian waters, p.1-16. *In* W. D. Bowen [ed.] Population biology of sealworm (*Pseudoterranova decipiens*) in relation to its intermediate and seal hosts. Can. Bull. Fish. Aquat. Sci. 222.

Researches on the cod nematode, *Pseudoterranova decipiens*, and to a limited degree, the nematode *Anisakis* sp. in eastern Canadian waters up to about 1980 are discussed. The changes in the generic name of the cod nematode are described, from *Ascaris decipiens*, Krabbe, 1878 to *Pseudoterranova decipiens* (Krabbe, 1878). Adult *P. decipiens* were more numerous in grey than in harbour seal stomachs and were scarce in harp seals. Adult *Anisakis* sp. (usually *A. simplex*) were scarce in seals but plentiful in cetacean stomachs where adult *P. decipiens* were scarce. During the period harbour seals decreased, grey seals increased greatly, especially on Sable Island, and harp seals decreased considerably and then probably increased. In the 1950's, the greatest intensity of infection by larval *P. decipiens* in cod fillets was in the southern Gulf of St. Lawrence and the lowest on eastern Newfoundland offshore banks where seals infected by the nematode were scarce. Cod nematode infection rates in groundfish were higher inshore than offshore. The flesh of most other groundfish was also infected by *P. decipiens*. Infection rates of cod fillets by *Anisakis* sp. were low. The results from candling of groundfish fillets for the removal of nematodes are described.

Les résultats de recherches entreprises sur le ver du phoque, *Pseudoterranova decipiens*, et à un degré moindre, sur le nématode *Anisakis* sp. dans les eaux de l'est du Canada jusqu'aux environs de 1980 sont examinés. Les modifications du nom générique du ver du phoque sont décrits, d'*Ascaris decipiens*, Krabbe, 1878 à *Pseudoterranova decipiens* (Krabbe, 1878). *P. decipiens* adulte est plus répandu dans l'estomac des phoques gris que communs et plus rare chez les phoques du Groenland. *Anisakis* sp. adulte (habituellement *A. simplex*) est rare chez les phoques, mais répandu dans l'estomac des cétacés où *P. decipiens* adulte est rare. Au cours de la période considérée, les effectifs des phoques communs ont diminué, ceux des phoques gris ont beaucoup augmenté, notamment dans l'île de Sable, et ceux des phoques du Groenland ont décliné considérablement, puis probablement augmenté. Dans les années 50, le taux d'infestation des filets de morue *P. decipiens* à l'état larvaire a été le plus élevé dans le sud du golfe du Saint-Laurent et le plus bas, dans les bancs au large de la côte est de Terre-Neuve où les phoques parasités par le nématode étaient rares. Les taux d'infestation des poissons de fond par le ver du phoque étaient plus élevés sur la côte qu'au large des côtes. La chair de la plupart des autres poissons de fond était également infestée par *P. decipiens*. Les taux d'infestation des filets de morue par *Anisakis* sp. étaient faibles. Les résultats des expériences de mirage des filets des poissons de fond afin d'éliminer les nématodes sont décrits.

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[1] This paper was originally presented in June 1986 at the Huntsman Marine Laboratory (St. Andrews, N.B.) in their "HML Marine Science Symposium" series. The symposium, "The cod (or seal) worm — past, present and future" was chaired by Michael D. B. Burt (University of New Brunswick).

Introduction

The two most important nematodes in fish flesh of Canadian Atlantic waters are larval *Pseudoterranova decipiens* (the seal worm or cod worm) and larval *Anisakis* sp., usually *A. simplex*, often called the herring worm. These two nematodes and especially the former occur widely in the flesh of groundfish species in many areas of the Canadian Atlantic. The costs of removing these nematodes from the fillets at the groundfish filleting plants amount to many millions of dollars and the loss of customers and downgrading of the product cost additional millions.

In the late 1940's and in the 1950's there was in consequence considerable research on the occurrence and life cycle of *P. decipiens* and some incidental researches on the occurrence of *Anisakis* sp. at the Stations of the Fisheries Research Board of Canada at St. Andrews (New Brunswick) and St. John's (Newfoundland). Researches on the methods and success of commercial extraction of the nematodes from groundfish fillets, especially of Atlantic cod (*Gadus morhua*) and American plaice (*Hippoglossoides platessoides*), were carried out at the Technological Station of the Fisheries Research Board in Halifax (Nova Scotia) and by the Halifax Inspection Laboratory and the Inspection Division of the Canadian Department of Fisheries. Researches on *P. decipiens* were also carried out at the Institute of Parasitology at Macdonald College of McGill University (Montreal, Que.) and later in the Department of Biology at Guelph University (Ontario).

Anisakis sp. larvae are small whitish or flesh-coloured nematodes whose lengths from cod fillets are about 17-34 mm (preserved). *Pseudoterranova decipiens* is considerably larger, about 15-58 mm long (preserved) from cod fillets, with the greatest number between 35 and 42 mm. It is also much thicker and of much greater bulk and with its yellowish or sometimes reddish brown colour, is much more visible and obvious to the consumer than *Anisakis* sp. *Pseudoterranova decipiens* is also much more plentiful in cod fillets than is Anisakis sp., *Pseudoterranova decipiens*, therefore, usually presents the chief problem in the marketing of nematode infected cod, especially for the fillets (Templeman et al. 1957). Its final host is typically a seal, whereas the usual final host of *Anisakis* sp. is a cetacean. In this review, except when it is necessary to mention *Anisakis* sp. infection for reasoning about the relative importance of *P. decipiens*, the information and reasoning will be about *P. decipiens*.

A symposium on sealworm was held in Quebec City on October 8-9, 1956. It brought together the researchers on *P. decipiens* (and to a lesser degree *Anisakis* sp.) in eastern Canada. At about this time plans were being made to carry out experiments on the effects of reduction of harbour seals in two areas: in St. Mary's Bay, Newfoundland by the St. John's Biological Station and near Lockeport, N.S. by the St. Andrews Biological Station but neither of these experiments was funded and undertaken. The chief research scientists engaged in the seal-fish nematode relations in the 1950's at St. Andrews dispersed to other regions. At St. John's some new work on *P. decipiens* was carried out by Wiles (1968) but the new research vessel, the *A.T. Cameron*, began work in 1958; the St. Andrews Station also soon got a new vessel, the *E.E. Prince*, and the groundfish workers were swamped with sea-work and data from these ships. The seal researchers had meanwhile been transferred to the Arctic Biological Station near Montreal. As a result, researches on seal-borne nematodes and their effects in parasitizing fish disappeared as major research objectives at the St. Andrews and St. John's stations over the period when the grey seal, especially on Sable Island, was increasing so rapidly after the early 1960's and 1970's, and most of the attention of the seal researchers was directed to counting and studying the herds of harp seals, although grey seals and harbour seals also received some attention.

The ensuing account describes researches pertinent to occurrence and life cycle of the nematodes *P. decipiens*, *Anisakis* sp. and, incidentally, other nematodes found as larvae and adults in the gastrointestinal tract of grey, harbour, and harp seals, and from cetaceans of eastern Canadian Atlantic waters, and on larvae of *P. decipiens* and to a minor degree of *Anisakis* sp. as found in fish flesh of these waters up to the late 1970's.

Systematics and Nomenclature

Much of the following taxonomic account is based on Myers (1959) and Gibson (1983). Krabbe (1878a, 1878b) described *Ascaris decipiens* Krabbe, 1878 from six species of seals from Greenland. Raillet and Henry (1912) introduced the genus *Porrocaecum*, with *P. crassum* from a bird as the type species (possessing interlabia, ventriculus and a forwardly directed intestinal caecum).

The genus *Terranova* was established by Leiper and Atkinson (1914) for the nematode species *Terranova antarctica* from the stomach of the elasmobranch, *Mustelus antarcticus*, with the following diagnosis of the genus: an ascarid with three simple lips, no interlabia, oesophagus simple, no oesophageal appendix. Gut with an anterior caecal prolongation.

Baylis (1920) emphasized the form of the oesophagus for separation of genera of the Ascaridae. He noted that *Terranova antarctica* possessed a ventriculus; he did not consider the absence of interlabia in *Terranova* to be significant, and thus placed *Terranova* as a synonym of *Porrocaecum* and accepted the change of *Ascaris decipiens* Krabbe to *Porrocaecum decipiens* (Krabbe). Subsequent authors for many years accepted this synonomy.

Johnston and Mawson (1945) restricted the genus *Porrocaecum* to species possessing interlabia and thus confined *Porrocaecum* to species whose final host was birds. They reinstated the genus *Terranova* for species of the *Porrocaecum* group lacking interlabia, a wide group of species restricted as adults to elasmobranch, teleost fish, aquatic reptile, and marine mammal, mainly seal, hosts. Karokhin (1946) was first to use the *decipiens* in the combination *Terranova decipiens* (Krabbe). Lacking interlabia, this species was clearly separated at the generic level from *Porrocaecum* (from birds) which possesses interlabia but, according to Gibson (1983) it was not until the work of Hartwich (1957) that this was generally accepted. Dollfus (1953) preferred *Porrocaecum* (*Terranova*) *decipiens*, regarding *Terranova* as sub-generic in status.

Myers (1959) erected the genus *Phocanema*, containing one species, *Phocanema decipiens*, on the basis of differences from *Terranova* species in fishes "in the cephalic region and in the tail region of the male", but she did not mention what these differences were. Myers had, however, separated *Terranova* in marine mammals, as represented by *Phocanema decipiens*, from *Terranova* in other vertebrates.

Johnston and Mawson (1939) described *Porrocaecum kogiae* from the pygmy sperm whale (*Kogia breviceps*), and Johnston and Mawson (1945) changed the name to *Terranova kogiae*. Mozgovoi, in Skrjabin et al. (1951), erected the genus *Pseudoterranova* for this species based on the position of the excretory pore as reported in Johnston and Mawson (1939) which was later (Gibson and Harris 1979; Gibson 1983) shown to be in error.

Canadian researchers working out of the east coast fisheries laboratories in the 1950's and 1960's largely followed Baylis (1920) and used the name *Porrocaecum decipiens*. Even as late as 1968, Wiles, and 1977, Mansfield and Beck, used *Porrocaecum*. Margolis (1956) reviewed the relevant literature and accepted the view of Johnston and Mawson (1945) that genera of this type, lacking interlabia, should be referred to *Terranova*. Young (1972) concluded that a study of Myers' (1959) generic diagnosis indicates that *Phocanema* is similar in all essential features to *Terranova* and should therefore be suppressed. Margolis (1977) said that authorities on nematode systematics agree that *Porrocaecum* should no longer be used for this nematode but observed that its allocation to *Terranova* or *Phocanema* is not unanimous and that both names may be found in current literature. Because Myers' generic separation of *Phocanema* from *Terranova* was indefinite and depended on statements without the presentation of evidence, many scientists throughout the world did not recognize *Phocanema* and used *Terranova decipiens*. In eastern Canada, the group working from the Institute of Parasitology of McGill University and in recent years most of the Halifax group used *Phocanema decipiens*, and the Guelph school used *Terranova decipiens*.

Gibson (1983) concluded that: "current criteria for distinguishing *Phocanema* and *Pseudoterranova* as distinct from *Terranova* are, therefore, weak or defunct", and that "as there is no other case of an ascaridoid genus which contains adults which can mature in both poikilotherms and homoiotherms, it seems improbable that *Terranova* should be an exception". He consequently compared *T. decipiens* and *T. kogiae* with most of the other species of *Terranova* and found some quantitative differences in the excretory system and the lip lobes, on which he separated these two species of *Terranova* from marine mammals, at the generic level, from the remaining *Terranova* species. He accepted *Pseudoterranova* as the oldest available name for the genus, with *Phocanema* as a synonym. Recently, Deardorff and Overstreet (1981) described a species of *Pseudoterranova* from another species of pygmy sperm whale, as *Terranova ceticola*. Gibson and Colin (1982) transferred this species to *Pseudoterranova* and *P. ceticola* became the third species of *Pseudoterranova*. Pygmy sperm whales are rare in North Atlantic waters (Miller and Kellogg 1955). Although the features separating *Pseudoterranova* from *Terranova* are quantitative rather than absolute, the use of *Pseudoterranova* as a genus provides a useful separation (as did the *Phocanema* of Myers 1959) of adult nematodes from homoiothermous marine mammalian final hosts, from the *Terranova* nematode species of the poikilothermous elasmobranchs, teleosts and aquatic reptiles. This new name, *Pseudoterranova decipiens* (Krabbe) was used by Gibson and Colin (1982), Gibson (1983), Hurst (1984a, 1984b), Smith and Wootten (1984), and McClelland et al. (1985), and will be used in this paper.

Nematodes in Seals

Preliminary studies (Scott 1950; Fisher 1950, 1951) showed that *P. decipiens* occurred in the harbour seal (*Phoca vitulina*), the grey seal (*Halichoerus grypus*), and in the harp seal (*Pagophilus groenlandicus*) of the Gulf of St. Lawrence. Scott and Fisher (1958b) identified *P. decipiens* (and also *Anisakis* and *Contracaecum*) from the stomachs of 318 harbour seals, 127 grey seals, and 812 harp seals from the Atlantic coast of Canada. The average abundance (mean number per seal) of adult *P. decipiens* was about 20 in harbour seals, 100 in grey seals and 2 in harp seals from the Gulf of St. Lawrence. *Pseudoterranova decipiens* was not observed in harp seals migrating southward into the Gulf of St. Lawrence in January, in only 10 % during their northward migration out of the Gulf in June and in only 2 % of the harp seals collected from the east coast of Newfoundland. It was found, usually in very small numbers, in harp seals of the Gulf after they had time to feed on the *P. decipiens*-infected groundfish there. Harbour seals were the most important hosts of *P. decipiens* within the Bay of Fundy and in southwestern Nova Scotia. Elsewhere, harbour seals and grey seals were approximately equal in numbers, with the grey seals being more important hosts because of their greater abundance of *P. decipiens*. Harp seals had some importance in the Gulf because of their large numbers of lightly infected seals.

Mansfield and Beck (1977) reviewed the available data on *P. decipiens* in seals of eastern Canadian waters, introducing some of Mansfield's unpublished data and unpublished data of Grigg and Wiles, and Wiles. They found the average numbers of adult female *P. decipiens* for grey, harbour and harp seals of the Gulf of St. Lawrence to be 102, 8, and 1.5. Mansfield and Beck also concluded that the relative overall importance of grey and harbour seals as vectors of this nematode in eastern Nova Scotia was approximately 4 to 1, and that for the southern Gulf (NAFO Div. 4T Fig. 1), the relative overall importance was grey, 80; harp, 18; and harbour, 2.

Most of the investigations of these nematodes in seals have been related to their presence in the seal's stomach, but Montreuil and Ronald (1957) noted that the intestine of the grey, harbour, and harp seals is also a site of infection by nematodes, sometimes in numbers equal to or greater than those in the stomach. Mansfield and Beck (1977) reported that the percentages of intestinal nematodes of the total *P. decipiens* from the stomach and intestine combined, were 7.0 from 14 harbour seals, 1.7 from 8 grey

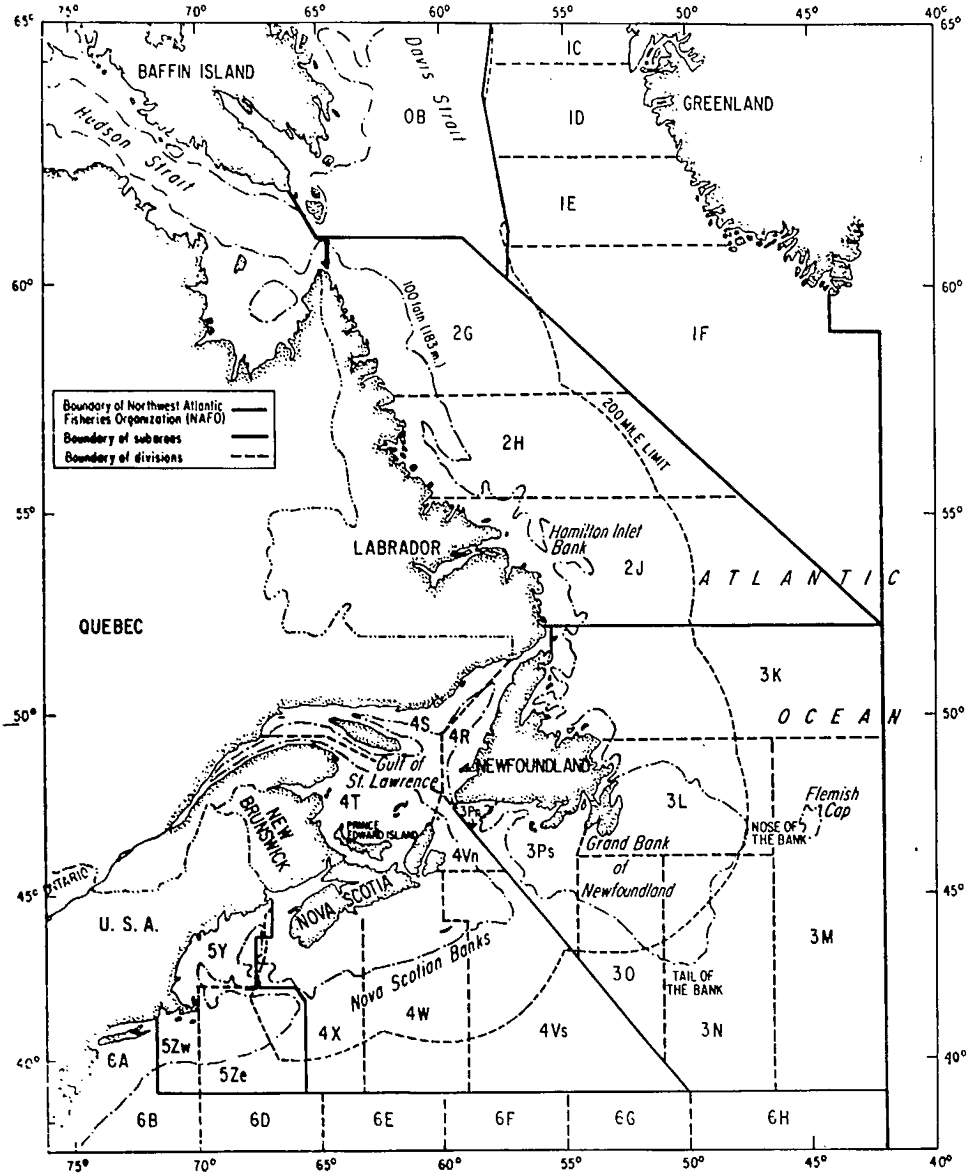

FIG. 1. Subareas and divisions of the Northwest Atlantic used by the Northwest Atlantic Fisheries Organization (NAFO).

seals, and 22 from 33 harp seals. Investigators, however, have usually continued to consider only the numbers of nematodes in the stomachs.

Except for *P. decipiens*, little specific classification of other nematodes from seal stomachs occurred in eastern Canada during the early period. Myers (1957) reported *P. decipiens, Contracaecum osculatum*, and *Phocascaris sp.* from the harp seal. Scott and Fisher (1958b) found *P. decipiens*, *Contracaecum* sp., and *Anisakis* sp. in grey, harbour, and harp seals, and said that some which they called *Contracaecum* may have been *Phocascaris.* In harbour seals, *P. decipiens* made up 90-100 % of the nematodes. Very few adult *Contracaecum* sp. and adult *Anisakis* sp. were observed. In grey seals, *P. decipiens* were 50-98 % of the nematodes examined; the remainder were mainly adult and immature *Contracaecum* sp. In the harp seal, *Contracaecum* sp. (including presumably *Phocascaris)* and *Anisakis* sp. were by far the most numerous nematodes and *P. decipiens* relatively scarce. Adult *Anisakis* sp. were rare in seals. Mansfield and Beck (1977) reported *P. decipiens*, *Contracaecum* sp. and *Anisakis* sp. from the grey seal, respectively 69, 7 and 25 % for E. Cape Breton Island and 80, 16, and 5 % for Northumberland Strait.

Nematodes in Cetaceans

Vladykov (1944) reported that all independently feeding white whales (*Delphinapterus leucas*) of the St. Lawrence estuary had nematode parasites, especially *Anisakis simplex*, in their stomachs: up to a gallon (4.5 L) of these nematodes was found in a single stomach.

Scott and Fisher (1958a) found only 1 mature male and small numbers of immature *P. decipiens* in the stomachs of 150 common porpoises (*Phocoena phocoena*), all except one from near Passamaquoddy Bay of the Bay of Fundy, an area with a high prevalence (% fish infected) of *P. decipiens* in fish. *Anisakis* sp. and *Contracaecum* sp. were more common than *P. decipiens* and several of each of these two genera were adults. Of 507 nematodes from the stomach of a white whale from Mace's Bay, N.B., 80 larval but no adult *P. decipiens* were found. The remaining nematodes were *Anisakis* sp., half of them mature. Sergeant (1962) reported *Anisakis simplex* from stomachs of the pilot whale (*Globicephala melaena*) from coastal waters off Newfoundland. Cowan (1967) noted several dozen to several hundred *Anisakis* sp. in each of the stomachs of 55 pilot whales from eastern Newfoundland. No *P. decipiens* were reported. Although many cetacean species of the western Atlantic were not examined, there was no evidence from those examined that the cetaceans of the area were important final hosts of *P. decipiens*. The first intermediate hosts of *Anisakis simplex*, whose final hosts are mainly cetaceans, include five species of euphausiids (Smith 1971, 1983). These euphausiids are eaten by baleen whales and also by fish, especially pelagic ones such as herring, mackerel, and capelin and also by squid.

Generic and Specific Identifications of Larval Nematodes from Fish Flesh in Eastern Canadian Waters

Scott and Martin (1957) said that all larval nematodes which they identified from cod fillets were *Pseudoterranova* (*Porrocaecum*). In Templeman et al. (1957), reporting for nematodes in cod fillets, all of 427 nematodes identified from the southern part of the Gulf of St. Lawrence (NAFO Div. 4T) were *Pseudoterranova.* From off the West Coast of Newfoundland (Div. 4R of the Gulf), the Scotian banks (Div. 4VW), St. Pierre Bank and the South Coast of Newfoundland (Div. 3P), 96 % of 980 nematodes were *Pseudoterranova.* From the North Shore of the Gulf (Div. 4S), 84 % of 50 nematodes were *Pseudoterranova*. Thus, in areas which had highly infected cod fillets, almost all the nematodes were *Pseudoterranova.* Similarly in the inshore areas of eastern

Newfoundland and Labrador, where nematodes in fish flesh were scarce, 90 % of 61 nematodes were *Pseudoterranova*. Smaller proportions of *Pseudoterranova* were present in the offshore areas of eastern Newfoundland and Labrador, distant from harbour and grey seal colonies, where nematode infection of fish flesh was very low: on the northern Grand Bank (Div. 3L), 75 % of 24 nematodes identified were *Pseudoterranova*; on the southern Grand Bank (Div. 3NO), 34 % of 21 nematodes and in offshore Labrador 36 % of 11 nematodes were *Pseudoterranova*; on Flemish Cap only 3 nematodes were examined and none were *Pseudoterranova*. The remaining nematodes in each case were *Anisakis*. In Scott and Martin (1959), of 517 larval nematodes identified from cod fillets in the Lockeport, N.S. area, 97 % were *Pseudoterranova* and the remainder were tentatively identified as *Anisakis*. All of about 1000 nematodes taken from fillets, mainly cod, from the Bras d'Or Lakes of the Cape Breton area, were *Pseudoterranova* (Scott and Black 1960). Templeman et al. (1957), for larval nematodes from cod fillets, demonstrated that in *Pseudoterranova* the pharynx was shorter in relation to the total length of the nematode and to the ventriculus length than in the nematodes without caeca (assigned to Anisakis).

Transmission of *Pseudoterranova decipiens* Between Seals and Fish

Larval *Pseudoterranova* sp. occur commonly in the musculature of Atlantic cod (*Gadus morhua*) in Canadian Atlantic waters (Scott 1950). Although the larval *Pseudoterranova* in fish flesh could be identified to genus, the larval characters are not sufficient to identify the species. In experiments carried out at the St. Andrews Biological Station in 1947-48, Scott (1953) showed that larval nematodes from the flesh of Atlantic cod (*Gadus morhua*), rainbow smelt (*Osmerus mordax*), American plaice (*Hippoglossoides platessoides*), and ocean pout (*Macrozoarces americanus*), when fed to the harbour seal, infected the seal and grew to maturity in its stomach, when they were identified as *P. decipiens*. Some male and female *P. decipiens* matured before the 20th day after transference to the seal.

Pseudoterranova sp. larvae were found in smelt and in the flesh of 13 species of groundfish in Canadian Atlantic waters. As only one species of *Pseudoterranova* has been found in these waters (Scott 1956), in can be assumed that they are larvae of *P. decipiens* (Scott 1954). Scott's experiments (1954) showed that when *Pseudoterranova* from smelt were fed to cod, some of these nematodes passed through the stomach wall and penetrated the body muscle of the cod, thus showing that a fish may obtain *P. decipiens* larvae in its flesh by eating other infected fish.

Pseudoterranova sp. larvae from cod matured in vitro so that they could be recognized as *P. decipiens* (Townsley et al. 1963). McClelland and Ronald (1970) hatched *P. decipiens* eggs from adults taken from seals and raised the larvae in vitro to 10 mm in length in 4 months. McClelland and Ronald (1974) raised *P. decipiens* larvae (hatched from the eggs in seawater) in vitro to the pre-adult stage. The characteristic anteriad intestinal caecum was lacking in larvae < 2 mm in length.

Myers (1960) described the morphology of *Pseudoterranova decipiens* and carried out experiments on its early life history. The eggs of this nematode were in the morula stage when passed in the faeces of the seal. The eggs, obtained from adult female *P. decipiens* from seal stomachs, were hatched in salt water. After emerging from its shell the larva soon became attached by its tail to bottom particles. Experimental infections of small to large numbers of 29 species of marine invertebrates and 4 species of marine fish by these second stage produced no further development, the larvae surviving in these invertebrates and fish typically for not more than 24 h.

Scott and Black (1960), working in the Bras d'Or Lakes found 110 nematodes in 8 000 mysids. Only one of those was definitely and another was probably *Pseudoterranova* sp. Most of these larvae were longer than 20 mm and none were shorter than 10 mm, suggesting that there was an earlier intermediate host.

Number of Harbour, Grey and Harp Seals

Harbour seals were common (some thousands) at Sable Island in 1854 (Gilpin 1870, 1874), (common) in the 1920's and several hundred in 1961 (Mansfield 1967a) and estimated at 1 250 in 1973 (Boulva and McLaren 1979). Small colonies of harbour seals are commonly distributed around the coasts of the Atlantic provinces and Quebec (Table 1) and are also found on the coast of Labrador (Templeman et al. 1957), Hudson's Bay and the eastern Arctic (Mansfield 1967b). Harbour seals were considerably reduced between 1949 and 1973 (Table 1) by a bounty, and have apparently been increasing slowly since the removal of the bounty in 1976.

Grey seals increased greatly since the early 1960's (Table 1) especially on Sable Island where about half the population breeds. They are now much more plentiful than the harbour seals as well as being much larger. They migrate widely in summer-autumn and in some areas establish summer concentrations.

TABLE 1. Populations of seals in eastern Canadian waters south of Labrador.

Location	Dates	Population	Ref.[a]
Harbour seal			
Sable Island	1854	Common (some thousands)	1
	1920's	Common	2
Maritime Provinces not including Sable I.	1949	10 000-15 000	3
	1973	5 453	4
E. Canada not including Labrador and Arctic	1973	12 700	4
Quebec (including Magdalen Is.)	1973	1 580	4
Sable I.	1961	290+	2
	1973	1 250	4
Grey Seal			
Sable I.	1854	several hundred + pups	1
Miramichi	1949	about 500	5
Deadman I. (Magdalen Is.)	1951	100-200 (mostly pups taken)	5
Souris Harbour	1951	1 200-1 500 pups	5
SE Gulf of St. Lawrence	1954-55	about 1 000 pups	5
Sable I.	1962	350 pups	6
E. Canada	1965	5 000-7 000	5
	1976	24 000 age 1+	5
	1980	44 000-48 000 age 1+	6
Sable I.	1980-84	Half the total population	7
Harp seal			
Canada	1946	1 880 000	8
	1948-49	1 960 000	8
	1952	2 470 000	9
	1953	2 400 000	9
	1971	964 000	8
	1972	1 084 000	9
	1978	1 299 000	9

[a] References — 1, Gilpin (1870, 1874); 2, Mansfield (1967a); 3, Fisher (1949); 4, Boulva and McLaren (1979); 5, Mansfield and Beck (1977); 6, Zwanenburg et al. (1981); 7, Anon. (1984); 8, Allen (1975); 9, Winters (1978).

Harp seal numbers increased to more than 2 million seals of 1 yr of age and older due to a great reduction in hunting during and for a while after the second world war (Table 1 and Templeman 1966). Under intensive hunting, they decreased to about 1 million age 1 + seals, and probably increased somewhat after the introduction of quotas in 1971 (ICES 1983). With the relative lack of hunting in recent years they are presumably increasing rapidly.

Possible Role of Temperature in Nematode Infection of Fish Flesh

The scarcity of *P. decipiens* in cod of southern Labrador, in spite of the large numbers of residential harbour seals and of migrating harp and grey seals, led Templeman et al. (1957) to speculate that the lower summer temperatures of inshore Labrador compared with the considerably higher inshore summer temperatures of the southern Gulf may interfere with the transmission of *P. decipiens* from seal to fish.

In experiments on the development of the eggs of *P. decipiens* in sea water (Scott 1955) the gastrula stage was reached in 3 d at 17-25°C, 5 d at 13-14°C and in 18 d at 2-4°C. The eggs hatched in 8-9 d at 17-25°C, 13-14 d at 13-14°C. At 2-4°C in 27 d no movement of larvae had been detected in the eggs. In Myers (1960), eggs in the morula or the uncleaved stage, obtained from adult *P. decipiens* from seal stomachs, were hatched in salt water in 7 d at 24°C and 14 d at 14°C. Temperatures above 24°C were lethal and at 4°C there was no development beyond the morula stage. McClelland and Ronald (1974) reported that *P. decipiens* eggs in sea water at 15°C hatched in 10-14 d, and at 5°C in 50-60 d. In 18 wk subsequent in vitro development of these larvae, at 15°C the larvae grew to 11.4 mm in length, at 10°C to 5.5 mm, and at 5°C there was no growth, but the larvae were alive and according to McClelland and Ronald (1970) could be stored indefinitely.

In experiments at St. Andrews, N.B. (Scott 1954), smelt containing *P. decipiens* were fed to cod, mainly in July 4-21 in tanks at the St. Andrews Station. Temperatures in the tanks were not reported but on July 4-21 they should have been in the vicinity of 12-13°C (Templeman 1937). Apparently more than 24 and less than 48 h were needed for the majority of the larvae to complete their movement into the body wall of the cod.

Ronald (1960) carried out experiments on the penetration of fish tissue in physiological saline by larval *P. decipiens* from cod muscle. Penetration by the greatest number of larvae was at 15°C and by approximately half these numbers at 0°C.

There is thus a possibility that fewer *P. decipiens* larvae would develop in intermediate hosts to the point where they could infect groundfish and that fewer would free themselves from invertebrate and smaller fishes in food of larger fishes, attach themselves to the stomach wall and bore through to the body cavity at or slightly above 0°C than at higher temperatures before they were eliminated from the gut in the faeces of the fish.

Pseudoterranova decipiens in Fish Flesh in Eastern Canadian Waters

The principal earlier investigations on the relative abundance of *P. decipiens*, mainly in cod fillets but with some information on infection in flounders and other fishes, in the eastern Canadian area, are those of Templeman et al. (1957), Scott and Martin (1957, 1959), Scott and Black (1960), and Wiles (1968). In Scott and Martin (1957) the nematodes were noted by research technicians as they were picked out by commercial employees or occasionally by the technicians themselves from candling operations (see below) on whole fillets at the fish plants. In the remainder, the obvious nematodes were removed and the fillets, apart from the smallest, cut into thin slices before being candled to note the remaining nematodes. Power (1961) found, for heavily infected cod fillets, that the percentages of total nematodes extracted by candling whole fillets ranged from 94 for small fillets to 67 and 61 for medium and medium large and 15 for large, as compared with those obtained by candling, cutting into 13 mm slices and recandling the slices. In another experiment by Power for small, medium, and large cod fillets averaging 0.25, 0.35, and 0.52 kg, 27, 24, and 22 % of the nematodes respectively were removed by the candling of whole fillets.

Control of *P. decipiens* (and *Anisakis*) in Fish Processing

Hess (1945) described a candling table used in the detection and removal of nematodes from fish fillets and other fish products. Knowledge of the most suitable lighting conditions for candling was improved by Power (1958), and Power (1961) reported the additional efficiency in nematode removal from slicing fillets mechanically to 13 mm thickness, followed by candling.

Frick (1956), reporting for four groups of filleting plants in the Maritimes, found that the infection density (average number of nematodes per unit fillet weight) of nematodes per 45.4 kg of cod fillets was much greater in the southern Gulf of St. Lawrence (233) compared with eastern Cape Breton (120), east Mainland Nova Scotia (94) and SW Nova Scotia (88). This is much different from recent years for which Odense (1978) reported the greatest density of infection in cod of Sydney Bight (Div. 4Vn). More nematodes (60/45.4 kg of fillet) remained after the candling of Gulf cod compared with 25-42 for the other areas. The ratio of candlers to filleters was greater in the Gulf (1.4) compared with 0.7 off eastern Cape Breton and 0.3 for the other two areas.

In Homans and MacFarlane (1956) the average efficiency of nematode removal from cod fillets in the 8 plants examined in the Maritimes was about 50 %. In tests with cod fillets in 16 samples totalling 2 000 lb (907 kg), the following results were obtained: in cod fillet samples averaging 190 nematodes per 45.4 kg, plant workers removed 95 (50 %) and failed to remove 50 %. Fisheries inspectors found an additional 41 nematodes (22 %) by a second candling. The remaining 54 (28 %) were only detected by slicing the fillets into 3 mm slices and candling these. The authors stated that plant workers are unable to work as slowly and carefully as the fisheries inspectors did in this survey. Slicing and repeated candlings lower the quality and grade of the fillets.

Ronald (1956) using ultraviolet light in candling for *P. decipiens*, noted that when the nematodes were fluorescent they were detected more easily in the flesh by ultraviolet light rather than by the usual transmitted light method. The parasites, however, were fluorescent only after they were dead, either in frozen or boiled fish or after natural death of the parasite.

General Distribution of *P. decipiens* in Cod of the Eastern Canadian Area in the Earlier Period

In Templeman et al. (1957), the numbers of larval *P. decipiens* in fillets of 100 cod, 41 cm and over, in 1947-53 declined from 311 in the southwestern Gulf of St. Lawrence to very low levels of 1 to 2 in the Newfoundland eastern offshore regions (Table 2). The great infection densities in the southern Gulf could be related to the presence of breeding colonies of grey and harbour seals, seasonal migrations and summer concentrations of grey seals and to the seasonal visits of a large herd of harp seals. In the northern Gulf, infection levels could be ascribed to harbour seal colonies, harp seals, and visiting grey seals; on the western and central parts of the South Coast of Newfoundland to harbour seal colonies, a summer-autumn concentration of grey seals on Miquelon Island and migrating grey seals. The small numbers of *P. decipiens* in eastern coastal Newfoundland were related to the small number of resident harbour seals and of migrating grey seals, and the very low densities of infection on the Grand Bank to distances from seal colonies and lack of migrants from coastal areas with high infec-

TABLE 2. Numbers of *Pseudoterranova decipiens* in fillets of 100 cod 41 cm and over in 1947-53 in declining order (from Templeman et al. 1957).

Area	NAFO Div.	No. of P. *decipiens* in fillets of 100 cod, 41 cm+
SW Gulf of St. Lawrence	4T	311
W part of S Coast Newfoundland	3Pn	96
S part of W Coast Newfoundland	4R	94
Central part S Coast Newfoundland	3Ps	52
Slope Magdalen Islands	4T	39
N part W Coast Newfoundland	4R	37
NE Scotian Shelf	4VW	30
NE Gulf of St. Lawrence	4S	28
Fortune and Placentia Bays	3Ps	18
Southern Avalon Peninsula	3L	12
Southern St. Pierre Bank	3Ps	6
E Coast Newfoundland, Coastal	3KL	4
SW Grand Bank	3O	1-2
E parts of northeastern Grand Bank	3L	1-2
Offshore NE Newfoundland	3K	1-2
Offshore Labrador	2GHJ	1-2
SE Grand Bank	3N	1
Flemish Cap	3M	0

tion rates. There were very few nematodes in cod off Labrador in spite of the presence of many colonies of harbour seals and of harp seals in season. Because the fish they eat in the Labrador area are little infected with *P. decipiens*, (the capelin, forming a large part of their food, are apparently not infected by this species, Templeman 1948, 1968, Templeman et al. 1957), the seals also should have low infection rates. The harp seals migrating from the Gulf apparently lose most of their infection with *P. decipiens* before leaving the Gulf. It has also been considered possible that the transmission of the nematode through intermediate hosts from seals to fish is not very effective in the northern colder water.

In the data reported by Scott and Martin (1957), percentage infections of cod fillets with larval *P. decipiens* in 1946-56 were highest in coastal areas of the southern Gulf of St. Lawrence, including near the Magdalen Islands (89-92), on Orphan Bank and Bradelle Bank of the southern Gulf (76), in Passamaquoddy Bay (66) and in the southeastern Gulf off Cape Breton (55). Percentage infections with *P. decipiens* were lower (22-24) in eastern Cape Breton and coastal SE Nova Scotia (14-16) and low (5-7) on the offshore Scotian banks including Sable I. Bank. Coastal infection percentages were higher than offshore. The infections in southern Nova Scotia were mainly from the harbour seal, those of the northeastern Scotian Shelf mainly from grey and incidentally harbour seals, and those of the Gulf from grey, harp, and harbour seals. In the southern Gulf, prevalence of *P. decipiens* infection in samples of cod landed at Caraquet declined from 1946 to 1956, coincident with the landing of smaller cod as the fishery changed from line fishing to otter trawling, increased use of offshore areas for fishing, and an increase in the growth rate of cod. Scott and Martin (1959) reported the results of investigations on nematode numbers in the fillets of young cod from coastal areas, all 10 miles or less from shore near Lockeport, N.S. and from six areas in the southern Gulf of St. Lawrence. About 97 % of the nematodes from the Lockeport area were *P. decipiens* and the remainder *Anisakis* sp. Infection rates in cod of the Magdalen Islands area were considerably less than in New Brunswick coastal areas to the southwest of these islands, and Scott and Martin concluded that because harp seals are much more numerous near the Magdalen Islands than in the New Bruswick areas, there was no evidence from their study that the harp seal was the principal source of *P. decipiens* for cod in the southwestern Gulf of St. Lawrence. Near Lockeport the cod were apparently infected by the *P. decipiens* from a small number of harbour seals, probably not exceeding 50 within a 5-mile radius of Lockeport. These harbour seals are closely related to the shore. Prevalence of the parasite typically increased from younger to older cod and infection rates of age-4 fish ranged from 71 to 79 %. Similarly, Scott and Black (1960) reported a very heavy infection of cod with *P. decipiens* in Bras d'Or Lakes from the presence of several hundred harbour and grey seals in this area from late November until March. No seals were seen in the lakes during the summer. Although cod 5 years of age from Baddeck Bay and Kempt Head of the Bras d'Or Lakes had an infection rate of 18 *P. decipiens* in their fillets, 5-y old cod from the adjacent Whycocomagh Bay (of these lakes), only about 15 nautical miles distant, with a narrow entrance which seals rarely entered, had a nematode infection rate of only 1 %.

McCracken and Fitzgerald (1964) examined cod fillets from the Nova Scotian Shelf and the Gulf region for nematodes using the methods of Scott and Martin (1957). The relative numbers of nematodes were least from the offshore Nova Scotia banks (Western, Middle, Sable I. and Emerald banks and Banquereau) intermediate for southwestern Nova Scotia (Div. 4Y) and largest for the Cape Breton region and the southern Gulf of St. Lawrence (Div. 4T) averaging approximately per 45.4 kg of fillets for market cod in these regions respectively, 10, 30, 70, and 80 nematodes. These results are comparable but of course low because of the superficial methods of examination for nematodes. Nematode prevalence in fillets of cod landed at Caraquet in the southern Gulf showed a progressive reduction from 90 in 1946 and 66 % for the period 1946-54 to 43 % in 1955 and to 20 % in 1963. McCracken and Fitzgerald conclude that although reduction in prevalence has been associated with reduction in size of fish landed, there also appears to have been a real reduction in infection of fish of larger size.

Wiles (1968) noted some increases and decreases in infection of cod fillets with nematodes between 1947-53 (Templeman et al. 1957) and 1966-67 for (a) % cod infected, (b) nematodes/100 cod, (c) nematodes/infected fish. The results were: for Div. 3Pn off the SW Coast of Newfoundland, a non-significant increase in (a) and significant decreases in (b) and (c); for Div. 4R, West Coast of Newfoundland, significant decreases in (a) and (b) and a significant increase in (c); and for Div. 4S, North Shore of Gulf of St. Lawrence, significant increases in (a, b, c).

Nematodes in Relation to Length and Age of Cod Host

Templeman et al. (1957) found that the average number of nematodes in cod fillets per infected cod usually increased with increase in fish length. The number of nematodes per unit of cod weight usually increased from the 31-50 cm to the 51-70 cm fish length class and usually decreased at larger sizes. In areas with few nematodes in the fillets and where *Anisakis* sp. was an important percentage, nematodes per unit weight of cod fillets declined considerably from the smallest to the largest fish sizes. This and the smaller numbers of nematodes per unit weight at the larger fish sizes generally, may have been partly due to a higher percentage of the *P. decipiens* remaining in the napes or belly flaps (the lateral and ventral walls of the body cavity) in the larger cod and also to larger cod in deeper water and farther away from the sources of infection. In an offshore sample from Div 4T of the southern Gulf, the largest and more migratory cod had more nematodes per unit weight than the more residential smaller cod.

The prevalence of nematodes, almost all *P. decipiens*, and the mean number of nematodes in cod fillets typically increased with age in small cod of ages 2-5 from near Lockeport, N.S. and in the southern Gulf of St. Lawrence (Scott and Martin, 1959). The mean number of *P. decipiens* larvae in fillets of cod in Baddeck Bay of the Bras d'Or Lakes increased gradually from 2 at age 1 (23 cm) and 10 at age 2 (31 cm) to 98 at age 11 (69 cm) and to 330 at age 13 (83 cm).

Nematodes in Flounder Fillets

Homans and MacFarlane (1956) candled samples of flatfish fillets for nematodes after slicing the fillets to 3 mm thickness. They found no nematodes in the flesh of samples of winter flounder (*Pseudopleuronectes americanus*) from St. Mary and Shelburne bays, N.S. In witch flounder (*Glyptocephalus cynoglossus*), the average number of nematodes per 45.4 kg of fillets varied from 1 to 6 in witch from the offshore banks to a high of 27 and 34 in those caught in Sydney Bight and in the Gulf of St. Lawrence respectively. The number of nematodes per 45.4 kg of fillets of American plaice (*Hippoglossoides platessoides*) ranged from 3 to 6 in fish caught on the Grand Bank and Banquereau, 11-19 in fish from the south shore of Nova Scotia and St. Pierre Bank, and 84-112 in plaice caught off Cape Breton and in the Gulf of St. Lawrence.

For American plaice, Templeman et al. (1957) found nematode infection rates per 45.4 kg of fillets averaged for 31-40 cm and 41-50 cm fish length ranged from 132 for the southern Gulf (Div. 4T) to 52 on the North Shore of the Gulf (Div. 4R), 25 in Div. 3P including St. Pierre Bank, 19 on the northeastern Scotian Shelf (Div. 4V) and 0.2 in the eastern Newfoundland area (Div. 2J, 3K LMNO). The number of nematodes per unit weight of fillets declined very rapidly from smaller to larger fish in ranges from 11-20 to 51-60 cm. Witch flounder were lightly infected, averaging at 41-50 cm per 45.5 kg of fillets: 6 nematodes in Div. 4RT (Gulf) and in Div. 4VW (Scotian Shelf) to 1 in the southern Newfoundland (Div. 30P) and 0 nematodes in the eastern Newfoundland area (Div. 3KL). The rapid decrease in infection per unit weight with increase in fish size was not evident in the witch whose young are typically inhabitants of deep water, and were not infected up to size of 30 cm.

Infection in Flesh of Other Fish by Larval *Pseudoterranova* and *Anisakis*

Templeman et al. (1957) reported very low infection by larval *P. decipiens* and *Anisakis* sp. in the flesh of haddock (*Melanogrammus aeglefinus*) and redfish (*Sebastes* sp.). The sea raven (*Hemitripterus americanus*) was highly infected, and the smelt (*Osmerus mordax*) was usually moderately infected individually but highly infected by unit of weight; the longhorn sculpin (*Myoxocephalus octodecemspinosus*) had a moderate rate of infection at the larger sizes; the common angler (*Lophius americanus*), the Greenland cod (*Gadus ogac*), Greenland halibut (*Reinhardtius hippoglossoides*), pollock (*Pollachius virens*), yellowtail flounder (*Limanda ferruginea*), and tomcod (*Microgadus tomcod*) had some infection, but the three species of wolffish (*Anarhichas lupus, A. minor* and *A. denticulatus*) showed no infection in their fillets. Apart from smelt, there were not enough specimens of these species examined to make very definite comparative statements. The nematode parasites found in capelin by Templeman 1948, 1968 (see also Templeman et al. 1957) almost all possessed the *Contracaecum*-type caeca, but a smaller proportion were *Anisakis*, sp. Mr. Per Høst, who described the nematode, *Phocascaris phocae*, from the harp seal (Høst 1932), examined in 1949 some of my specimens of larval nematodes taken from Newfoundland capelin in May, 1946 and found 5 of 14 to be *Anisakis* sp. and 9 *Contracaecum* sp. or *Phocascaris* sp. In addition to the fishes mentioned above, Scott (1950, 1954) found *Pseudoterranova* larvae in the flesh of the mailed sculpin (*Triglops murrayi*), the shorthorn sculpin (*Myoxocephalus scorpius*), the common eelpout (*Macrozoarces americanus*), the white hake (*Urophycis tenuis*), and the winter flounder (*Pseudopleuronectes americanus*). Scott and Black (1960) add the ribbed sculpin (*Triglops pingeli*) as a host but either the common name or the species is in error as these authors call the species the mailed sculpin.

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Group Report 1: Hatching and Infection of Intermediate Hosts

G. McClelland (*Rapporteur*) A. Bjørge, J. Brattey, M. Burt, S. des Clers, P. Fanning, G. Hare, L. Jarecka, T. Landry, L. Margolis, S. McGladdery, R. Misra, R. Mohn, H. Möller, J. Pálsson, J. Smith, W. Stobo, and R. Wootten

Ova

Ova of *Pseudoterranova decipiens*, 40-50 µm in diameter and at the 2 to 16 cell stage when passed with the faeces of seals, settle in seawater and adhere to the substrate (Scott 1955; Myers 1960; McClelland 1982; Brattey 1990). Settling rates of the eggs and the influence of oceanic currents on their dispersal have not been determined but it is doubtful that they are carried a significant distance from the point where they are passed by a seal. It is also unlikely that the ova remain suspended in the water column where they or the larvae emerging from them might be consumed by planktonic organisms; the parasite has not been found in pelagic invertebrates and is seldom found in pelagic fish.

Pseudoterranova decipiens ova complete embryonation and hatch at temperatures ranging from 1.7 to 26.0°C, in fresh and brackish water as well as in seawater (McClelland 1982; Brattey 1990; Burt et al. 1990b). Development time to hatch varies from 5 d at 22°C to 125 d at 1.7°C, the hatching time-temperature relationship being described by a hyperbolic curve. Prehatch mortality varies from 3 to 28 % in the 1.7 to 17.0°C range but prolonged incubation ($\geq$150 d) at lower temperatures ($\leq$ 1.0°C) may result in much higher mortality ($>$70 %).

Developmental rates at temperatures $<$1.7°C and the lower lethal temperature for eggs remain to be determined. Information on egg mortality resulting from prolonged exposure to sublethal temperatures in the lower range may also help explain geographic variation in the abundance of the parasite.

Free-Living Ensheathed Larva

Larvae which emerge from ova are approximately 200-215 µm in length (heat-relaxed) and retain the cuticle of the previous larval stage as a tight-fitting sheath (McClelland 1982). As light microscopy and TEM studies have revealed the occurence of a single moult in the ova (M.D.B. Burt, Dep. of Biology, University of New Brunswick, Fredricton, N.B., Canada, pers. comm.), freshly-hatched larvae are assumed to be in the second stage (L_2). The larvae adhere to the substrate by their tails and alternately arch and extend their bodies to produce a "flicking" motion (McClelland 1982), They are extremely active at temperatures $>$10°C but sluggish to immobile at $<$5°C.

Post-hatch longevity of the ensheathed free-living larvae varies inversely with temperature, the survival time-temperature, relationship again being described by a hyperbolic curve (McClelland 1982; M. D. B. Burt, unpublished data). While larvae survive but a few hours at temperatures of 20 to 25°C, they persist for 120-140 d at 4 to 5°C and remain infective to first intermediate hosts (copepods) for 111 d at the latter temperatures.

Longevity and infectivity of ensheathed larvae at lower temperatures ($<$4°C), lower lethal temperatures and the sublethal effects of prolonged exposure to cold should be investigated in the future. As is the case with ova (above), temperature may limit the range of the parasite and influence variation in parasite abundance within that range.

Copepod Host

Ensheathed larvae of *P. decipiens* have been transmitted experimentally to a broad spectrum of copepods including marine benthic harpacticoid and cyclopoid, marine pelagic calanoid and freshwater clyclopoid species (Table 1). The range of susceptible copepod species narrows considerably however, when exposures are conducted at temperatures <5°C and only *Tisbe furcata* has proven susceptible to infection at 0°C. It is unlikely that there would be a detectable prevalence of the parasite in natural populations of copepods or, that natural infections would occur in pelagic species.

On ingestion by mature copepods, *P. decipiens* larvae exsheath and penetrate the mid-gut wall to the haemocoel. The nematodes grow (in body length) at an exponential rate in copepod haemocoels and the growth rate is approximately 6 times more rapid at 15°C than at 5°C (McClelland 1982). The nematodes grow as large as 2 mm in length in the calanoid *Tortanus discaudata* (Jarecka et al. 1988) and at this size, they may be infective to fish (see below). In most copepod hosts, however, sealworm larvae grow no larger than 300-500 μ m in length, far too small (and perhaps in the wrong larval stage) to be infective to fish. The growth and development of *P. decipiens* in copepods is limited by the longevity of the host. Most copepod hosts are short-lived, surviving 3-5 wk at 5°C and <2 wk at temperatures >10°C (McClelland 1982).

TABLE 1. Natural and experimental *P. decipiens* infections in invertebrate hosts.

Host					*P. decipiens* Infections			
Phylum	Class/ Subclass	Order	Species	Location	Natural	Laboratory transmission		Source
						Direct[a]	Serial[b]	
Annelida	Polychaeta		*Lepidonotus squamatus*	White Sea, USSR	+	–	–	Val'ter and Popova (1974)
			Phyllodoce sp.	Canada	–	–	+	McClelland (1990)
Arthropoda	Copepoda	Calanoida	*Calanus finmarchus*	Canada	–	+	–	Jarecka et al. (1988)
			Centrophages typicus	Canada	–	+	–	Jarecka et al. (1988)
			Eurytemora sp.	Canada	–	+	–	Jarecka et al. (1988)
			Acartia sp.	Canada	–	+	–	Jarecka et al. (1988)
			Tortanus discaudata	Canada	–	+	–	Jarecka et al. (1988)
		Harpacticoida	*Helectinosoma* spp.	Canada	–	+	–	McClelland (1982)
			Danielsennia typica	Canada	–	+	–	McClelland (1982)
			Tachidius brevicornis	Canada	–	+	–	Jarecka et al. (1988)
			Tisbe furcata	Canada	–	+	–	McClelland (1982)
			Tisbe spp.	Canada	–	+	–	McClelland (1982)
			Alteutha sp.	Canada	–	+	–	McClelland (1982)
			Ameira longipes	Canada	–	+	–	McClelland (1982)
			Diosaccidae g(aff Robertgurneya) sp.	Canada	–	+	–	McClelland (1982)
			Enhydrosoma curticauda	Canada	–	+	–	McClelland (1982)
			Macrostella sp.	Canada	–	+	–	Jarecka et al. (1988)
			Phyllothalestris sp.	Canada	–	+	–	McClelland (1982)
			Parathalestris sp.	Canada	–	+	–	Jarecka et al. (1988)
		Ciclopoida	*Paracylopina* sp.	Canada	–	+	–	McClelland (1982)
	Malacostraca	Mysidacea	*Mysis* and *Erythrops* spp. and unidentified mysids	Canada	(+)[c]	–	–	Scott and Black (1960)
			Mysis stenolepis	Canada	–	–	+	McClelland (1990)
		Amphipoda	*Gammarus oceanicus*	Canada	–	+	+	Jarecka et al. (1988)
			Gammarus lawrencianus	Canada	+	+	+	McClelland (1990)
			Marinogammarus obtusatus	White Sea, USSR	+	–	–	Val'ter (1987)
			Unciola irrorata	Canada	+	+	+	McClelland (1990)
			Caprella septentrionales	White Sea, USSR	+	–	–	Val'ter (1978)
		Isopoda	*Idotea neglecta*	Norway	(+)[d]	–	–	Bjbrge (1979)
			Edotea montosa	Canada	–	–	+	McClelland (1990)
		Cumacea	*Diastylis polita*	Canada	–	–	+	McClelland (1990)
		Decapoda	*Palaemonetes vulgaris*	Canada	–	–	+	McClelland (1990)
			Crangon septemspinosa	Canada	–	–	+	McClelland (1990)
			Sclerocrangon boreas	Barents Sea	(+)[c]	–	–	Uspenskaya (1963)
			Hyas araneus	Canada	–	(+)[f]	–	Jarecka et al. (1988)
			Hyas coarctatus	Canada	–	(+)[f]	–	Jarecka et al. (1988)
			Cancer borealis	Canada	–	(+)[f]	–	Jarecka et al. (1988)
Mollusca	Gastropoda	Nudibranchia	*Coryphilla* sp.	Canada	–	–	+	McClelland (1990)

[a] Infected by consuming the freshly hatched larvae of *P. decipiens*.
[b] Infected by consuming a carrier host, usually a copepod.
[c] *Pseudoterranova* (*Porrocaecum*)-like larvae.
[d] Infected isopod recovered from stomach of cod.
[e] Nematode described by Uspenskaya (1963) appeared to be fourth-stage *P.* (*Terranova*) *decipiens* larva (Val'ter 1978).
[f] Zoea larvae of crabs susceptible to infection.

Macroinvertebrate Host

In the laboratory, larval grammaridean amphipods (*Gammarus oceanicus, Gammarus lawrencianus*, and *Unciola irrorata*) and the zoea larvae of crabs (*Hyas* and *Cancer* spp.) become infected with *P. decipiens* by ingesting the newly-hatched ensheathed larvae (Jarecka et al. 1988; McClelland 1990) but <1 % of the nematodes consumed by amphipods exsheath and penetrate to the haemocoel. Transmissions to amphipods via copepod transfer hosts appear to be much more efficient as >50 % of the nematodes infecting ingested copepods successfully invade the amphipod haemocoel. Sealworm larvae have also been transmitted via copepods to polychaetes, mysids, isopods, cumaceans, decapods, and gastropods in the laboratory (McClelland 1990) while natural infections have been reported in polychaetes (USSR), mysids (Canada), amphipods (Canada and USSR), isopods (Norway), and decapods (USSR) (Table 1). Natural infections invariably involve a single worm and are usually of extremely low prevalence (<1 %).

In amphipod haemocoels, *P. decipiens* larvae grow exponentially to a length of 2-3 mm with subsequent growth (in body length) becoming asymptotic (McClelland 1990). The exponential growth phase requires 4 wk at 15°C and ~20 wk at 5°C. The nematodes reach a maximum of 10 mm in length in amphipods after 12 wk at 15°C but possibly grow much larger over the natural life span (1-2 yr) of the amphipod hosts. Sealworm larvae also grow >5 mm in length in the haemocoel of experimentally infected larval crabs (*Hyas* spp.), surviving the host moult from zoea to megalops stage (Jarecka et al. 1988). It is doubtful, however, that planktonic crab larvae are important natural hosts of *P. decipiens*, given the scarcity of the parasite in pelagic consumers of plankton such as mackerel and herring (McClelland et al. 1990).

According to recent evidence, the second moult (M_2) i.e. from second (L_2) to third (L_3) stage larvae, in the life cycle of *P. decipiens* may occur in the macroinvertebrate host (L. Jarecka, Dep. of Biology, University of New Brunswick, Fredicton, N.B., Canada pers. comm.). Sealworm larvae, 1.5-2.0 mm in length, recovered from moribund amphipods, appeared to moult when subsequently transferred to an *in vitro* system. Unfortunately, this moult has not been observed in the development of *P. decipiens* larvae cultivated continuously *in vitro* from time of hatch (McClelland and Ronald 1974).

Although *P. decipiens* in amphipods or other invertebrate hosts may be of sufficient size and in the appropriate (infective L_3) stage, it is unlikely that invertebrate transmissions contribute significantly to infections in seals (McClelland 1990). Sealworm larvae have not been identified in invertebrates such as squid and large decapods which are commonly found in seal diets (Benoit and Bowen 1990a).

Longevity *P. decipiens* in invertebrate hosts and efficiencies of sealworm transmission through macroinvertebrate intermediaries are important considerations in the development of mathematical models of the parasite population. While existing experimental data may prove useful, additional experimentation and information on *P. decipiens* abundance in natural invertebrate populations will be required. Experimental systems should be established to study factors such as: parasite transmission and growth rates; influence of host response on the survival and development of the nematodes; parasite and host longevities; pathogenicity of the parasite including sublethal effects such as behavioral modifications which render the host more susceptible to predation. Natural abundances of *P. decipiens* in invertebrate populations can be determined not only by direct surveys of invertebrates but also by investigating diets of heavily infected non-migratory fish hosts such as smelt (*Osmerus mordax, O. eperlanus*), sculpins and flatfishes.

Fish Host

Sealworm larvae infect a wide range of fish species in the North Atlantic and adjacent waters (McClelland et al. 1990). Abundances and intensities of infection are generally greatest in piscivorous demersal fish such as monkfish (*Lophius americanus*), Atlantic cod (*Gadus morhua*) and sea raven (*Hemitripterus americanus*). The greatest densities of infection (numbers per unit host weight), however, are often found in small benthophagous fish including ocean pout (*Macrozoarces americanus*), sculpins (*Myoxocephalus octodecemspinosus, M. scorpius*) and American plaice (long rough dab, *Hippoglossoides platessoides*). In coastal waters, even pelagic feeders such as smelt (*Osmerus eperlanus, O. mordax*) may have high sealworm densities (Templeman et al . 1957; Landry and Hare 1990; Möller and Klatt 1990).

In laboratory experiments, larval *P. decipiens* have been transmitted via gammaridean amphipods to alewife (*Alosa pseudoharengus*), Atlantic salmon (*Salmo salar*), brook trout (*Salvelinus fontinalis*), smelt, cod, pollock (*Pollachius virens*), mummichog (*Fundulus heteroclitus*), Atlantic silverside (*Menidia menidia*), threespine stickleback (*Gastosteideus aculeatus*), cunner (*Tautogolabrus adspersus*), grubby (*Myoxocephalus aenaeus*) and winter flounder (*Pseudopleuronectes americanus*) (McClelland, unpublished data). Sealworm larvae ≥ 2 mm in length were infective to fish but larger *P. decipiens* (>4 mm in length) were more successful in penetrating to the flesh. Results of experiments in which amphipods containing known numbers of sealworm larvae (the amphipods were inspected microscopically prior to being fed to the fish) were fed to trout, smelt, mummichog and stickleback, indicated that the majority (60-100 %) of the nematodes were successfully transmitted from amphipods to fish.

The minimum size or age of naturally infected fish hosts varies. Larval *P. decipiens* 3-4 mm in length have been reported in yearling cod from Icelandic waters (Pålsson 1979). In the Elbe estuary, smelt as small as 6 cm in length (5 months old) are infected (Möller and Klatt 1990) while witch flounder (*Glyptocephalus cynoglossus*) and long rough dab <15 cm in length may be infected in British waters (Wootten and Waddell 1977). Sculpins <10 cm in length from the Elbe estuary (Möller and Schröder 1987) and eastern Canada (McClelland et al. 1990) are also frequently infected. In eastern Canada, however, cod, sea raven and monkfish <25 cm in length are usually lightly infected and while various flatfishes, including American plaice and windowpane (*Scophthalmus aquosus*) are occasionally infected at <15 cm in length, the smallest infected grey sole (witch flounder) are usually >30 cm in length. Prevalence and abundance of sealworm usually increases with the size or age of the fish host but appears to be most strongly correlated to host size (Platt 1975). As studies on Icelandic cod show, abundances of ascaridoid larvae may vary significantly with the length of fish hosts belonging to a single cohort (Pålsson, unpublished data).

Larval sealworm abundances seem to be increasing in fish populations throughout the North Atlantic (Table 2), but examination techniques used in the time series shown were not consistent. In many surveys, particularly those conducted by industry, only the fillets were inspected. Scott and Martin's (1957) survey, for example, documents worm counts in graded cod fillets determined by routine candling procedures at eastern Canadian fish plants and with no effort to separate *P. decipiens* from *Anisakis simplex* larvae. In a survey conducted by Templeman et al. (1957) and in most recent scientific surveys, fillets were examined by slicing or systematic destruction of the flesh and lengths, weights and ages (sometimes) were recorded. Napes and belly flaps (hypaxial musculature surrounding the body cavity) were usually examined in recent surveys and infections in the body cavity were reported in some Canadian (McClelland et al. 1983a. b, 1985, 1990) and Icelandic studies (Pålsson 1979: Pålsson et al. 1985).

Longevity of *P. decipiens* in fish hosts is not known. In unpublished experimental studies (McClelland), larvae (2-5 mm in length) transmitted via amphipods to various

TABLE 2. Time series studies of larval sealworm (*Pseudaterranova decipiens*) infections in marine fish.

Location	Fish species	Time frame	Source	Trends in prevalence or abundance of larval *P. decipiens*
Iceland	*Gadus morhuo*	1937-38 1971-73 1975 1984 1985	Kahl (1939) Platt (1975) Pálsson (1979) Hauksson (1984) Pálsson et al. (1985)	inconclusive
Iceland	*G. morhua*	1963-present	Industrial data	- abundance increasing
Norway	*G. morhua*	1937-38 1978-1981	Kahl (1939) Bjórge et al. (1985)	- inconclusive
Germany	*Osmerus eperlanus*	1936 1984-present	Kahl (1936) Möller and Klatt (1990)	- prevalence increasing
Germany	*G. morhua* *Molva molva* *Pallachius virens* *Sebastes* sp.	1935-present	Industrial data	- stable from '35 to '82; dramatic increases since '82 but, no distinction between *P. decipiens* and *Anisakis simplex* larvae
Great Britain	*G. morhua*	1958-70 1968-70 1971-73 1978-1979	Rae (1972) Young (1972) Wootten and Waddel (1977) Smith and Wootten (1979)	inconclusive: no distinction between *P. decipiens* and *A. simplex* in Rae's study
Northeastern and southern Newfoundland	*G. morhua*	1947-53 1984	Templeman et al. (1957) McClelland et al. (1985)	- abundance increasing on Whale Bank
		1984-85	Chandra and Khan (1988)	- abundances increasing off Avalon Peninsula and off northeastern and southern Newfoundland
		1984-86	Brattey et al. (1990)	- abundance increasing off southern Newfoundland
Northern Gulf of St. Lawrence	*G. morhua*	1947-53 1984 1984-85	Templeman et al. (1957) McClelland et al. (1985) Chandra and Khan (1988)	abundance increasing
Southern Gulf of St. Lawrence	*G. marhua*	1947 1949-56 1980-1981	Templeman et al. (1957) Scott and Martin (1957) McClelland et al. (1983a)	no apparent change in abundance
Breton Shelf and eastern Scottian Shelf	*G. marhuo*	1947-53 1949-56 1982	Templeman et al. (1957) Scott and Martin (1957) McClelland et al. (1983a, b)	dramatic increases in abundance
Southwestern Shelf and Lower Bay of Fundy	*G. morhua*	1944-1956 1983-1984	Scott and Martin (1957) McClelland et al. (1985)	- abundance increasing on southwestern Scotian Shelf
Eastern Canada	*Hippoglassoides platessaides*	1947-53 1980-81 1983-84 1985-86 1987-88	Templeman et al. (1957) McClelland et al. (1983a) McClelland et al. (1985) McClelland et al. (1987) McClelland et al. (unpublished)	prevalence and abundance increasing off southern Newfoundland, in the Gulf of St. Lawrence and in the Breton and eastern Scotian Shelves
Breton Shelf and eastern Scotian Shelf	*Glyptocephalus cynoglossus*	1947-53 1980-1982	Templeman et al. (1957) McClelland et al. (1983a, b)	abundance increasing
Sable Island Bank	*G. morhua* *Melanogrammus aegelfinus* *Sebastes fasciatus* *G. cynoglossus* *H. platessoides* *Limanda ferruginea*	1947-53 1982-87	Templeman et al. (1957) McClelland et al. (1983b, 1985, 1987, 1990)	prevalence and/or abundance increasing

fish hosts, grew at a linear rate once established in the flesh. The nematodes reached 27 (23-31) mm in length after 8 wk in smelt maintained at 15°C, but over the same time frame and the same temperature, larvae in mummichog and winter flounder were only 10-20 mm in length. Growth rates at lower temperatures have not been determined, but if developmental rate-temperature relationships observed for hatching and larval growth in invertebrate hosts (above) are indicative, growth of sealworm larvae in fish at temperatures $\leq 5°C$ may continue for several months.

It is also not clear how long larvae persist in the fish host after reaching their maximum size. Groups of cod and smelt used as controls for the experiments above were still infected with viable *P. decipiens* of natural origin after 10 months in captivity on a diet of frozen herring (McClelland, unpublished data). In the U.K., herring retained viable *Anisakis simplex* infections after at least 60-61 wk and possibly >3 yr in captivity (Smith 1984). While moribund worms are frequently observed in naturally infected fish, they are, usually, greatly outnumbered by viable worms. Only 1 % of infected yearling smelt from the Elbe estuary hosted degenerating *P. decipiens* larvae; the proportion of 2-4-yr-old fish hosting degenerating sealworm was, however, 8 to 14 % (Möller and Klatt 1990).

Experimental transmission of *P. decipiens* to *Fundulus heteroclitus* resulted in a 30 % host mortality attributable to heavy infections in the viscera or invasion of the heart, dorsal aorta or central nervous system (McClelland, unpublished data). There is, however, no evidence of mortality in naturally infected fish. The condition factor of infected smelt in the lower Elbe is significantly lower than that observed in uninfected smelt (Möller and Klatt 1990) but, in contrast, the condition factor of Icelandic cod increases with sealworm abundance (Pálsson et al. 1985).

In light of experimental evidence of fish to fish transmission (Scott 1954) and the great natural abundances of the parasite in large piscivorous fish such as monkfish, cod and sea raven, it is apparent that *P. decipiens* may pass through two or more fish hosts. A recent study shows, however, that sealworm lose vigor on repeated transmissions through fish (Burt et al 1990a) and many, rather than reestablishing themselves in successive fish hosts, may simply be lost from the system. Moreover, seals feed primarily on smaller fish (SMRU 1984; Benoit and Bowen 1990b) and the second or third fish host, while heavily infected and a nuisance for fish processors, may not contribute significantly to parasite production (McClelland et al. 1990).

While general information on fish host biomass may be useful to our considerations of the dynamics of the parasite, data on available biomass of fish species in areas where seals feed, i.e., adjacent to haulouts, would perhaps be more pertinent. Special attention should be given to non-migratory species and to species commonly found in the diets of seals in the area. Fish surveyed should also be similar in size or age to those consumed by seals. It follows that more study is needed on the diets of seal hosts and that knowledge of the size or age of fish consumed by seals is as important as the specific identities of prey.

Much of the available information on *P. decipiens* infestation in natural populations has been documented in terms of host length strata. But given the variation in growth rate of a given host species in the North Atlantic and the considerable overlap in length between host age classes (des Clers 1989), more studies of worm count-host length variation within host cohorts would be desirable.

In view of the importance of environmental temperature as a rate-and range-limiting factor in the hatching and subsequent development of *P. decipiens* in cold-blooded intermediate hosts, there should be an effort to amass up-to-date information on geographical and seasonal trends for bottom temperatures in relevant areas of the North Atlantic.

Recent electrophoretic analyses of gene-enzyme systems in *P. decipiens* from North Atlantic fish and seals (Mattiucci and Paggi 1989; J. Brattey pers. comm.) have revealed the existence of three morphologically similar sibling species. In the northeast Atlantic, the adults of sibling A are usually found in grey seals (*Halichoerus grypus*), while harbour (*Phoca vitulina*) and bearded seals (*Erignathus barbatus*) appear to be primary definitive hosts of siblings B and C, respectively. Sibling B seems to be the predominant species infecting fish and (harbour and grey) seals from the northwest Atlantic although larvae of sibling C have been identified from cod collected off northern Labrador. Given the lack of opportunity for mixing of gene pools, northeastern and northwestern Atlantic populations of a sealworm sibling, e.g. *P. decipiens* B, may be distinct variants of the species differing in regard to host spectra and developmental rates. Clearly, comparative life history studies are required for northeastern and northwestern Atlantic populations of each sibling species.

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Effect of Temperature on Egg Hatching in Three Ascaridoid Nematode Species from Seals

John Brattey

Department of Fisheries and Oceans, Science Branch,
P.O. Box 5667, St. John's, Nfld., Canada A1C 5X1

BRATTEY, J. 1990. Effect of temperature on egg hatching in three ascaridoid nematode species from seals, p. 27-39. *In* W. D. Bowen [ed.] Population biology of sealworm (*Pseudoterranova decipiens*) in relation to its intermediate and seal hosts. Can. Bull. Fish. Aquat. Sci. 222.

Eggs of *Pseudoterranova decipiens* from grey seals (*Halichoerus grypus*), and *Contracaecum osculatum* and *Phocascaris phocae* from harp seals (*Phoca groenlandica*) were incubated in seawater at various constant temperatures from 1.7 to 12.0°C and hatching times determined. Eggs of each species hatched at all temperatures and the proportion which hatched was similar at each temperature but differed among species. Mean time to hatch ranged from 16 d at 12.0°C for eggs of *P. decipiens* to 174 d at 1.7°C for eggs of *C. osculatum*. There was a declining curvilinear relationship between temperature and mean time to hatch for each species, but the shape of the curves differed among the species. Eggs of *P. decipiens*, which were smaller than those of the other two species, developed and hatched more quickly at all temperatures. For all species, incubation of eggs in seawater at −0.5°C for up to 3 mo did not reduce the percentage hatch when the temperature was subsequently increased to 12.0°C, compared to eggs incubated directly at 12°C. In those offshore areas off eastern Canada where *P. decipiens* is common, bottom temperatures are generally in the range 1.5-8.0°C and eggs of *P. decipiens* would require about 1-5 mo to hatch. In shallow inshore areas temperatures show a pronounced seasonal cycle; during summer when temperatures are generally above 12°C eggs would hatch within a few weeks, but during winter when temperatures are generally below 0°C development and hatching would probably be extremely slow or completely inhibited.

Des oeufs de *Pseudoterranova decipiens* provenant de phoques gris (*Halichoerus grypus*) et de *Contracaecum osculatum* et de *Phocascaris phocae* provenant de phoques du Groenland (*Phoca groenlandica*) ont et incubés dans de l'eau salée à différentes températures constantes variant de 1,7 à 12 °C, et le temps écoulé jusqu'à l'éclosion a été calculé. Des oeufs de chaque espèce ont éclos pour toutes les températures, et la proportion d'oeufs éclos était similaire à toutes les températures mais variable selon l'espèce. La durée moyenne de l'incubation a varié de 16 jours à 12 °C pour les oeufs de *P. decipiens*, à 174 jours à 1,7 °C pour les oeufs de *C. osculatum*. Une relation curviligne inverse a été relevée entre la température et le temps moyen d'éclosion pour chaque espèce, mais la forme des droites a différé selon l'espèce. Les oeufs de *P. decipiens*, plus petits que ceux des deux autres espèces, se sont développés et ont éclos plus rapidement à toutes les températures. Chez toutes les espèces, l'incubation des oeufs dans l'eau salée à −0.5 °C pendant trois mois puis à 12 °C n'a pas réduit le pourcentage d'oeufs éclos, comparativement aux oeufs incubés dès le départ à 12 °C. Dans les régions au large de la côte est du Canada où *P. decipiens* est répandu, les températures sur le substrat varies généralement de 1,5 à 8 °C, et les oeufs de *P. decipiens* nécessiteraient environ 1 à 5 mois pour éclore. Dans les eaux côtières peu profondes, les températures fluctuent selon les saisons. En été, les températures sont habituellement supérieures à 12 °C, de sorte que les oeufs éclosent au bout de quelques semaines; par contre, en hiver, elles sont généralement inférieures à 0 °C, de sorte que le développement et l'éclosion sont probablement extrêmement lents ou complètement inhibés.

Ascaridoid nematodes of the genera *Contracaecum*, *Phocascaris* and *Pseudoterranova* are common in the gastrointestinal tract of pinnipeds in the North Atlantic. The taxonomy of these nematodes is somewhat confused and recent studies, using multilocus electrophoresis, have revealed several undescribed species among these genera infecting seals in the northeast Atlantic (Nascetti et al. 1986; Orecchia et al. 1986). In the northwest Atlantic (Canadian coast) species of *Contracaecum* and *Phocascaris* are found mainly in arctic or sub-arctic seals such as harp (*Phoca groenlandica*), hooded (*Cystophora cristata*), bearded (*Erignathus barbatus*) and ringed (*Phoca hispida*) seals (Lyster 1940; Myers 1957a, b; Scott and Fisher 1958). Sealworm (*Pseudoterranova decipiens*) has a more boreal distribution and is common in grey (*Halichoerus grypus*) and harbour (*Phoca vitulina*) seals, particularly in the Bay of Fundy, Scotian Shelf, Gulf of St. Lawrence, and off southern Newfoundland (Scott and Fisher 1958; Mansfield and Beck 1977; McClelland 1980; Stobo et al. 1990).

As far as is known the life cycle of species within each genus is similar; gravid female worms in the gastrointestinal tract of seals release eggs that are voided with the host's faeces. The eggs sink to the bottom, develop, and hatch releasing ensheathed (second stage ?) larvae that are ingested by invertebrates. Larval stages (second and third ?) occur in various species of invertebrate and marine fish.

The larvae of *P. decipiens* occur in the flesh of several species of marine fish (Templeman et al. 1957; McClelland et al. 1983a, b, 1985) and pose a chronic cosmetic problem for the commercial fishing industry off eastern Canada. Recent increases in the abundance of larval *P. decipiens* in eastern Canadian fisheries (McClelland et al. 1985, 1987; Brattey et al. 1990) have provided a stimulus for further research on the life history and population dynamics of the nematode. The purpose of the present study is to provide estimates of the time required for eggs of *P. decipiens* to develop and hatch over the range of temperatures encountered in waters off eastern Canada. This information would be a useful first step toward determining the generation time of *P. decipiens* in the natural habitat.

This paper (i) summarizes available data on bottom temperatures from various regions off eastern Canada, to determine the range of temperatures to which eggs of *P. decipiens* would normally be exposed, (ii) estimates hatching times of eggs over most of the natural temperature range, (iii) examines the effects of exposure to low temperatures (< 0°C) on percentage hatch of eggs, and (iv) compares the effect of temperature on egg hatching time of *P. decipiens* with that of *C. osculatum* and *P. phocae*. Myers (1960), Scott (1955), and McClelland (1982) provided some information on hatching times of *P. decipiens*, but the present study incorporates lower temperatures than those used previously. Aside from the paper by Davey (1969) little is known about the effect of temperature on egg hatching in *C. osculatum* and *P. phocae*.

Materials and Methods

Gravid females of *P. decipiens* were obtained from the stomach of a freshly killed adult grey seal obtained from Sable Island off Nova Scotia on May 19th, 1987; the other two nematode species were obtained from the stomach of an adult harp seal freshly killed (< 1 h) near St. Anthony, Newfoundland on February 26th, 1987. Whole worms were kept at < 4°C during the 32-36 h interval between collection and initiation of the experiments. The uterus of each gravid female was dissected out intact and washed twice in chilled (1°C) 0.85 % saline; the remainder of the worm was fixed and stored in glycerin alcohol. To release the eggs the uterus was torn apart in chilled (1°C), filtered seawater (32°/$_{oo}$). The eggs were transferred in approximately equal numbers to 10 wide-mouthed glass jars (75 mm bottom diameter by 120 mm height) each containing 250 mL of filtered seawater (32°/$_{oo}$). The jars were covered with lids provided with a small hole to minimize evaporation but permit exchange of air. Seven of the jars were placed in incubators at mean temperatures of −0.5, 1.7, 4.1, 6.1, 8.0, 10.0, and 12.0°C;

the remaining three jars were initially kept at −0.5°C then transferred to 12.0°C after 1, 2, and 3 mo, respectively. The procedure described above was repeated for five specimens of *P. decipiens* and three specimens each of *C. osculatum* and *P. phocae*. Mean temperatures were calculated from daily temperature recordings. Photoperiod was not controlled. The eggs adhered firmly to the bottom of the jars and the seawater was changed approximately every 3-4 d at 8.0, 10.0, 12.0°C, weekly at 4.1 and 6.1°C, and every 2 wk at −0.5 and 1.7°C. Eggs were examined daily by placing the jars directly under a stereomicroscope and counts were made of the number of hatched larvae, and the proportion of dead eggs, empty shells, and live but unhatched eggs in a small (1-2 cm^2) randomly selected area on the bottom of the jar. Small samples (~50) of unhatched eggs were also removed with a fine artist's brush and examined under a compound microscope to confirm whether the eggs contained developing larvae; dead eggs were easily recognized by their granular amorphous contents. The following information was calculated for each jar: days until first egg hatched, mean hatching time (days until 50 % of viable eggs hatched), percentage of eggs which hatched, duration of the hatching period. A small sample of eggs from one worm of each species was placed on a microscope slide with seawater and the length and width of 18-20 eggs was measured under a compound microscope at ×800 using an ocular micrometer; the length and width of 25 hatched larvae (excluding the sheath) from one individual of each species was determined in a similar manner, except that larvae were measured after fixation in neutral buffered 10 % formalin.

Since eggs of each nematode species were obtained directly from worms in the stomach of seals, rather than from seal faeces, the eggs used in the experiments would not have been exposed to passage along the host's intestine, as occurs in nature. Consequently, hatching times could be overestimated if further development of embryos occurred during passage along the host's intestine. To investigate this possibility faecal samples and stomachs were collected simultaneously from two freshly killed (<2h) heavily infected harp seals (for *C. osculatum* and *P. phocae*) and a grey seal (for *P. decipiens*) and immediately fixed in neutral-buffered 10 % formalin. Eggs in faecal smears were examined under a compound microscope (× 800) and stages of development compared with those of eggs removed directly from the uterus of gravid female worms in the stomach.

In view of the recent discovery of undescribed species among the nematode genera investigated here (see Nascetti et al. 1986; Orecchia et al. 1986) it was necessary to confirm the identity of the specimens used in the present study. Additional specimens from each genus were obtained from the stomach of grey and harp seals collected off eastern Canada and frozen (−60°C). These specimens were sent to Prof. Lia Paggi and coworkers at the Institute of Parasitology, University of Rome, Italy, for identification using multilocus electrophoresis. Their analysis indicated that grey seals from eastern Canada harboured *P. decipiens* Type B, whereas harp seals were infected with *C. osculatum* Type B and *Phocascaris phocae*. Therefore, it was assumed that these were the species used in the experiments reported here.

Water Temperatures

Bottom temperatures over an approximately 12-mo period (October 1984-September 1985) for four widely separated inshore locations off eastern Canada (Fig. 1, 2) were obtained from Walker et al. (1986, 1987). Temperatures in eight offshore areas (see Fig. 1, 3) were obtained from the Marine Environmental Data Service (MEDS), Ottawa. For each offshore area, all temperature records taken within 15 m of the bottom were extracted from the data base provided the depth sounding indicated that the temperature recording was taken within a specified depth range (see Fig. 3). For each area records obtained over several years were summarized by month (means ± one standard deviation).

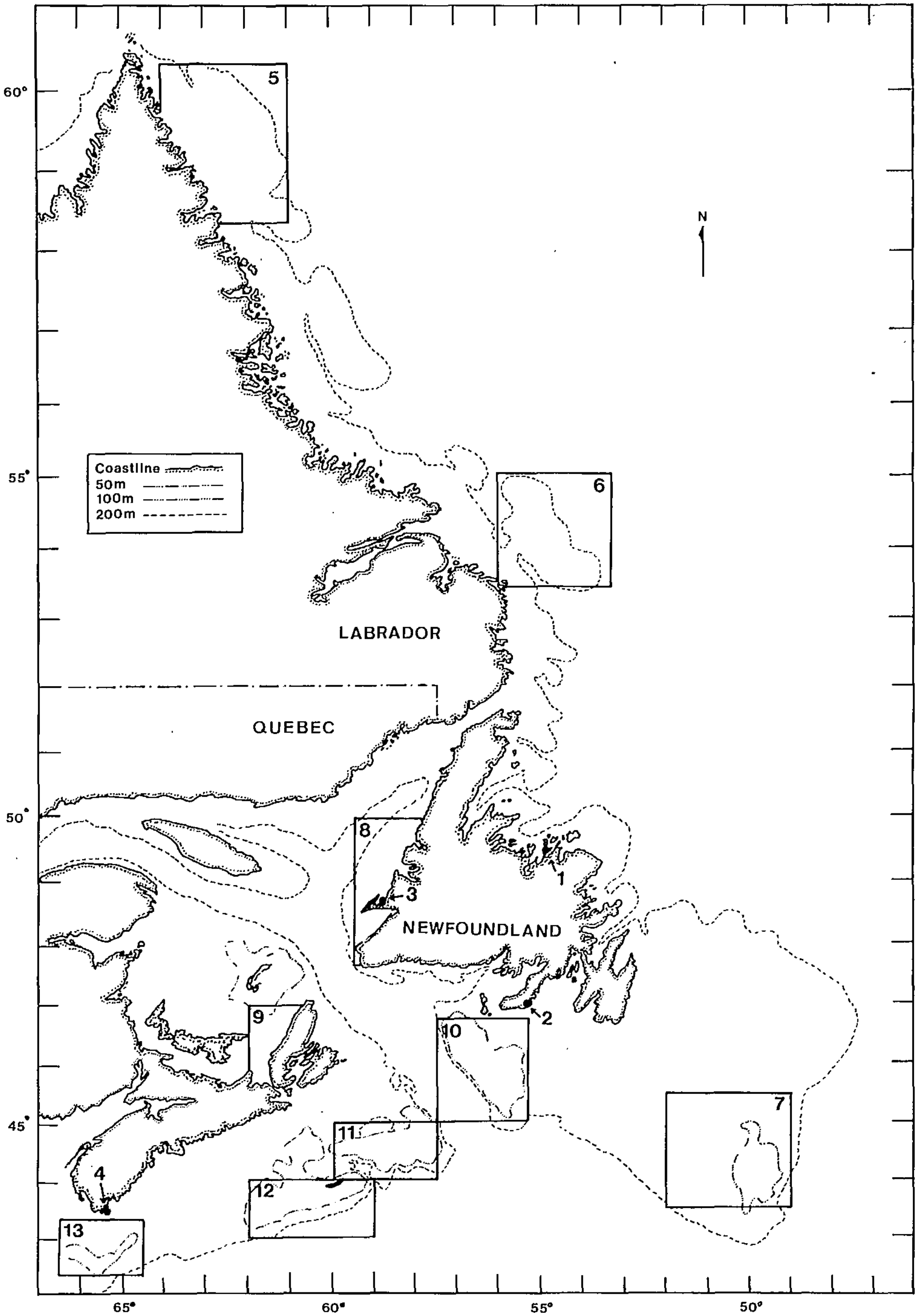

FIG. 1. Eastern Canada showing inshore locations (numbered 1-4) and offshore areas (5-13) from which temperature data were obtained (1 = Comfort Cove, 2 = Corbin cove, 3 = Port au Port, 4 = Cape Sable Island, 5 = Saglek Bank, 6 = Hamilton Inlet Bank, 7 = Grand Bank, 8 = North East Gulf of St. Lawrence, 9 = South East Gulf of St. Lawrence, 10 = St. Pierre Bank, 11 = Banquereau Bank, 12 = Sable Island Bank, 13 = Browns Bank and Baccaro Bank).

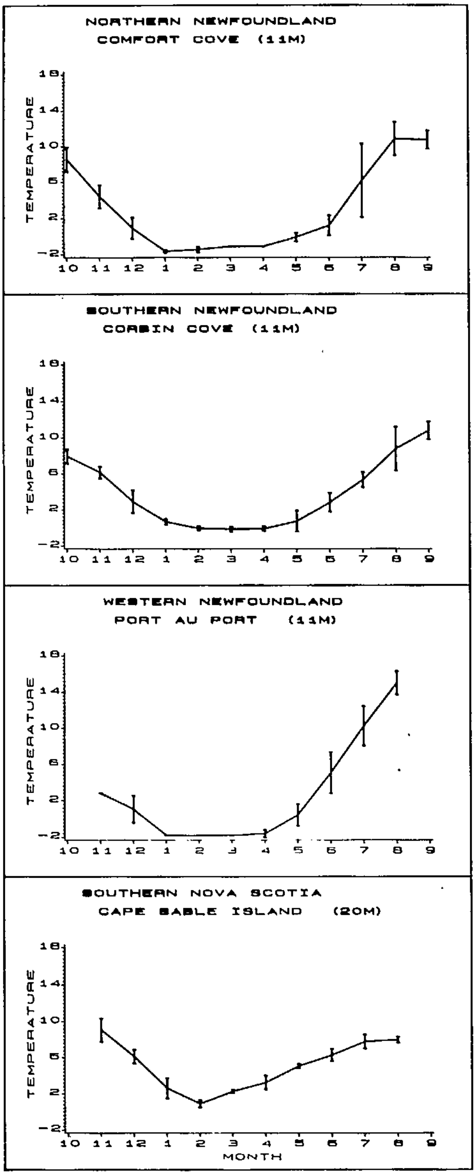

FIG. 2. Seasonal changes in bottom temperature (monthly means ± one standard deviation) during September 1984-October 1985 at four inshore locations off eastern Canada (see Fig. 1).

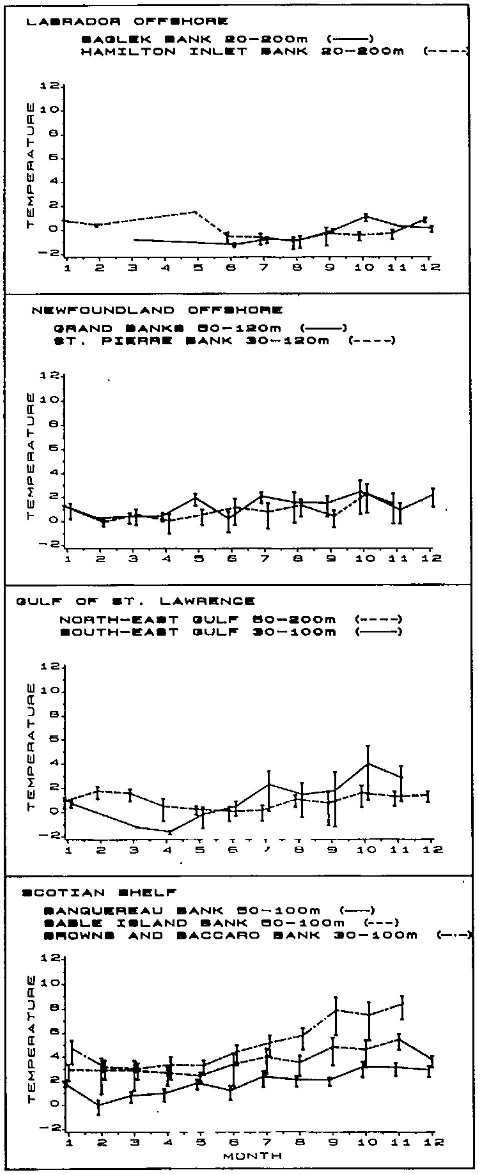

FIG. 3. Seasonal changes in temperature (monthly means ± one standard deviation, averaged over several years) within 15 m of the bottom for nine offshore areas off eastern Canada (see Fig. 1).

Statistical Analyses

The relationship between incubation temperature (*T*) and mean hatching time (*Y*) was non-linear for each nematode species (Fig. 4). Initially this relationship was modelled separately for individual worms of each species using Belehradek's (1935) equation of the form $y = a(T - \alpha)^b$, where a, b, and α are fitted constants (see McLaren 1963, McLaren et al. 1969 for discussion of the significance of these parameters). Although the model gave good fits to the data for each species ($r^2 > 0.9$) the assumptions of non-linear least squares regression were clearly violated in each instance by increasing variance at lower temperatures. Consequently, the model would not necessarily give accurate prediction of the hatching times of eggs from individual worms at lower temperatures. Hatching times were therefore $1/\sqrt{}$ transformed and the relationship modelled using a linear equation of the form $Y = a + bT$. The constants a and b were calculated using least squares regression after transforming Y. The appropriateness of the regression model was examined and tested by graphing residuals to check for skewness and constant variance. Initially, equations for individual worms of each species were calculated and compared using ANCOVA. There were no significant differences in slopes ($P > 0.05$) or elevations ($P > 0.05$) among worms within each species; therefore, data from individual worms were pooled and a common regression line was calculated for each species.

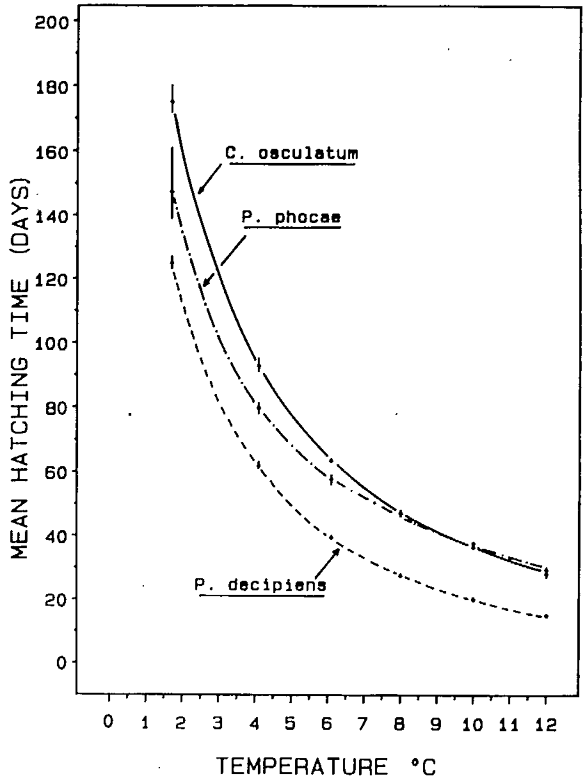

FIG. 4. Relationship between incubation temperature (°C) and mean time to hatch (t ± range, in days) for eggs of three species of ascaridoid nematode from seals. $n = 5$ at each temperature for *P. decipiens*, $n = 3$ at each temperature for *C. osculatum* and *P. phocae*.

Results

Dimensions of Eggs and Larvae

Eggs of each nematode species were sub-spherical and developing larvae were mostly at the 2-16 cell stage when eggs were removed from the uterus. Eggs in the faeces were at a similar stage of development to those removed directly from the uterus of the worm, indicating that no significant development occurred during passage along the intestine. Although lengths and widths of eggs differed significantly among the three species ($P < 0.05$, Table 1), eggs of *P. decipiens* were much smaller than those of the two arctic species. Lengths and widths of newly hatched larvae were variable (Table 1) but the means generally differed significantly ($P < 0.05$) among species; the only exception was for width of *P. phocae* versus *C. osculatum* ($P > 0.05$). An interesting finding was that the larvae of *P. phocae* were longer than those of *C. osculatum* even though *C. osculatum* had the larger eggs.

TABLE 1. Dimensions in microns (means ± one standard deviation) of eggs and hatched larvae of three species of ascaridoid nematode from seals. Means in the same row not sharing the same letter are significantly different ($P < 0.05$, Student-Newman-Keuls test). Eggs were measured fresh in seawater; larvae (excluding sheath) were measured after fixation in 10 % neutral buffered formalin.

		Nematode species		
		C. osculatum	*P. phocae*	*P. decipiens*
Eggs				
	n	20	20	18
	Length	$82.3^a \pm 4.21$	$78.4^b \pm 2.82$	$44.3^c \pm 0.91$
	Width	$73.0^a \pm 3.95$	$68.8^b \pm 2.40$	$40.2^c \pm 1.64$
Larvae				
	n	25	25	25
	Length	$407.0^a \pm 40.84$	$452.2^b \pm 33.02$	$189.4^c \pm 13.14$
	Width	$22.0^a \pm 5.69$	$21.9^a \pm 2.87$	$16.5^b \pm 1.62$

Water Temperatures

Bottom temperatures at each of the four inshore locations showed a pronounced seasonal cycle (Fig. 1, 2). Temperatures were generally below 0°C during the first 4 mo of the year in all locations except Cape Sable Island, Nova Scotia (~ 2°C). During April or May temperatures increased and monthly means reached a maximum of 12-14°C off northern and southern Newfoundland, 15°C off western Newfoundland, and 8-10°C off southwestern Nova Scotia. The slightly narrower range of temperatures recorded at the latter site may be due to the greater depth (20 m).

Monthly mean temperatures in the offshore areas showed little or no seasonal cycle and were consitently low (<8°C), although data were sparse for the most northerly areas and the southeast Gulf of St. Lawrence (Fig. 1, 3). Temperature variation within each month was often high, particularly for areas on the Scotian Shelf and off southern and southeastern Newfoundland; these areas may have been influenced periodically by warm water from the Gulf Steam. The variation within each month may also reflect differences in temperature among years and the wide range of depths within some of the areas. Nonetheless, the observed monthly means indicate a general north to south trend, with the coldest monthly means (−1 to 2°C) off Labrador, slightly warmer temperatures (1-4°C) off Newfoundland and in the Gulf of St-Lawrence, and the warmest temperatures (1.5–8°C) on the Scotian Shelf. There was also a general increase in bottom temperature from north to south among the three areas on the Scotian Shelf.

Hatching Times at Constant Temperatures

Eggs of each nematode species developed and hatched at all temperatures in the range 1.7–12.0°C (due to an incubator malfunction after 3.5 mo no hatching time was obtained for eggs kept at −0.5°C). Mean hatching times ranged from 16 d at 12.0°C for *P. decipiens* to 174 d at 1.7°C for *C. osculatum* (Fig. 4). Hatching times were similar for *P. phocae* and *C. osculatum* at temperatures above 6.0°C, but below 6.0°C eggs of *P. phocae* hatched more quickly. Eggs of *P. decipiens* developed and hatched more quickly than those of the two arctic species at all temperatures in the range 1.7–12.0°C.

For each nematode species there was a declining curvilinear relationship between incubation temperature and mean time to hatch (Fig. 4). The range of mean hatching times tended to increase at lower temperatures and the duration of the hatching period for eggs from individual worms increased from 2–3 d at 12.0°C to 4–5 wk at 1.7°C. However, the $1/\surd$ transformation removed the heteroscedasticity in mean hatching time and changed the relationship to a linaear one. For each nematode species the slope, b, was significantly different from zero ($P < 0.0001$). Although values of b for *C. osculatum* and *P. phocae* were similar (Table 2), ANCOVA revealed significant differences in slopes among all three species. The high values of the correlation coefficients (>0.993) suggest that other environmental factors such as photoperiod did not have a significant effect on hatching time form any of the nematode species.

TABLE 2. Parameter estimates for linear regression equations of the form $y = aT + b$ describing the relationship between incubation temperature and mean time to hatch for eggs of three species of ascaridoid nematode from seals. $Y = 1/\surd$ mean time to hatch in days, T = temperature in degrees Celsius (range 1.7 to 12°C), a and b are fitted constants, r^2 = coefficient of determination, SE = standard error of b, n = sample size.

Nematode species	Regression constants				
	a	b	SE	r^2	n
Contracaecum osculatum	0.059	0.011	0.0002	0.997	18
Phocascaris phocae	0.070	0.009	0.0002	0.993	30
Pseudoterranova decipiens	0.061	0.016	0.0006	0.999	30

Percentage Hatch at Constant Temperatures

The effects of nematode species and temperature on percentage hatch were investigated by two-way ANOVA after arcsin$\surd$ transformation. The effect of temperature and the interaction term were not significant (both $P > 0.5$) but nematode species had a significant effect on percentage hatch ($P < 0.001$). Percentage hatch was clearly much higher for *P. decipiens* (70–96 %) than for the other two species (25–65 %) at all temperatures (Fig. 5).

Effect of Exposure to −0.5°C

The effects of nematode species and number of months at −0.5°C on percentage hatch at 12.0°C were investigated as described above. Number of months at −0.5°C and the interaction term were not significant ($P > 0.1$) but nematode species had a significant effect on percentage hatch ($P < 0.001$). Percentage hatch was again much

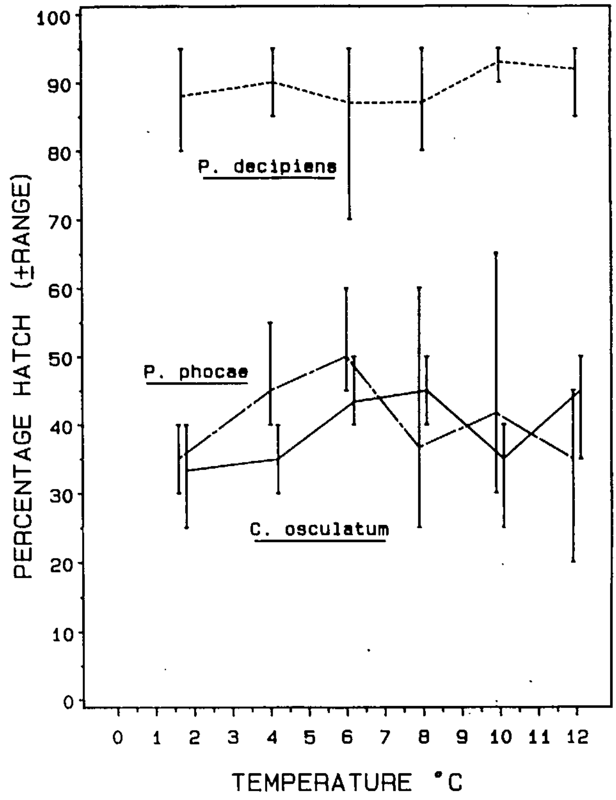

FIG. 5. Relationship between incubation temperature (°C) and percentage hatch for eggs of three species of ascaridoid nematode from seals. $n = 5$ at each temperature for *P. decipiens*, $n = 3$ at each temperature for *C. osculatum* and *P. phocae*.

higher for *P. decipiens* (72-96 %) than for the other two species (22-66 %) at all temperatures (Fig. 6).

Discussion

Eggs of the nematode species investigated here sink in seawater and would therefore be exposed to bottom temperatures during most of their development period. Although sinking rates have yet to be quantified, the eggs are probably not carried extensive distances beyond the point where they are released from the seal because larvae of the three species are rare in areas beyond the range of their respective definitive hosts. The eggs were also adhesive and readily adhered to the substrate which would prevent further dispersal after reaching the ocean bottom.

The nematode eggs would clearly be exposed to various temperature regimes in waters off eastern Canada. In the offshore areas monthly mean temperatures were generally low (−1.5 to 8.0°C) throughout the year and the temperature-hatching curves suggest that eggs of sealworm would require approximately 1-4 mo to hatch on the Scotian Shelf (temperatures of 1.5-8°C), 2-5 mo on the offshore areas in the Gulf of St-Lawrence and off Newfoundland (1-4°C), and >4 mo off Labrador (−1.5 to 2°C). While these general estimates of egg hatching time are probably reasonably accurate, more precise predictions of egg hatching times in the natural habitat should be avoided

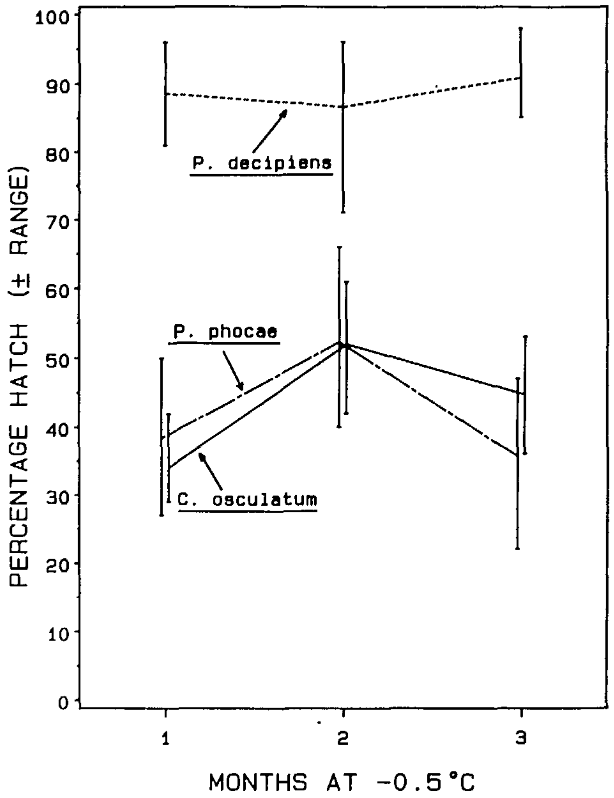

FIG. 6. Relationship between number of months in seawater at −0.5°C and percentage hatch when the temperature was subsequently increased to 12°C for eggs of three species of ascaridoid nematode from seals. n = 5 at each temperature for *P. decipiens*; n = 3 at each temperature for *C. osculatum* and *P. phocae*.

because the experiments were conducted at constant temperatures whereas eggs in the ocean could be exposed to wider fluctuations in temperature. Also the lower temperature threshold for development and hatching of eggs of each species remains unknown.

In the shallow (<10 m) inshore areas eggs would by exposed to extreme cold (<0°C) for 3-4 mo during winter followed by increasing temperatures in spring. Although hatching times of eggs deposited in these areas would therefore be difficult to predict without further experiments, present findings suggest that development of eggs in shallow inshore areas would be very slow or completely inhibited during winter. For eggs shed and retained in the inshore environment most development and hatching would probably be restricted to the warmer months; the results reported here and in McClelland (1982) suggest that eggs of *P. decipiens* shed inshore during summer would hatch within a few weeks.

Although the temperature hatching-time curves reported here suggest little intraspecific variation in mean hatching time of eggs, particularly at warmer temperatures (>4°C), the curves are based on eggs from a small number of females worms recovered from individual seals. Consequently, the influence of other factors such as host effects, seasonality, and worm burden on egg hatching remain to be investigated; these would possibly result in more variable hatching times than those reported here. Nonetheless, the results indicate distinct differences in the temperature-hatching time relationships among the three species of nematode. The most notable difference is that while the eggs of the two arctic species are larger, they develop and hatch more slowly than the smaller eggs of *P. decipiens* at all temperatures between 1.7 and 12°C. Eggs of *C. osculatum* also develop more slowly than those of *P. phocae*; therefore, the results are consistent with the general finding that large eggs tend to develop more slowly than small eggs among related organisms (Berrill 1935; McLaren 1965, 1966; Bottrell 1975).

The most enigmatic result of the experiments described here was the low percentage hatch among eggs of *C. osculatum* and *P. phocae*. The failure of some eggs to hatch could be attributed to their being not fully developed when removed from the uterus, particularly for eggs from the proximal end of the uterus nearest the ovaries; however, it is unlikely that this would account for more than a small proportion of the total uterine egg content. Also, in this laboratory a much higher percentage hatch of eggs has been observed among other specimens of *C. osculatum* and *P. phocae* obtained from other harp seals; therefore, the reasons for the low hatch success in the experiments remain unknown.

The declining curvilinear relationship between temperature and mean hatching time has been reported previously for *P. decipiens* (McClelland 1982) but is reported here for the first time for *C. osculatum* and *P. phocae*. Similar declining curvilinear relationships have been reported for other parasitic nematode species (Crofton 1964) and for other taxa including copepods (McLaren 1966), insects (Elliott 1978; Humpesch 1980), and ascidians (Berrill 1935). Hatching times reported here for *P. decipiens* at 4-12°C are similar to those described by McClelland (1982) and (Burt et al. 1990) but the present study extends the lowest known temperature at which eggs of *P. decipiens* will hatch down to 1.7°C. Although Myers (1960) reported that egg development in *P. decipiens* was inhibited at temperatures <4°C, Scott (1955) had previously shown that some development occurred after 27 d at 2-4°C. McClelland (1982) also showed that eggs of sealworm would develop and hatch at much higher temperatures (15-20°C) than those used here, and that temperatures >24°C were lethal to *P. decipiens*. The maximum temperature at which eggs of *C. osculatum* and *P. phocae* will develop and hatch has yet to be determined.

The temperature-hatching curves also indicate that the duration of the hatching time of each species increases rapidly at temperatures below about 4°C. Consequently, in waters north of Newfoundland, the eggs of each species would probably require several months to develop and hatch. McClelland (1982) and McClelland et al. (1985) suggested that the general scarcity of larval *P. decipiens* in the more northerly cod stocks was due to cold water temperatures retarding hatching and larval development and perhaps proving lethal to the embryos. Although present fundings indicate that most embryos of each species can tolerate up to three months at -0.5°C, clearly more information on temperature-hatching time relationships of *P. decipiens* below 1.7°C is needed before this hypothesis can be tested.

The estimates described here for egg hatching time at various temperatures provide a first step toward calculating the generation time of *P. decipiens* in various regions off eastern Canada. The only other stage in the life cycle for which survival time is available is the adult worm infection in seals (McClelland 1980). Experimental studies should therefore be undertaken to investigate the time required for growth and survival of the remaining components in the life cycle, namely larval stages in the various invertebrate and fish hosts.

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Pseudoterranova decipiens (Nèmatoda: Ascaridoidea): Time of Development to Hatching of Larvae at Different Temperatures and Salinities

M. D. B. Burt

Department of Biology, University of New Brunswick,
Fredricton, N.B., Canada E3B 6E1

J. W. Smith

Department of Agriculture and Fisheries for Scotland, Marine Laboratory,
Torry, Aberdeen, Scotland

A. Jarecka

Department of Biology, University of New Brunswick,
Fredricton, N.B., Canada E3B 6E1

A. W. Pike

Department of Zoology, University of Aberdeen,
Tillydrone Avenue, Aberdeen, Scotland

R. Wootten

Department of Agriculture and Fisheries for Scotland,
Marine Laboratory, Torry, Aberdeen, Scotland

and G. McClelland

Fish Health Laboratory, Department of Fisheries and Oceans,
Lower Water Street, Halifax, N.S., Canada

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Eggs of *Pseudoterranova decipiens* (Nematoda: Ascaridoidea) start hatching in 5 d at 22°C but take at least 57 d to start hatching at 4°C. Neither the time taken to hatch nor the hatching success rate was influenced by the salinity of the water in which the eggs were incubated (full strength sea water of 34 $^{\circ}/_{\circ\circ}$ salinity; an equal mixture of seawater and distilled water of 17 $^{\circ}/_{\circ\circ}$ salinity; and distilled water). Survival times of larvae varied from 3 d at 22°C to at least 60d at 4°C in either seawater or the equal mixture of sea water and distilled water. In distilled water, however, larvae were dead after 2 d at 22°C and after 4 d at 4°C. Larvae hatched in either seawater or in the equal mixture of sea water and distilled water were infective to the marine harpacticoid copepod *Tisbe furcata*; larvae hatched in distilled water were infective to the freshwater cyclopoid copepod *Macrocyclops albidus*.

Les oeufs de *Pseudoterranova decipiens* (Nématodes: Ascaridoidea) commencent à éclore au bout de 5 jours à 22 °C, et jusqu'à 57 jours au moins à 4 °C. La salinité de l'eau dans laquelle sont incubés les oeufs (eau salée non distillée à salinité de 34 $^{\circ}/_{\circ\circ}$, mélange égal d'au salée et d'eau distillée à salinité de 17 $^{\circ}/_{\circ\circ}$, et eau distillée) n'a aucun effet sur la durée de l'incubation ni sur le taux de succès de l'éclosion. La période de survie de ces larves varie de 3 jours à 22 °C à au moins 60 jours à 4 °C dans l'eau salée ou dans un mélange égal d'au de mer et d'eau distillée. Toutefois, dans l'eau distillée, les larves meurent au bout de 2 jours à 22 °C et de 4 jours à 4 °C. Les larves écloses dans l'eau salée ou dans un mélange égal d'eau salée et d'eau distillée peuvent infester *Tisbe furcata*, copépode marin du sous-ordre des Harpacticoïdés, tandis que celles écloses dans l'eau distillée peuvent infester *Macrocyclope albidus*, copépode d'eau douce du sous-ordre des Cyclopoïdés.

Introduction

The marine ascaridoid nematode, *Pseudoterranova decipiens*, is increasing in abundance in the flesh of many benthic fish species caught off the Atlantic coast of Canada (McClelland et al. 1983). This increase in abundance is undoubtedly linked to the increase in abundance of the seal definitive hosts in which the worms mature and reproduce. Estimates of populations of grey seals, the most important species in the life cycle, show substantial increases over the past 25 yr to about 70 000 in 1984 with a continuing annual increase at least on Sable Island of about 13 % (Malouf 1986; Zwanenburg and Bowen 1990). Although intensities of infection in harbour seals are lower than in grey seals, the former seal species are also increasing in numbers, and may be important in the population dynamics of *P. decipiens* in shallow, inshore waters; it may be relevant that harbour seals frequently occur in estuarine waters of varying salinity. Preliminary work on the time of development of the eggs to hatching of larval worms in sea water was reported by McClelland (1982) for temperatures from 5 to 20°C.

In view of the importance of data on hatching times, larval survival, and infectivity of larvae not only in the sea, but also under estuarine (and possibly even fresh water) conditions, the present study was designed to: (1) examine hatching times over a broader range of temperatures than tested by McClelland (1982); (2) investigate hatching times and success of hatching in brackish and fresh water; (3) determine the viability of larvae hatched and maintained at different temperatures; and (4) determine if larvae, hatched in waters of different salinity, were infective to crustacean hosts.

Materials and Methods

Uteri and eggs were collected from gravid female *P. decipiens* recovered from a grey seal killed at Port Hood, N.S., the southern Gulf of St. Lawrence. The eggs and uteri were placed in a jar with sea water and kept on ice prior to being randomly divided into two, approximately equal, samples: one sample was maintained at the Department of Agriculture and Fisheries for Scotland (DAFS), Marine Laboratory, Aberdeen; the other sample was maintained in the Zoology Department, University of Aberdeen. Each sample was shaken and 10 mL subsamples of the suspension were pipetted into clean petri dishes.

The eggs and uteri were allowed to settle to the bottom of each petri dish and as much of the supernatant sea water as possible was pipetted off, without allowing the material to dry. About 50 mL of either sterilized sea water, or distilled water, or an equal mixture of both, was poured into the petri dishes and, as before, the supernatant was pipetted off after the material settled to the bottom. Another 50 mL of sterilized sea water, distilled water, or an equal mixture of both was added to each petri dish containing *P. decipiens* eggs and uteri and one subsample, in each of the three salinities, was kept covered in an incubator or temperature-controlled chamber at different temperatures. Each subsample contained more than 5 000 eggs.

One series of subsamples was maintained at the Marine Laboratory at 22, 14, 12, and 8°C; the other was maintained in the Zoology Department, at 21, 15, 11, 7, and 4°C.

Material was examined as follows: every day at 22, 21, 15, and 14°C; every second day at 12 and 11°C; every third day at 8 and 7°C; and every seventh day at 4°C.

TABLE 1. Hatching and survival time of *Pseudoterranova decipiens* larvae at different temperatures and salinities.

		Hatching times (days)			Larval survival (days post-hatching)			
Temp. °C	Salinity	Start of hatching	Ca. 50 % hatched	Ca. 85 % hatched	Active	Slowing	Very sluggish	Dead
22	S[a]	5	7	8	1	2	3	4
	S/F[a]	5	7	8	1	2	3	4
	F[a]	5	7	8	1	—	—	2
21	S	6	7	8	1	2	3	4
	S/F	6	7	8	1	2	3	4
	F	6	7	8	1	—	—	2
15	S	8	9	10	11	12	14	21
	S/F	9	9	10	7	8	14	21
	F	9	9	10	2	—	—	3
14	S	9	9	10	12	13	14	21
	S/F	9	9	10	7	8	14	21
	F	9	9	10	2	—	—	3
12	S	23	24	24	16	17	24	38
	S/F	19	20	21	16	17	24	38
	F	19	20	21	2	—	—	3
11	S	23	24	24	17	18	24	40
	S/F	20	21	22	17	18	24	40
	F	20	21	22	2	—	—	3
8	S	33	35	37	26	27	39	55
	S/F	32	35	37	26	27	39	56
	F	33	34	34	2	—	3	4
7	S	34	35	36	28	29	42	58
	S/F	34	34	36	28	29	42	58
	F	34	34	35	2	—	3	4
4	S	57	58	59	60+	worms still active at termination of experiment.		
	S/F	57	58	58	60+			
	F	57	57	58	2	3	3	4

[a] S = Sea water (34 °/∞ salinity); S/F = Equal parts sea water and distilled water (17 °/∞ salinity); F = Distilled water.

Estimates of the proportions of eggs hatched were made by counting hatched and unhatched eggs in five, wild M5 stereo microscope fields at x 50 magnification. It was not necessary to add water during the time of the experiment as the petri dishes were kept covered and evaporation was negligible.

In a subsequent experiment, adult female worms, collected from a grey seal from Grand Manan, N.B., were used as the source of eggs and these were maintained in salinities and at temperatures similar to those above. Larvae hatched from these eggs were used in experimental infections to determine whether they were infective. Larvae, hatched in sea water or in the equal mixture of sea water and distilled water, were fed to *Tisbe furcata*, a marine harpacticoid copepod; larvae hatched in distilled water were fed to *Macrocyclops albidus*, a freshwater cyclopoid copepod.

Results

Hatching times and larval survival times at each temperature and salinity regime are summarized in Table 1. Not all eggs were fertilized ahd only about 85 %, in any given subsample, hatched. Table 1 shows: (a) when hatching was first seen; (b) when about 50 % of all eggs had hatched; and (c) when hatching was completed (about 85 %). Although the terms "slowing" and "very sluggish" are arbitrary, they reasonably well describe the behaviour of virtually all of the worms, particularly at the lower temperatures. Often the worms would lie motionless but, as they were being examined, the concomitant temperature increase stimulated some of those initially presumed to be dead to start making feeble movements. In Table 1, the last column indicates the number of days post-hatching when all larvae in the given subsample were dead.

It should be noted that the times shown relate to the number of days that the material was under observation at the Marine Laboratory and in the Zoology Department. The material was already 11-d-old when the above series were started but it had been maintained on ice near 0°C throughout this time.

In the second experiment, times of hatching and larval survival at different temperatures agree with those above. The larvae that hatched in sea water and in the equal mixture of sea water and distilled water, at all temperatures, successfully infected *Tisbe furcata*; those that hatched in distilled water at all temperatures, successfully infected *Macrocyclope albidus*. In each case, the presumed L_2 larvae were liberated from the L_1 sheath and penetrated the gut wall of the respective copepod hosts and entered the host haemocoel.

Discussion

As may be seen from Table 1, eggs can develop, hatch and produce active and infective larvae in diluted sea water and even in distilled water. Moreover, development at 11 and 12°C is most rapid in distilled water. These differences in development time to hatch in different salinities are however, proportionately small. Although the hatched larvae do not survive long in distilled water (about 1 d at 21-22°C to about 5 d at 4°C) they can survive in an equal mixture of sea water and distilled water (about 17 $^{\circ}/_{\circ\circ}$ salinity) for as long as they survive in full-strength (34 $^{\circ}/_{\circ\circ}$) sea water. As seals (especially harbour seals) frequently inhabit estuarine waters and are not infrequently found in rivers, *P. decipiens* eggs released in these different habitats may represent a further source of infection. If fresh water or estuarine (brackish water) copepods become infected naturally then there is a correspondingly greater biotic potential for the parasite. It is interesting to note that two related ascaridoids have been reported to develop in hosts in fresh water, namely, *Contracaecum osculatum* in the landlocked Baikal seal (see Sudarikov and Ryzhikov 1951) and (experimentally) *Hysterothylacium aduncum* in rainbow trout, *Salmo gairdneri* (now known as *Oncorhynchus mykiss*) (see Yoshinaga et al. 1987).

Although we have shown that survival times of larvae, particularly at lower temperatures, can be long we do not yet know for how long they remain infective. For example, at 7°C larvae became very sluggish at about 42 d post-hatching. When these were warmed slightly (a result of examining them at room temperature) they became more active but it is not known wheter they were still infective. The worms kept at 4°C were still active in sea water after 60 d and were infective at least up to 48 d. The times of hatching compare favourably with those reported by McClelland (1982) who found hatching to occur in 8 d at 20°C and 52 d at 5°C. Wootten and Smith (unpublished data) found that hatching required 6-10 d at 20°C and 10-15 d at 15°C. The slightly earlier times found in the present study probably relate to the delay of 11 d before the eggs were started at the various temperature regimes. As this material was kept near 0°C during these 11 d, however, this delay did not have any major effect, advancing the hatching time by, perhaps, 10 % at the higher temperatures. This estimate is based on a subsequent experiment with eggs from worms recovered within 4 h of the post-mortem examination of a seal and in which the eggs hatched, at 14°C, in 10-11 d compared to 9-10 d in the series described above (Table 1).

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Larval Sealworm (*Pseudoterranova decipiens*) Infections in Benthic Macrofauna

Gary McClelland

Department of Fisheries and Oceans, Marine Fish Division, Bedford Institute of Oceanography,
P.O. Box 1006, Darmouth, N.S., Canada B2Y 4A2

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Larval sealworm (*Pseudoterranova decipiens*), 1.1-3.7 mm in length, were found in four (0.16 %) of 2 500 amphipods (*Gammarus lawrencianus* and *Unciola irrorata*) collected from the Northwest Arm, Halifax, N.S. In the laboratory, newly-hatched larvae of *P. decipiens* were transmitted directly to both species of amphipods but serial transmissions employing benthic copepods (*Halectinosoma, Tisbe, Ameira* and *Paracyclopina* spp.) as precursor hosts proved more efficient. Sealworm were also transmitted via copepod carrier hosts to polychaetes (*Phyllodoce* sp.), nudibranchs (*Coryphilla* sp.), mysids (*Mysis stenolepis*), cumaceans (*Diastylis polita*), isopods (*Edotea triloba*) and decapods (*Crangon septemspinosus* and *Palaemonetes vulgaris*). While sealworm larvae infecting mysids, cumaceans, isopods and decapods were invariably immobilized and destroyed by haemocytic encapsulation, those developing in amphipod haemocoels were seldom encapsulated. Sealworm did not seem to affect the growth, reproduction and survival of its amphipod hosts but chronically infected amphipods exhibited altered behavior. Growth of *P. decipiens* in amphipods was influenced by temperature and by a "crowding effect" in which nematode size was inversely related to intensity of infection. After 84 d in lightly infected (Intensity = 1-2) amphipods at 15°C, larval *P. decipiens* were 7.3 (5.9-10.1) mm in length and morphologically similar to suspected sealworm larvae naturally infecting marine macroinvertebrates.

Des larves de ver de phoque (*Pseudoterranova decipiens*) de 1,1-3,7 mm de long ont été trouvées dans quatre amphipodes sur 2500 examinés (*Gammarus lawrencianus* et *Unciola irrorata*), soit dans 0,16 % de l'échantillon, qui ont été prélevés dans le Northwest Arm à Halifax, N.-É. Au laboratoire, les larves nouvellement écloses de *P. decipiens* ont été transmises directement aux deux espèces d'amphipodes, mais les transmissions en série grâce à des copépodes benthiques comme hôtes précurseurs (*Halectinosoma, Tisbe, Ameira* et *Paracyclopina* spp.) se sont révélées plus efficaces. Le ver de phoque est également transmis par l'intermédiaire de copépodes comme hôtes précurseurs à des polychètes (*Phyllodoce* sp.), des nudibranches (*Coryphilla* sp.), des mysidacés (*Mysis stenolepis*), des cumacés (*Diastylis polita*), des isopodes (*Edotea triloba*) et des décapodes (*Crangon septemspinosus* et *Palaemonetes vulgaris*). Alors que les larves de ver de phoque qui infectaient les mysidacés, les cumacés, les isopodes et les décapodes étaient invariablement immobilisées et détruites par encapsulation hémocytique, celles qui se développaient dans les hémocèles des amphipodes étaient rarement encapsulées. Le ver de phoque ne semble pas avoir nui à la croissance, à la reproduction et à la survie de ses hôtes amphipodes, mais les amphipodes chroniquement infectés avaient un comportement altéré. La croissance de *P. decipiens* chez les amphipodes était modifiée par la température et par un «effet de foule» où la taille des nématodes était inversement reliée à l'intensité de l'infection. Après 84 jours dans des amphipodes légèrement infectés (intensité = 1-2) à 15 °C, les *P. decipiens* larvaires mesuraient 7,3 mm (5, 9-10,1) et ils étaient similaires, sur le plan morphologique, aux larves qu'on suspecte d'infester naturellement les macroinvertébrés marins.

Introduction

Larval sealworm, *Pseudoterranova* (*Phocanema, Terranova* or *Porrocaecum*) *decipiens*, have been described or tentatively identified in various marine benthic macroinvertebrates including a polychaete (Val'ter and Popova 1974), amphipods (Val'ter 1978; 1987), an isopod (Bjørge 1979), mysids (Scott and Black 1960) and a decapod (Uspenskaya 1963) but attempts to infect marine macroinvertebrates (amphipods, isopod, mysids, decapods, annelids, molluscs and echinoderms) with freshly hatched sealworm larvae were unsuccessful (Myers 1960). However, macroinvertebrate hosts of freshwater and marine ascaridoids may become infected via smaller precursor hosts such as copepods rather than by direct consumption of the larval nematodes (Overstreet 1983). Although records of natural sealworm infections in copepods are lacking, newly-hatched larvae of *P. decipiens* are infective to a broad range of benthic and epibenthic marine copepods in the laboratory (McClelland 1982). The objectives of the present study were to investigate the possibility that *P. decipiens* is transmitted to marine macrobenthos by copepod precursor hosts and, to describe the development of the parasite in suitable macroinvertebrate hosts.

Materials and Methods

Gravid female *Pseudoterranova decipiens* were collected from experimentally infected grey seals (*Halichoerus grypus*) housed in the Aquatron Laboratory, Dalhousie University, Halifax, N.S. (McClelland 1980) and from free-living grey seals from the Northumberland Strait, Cape Breton Island and the eastern Nova Scotia mainland. Procedures for incubation of ova and for collection, maintenance and exposure of marine copepods were similar to those described in an earlier study (McClelland 1982). Ova dissected from the vagina and uterus of the nematodes were transferred to finger bowls containing approximately 250 mL of fresh prefiltered seawater and incubated at 5, 10 and 15°C. Temperature, development of ova and the condition of ensheathed larvae emerging from the ova were monitored daily. Marine benthic and epibenthic copepods including the harpacticoids, *Halectinosoma* sp., *Tisbe furcata* and related *Tisbe* spp. and *America longipes*, and the cyclopoid, *Paracyclopina* sp., were collected from the Northwest Arm, Halifax. Two hundred copepods (one copepod cm^{-2} bottom area) and 20 000 ± 2 000 recently hatched ensheathed larvae of *P. decipiens* (approximately 100 nematodes cm^{-2} bottom area) were placed in 4 L jars of fresh prefiltered seawater with a thin sediment (1-2 mm deep) of fine organic detritus from the Northwest Arm. The detritus and the microflora and-fauna therein provided a source of food for the copepods as well as a substrate to which the ensheathed *P. decipiens* larvae could adhere. Copepods were exposed for periods of 24 h to 7 d at 5, 10 and 15°C. During incubation of ova and maintenance of ensheathed *P. decipiens* larvae and copepods, approximately 80 % of the seawater was replaced weekly at 5°C, every second day at 10°C and daily at 15°C.

Benthic and epibenthic macroinvertebrates were collected intertidally and sublittorally at depth <7 m, from rocky and sandy bottom and from loose sediment. Specimens from the Northwest Arm included errant polychaetes (*Phyllodoce* sp.), nudibranchs (*Coryphilla* sp.), cumaceans (*Diastylis polita*), isopods (*Edotea triloba*), amphipods (*Gammarus lawrencianus*, and *Unciola irrorata*) and decapods (*Crangon septemspinosus, Palaemonetes vulgaris*). Mysids (*Mysis stenolepsis*) and additional specimens of sand shrimp (*C. septemspinosus*) were collected from the Head of St. Margaret's Bay, Halifax County. One to 20 macroinvertebrates were placed in finger bowls containing 250 mL of seawater and 10 000 ± 1 000 recently hatched *P. decipiens* larvae (approximately 100 nematodes cm^{-2} bottom area) or in 4 L jars of seawater containing 20 000 ± 2 000 larvae (approximately 100 nematodes cm^{-2} bottom area). One to 20 macroinvertebrates were also placed in 4 L jars of seawater with 10-200 copepods previously exposed to recently hatched *P. decipiens* larvae. Exposures to ensheathed *P. decipiens* larvae or to infected copepods were of 12 h to 14 d duration. For studies of the parasite's growth rate, lab reared larval amphipods (*G. lawrencianus*) 2-3 mm in length were exposed directly to recently hatched nematodes for a maximum of 24 h. During and after exposure, macroinvertebrates were fed finely ground Tetramin™ Staple Food and approximately 80 % of the seawater in holding containers was replaced daily at 15°C, every second day at 10°C and every 5 d at 5°C. Unexposed macroinvertebrates were maintained on a Tetramin™ diet in 0.8 × 0.5 × 0.3 m fiberglass aquaria with a continuous flow (approximately 0.3 L min^{-1}) of fresh prefiltered seawater at ambient temperature.

Macroinvertebrates were sampled daily during exposure and at 5-28 d intervals following exposure to ensheathed *P. decipiens* larvae or infected copepods. Nematodes recovered by dissection of exposed and unexposed macroinvertebrates were preserved in hot glycerine alcohol, cleared in glycerine and subsequently identified, measured and counted. The nematodes were compared with preserved specimens of *P. decipiens* grown *in vitro* (in Eagle's MEM supplemented with foetal calf serum) during an earlier study (McClelland and Ronald 1974). Whole amphipods were fixed in 70 % ethanol and routinely dehydrated, cleared, embedded and sectioned at 5 µm; the sections were stained with H&E.

SYSTAT ANOVA and ANCOVA procedures (Wilkinson 1987) were employed in analyses of nematode abundance, growth and morphometry. Quantitative terms such as prevalence (P), abundance (A), and intensity (I) are defined according to Margolis et al. (1982).

Results

Natural Infections

Natural nematode infections were found in the gammaridean amphipods, *Gammarus lawrencianus* and *Unciola irrorata*, and in the isopod *Edotea triloba*. Single ascaridoid larvae occurred in the haemocoels of 11 of 2 000 *G. lawrencianus*, 9 of 500 *U. irrorata*, and 1 of 100 *E. triloba*. Three nematodes, 1.1, 2.3, and 3.7 mm in length from *G. lawrencianus* and a 2.1 mm specimen from *U. irrorata* proved to be *P. decipiens* while the remaining 17 nematodes from amphipod and isopod hosts were *Hysterothylacium* sp. larvae, 1.8-8.3 mm in length. Samples (n = 50-500) of polychaetes (*Phyllodoce* sp.), sea slugs (*Coryphilla* sp.), mysids (*Mysis stenolepis*), cumaceans (*Diastylis polita*), sand shrimp (*Crangon septemspinosus*) and grass shrimp (*Palaemonetes vulgaris*) were not infected.

Direct Transmission

The amphipods *G. lawrencianus* and *U. irrorata* readily consumed the ensheathed newly hatched larvae of *P. decipiens* and exsheathed nematodes were found in amphipod haemocoels after 12 h of exposure at 10 and 15°C and after 48 h at 5°C. Larval amphipods <5.0 mm in length were most susceptible to infection. The parasite was frequently found in the gut but rarely in the haemocoel of late larval instar or mature amphipods (≥5.1 mm in length). Apparently, only a small percentage of the nematodes ingested successfully exsheathed and migrated to the amphipod haemocoel. After being exposed to approximately 20 000 *P. decipiens* larvae for 7 d at 10°C, groups of 20 amphipods were infected with maximum total of 177 larvae , <1 % of the available nematodes (Table 1) The remaining nematodes were found fully or partially embedded in amphipod faecal tailings, indicating they had been ingested and passed by the crustaceans.

Pseudoterranova decipiens larvae were also consumed by other benthic crustaceans including mysids (*M. stenolepis*), sand shrimp (*C. septemspinosus*) and grass shrimp (*Palaemonetes vulgaris*). However, following exposures of up to 2 wk duration at 10 and 15°C, the parasite was not detected in the haemocoel of these latter crustacean species. Polychaetes (*Phyllodoce* sp.) and seaslugs (*Coryphilla* sp.) did not seem to ingest sealworm larvae.

TABLE 1. Direct and serial transmissions of *Pseudoterranova decipiens* larvae to benthic amphipods, *Gammarus lawrencianus* and *Unciola irrorata.*

Transmission	*Amphipod body length (mm)*[a]	*P. decipiens* in haemocoels of					
		G. lawrencianus (*n* = 20)			*U. irrorata* (*n* = 20)		
		P	A	I	P	A	I
Direct[b]	≤2.0	25	0.30	1-2	80	1.60	1-4
	2.1-5.0	55	1.85	1-9	100	8.85	3-22
	5.1-10.0	10	0.15	1-2	45	1.00	1-6
	≥10.1	0	0		5	0.05	1
Serial[c]	≤2.0	0	0		0	0	
	2.1-5.0	65	7.20	4-23	70	9.35	5-35
	5.1-10.0	100	69.60	12-157	100	56.95	8-116
	≥10.1	100	60.15	21-163	100	63.15	38-132

[a] Rostrum to telson.

[b] Groups of 20 amphipods exposed to 20 000 recently hatched *P. decipiens* larvae (~ 100 nematodes cm^{-2} bottom area) for 7 d at 10°C.

[c] Groups of 20 amphipods exposed to 200 copepods (one copepod cm^{-2} bottom area) for 7 d at 10°C; copepods previously exposed to *P. decipiens* larvae for 7 d at 10°C.

Serial Transmission

Pseudoterranova decipiens larvae were first detected in haemocoels of *G. lawrencianus* and *U. irrorata* after 3-5 d of exposure to infected copepods at 10 and 15°C and after 5-12 d exposure at 5°C. Intact copepods were found in amphipod foreguts and larval *P. decipiens* were observed escaping from partially digested copepods and penetrating the wall of the fore- and midgut. The parasites were most numerous in the haemocoels of late instar and adult amphipods (>5 mm in length). First instar larvae (<2 mm in length) were incapable of ingesting whole copepods and did not become infected (Table 1).

Viable *P. decipiens* larvae often occurred in dead and degenerating copepods recovered from the detritus in the exposure vessels and thus, amphipods may have become infected primarily by scavenging on copepod remains. Prolonged observation of amphipods during exposure revealed that they were, at best, chance or contact predators of copepods and did not actively pursue the smaller crustaceans.

Serial transmissions of *P. decipiens* to late instar and adult amphipods appeared to be extremely efficient. The majority of nematodes ingested by copepod carrier hosts were ultimately found in amphipods haemocoels. Following the first phase of serial transmissions described in Table 1, four control groups of copepods (*n* = 200) were infected with 1 607 to 2 021 *P. decipiens* larvae, approximately 7-11 % of the 20 000 ± 2 000 nematodes to which each group was exposed. The remaining nematodes were ensheathed and caudally attached to the detritus and did not appear to have been disturbed. Following the second phase of the experiment, four groups of amphipods (n = 20) were infected with 1 139-1 392 *P. decipiens* larvae, approximately 5-8 % of the nematodes available to copepod precursor hosts.

Frequency distributions of nematode counts in amphipods were positively skewed, the degree of skewedness varying with the mode of transmission (direct or serial) and the length of exposure (Fig. 1). However, the distributions were brought close to normality by a $\log_{10}(n+1)$ transformation. A three-way ANOVA on transformed data from Table 1, revealed that variations in nematode abundance with mode of transmission and amphipod length were highly significant ($P < 0.001$). Subsequent contrasts of *P. decipiens* abundace in the two amphipod species indicated that the parasite was significantly more numerous ($P < 0.001$) in *U. irrorata* than in *G. lawrencianus* following direct transmissions, but nematode abundances in corresponding length groups of the two amphipod hosts did not vary significantly ($P \geq 0.276$) following serial transmissions.

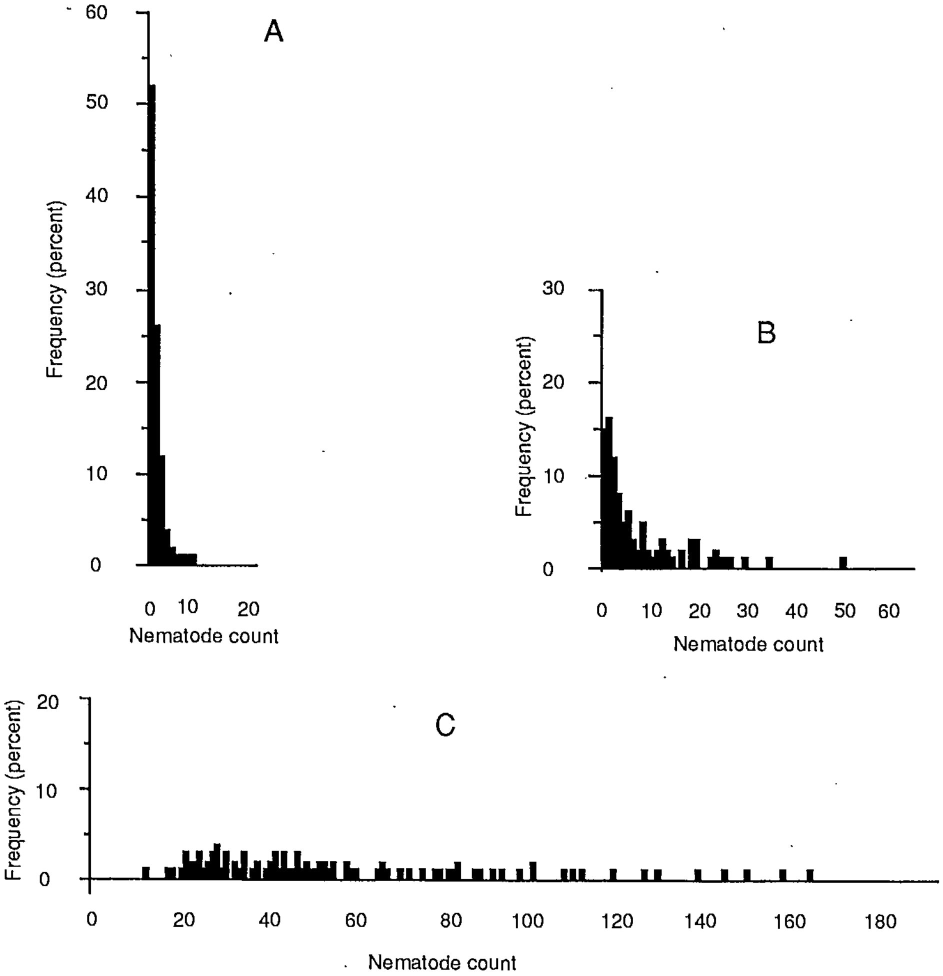


FIG. 1. Frequency distribution of counts of *Pseudoterranova decipiens* larvae in *Gammarus lawrencianus* (n = 100) after 7 d of exposure to (A) freshly hatched sealworm larvae, (B) copepods previously exposed to newly hatched sealworm for 24 h and (C) copepods previously exposed to sealworm for 7 d; all transmissions were conducted at 10°C.

Various macrobenthic species which were not susceptible to infection on direct exposure to *P. decipiens* larvae, became infected when exposed to copepod carrier hosts (Table 2). Mysids actively pursued and consumed infected copepods at 10 and 15°C and the prevalence of *P. decipiens* larvae in mysid haemocoels reached 100 % within 24 h of exposure. The parasite also occurred in the haemocoels of cumaceans, isopods, sand shrimp and grass shrimp, and in the coeloms of errant polychaetes and nudibranchs. In these latter hosts however, infections were detected only after prolonged exposure (7-14 d) at 10 and 15°C and were of low prevalence and intensity.

TABLE 2. Serial transmissions of *Pseudoterranova decipiens* to benthic macroinvertebrates.[a]

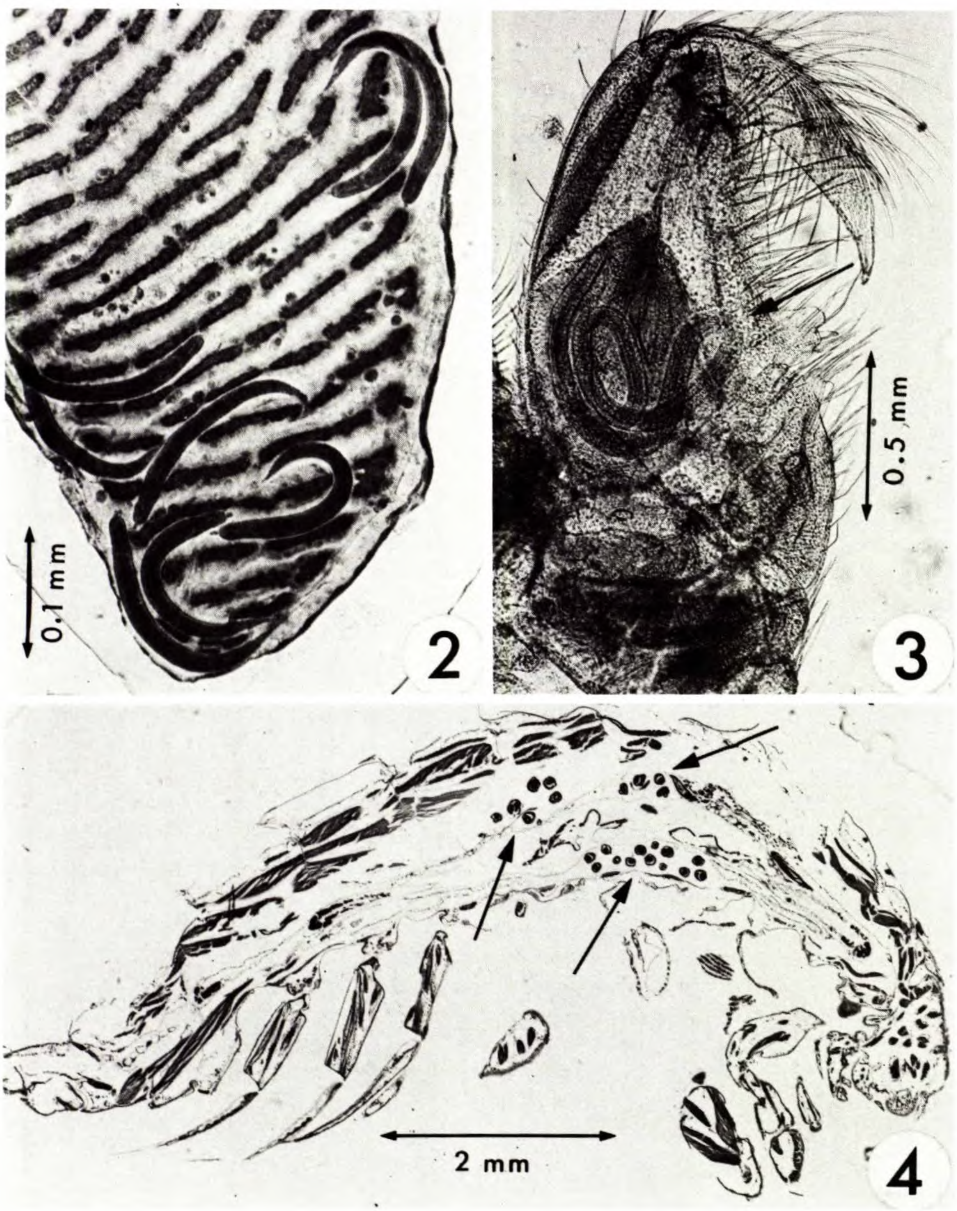
Host			Prevalence	Mean Intensity (range)
Species	Body length (mm)	*n*		
Annelida: Polychaeta				
Phyllodoce sp. (immature)	15-30	50	14	(1)
Mollusca: Gastropoda				
Coryphella sp. (juvenile)	10-20	50	8	(1-2)
Arthropoda: Crustacea				
Mysidacea				
Mysis stenolepis	30-40	50	100	9.9(3-27)
Cumacea				
Diastylis polita	5-10	50	6	(1)
Isopoda				
Edotea triloba	5-10	50	16	(1)
Decapoda				
Crangon septemspinosus	30-50	50	28	1.4(1-2)
Palaemonetes vulgaris	30-40	20	10	(1-2)

[a] Macroinvertebrates exposed individually to 10 copepods: mysids exposed for 24 h at 15°C, polychaetes, seaslugs, cumaceans, isopods and decapods for 7 and 14 d at 15 and 10°C, respectively; copedods previously exposed to *P. decipiens* larvae for 7 d at 10°C.

Larval *P. decipiens* were also transmitted serially to mysids (n = 20), sand shrimp (n = 10) and grass shrimp (n = 10) through copepod and amphipod precursor hosts with the resultant prevalence of the nematode in mysid and decapod haemocoels being 100 %. Such transmissions, however, were successful only when recently exposed amphiphods were used as precursor hosts, as nematodes which had grown >0.5 mm in length were usually damaged or destroyed by the mastificatory appartus of a mysid or shrimp.

Host-Parasite Interactions

In recently infected amphipods, *P. decipiens* larvae occurred pimarily in the thoracic haemocoel but were also found in the cephalic and abdominal sinuses and in the sinuses of cephalic, thoracic and abdominal appendages of heavily infected ($I \geq 10$) specimens (Fig. 2). In older infections, however, the nematodes had apparently outgrown the sinuses of all but the largest appendages (Fig. 3) and were confined to the thoracic and abdominal haemocoel. In lightly infected amphipods ($I \leq 5$), *P. decipiens* larvae were invariably located in the thoracic sinuses in proximity to the heart, midgut glands or coxal gills (branchial epipods of thoracic appendages) (Fig. 4).



FIGURES 2-4

FIG. 2. *Pseudoterranova decipiens* larvae, 200-300 µm in length, in coxal gill of heavily infected (I > 100), preserved specimen of *Gammarus lawrencianus*, following 7 d exposure to infected copepods at 10°C: cleared in glycerin and stained with methylene blue. FIG. 3. *P. decipiens* larva, approximately 2.5 mm in length, in gnathopod of heavily infected (I > 30), preserved *Unciola irrorata* male after 42 d (PE) at 15°C: cleared in glycerin. FIG. 4. Cross-sections of *P. decipiens* larvae in the thoracic haemocoel of mature *G. Lawrencianus* male after 42 d (PE) at 10°C: amphipod sectioned longitudinally at 5 µm and stained with H&E.

Larval *P. decipiens,* readily observed through the transparent amphipod integument in fresh whole mounts at 15°C, were fully extended and moving in a serpentine manner. At 5 and 10°C, the nematodes were spirally coiled and inactive at first but uncoiled and resumed activity after exposure to the warmth of the microscope stage. The fact that the nematodes consumed host haemolymph was evident from the rapid peristaltic contractions of their preventriculi and the conspicuous vortices in the haemolymph near their mouths.

The host haemocytic reaction to *P. decipiens* was most apparent in the amphipods with heavy infections ($I > 20$) of > 30 d duration. The haemolymph, clear and colourless in uninfected and lightly infected amphipods, appeared "milky" in heavily infected specimens. Examination of sectioned and stained specimens subsequently revealed that the "milkiness" was attributable to clusters of haemocytes and to other cellular and acellular debris suspended in the haemolymph. Haemocytes also lined the visceral serosae and sinus membranes. Only two instances of haemocytic encapsulation of *P. decipiens* were detected, however, and both occurred in heavily infected *U. irrorata* maintained at 10°C. In each case, the capsule was thin-walled and delicate and the loosely coiled worms within, large and robust.

While there was no mortality among larval *P. decipiens* in amphipod haemocoels, growth of the parasite was evidently retarded in multiple nematode ($I \geq 3$) infections. In infections of a given duration, the lengths of the nematodes were inversely related to the intensity of infection (Fig. 5). Nematodes from lightly infected ($I = 1$-2) *G. lawrencianus,* for example, were 3.0 (1.5-5.4) ($n = 20$) mm in length after 28 d at 15°C while those from heavily infected ($I > 20$) hosts were 1.1(0.4-1.6) ($n = 114$) mm in length.

Amphipods which were exposed to *P. decipiens* as 2-3 mm instar larvae subsequently grew to maturity and reproduced. There was no mortality among infected amphipods maintained for as long as 84 d post exposure (PE) at 15°C and 140 d PE at 5°C. Nor, evidently, was growth retarded in infected amphipods. After 56 d PE at 15°C, the body length of *G. lawrencianus* did not vary significantly ($P = 0.989$ for female and 0.184 for male amphipods) with intensity of sealworm infection (Table 3). The genitalia of

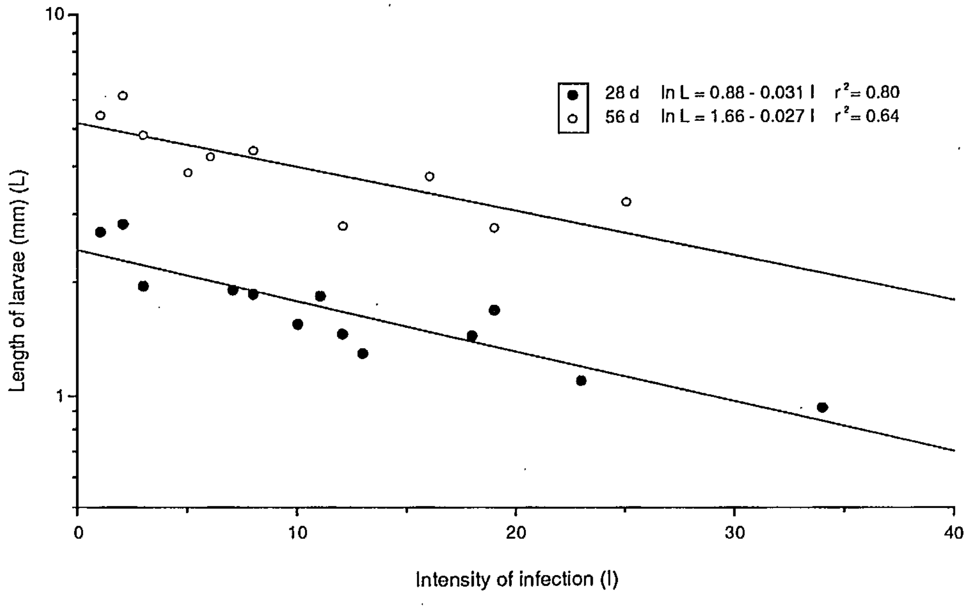


FIG. 5. Relationship of body length of *Pseudoterranova decipiens* larvae (mm) and intensity of infection in *Gammarus lawrencianus* after 28 and 56 d (PE) at 15°C.

even the most heavily infected amphipods appeared normal in sectioned material but the numbers of progeny produced by infected and uninfected hosts were not compared. Infected amphipods were indistinguishable from uninfected controls but for behavioral changes observed in the former at 30-40 d PE. Whereas uninfected amphipods were usually found foraging among the detritus, infected specimens often occurred off bottom, *G. lawrencianus* swimming lethargically near midwater level in their containers and, *U. irrorata*, clinging to the walls of their containers near the surface.

TABLE 3. Body length of mature *Gammarus lawrencianus* 56 d after exposure to *Pseudoterranova decipiens*) larvae.

Intensity of *P. decipiens* infection	Body length of host (mm)[a]					
	Females			Males		
	n	$\bar{x}$	(range)	*n*	$\bar{x}$	(range)
0	13	13.2	(10.3-15.0)	10	15.7	(13.9-17.4)
1-2	15	11.3	(9.8-15.0)	11	14.8	(12.7-19.7)
3-10	9	13.1	(10.5-14.7)	6	16.0	(13.6-18.4)
>10	6	12.8	(10.1-14.6)	10	14.4	(13.0-16.2)

[a] Amphipods were 2-3 mm in length at time of exposure and were maintained at 15°C.

Larval *P. decipiens* was more pathogenic in mysids. Fifteen (30 %) of 50 *M. stenolepis* died within 5 to 10 d PE, the casualities subsequently proving to be the most heavily infected (I $\geq$9) specimens. Death in each case was preceded by rapid melanization of the host integument and, in some instances, by erratic swimming behavior (whirling and spinning) attributable to the presence of nematodes in the compound eyes. In surviving mysids, however, *P. decipiens* infections succumbed to a host haemocytic response; by day 10 PE at 15°C, there were haemocytes adhering to the integuments of the nematodes and by day 20, all nematodes were moribund and fully embedded in clots attached to the hypodermis.

Larval *P. decipiens* infecting cumaceans, isopod and decapod hosts, although apparently nonpathogenic, were, nevertheless, attacked and destroyed by a haemocytic response within 20 d PE at 15°C. In juvenile polychaetes and nudibranchs, the parasites appeard to be nonpathogenic, and there was no evidence of a host response.

Growth and Development of *P. depiciens* Larvae

Recently hatched ensheathed larvae of *P. decipiens* were 208 (200-215) μm in length (n = 100) in fresh, heat relaxed condition and 140 (134-145) μm in length (n = 100) after fixation and clearing. With body length increasing at an exponential rate (Fig. 6), exsheathed larvae in the haemocoels of lightly infected (I = 1-2) amphipods at 15°C grew to 2.8 (1.4-5.4) mm in length (n = 28) in 28 d PE while those cultivated in an *in vitro* system at 15°C reached 2.4 (2.0-3.1) mm in length (n = 20) in 42 d. Nematodes growing in the haemocoels of lightly infected amphipods for 56 d PE at 10°C and 140 d at 5°C were 2.2 (1.5-4.2) (n = 20) and 1.8 (1.2-2.9) (n = 20) mm in length, respectively. ANCOVA indicated that the difference in the exponential growth rate of *P. decipiens* larvae in amphipods and *in vitro* at 15°C was highly significant (P <0.001 for nematode length-treatment interaction).

As they reached the 2-3 mm length range (Fig. 6), *P. decipiens* larvae infecting amphipods entered an asymptotic growth phase. Although the nematodes ultimately grew to 7.3 (5.9-10.1) mm in length (n = 8) after 84 d in amphipods at 15°C, daily length increments, 0.132 mm d^{-1} between days 28 and 42 PE, fell to 0.052 mm d^{-1} between days 56 and 84 PE. Larvae growing *in vitro*, on the other hand, entered a linear

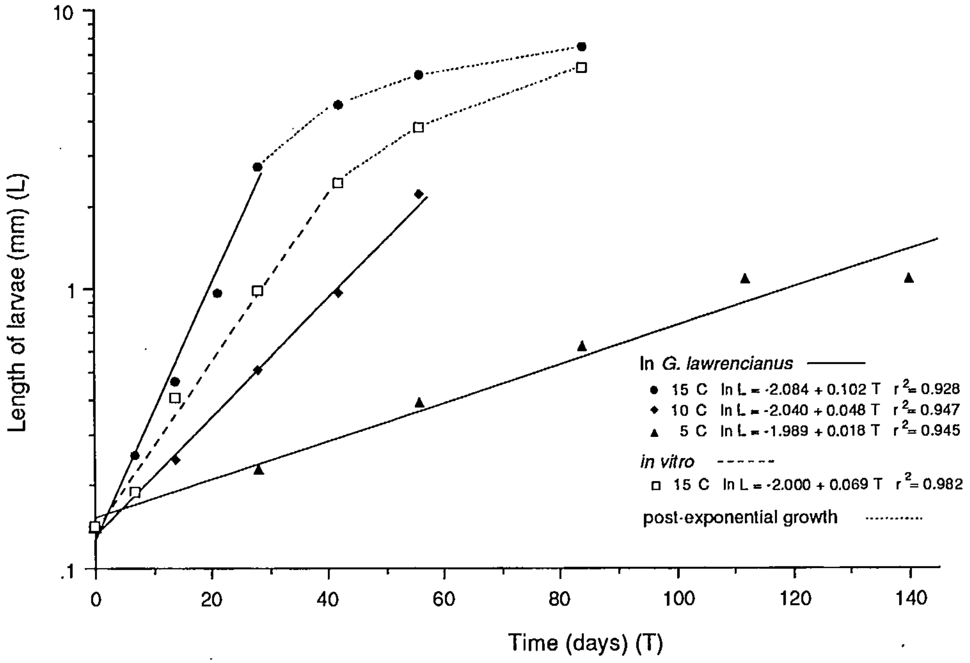


FIG. 6. Relationship of body length of *Pseudoterranova decipiens* larvae (mm) to time (days PE) in the haemocoel of lightly infected *Gammarus lawrencianus* at 15, 10 and 5°C and *in vitro* at 15°C.

growth phase on reaching the 2-3 mm length range. The linear growth rate *in vitro* between 42 and 182 d was 0.097 mm d^{-1} with the nematodes reaching 6.0 (5.5-7.4) mm in length (n = 20) after 84 d and 15.7 (13.9-17.6) mm in length (n = 20) after 182 d of cultivation.

Larval *P. decipiens* in mysids grew to a maximum length of 500 μm and those in cumaceans, isopods and decapods to a maximum length of 350 μm before succumbing to the host haemocytic response. Two *P. decipiens* larvae recovered from a juvenile sea slug on day 21 PE were 450 and 550 μm in length, respectively, while a third larva found in the coelom of a juvenile polychaete on day 42 PE was 1.4 mm in length.

Development of *P. decipiens* larvae in amphipod haemocoels was similar to that described for nematodes cultivated *in vitro* (McClelland and Ronald 1974). Elements of the gut including the preventriculus, ventriculus, intestine, rectum and associated glands, muscles and ligaments and surface features such as the cephalic and cervical papillae, excretory pore, amphids and phasmids were rudimentary or indistinct in freshly hatched larvae but had become well defined by the time the larvae had grown to 1 mm in length. The characteristic dorsal anteriad intestinal caecum had developed at the ventriculo-intestinal junction of larvae ≥1.5 mm in length and the genital primordium, unicellular in recently hatched *P. decipiens*, was multicellular and sexually dimorphic in nematodes >2 mm in length. The proximal end of the female primordium lay in the ventral hypodermis near the cuticle, while the bilobed distal end ran posteriad in the ventral pseudocoel. The male primordium was an elongate cylindrical structure with a recurved anterior end and lay in the sublateral hypodermis, parallel and ventral to the left lateral excretory canal. The parenchyma of three bilobed lips were distinctly visible beneath the cephalic cuticle in *en face* preparations of larvae >3 mm in length.

Although *P. decipiens* larvae from amphipod haemocoels appeared to be morphometrically similar to those grown *in vitro* (Fig. 7), ANCOVA revealed that the former

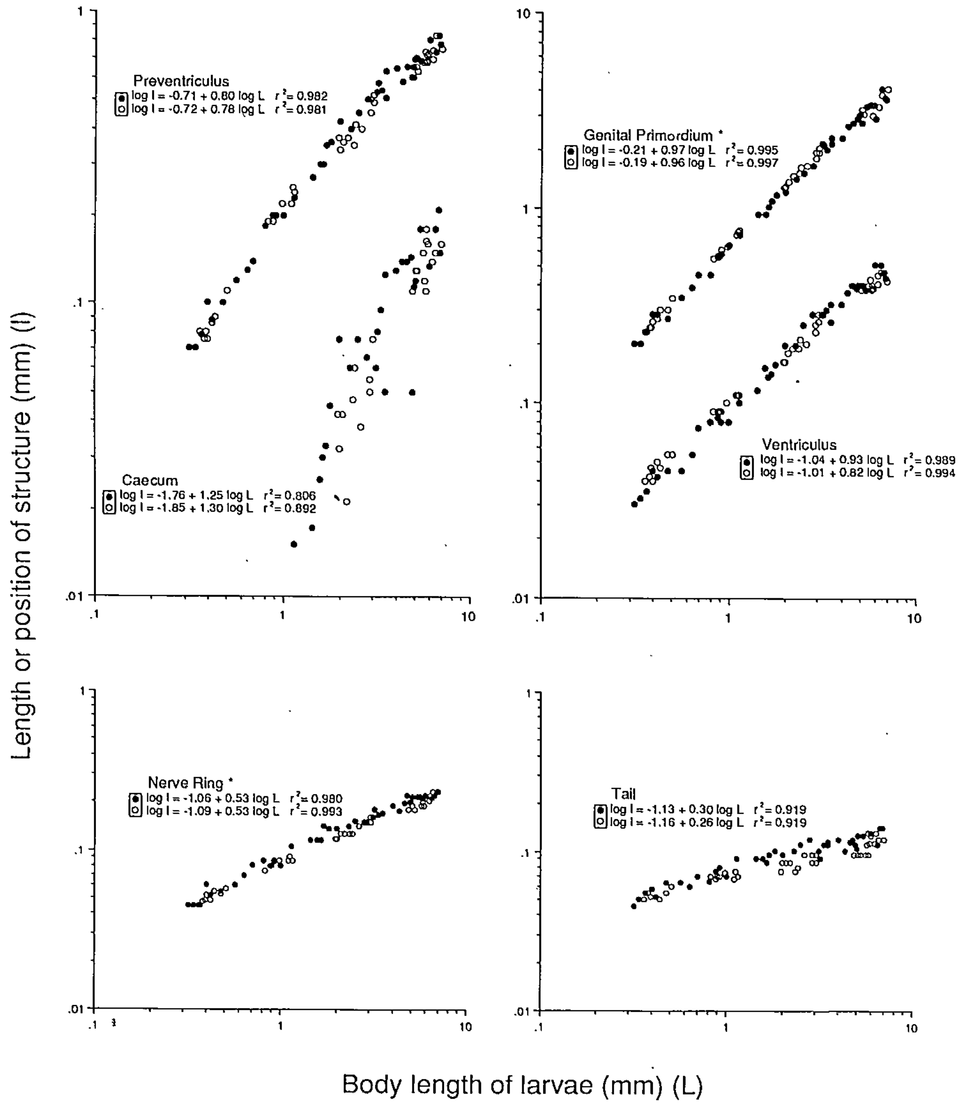


FIG. 7. Morphometric regressions for lengths or positions of various structures in *Pseudoterranova decipiens* larvae ($n = 40$) from the haemocoel of experimentally infected *Gammarus lawrencianus* (•) and from an *in vitro* (O): asterisk (*) indicates distance from anterior extremity.

differend from the latter in respect to morphometric regressions for ventriculus length ($P < 0.001$ for the ventriculus length-treatment interaction), tail length and position of the nerve ring ($P < 0.001$ for adjusted means). ANCOVA also indicated that nematodes ≥ 3.0 mm in length were sexually dimorphic in regard to the position of the genital primordium and tail length. The female primordium ($n = 21$) lay significantly anterior ($P < 0.001$) to the male primordium ($n = 21$) and the tail of female larvae was significantly longer ($P < 0.001$) than that of the males; taillength was 125 (110-140) µm ($n = 21$) in females, 100 (85-110) µm ($n = 21$) in males.

Pseudoterranova decipiens did not appear to perform a moult during development in amphipod hosts. Neither moulting nematodes nor cast cuticula were detected in the gut or haemocoel of amphipods, nor was there indirect evidence of moulting such as changes in the parasite's morphometric development which are usually indicative of the passage from one larval stage to the next.

Discussion

Marine ascaridoids use a wide range of invertebrates as intermediate or paratenic hosts. *Pseudoterranova decipiens* larvae have been detected in an errant polychaete (Val'ter and Popova 1975), various amphipod species (Val'ter 1978; Val'ter 1987; herein), and, possibly, in mysids (Scott and Black 1960), an isopod (Bjørge 1979) and a decapod (Uspenskaya 1963; Val'ter 1978). Harpacticoid and cyclopoid copepods (McClelland 1982) and, in the present study, an errant polychaete, a gastropod mollusc (nudibranchia) and various crustaceans (mysids, amphipods, isopods, cumaceans and decapods) proved susceptible to *P. decipiens* infection in laboratory experiments. *Anisakis* sp(p). larvae have been described from errant polychaetes, caprellid amphipods, euphausiids, caridean prawns and brachyuran crabs (Smith and Wootten 1978) as well as from sepioid, myopsid and oegopsid cephalopods (Smith 1984). *Hysterothylacium* sp(p.) larvae, the ascaridoids most frequently reported in marine invertebrates, have been found in benthic, planktonic and nektonic species beloging to no less than seven invertebrate phyla. Hosts of *Hysterothylacium* larvae include cnidarians (hydrozoans and scyphozoans), ctenophorans, molluscs (gastropods and cephalopods), annelids (polychaetes), arthopods (crustaceans), echinoderms (asteroids) and chaetognaths (Norris and Overstreet 1976).

As a given species of larval ascaridoid may occur in invertebrates occupying different trophic levels in marine food webs, it is probable that those parasites utilize not just one but two or more invertebrate hosts in series (Norris and Overstreet 1976, Overstreet 1983). Smith (1983; 1984), for example, speculated that euphausiid intermediate hosts of *Anisakis* sp(p.). larvae may be infected via copepod transfer hosts and that cephalopod paratenic hosts may become infected in turn by feeding on euphausiids. As demonstrated experimentally in the present study, transmission of *P. decipiens* larvae to benthic macrofauna is dramaticaly enhanced with the participation of a copepod precursor host. Further experiments showed that larval sealworm can be transmitted serially through copepods and amphipods to larger crustaceans suc has mysids (*Mysis stenolepis*), sand shrimp (*Crangon septemspinosus*) and grass shrimp (*Palaemonetes vulgaris*).

While records of natural *P. decipiens* infections in copepods are lacking, experimental evidence indicates that these meiofaunal crustaceans are involved in the transmission of larval sealworm to macrofauna. In the laboratory, newly hatched ensheathed sealworm larvae are readily consumed by and subsequently infect a variety of copepods, especially marine benthic harpacticoids and cyclopoids (McClelland 1982; Jarecka *et al.* 1988). The nematodes, approximately 200 µm in length (heat relaxed) exsheathe in the copepod gut and penetrate to the haemocoel where they begin to grow and develop. Within the brief life span of its copepod host, sealworm larvae reach a maximum of 300-500 µm in length (heat relaxed), not large enough (>2 mm in length) to infect a fish host (McClelland *et al.* 1983) but, as shown in the present study, capable of infecting various macroinvertebrates (polychaetes, nudibranchs, mysids, mature amphipods, isopods, cumaceans and decapods) which are not susceptible to infection on direct exposure to the free-living ensheathed larvae of the parasite. Growth of the sealworm larvae to 2.5 mm in length in an experimentally infected marine calanoid (*Tortanus discaudata*) (Jarecka *et al.* 1988) appears to be an exceptional case. It is unlikely, in any event, that a planktonic calanoid copepod in its natural environment would consume the newly hatched benthic larvae of *P. decipiens*. We cannot rule out the possibility, however, that sealworm might be transmitted to fish hosts by as yet unidentified benthic copepods which are of sufficient size and have sufficient life spans to accommodate sealworm growth similar to that observed in *T. discaudata*.

Temporary meiofauna such as early larval instars of the grammaridean amphipods, *Gammarus oceanicus* (Jarecka *et al.* 1988), *G. lawrencianus* and *U. irrorata* (this study) and zoaea larvae of the brachyuran decapods, *Cancer borealis*, *Hyas araneus* and *H. coarctatus* (Jarecka *et al.* 1988) have also proven susceptible to infection with freshly hatched ensheathed larvae of *P. decipiens*. In the present study, however, the great majority ($>$99 %) of sealworm larvae ingested by young amphipods failed to exsheathe and were subsequently passed with the faeces. Transmissions of larval sealworm to all but the smallest ($<$2 mm in length) of juvenile amphipods were more efficient when copepods were employed as precursor hosts. While considered excellent laboratory hosts for *P. decipiens* by Jarecka *et al.* (1988), zoaea larvae of crabs are planktonic in their free-living state and, like the calanoid copepod *T. discaudata* (above), are improbable natural hosts of a parasite with a benthic life cycle.

Although our knowledge of the natural transmission of larval sealworm by marine invertebrates is rudimentary at best, there is growing evidence that benthic and epibenthic amphipods play an important role. Natural sealworm infections have beem detected in the gammarids, *G. lawrencianus* (present study) and *Marinogammarus obtusatus* (Val'ter 1987), the corophid, *U. irrorata* (present study) and the caprellid, *Caprella septentrionalis* (Val'ter 1978) and laboratory experiments (present study) indicate that *G. lawrencianus* and *U. irrorata* are not only highly susceptible to *P. decipiens* infection but subsequently capable of accomodating significant sealworm growth and development. The apparent lack of pathogenicity exhibited by sealworm larvae in these two amphipod species is also indicative of a well developed host-parasite relationship. There was no host mortality and growth, maturation and reproduction of the host did not seem to be unfavorably influenced by the parasite. A host cellular response was evident only in the most heavily infected ($I > 20$) amphipods and this appeared to be directed to protection and repair of delicate visceral membranes rather than to parasite encapsulation. Other crustaceans which were susceptible to *P. decipiens* infection in this study proved to be unsuitable hosts for subsequent laboratory maintenance and development of the parasite. Heavy sealworm infections ($I \geq 9$) were, without exception, lethal to mysids (*M. stenolepis*) while infections with as few as a single nematode in mysids, isopods, cumaceans and decapods invariably provoked a host response in which the larval sealworm were immobilized and destroyed by haemocytic encapsulation similar to that which has been described in response to natural spirurid nematode (*Ascarophis* spp.) infections in decapods (Poinar and Hess 1977; Calderon-Perez 1986).

In discussing the evolution of nematode life cycles, Anderson (1988) speculates that, primitively, vertebrates (fish) were the intermediate hosts of aquatic ascaridoids and that invertebrates served as paratenic hosts. Anderson goes on to suggest that as a result of precocious development of larval ascaridoids in their primitive paratenic hosts, invertebrates may have replaced fish as intermediate hosts in some instances. *Anisakis* sp(p). larvae, for example, appear to develop to the infective stage (L_3) in krill (Euphausiacea) (Smith 1983). Baleen whales (Mysticeti), important definitive hosts of the parasite, may then become infected by preying on krill, a crustacean which they often consume in enormous quantities, while fish and squid which also prey on krill, assume the role of paratenic hosts, transmitting *Anisakis* to nekton — consuming definitive hosts, the toothed whales (Odontoceti). Similarly, it is possible that *P. decipiens* may be directly transmitted to definitive pinniped hosts by macroinvertebrate intermediaries. Despite their small size ($\leq$ 10 mm in length), sealworm which developed in experimental amphipod hosts in the present study and many of those naturally infecting marine invertebrates were clearly L_3 larvae (see also below). Larvae $>$ 3 mm in length are sexually dimorphic with respect to the morphology and position of the genital primordium and tail length, and possess an intestinal caecum and the primordia of L_4

lips. Larvae > 5 mm in length have proven capable of moulting to the L_4 *in vitro* (McClelland and Ronald 1974) and L_4s as small as 8 mm in length have been recovered from the stomachs of free-living seals (Boulva and McLaren 1979). Boulva and McLaren remarked that the young harbour seals (*Phoca vitulina*) hosting tiny L_4 larvae of *Pseudoterranova decipiens* were feeding, perhaps coincidentally, on small crustaceans including decapods (*Lebbeus groenlandicus* and *Pandalus* sp.) and unidentified amphipods.

The possibility that *Pseudoterranova decipiens* reaches the infective stage in an invertebrate host, however, does not detract significantly from the importance of fish hosts in the parasite's life cycle. Fish are clearly obligatory hosts of sealworm, not only in the ecological sense, in that they participate in the temporal and spatial dispersal of the parasite, thereby increasing the likelihood of the parasite being ingested by its definitive host, but also to the extent that they support significant larval growth (McClelland et al. 1983), thus improving the parasite's ability to establish itself and survive to maturity in the gastrointestinal tract of the final host. While apparently in the infective stage, larval sealworm from amphipod hosts herein and those naturally infecting marine macrofauna (Table 4) were barely as large as the smallest specimens (4-5 mm in length) detected in free-living cod (*Gadus morhua*) (Pálsson 1979). Sealworm larvae, as small as 2-5 mm in length, in invertebrate (prey) hosts, resume growth following transmission to fish (predator) hosts and ultimately reach > 30 mm in length in the latter hosts (McClelland et al. 1983).

There is much confusion as to the location of moults in the life cycles of aquatic ascaridoids but it is generally believed that the fist moult (M_1) occurs in the egg, the second (M_2) and possibly the third (M_3), in either fish or invertebrate intermediate hosts (Overstreet 1983; Smith 1983). It follows that nematodes emerging from the egg would be L_2s and those infecting definitive hosts, L_3s or L_4s. Assuming that sealworm is a "typical" nematode in regard to performing four moults in its life cycle, infective larvae of *P. decipiens* in fish and invertebrate hosts are L_3s and the final two moults (M_3 and M_4) in the parasite's maturation occur in the definitive host (McClelland 1980). Neither moulting nematodes nor cast cuticula, however, were detected in experimental amphipod hosts in the present study. Also lacking was indirect evidence of moulting such as changes in nematode morphometry similar to those associated with M_3 and M_4 in the final host (McClelland 1980). *In vivo* development of larval sealworm closely resembled that described in an *in vitro* study (McClelland and Ronald 1974) (Fig. 7) where freshly hatched *P. decipiens* exsheathed and developed directly to the infective stage without executing a moult. Thus, as previously surmised (McClelland 1982), sealworm may develop to the L_3 in the egg. Although considered a specialization (Anderson 1988), prehatch development to the L_3 has been reported in several ascaridoid genera (Maung 1978; Berry and Cannon 1981; Smith et al. 1983).

Given the inconsistencies in definition and usage of the term intermediate and paratenic hosts, particularly as they pertain to nematode life cycles, it is difficult to categorize the hosts of larval *P. decipiens*. If, in fact, larval sealworm which emerge from the egg are in the same stage (L_3) as those infecting definitive hosts, neither invertebrates (meio- and macrofaunal) nor fish can be considered true intermediate hosts of the parasite according to Overstreet's (1983) criteria, ie. hosts in which the larval nematode not only develops, but performs at least one moult. And yet, to refer to them (invertebrates and fish) as paratenic or even para-or metapartenic hosts (see Odening 1978) is to imply that they are not essential to the sealworm life cycle and that the parasite may be transmitted directly from seal to seal. As is clear in the discussions above, however, at least one intermediary, a macroinvertebrate, is obligatory in sealworm transmission while elements of physiological and ecological dependency are also evident in the nematode's relationship with copepod and fish hosts. Rhode's (1982) definition of an intermediate host as one which simply harbors the developing larval stage of a parasite

TABLE 4. Characteristic dimensions of suspected *Pseudoterranova decipiens* larvae naturally infecting marine benthic and epibenthic macrofauna.

Host		Nematode body length (mm)	Length or position of structure (mm)[a]					
Species	Source		Preventriculus	Ventriculus	Caecum	Nerve ring[b]	Genital[b] primordium	Tail
Lepidonotus squamatus	Val'ter and Popova (1974)	3.724	0.532*	0.245*	0.114*	0.189*	—	0.087
Mysis and *Erythrops* spp. and unidentified mysids	Scott and Black (1960)	4.300	0.660*	0.390*	—	—	—	—
		4.600	0.810*	0.560*	—	—	—	—
		4.700	0.620*	0.450*	0.160*	—	—	—
		5.500	0.700*	0.410*	—	—	—	—
		8.500	1.000*	0.560*	(0.080)?	—	—	—
Gammarus lawrencianus	present study	1.140	0.210*	0.095*	—	0.095*	0.660*	0.075*
		2.290	0.420*	0.200*	0.065*	0.150*	1.420*	0.090*
		3.700	0.590*	0.310*	0.115*	0.195*	2.150*	0.105*
Marinogammarus obtusatus	Val'ter (1987)	4.103	0.737*	0.319*	0.162	0.223*	2.134*	0.124*
Unciola irrorata	present study	2.100	0.440*	0.215*	0.040*	0.140*	1.320*	0.080
Caprella septentrionalis	Val'ter (1978)	5.808	0.693*	0.308*	0.118*	0.224*	—	0.110*

[a] Dimensions designated with an asterisk (*) lie within 95 % confidence intervals estimated from morphometric regressions for *P decipiens* from experimentally infected amphipods (Fig. 7).

[b] Distance from anterior end.

seems more appropriate in that it describes the copepod and fish hosts of sealworm as well as the macroinvertebrate hosts.

Larval parasitic helminths often seem to promote their own transmission by modifying the behavior of their crustacean hosts in ways which render the latter more susceptible to predation (Overstreet 1983). Copepods infected with the larvae of camallanid, philometrid and dracunculid nematodes, for example, become lethargic and remain near bottom where they may be more readily consumed by the fish hosts of the parasites (Moravec 1975; Uhazy 1977). Similar behavioral changes associated with *P. decipiens* infection observed in the present study, may have resulted in copepods being consumed by (primarily) detritivorous macroinvertebrates which they might otherwise have been capable of avoiding; only mysids pursued and captured natant copepods. As sealworm larvae usually remained viable in the decaying corpses of their former copepod hosts, it is also possible that detritivorous macrofauna become infected with the parasite by scavenging on copepod remains.

Whereas uninfected amphipods usually remained in the detritus, specimens with *P. decipiens* infections of > 30-40 d (PE) duration, often occurred off bottom, either swimming lethargically near midwater level (*G. Lawrencianus*) or clinging to the walls of their containers at the surface (*U. irrorata*). Erratic behavior such as swimming off the substrate or leaving the cover of detritus, rocks and vegetation, has previously been reported in amphipods hosting the larval stages of digeneans (Helluy 1984), cestodes (Sandeman and Burt 1972) and acanthocephalans (Bethel and Holmes 1973). Owing to their abnormal behavior, amphipods hosting larval helminths are more likely to be consumed by the vertebrate hosts of the helminths than are uninfected amphipods and, as a consequence, transmission of the helminths to their vertebrate hosts is enhanced (Bethel and Holmes 1976; Buckner et al. 1978; Kennedy et al. 1978). Assuming their behavior is similar to that displayed by infected laboratory hosts, free-living amphipods infected with larval *P. decipiens* would not only be more vulnerable to predation by the benthic consumers eg. gadid, cottid and pleuronectiform fishes which most frequently incur heavy sealworm infections but would also be available to predators such as smelt (*Osmerus mordax*) which, despite being pelagic feeders, often develop sealworm infections of greater density (numbers per unit weight) than those found in demersal fishes (Templeman et al. 1957).

In the laboratory, larval helminths developing in the haemocoels of crustacean hosts are often prone to "crowding effects" in which the size or growth rate of the parasite is inversely related to the intensity of infection (Shostak et al. 1985; Brattey 1986). Although unlikely to affect the growth of larval *P. decipiens* in natural crustacean hosts which are seldom infected with more than one asaridoid larva (Scott and Black 1960; Smith 1983; Hurst 1984; Val'ter 1987; herein), the influence of crowding on sealworm development was much in evidence in experimentally infected amphipod hosts in the present study (Fig. 5). Consequently, growth rates were computed for sealworm in lightly infected (I = 1,2) amphipods in order to provide the best approximation of the parasite's natural development.

Growth of larval helminths in crustacean hosts appears to be regulated to some extent by nutrient supply (Shostak and Dick 1985). Provided with an unlimited supply of nutrients in an *in vitro* system (McClelland and Ronald 1974), recently hatched exsheathed larvae of *P. decipiens* grew (in body length) at an exponential rate until they reached 2-3 mm in lenght and subsequently entered a prolonged phase of linear growth (Fig. 6). Larval sealworm in the haemocoels of lightly infected amphipods in the present study also completed an exponential growth phase upon reaching the 2-3 mm length range, growth *in vivo* at 15°C being somewhat more rapid than that observed *in vitro*. However, subsequent growth of the parasite *in vivo* was asymptotic. It is significant; perhaps, that the *in vivo* growth of sealworm became asymptotic at a time when the amphipod hosts were reaching maturity and, as a possible consequence of parasite induced behavioral changes (above), leaving the substrate, the source of their food. Thus, it would seem that having come into competition with host reproduction for diminishing nutrient supplies, larval sealworm were not capable of maintaining a (potential) linear rate of growth.

Development of *P. decipiens* in the egg and in crustacean hosts varies dramatically with temperature. The development time to hatch shows a declining curvilinear relationship with temperature and varies from 125 d at 1.7°C to only 8 d at 20°C (McClelland 1982; Brattey 1990). Embryonic development seems to be arrested at −0.5 to 1.0°C but even after prolonged periods (90 d) at temperatures in the latter range, development resumes when the temperature is elevated. As shown in the present (Fig. 6) and earlier studies (McClelland 1982), exponential growth in body length of larval sealworm in copepod and amphipod haemocoels is five to six times more rapid at 15°C than at 5°C.

Davey (1971) and Cheng (1976) speculate that temperature — dependent aspects of the life cycles of marine mammal ascaridoids, such as hatching and larval development in poikilothermic intermediate hosts, may influence the geographic distributions of the parasites. The fact that cod from northeastern Newfoundland, Labrador, Greenland and the Norwegian Arctic are seldom infected with larval sealworm (Templeman et al. 1957; Platt 1975), for example, may be attributable to retarded or arrested development of the parasite's eggs and larval stages in the cold waters found in these areas, rather than to a scarcity of suitable definitive hosts (McClelland 1982; McClelland et al. 1985). According to recent surveys (McClelland et al. 1983, 1985, 1987), however, geographic and temporal variations in abundance of sealworm in eastern Canadian groundfish seem most closely related to the distribution and population dynamics of a particular definitive host, the grey seal. Although moderate oceanic temperatures ($\geq$ 10°C) favor more rapid development of sealworm in the egg and in crustacean precursor hosts (McClelland 1982; present study), the foregoing surveys indicate that the parasite is becoming increasingly numerous in fish from waters (eg. southern Newfoundland and the Breton and Scotian shelves) where temperatures seldom exceed 5°C and may fall to $<$ 2°C for several months of each year (Drinkwater and Trites 1986, 1987; Brattey 1990).

Descriptions of the morphology and morphometry of early (L_3?) *P. decipiens* larvae from the present study should facilitate the identification of the parasite in natural invertebrate hosts. Larval nematodes naturally infecting mysids (Scott and Black 1960) and amphipods (herein) from Nova Scotian waters and those found in amphipods (Val'ter 1978; 1987) and a polychaete (Val'ter and Popova 1974) from the White Sea, USSR, are morphometrically consistent with sealworm larvae which developed in laboratory hosts (Table 4). Almost without exception, the characteristic dimensions (length of preventriculus, ventriculus, caecum, etc.) of the naturally occuring specimens fall within the 95 % confidence intervals of morphometric regressions computed for sealworm from experimentally infected amphipods.

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Geographic Distribution and Abundance of *Pseudoterranova decipiens* (Nematoda: Ascaridoidea) in the Musculature of Atlantic Cod, *Gadus morhua*, from Newfoundland and Labrador

John Brattey, Claude A. Bishop, and Ransom A. Myers

Department of Fisheries and Oceans, Science Branch,
P.O. Box 5667, St. John's, Nfld., Canada A1C 5X1

BRATTEY, J., C. A. BISHOP, AND R.A. MYERS. 1990. Geographic distribution and abundance of *Pseudoterranova decipiens* (Nematoda: Ascaridoidea) in the musculature of Atlantic cod, *Gadus morhua*, from Newfoundland and Labrador, p. 67–82. *In* W. D. Bowen [ed.] Population biology of sealworm (*Pseudoterranova decipiens*) in relation to its intermediate and seal hosts. Can. Bull. Fish. Aquat. Sci. 222.

The musculature of 12 652 Atlantic cod, collected in 21 regions around Newfoundland and Labrador during 1985–87, was examined for larval sealworm, *Pseudoterranova decipiens*. Infected cod were found in all regions. Larval *P. decipiens* were widely distributed throughout the musculature, but there were generally more in the left side and the percentage in the nape (= flesh surrounding the body cavity) increased with cod length. Prevalence and abundance were generally low (<18 % and <0.3 worms per fish) in cod collected off Labrador, northeast Newfoundland, and the Grand Bank; this homogeneity in distribution supports the suggestion that these fish form part of a common stock. Among cod from the south coast of Newfoundland, however, there was much greater geographic variability in the level of infection, including a general decline in prevalence and abundance from north to south across St. Pierre Bank, suggesting a more heterogeneous assemblage of stocks. High levels of infection (20–100 % and 0.3–22 worms per fish) among cod caught adjacent to the south coast of Newfoundland during winter were probably due in part to an influx of infected cod from the eastern Gulf of St. Lawrence. Abundances of nematodes, particularly larval sealworm, in the fillets of cod from southern Newfoundland were up to three times higher than those reported during 1947–53.

Les muscles de 12 652 morues de l'Atlantique, capturées dans 21 régions des environs de Terre-Neuve et du Labrador de 1985 à 1987, ont été examinés afin de déceler la présence de larves du ver du phoque *Pseudoterranova decipiens*. Des morues infestées ont été trouvées dans toutes les régions. Des larves de *P. decipiens* étaient largement distribuées dans tous les muscles, mais elles étaient généralement plus abondantes du côté gauche, et le pourcentage de larves dans la peau noire (membrane qui recouvre l'intérieur de la paroi abdominale) augmentait en fonction de la longueur du poisson. La prévalence et l'abondance étaient généralement faibles (18 % et 0,3 ver par poisson) dans les morues pêchées au large du Labrador, de la côte nord-est de Terre-Neuve et sur les Grands Bancs; cette homogénéité de la distribution appuie l'hypothèse que ces poissons appartiennent au même stock). Toutefois, parmi les morues capturées au large de la côte sud de Terre-Neuve, une variabilité géographique beaucoup plus grande a été relevée dans le taux d'infestation, y compris une baisse générale de la prévalence et de l'abondance du nord au sud sur le banc de Saint-Pierre, ce qui laisse croire à un assemblage plus hétérogène. Des taux d'infestation élevés (20 à 100 % et 0,3 à 22 vers par poisson) chez les morues prises dans les eaux adjacentes à la côte sud de Terre-Neuve durant l'hiver étaient probablement dus à l'afflux de morues parasitées de l'est du golfe du Saint-Laurent. L'abondance des nématodes, et en particulier du ver du phoque au stade larvaire, dans les filets de morue du sud de Terre-Neuve était jusqu'à trois fois supérieure à celle signalée entre 1947 et 1953.

Introduction

Parasitological surveys conducted during the early 1980's have shown that the abundance of larval sealworm, *Pseudoterranova decipiens* (formerly known as *Phocanema, Porrocaecum* or *Terranova*), in Atlantic cod, *Gadus morhua*, and other groundfish species off eastern Canada has increased considerably since the 1950's, particularly in the southeastern Gulf of St. Lawrence (NAFO Divisions 4S, 4T) and on the Cape Breton and Scotian shelves (4V, 4W) (McClelland et al. 1983a, b; 1985; 1987). However, there are several major cod stocks off Newfoundland and Labrador that were not examined for nematodes during these surveys.

This paper documents the results of an extensive survey of *P. decipiens* in the musculature of cod collected in 21 regions around Newfoundland and Labrador during 1985-87. The results are compared with a previous survey undertaken during 1947-53 (Templeman et al. 1957).

Materials and Methods

Sampling

Cod samples were collected during 1985—87 on Department of Fisheries and Oceans (DFO) research vessel cruises and from the commercial otter trawl fishery. Samples were taken widely over NAFO Divisions 2H, 2J, 3K, 3L, 3N, 3O and Subdivisions 3Pn and 3Ps (Fig. 1 and 2).

Commercial samples were examined at processing plants whereas research vessel samples were examined at DFO laboratories in St. John's. All individuals involved in the examination of cod were trained in the methods described by Templeman et al. (1957) for detecting nematodes. We duplicated the methods by strictly adhering to advice from several workers who were directly involved in the Templeman et al. (1957) study. Only the musculature of each fish was examined. Left and right fillet and nape (= muscle surrounding the body cavity) were examined on a candling table and the musculature of all but the smallest fish was sliced into thin strips during examination to reveal nematodes deeply embedded in the flesh. The approximate location of each nematode was recorded on a grid (Fig. 3) and all nematodes were fixed and stored in labeled vials of glycerin-alcohol. Most of the nematodes were easily identified by visual inspection; the largest brownish or yellowish worms were sealworm, *P. decipiens*, while the smaller tightly coiled specimens were *Anisakis simplex*. Specimens of uncertain identity were examined at x 100 magnification under a compound microscope after clearing in glycerin or lactic acid. Examination of approximately 500 specimens indicated that the visual inspection procedure was > 95 % accurate.

To determine the proportion of nematodes recovered by our examination procedures the flesh of 107 cod (Mean fork length ± SD = 57.6 ± 8.3 cm, range 42-107 cm collected in NAFO Subdivision 3Ps) was reinspected using a mechanical disintegration technique (Brattey 1988) which enables recovery of nematodes overlooked during candling and slicing. This procedure indicated that percentage recovery for *P. decipiens* during candling and slicing was 81 %. The proportion recovered was, therefore, comparable to that reported during recent surveys of nematodes in cod from other regions off eastern Canada (see McClelland et al. 1983a).

McClelland et al. (1983a, b, 1985) found that a small proportion (3 %) of the total *P. decipiens* burden occurred in the body cavity of cod rather than the flesh; also the proportion in the body cavity increased with cod size and was slightly higher for cod collected near Newfoundland. To determine the proportion of *P. decipiens* in the body cavity of cod in our survey, we examined for nematodes the viscera of 505 cod collected in Fortune Bay during January 1987. The mean fork length of the fish ± SD was

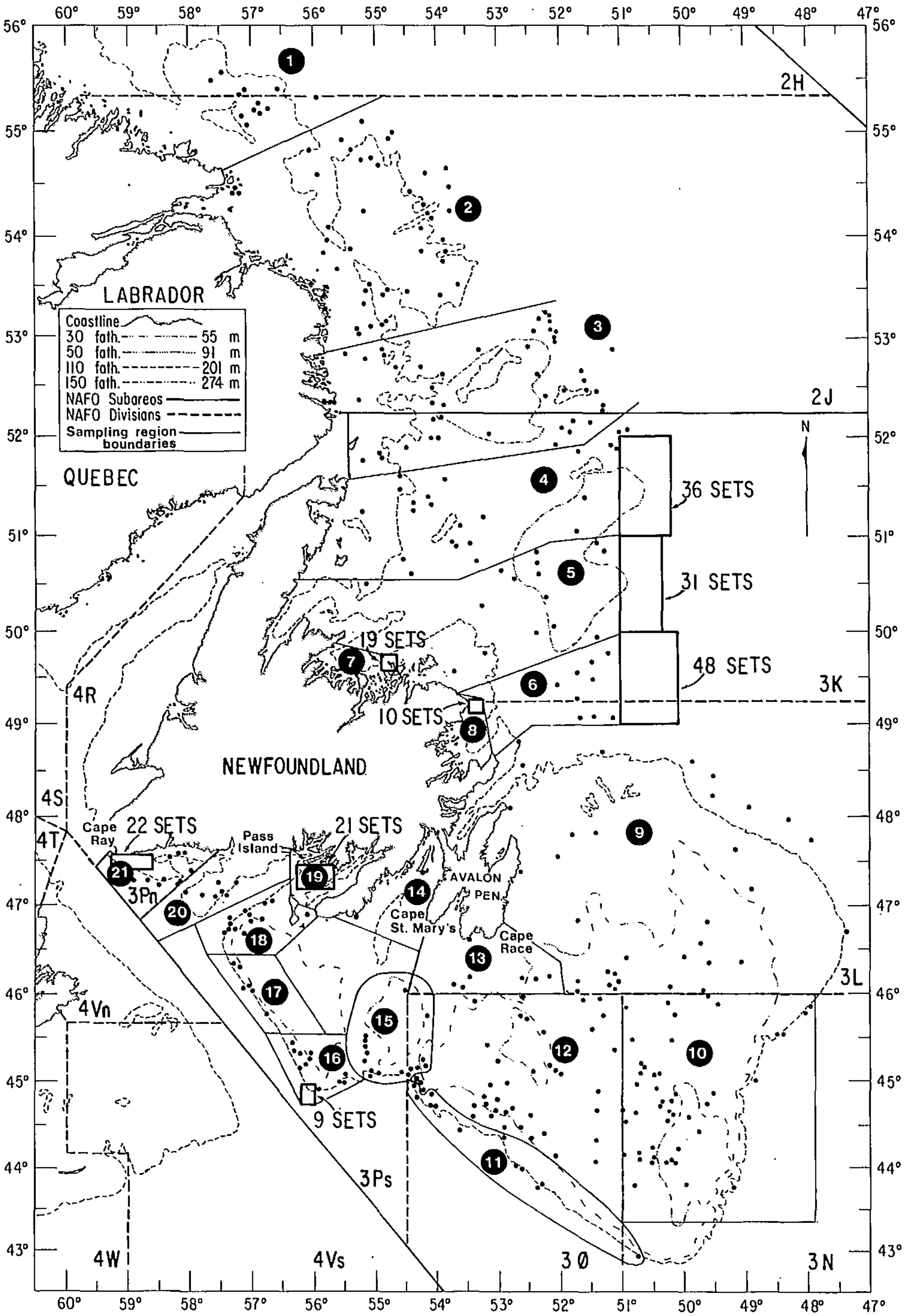


FIG. 1. Eastern Canada showing NAFO divisions and trawl locations (dots) from which samples of cod were obtained. Rectangles indicate boundaries of intensively sampled regions. Solid lines indicate boundaries of the 21 sampling regions (1 = Makkovic Bank, 2 = Hamilton Inlet Bank, 3 = Belle Isle Bank, 4 = northern Funk Island Bank, 5 = southern Funk Island Bank, 6 = northeast Newfoundland Shelf, 7 = Notre Dame Bay, 8 = Bonavista Bay, 9 = Grand Bank, 10 = southeast shoal of Grand Bank, 11 = southwest slope of Grand Bank, 12 = Whale Bank, 13 = southern Avalon, 14 = Placentia Bay, 15 = Green Bank, 16 = southern St. Pierre bank, 17 = western St. Pierre Bank, 18 = northern St. Pierre Bank, 19 = Fortune Bay, 20 = Burgeo Bank, 21 = Rose Blanche Bank).

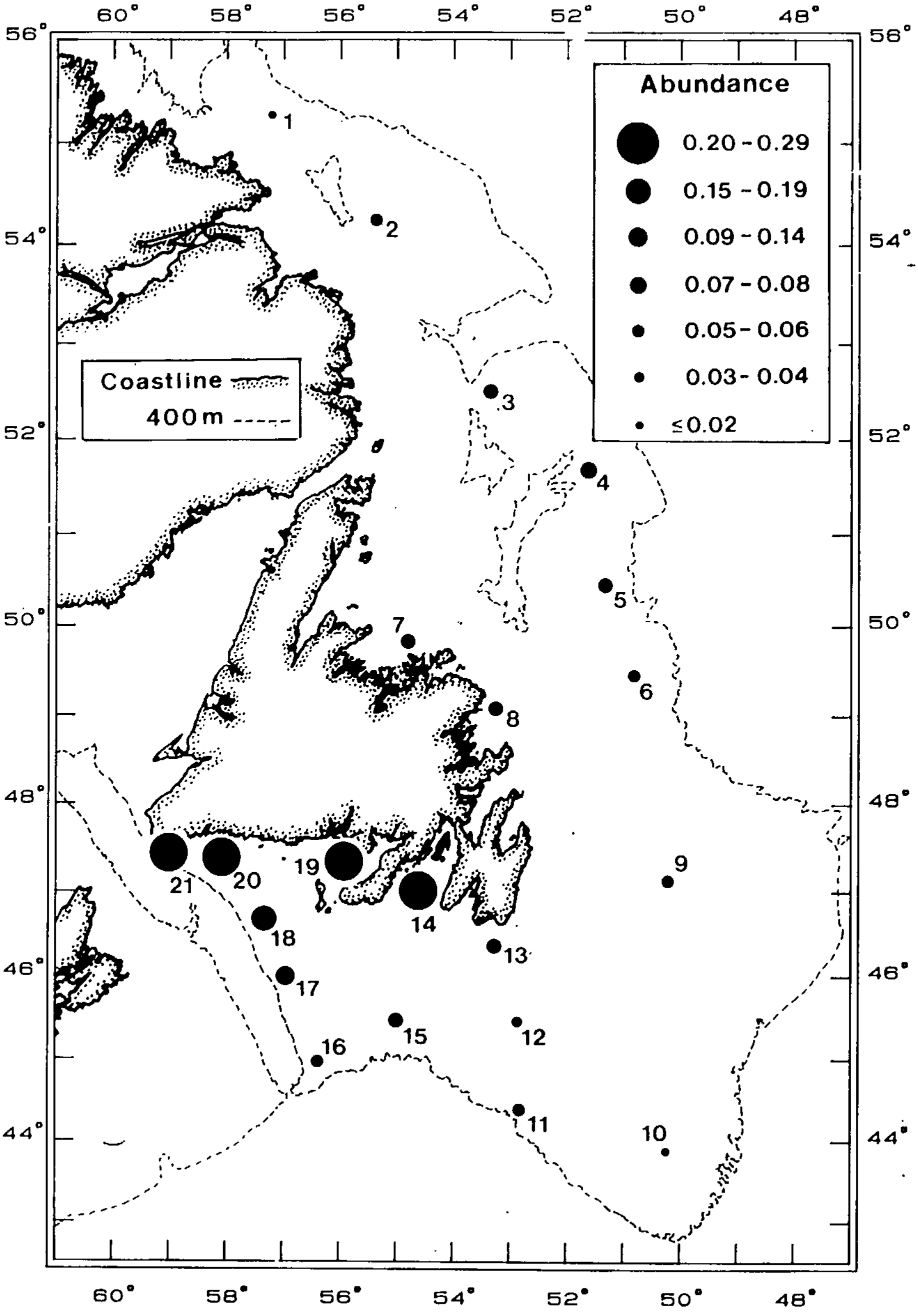


FIG. 2. Geographic variation in the abundance of larval sealworm, *P. decipiens*, in the fillets of cod 50 cm in length collected off Newfoundland and Labrador during 1985-87. The area of each circle is scaled proportional to the estimated abundance of the nematode in a cod 50 cm in length (see text for method of estimation). Numbers refer to sampling areas indicated in Fig. 1.

52.5 ± 4.7 cm (range 39-64). We found no specimens of *P. decipiens*; all large nematodes in the viscera and body cavity were *Phocascaris* sp. These findings do not exclude the possibility that some *P. decipiens* occur in the viscera and body cavity of larger cod; however, for most of the cod examined in this survey it appears that the proportion of sealworm in the viscera and body cavity was insignificant.

Statistical Methods

Terminology for nematode infection statistics follows Margolis et al. (1982) where prevalence = percentage hosts infected, abundance = mean number of nematodes per fish, and density = mean number of worms per kilogram of flesh including uninfected fish.

Clustering

Most commonly used statistical tests require that samples be independently and randomly selected. However, most samples of parasites from fish come from cluster sampling. That is, large numbers of fish typically come from the same fishing trawl, which is not a random sample of the population. The principle difficulty with this is that the standard statistical models which assume random sampling cannot be used to analyze the data because there may be considerable heterogeneity in the infection rates within regions.

The usual assumption in the analysis of binary data, such as whether a fish infected or not, is that the number of fish within a class, e.g. those infected, follows a binominal distribution. To analyze the heterogeneity within regions we assumed that in any one trawl, the number of cod that are infected follows a binomial distribution with parameter p, and that p varied as a beta distribution with parameters (α, β). The variation in the proportion of infected cod therefore follows a beta-binomial distribution (Paul and Plackett 1978). Within a sample, if there are n fish sampled from m trawls then the variance in the proportion infected is:

$$\frac{p(1-p)}{mn}\frac{(n\varepsilon+1)}{(\varepsilon+1)}$$

where $\varepsilon = 1/(\alpha+\beta)$. Therefore, the variance for the beta-binomial distribution is the heterogeneity factor $(n\varepsilon+1)/(\varepsilon+1)$ times the variance of the binominal distribution (Paul and Plackett 1978). The heterogeneity factor was computed using the mean number of fish per trawl, $\bar{n}$ (Table 1). Maximum likelihood estimates of α and β were obtained for each sample using a quasi-Newtonian algorithm and the number of fish examined was divided by the heterogeneity factor to adjust the sample size to the appropriate value needed for meaningful signifiance tests (Griffiths 1976).

Comparison of Sampling Regions

In comparing the abundance of *P. decipiens* in different sampling regions, we would have liked to use the data from all fish sampled in each region. However, this is difficult because infection is related to host size and there were differences in the size composition of the samples. Again, the standard statistical models are not of much use here: the large number of fish with no parasites preclude the use of models that assume normality and homoscedasticity, i. e. least square models (no suitable transformation could

TABLE 1. Heterogeneity factors for the proportions of cod infected with *P. decipiens* in the musculature. n = mean sample size per trawl, α and β are parameters of the beta binomial distribution, and $\varepsilon = 1/\alpha + \beta$).

Sampling area	Cod length class	Number of trawls	n	α	β	ε	Heterogeneity factor
Newfoundland east coast (inshore)	31-50	24	27.9	17.3	291.0	0.003	1.09
	51-70	23	33.6	5.3	79.7	0.012	1.38
	71-150	10	8.0	57.0	600.0	0.002	1.01
Labrador (inshore and offshore)	31-50	52	12.9	4.5	159.2	0.007	1.08
	51-70	54	11.1	5.5	139.0	0.021	1.21
	71-150	52	2.3	1.8	45.1	0.002	1.00
Newfoundland south coast (Cape Race to Pass Island)	31-50	23	11.7	144.9	657.8	0.001	1.01
	51-70	23	36.8	60.3	188.2	0.004	1.14
	71-150	20	9.3	1.2	4.8	0.168	2.18
St. Pierre Bank	31-50	14	8.1	0.3	1.9	0.452	3.22
	51-70	19	11.3	2.1	12.2	0.070	1.67
	71-150	22	7.3	1.7	4.6	0.160	1.87
Newfoundland south coast (Pass Island to Cape Ray)	31-50	25	9.5	310.0	548.6	0.001	1.02
	51-70	27	15.1	7.0	11.8	0.053	2.16
	71-150	20	5.3	3.3	3.3	0.152	2.72

be found) and the aggregation of nematodes within the fish host makes it inappropriate to use models that assume Poisson error, e.g. log-linear models. However, Myers and Brattey (1990) have shown that the following model provides a good description of the variation in the abundance of *P. decipiens* with the length of cod: the mean number of parasites was assumed to increase exponentially with cod length, with the variation in the number of parasites per fish described by a Poisson lognormal model in which the parameter, σ, is constant. In all cases the data fitted the model well, based on values of the log-likelihood ratio statistic G^2; however, in areas where the nematodes were rare, i.e. Makkovic Bank, southeast shoal of the Grand Bank, and southwest slope of the Grand Bank or where a narrow size range was examined, ie. Notre Dame Bay, Bonavista Bay, and Fortune Bay (Fig. 1) the mean abundance did not necessarily increase significantly with size. From the model, we estimated the mean number of parasites in a fish of length 50 cm and plotted the means on a map as a series of circular symbols with the area of the symbol scaled proportional to estimated nematode abundance (Fig. 2). The 50 cm size group was chosen for comparing areas because it was close to the mean size of fish sampled in each region. This method therefore uses all the information available to provide a common unit with which to compare sealworm abundance among sampling regions. The hypothesis that sealworm abundance increased with length of cod was tested using a likelihood ratio test, ie. the likelihood of a model in which abundance increased allometrically with length was compared to the likelihood of a model that assumed the abundance did not increase with length.

Results

Geographic Distribution

Larvae of *P. decipiens* were found in the flesh of cod in all 21 regions surveyed (Table 2; Fig. 2). Larvae of *A. simplex* were also common, but infection levels for this species will be described in detail elsewhere. A few specimens of *Contracaecum osculatum*, *Hysterothylacium* (= *Thynnascaris*) *aduncum* (Nematoda: Ascaridoidea) and *Echinorhynchus gadi* (Acanthocephala: Echinorhynchidae) were also recovered. These species are normally found in the viscera or alimentary tract and were probably introduced into the musculature accidentally during filleting; they are not included in further analyses.

Except among the largest size classes, the prevalence and abundance of sealworm were generally low (<18 % and <0.3 worms per fish) in the northern cod stock (NAFO Divisions 2J, 3K, 3L), and among cod from the southern Grand Bank (3NO), and southern St. Pierre Bank (3Ps); highest infection levels (20-100 % and 0.3-22 worms per fish) were in cod caught off southern Newfoundland, particularly on Rose Blanche Bank (3Pn), Burgeo Bank, northern and western St. Pierre Bank, and in Fortune Bay and Placentia Bay (3Ps) (Table 2, Fig. 2). There was also a notable decline in the prevalence and abundance of sealworm in cod from north to south across St. Pierre Bank. In almost all regions and size groups, the variance in the number of sealworms was greater than the mean indicating an aggregated distribution of nematodes; however, frequency distributions of sealworm among cod are investigated in more detail in Myers and Brattey (1990). Geographic changes in the density of sealworm were similar to those described above for prevalence and abundance. The average number of worms per kilogram was generally high (>1.0 worm/kg) only among cod caught off southern Newfoundland.

In most regions the abundance of sealworm increased with cod length ($P < 0.05$ in 15 of the 21 regions using a likelihood ratio test). The exceptions were in areas where sealworm was rare, i.e. Makkovic Bank, southeast shoal of the Grand Bank, southerwestern slope of the Grand Bank, or where a narrow size range of cod was examined, i.e. Notre Dame Bay, Bonavista Bay, and Fortune Bay (Table 2). On a per unit flesh weight basis (worms per kilogram) the relationship with cod length was variable and there was no consistent trend among the regions.

Comparison with Previous Survey

Before valid statististical comparisons of the proportion infected could be made between the Templeman et al. (1957) study and the present one we computed heterogeneity factors (Table 1) for cod length classes and sampling regions with our data grouped as closely as possible to that in table VIII in Templeman et al. (1957). For samples from Newfoundland east coast and Labrador, there was little heterogeneity within regions, i.e. the heterogeneity factor was in general slightly above one. There was greater heterogeneity within the three regions off the south coast of Newfoundland, where heterogeneity factors ranged from 1.01 to 3.22. We use these heterogeneity factors to adjust the sample size in the significance tests for our data as well as for Templeman et al. (1957). The original data used in the Templeman et al. (1957) study was not available to compute separate heterogeneity factors.

Numbers of nematodes (*P. decipiens* and *A. simplex*) in the fillets of cod in various length classes were compared with results obtained during Templeman et al.'s (1957) survey conducted during 1947-53 (Table 3). In most instances (12 of 15) prevalences observed during the present survey were higher than those observed previously, suggesting a general increase in the numbers of nematodes in the fillets of cod; the exceptions were mainly for cod off Labrador where current prevalences are similar to those

TABLE 2. Summary of infection statistics for *Pseudoterranova decipiens* in the musculature of Atlantic cod, *Gadus morhua*, collected off Newfoundland and Labrador during 1985-87. Prevalence = proportion of fish infected expressed as a percentage, abundance = mean number of *P. decipiens* per cod including uninfected fish, maximum = maximum number of *P. decipiens* found in a single cod. Density = mean number of *P. decipiens* per kilogram of flesh (including uninfected fish).

NAFO	Sample area	Dates	Length group (cm)	Number of fish	Prevalence	Abundance	Variance	Maximum	Density
2H, 2J	[a]1. Makkovik Bank	Oct. 1985; Sept., Nov. 1986	<30	10	0.00	0.00	0.00	0	0.00
			30-39	21	0.00	0.00	0.00	0	0.00
			40-49	33	3.03	0.03	0.03	1	0.10
			50-59	41	2.44	0.02	0.02	1	0.05
			60-69	17	0.00	0.00	0.00	0	0.00
			70-79	10	20.00	0.20	0.18	1	0.13
2J	2. Hamilton Inlet Bank	Oct.-Nov. 1985; Aug., Nov. 1986	30-39	81	4.94	0.06	0.08	2	0.38
			40-49	110	2.73	0.03	0.03	1	0.09
			50-59	137	2.19	0.02	0.02	1	0.04
			60-69	40	2.50	0.03	0.02	1	0.03
			70-79	31	0.00	0.00	0.00	0	0.00
			80-89	17	0.18	0.15	0.15	1	0.10
			°90	26	46.15	0.88	1.71	5	0.27
2J, 3K	3. Belle Isle Bank	Oct.-Nov. 1985; Aug., Nov.-Dec. 1986; Feb.-Mar. 1987	<30	23	4.35	0.09	0.17	2	1.78
			30-39	34	5.88	0.09	0.14	2	0.48
			40-49	350	7.43	0.11	0.20	4	0.24
			50-59	366	9.29	0.19	1.09	15	0.29
			60-69	67	4.48	0.06	0.09	2	0.06
			70-79	38	2.63	0.08	0.24	3	0.06
			80-89	23	4.35	0.04	0.04	1	0.02
			≥90	18	38.89	0.72	1.27	3	0.19
3K	4. northern Funk Isl. Bank	Nov. 1985; Jan. Mar., Nov.-Dec. 1986 Feb. 1987	30-39	17	17.65	0.53	1.89	5	2.32
			40-49	382	8.90	0.12	0.19	4	0.26
			50-59	601	12.48	0.20	0.46	8	0.31
			60-69	154	9.74	0.14	0.25	4	0.14
			70-79	31	9.68	0.68	10.49	18	0.44
			80-89	16	12.50	0.13	0.12	1	0.06
			≥90	15	13.33	0.27	0.50	2	0.07
3K	5. southern Funk Isl. Bank	Nov. 1985; Jan-Mar., Sept., Nov. 1986	40-49	172	7.56	0.09	0.12	2	0.23
			50-59	758	6.46	0.11	0.52	17	0.18
			60-69	335	9.85	0.14	0.42	9	0.15
			70-79	81	9.88	0.14	0.19	2	0.10
			80-89	21	14.29	0.19	0.26	2	0.09
3K, 3L	6. northeast Nfld. Shelf	Nov. 1985; Jan-Mar., Nov. 1986; Feb. 1987	30-39	13	7.69	0.08	0.08	1	0.46
			40-49	246	2.03	0.03	0.04	2	0.07
			50-59	851	7.76	0.18	2.52	42	0.29
			60-69	406	6.65	0.12	0.79	17	0.12
			70-79	95	18.95	0.28	0.52	4	0.20
			80-89	17	11.76	0.41	2.13	6	0.20
			≥90	17	17.65	0.47	1.64	5	0.13
3K	7. Notre Dame Bay	July-Sept. 1986	40-49	369	4.88	0.08	0.15	4	0.21
			50-59	371	6.74	0.10	0.24	7	0.18
			60-69	142	6.34	0.08	0.10	2	0.10
3L	8. Bonavista Bay	Aug.- Sept. 1986	40-49	172	5.23	0.10	0.27	5	0.30
			50-59	178	5.62	0.08	0.16	3	0.16
			60-69	105	9.52	0.12	0.17	2	0.14
			70-79	29	6.90	0.07	0.07	1	0.06
3L	9. Grand Bank	Feb.-Mar.,Aug.-Sept., Nov. 1986	30-39	29	0.00	0.00	0.00	0	0.00
			40-49	70	8.57	0.16	0.37	4	0.48
			50-59	178	5.62	0.08	0.15	3	0.15
			60-69	122	4.10	0.09	0.25	4	0.10
			70-79	86	16.28	0.28	0.51	3	0.21
			80-89	32	15.63	0.28	0.53	3	0.14
			≥90	35	17.14	0.86	9.48	17	0.23
3N	10. southeast Shoal of the Grand Bank	May, Sept. 1985; Apr.-May 1986	30-39	19	0.00	0.00	0.00	0	0.00
			40-49	20	5.00	0.05	0.05	1	0.17
			50-59	22	0.00	0.00	0.00	0	0.00
			60-69	20	0.00	0.00	0.00	0	0.00
			70-79	27	7.41	0.07	0.07	1	0.06
			80-89	27	0.00	0.00	0.00	0	0.00
			≥90	115	0.87	0.20	4.60	23	0.04
3O, 3N	11. southwest Slope of the Grand Bank	Apr. 1985; Jan., Mar.-Apr. 1986; Jan.-Mar. 1987	40-49	15	0.00	0.00	0.00	0	0.00
			50-59	96	6.25	0.06	0.06	1	0.11
			60-69	71	2.82	0.03	0.03	1	0.03
			70-79	31	6.45	0.10	0.16	2	0.07
			80-89	28	7.14	0.07	0.07	1	0.04
			≥90	10	0.00	0.00	0.00	0	0.00
3O	12. Whale Bank	Apr. 1985; Mar.-Apr., Nov. 1986; Feb. 1987	30-39	31	0.00	0.00	0.00	0	0.00
			40-49	29	0.00	0.00	0.00	0	0.00
			50-59	55	5.45	0.07	0.11	2	0.14
			60-69	63	3.17	0.05	0.08	2	0.06
			70-79	36	2.78	0.03	0.03	1	0.02
			80-89	27	7.41	0.07	0.07	1	0.04
			≥90	102	12.75	0.89	41.05	64	0.21

TABLE 2., *(Continued)*

NAFO	Sample area	Dates	Length group (cm)	Number of fish	Prevalence	Abundance	Variance	Maximum	Density
3L	13. southern ( ) Avalon	Feb., Sept., Nov. 1986; Feb. 1987	30-39	28	3.57	0.04	0.04	1	0.22
			40-49	46	10.87	0.11	0.10	1	0.35
			50-59	70	5.71	0.06	0.05	1	0.10
			60-69	63	7.94	0.08	0.07	1	0.09
			70-79	34	11.76	0.29	1.00	5	0.22
			80-89	27	11.11	0.30	0.83	4	0.14
			≥90	36	19.44	0.64	3.95	9	0.15
3Ps	14. Placentia Bay	Sept.-Oct. 1986	30-39	22	18.18	0.23	0.28	2	1.39
			40-49	57	21.05	0.25	0.26	2	0.80
			50-59	56	19.64	0.52	3.16	12	0.92
			60-69	57	29.82	0.86	5.87	17	0.95
			70-79	49	36.73	2.04	42.12	42	1.56
			80-89	19	78.95	3.47	111.93	47	1.80
			≥90	13	100.00	0.77	39.86	20	1.37
3Ps, 3O	15. Green Bank	Feb.-Apr. 1986; Feb.-Mar. 1987	40-49	38	5.26	0.18	0.97	6	0.45
			50-59	250	9.60	0.25	1.20	10	0.43
			60-69	189	10.05	0.16	0.26	3	0.18
			70-79	50	6.00	0.12	0.23	2	0.08
			80-89	29	17.24	0.24	0.40	3	0.11
			≥90	24	24.14	0.83	4.58	10	0.24
3Ps	16. southern St. Pierre Bank	Jan-Mar. 1986;	40-49	15	13.33	0.13	0.12	1	0.34
		Jan-Mar. 1987	50-59	171	1.75	0.05	0.30	7	0.08
			60-69	145	4.83	0.08	0.23	5	0.09
			70-79	59	1.69	0.02	0.02	1	0.01
			80-89	9	11.11	0.33	1.00	3	0.15
3Pn	17. western St. Pierre Bank	Jan.-Mar. 1986;	<30	12	0.00	0.00	0.00	0	0.00
		Jan., Feb. 1987	30-39	17	5.88	0.06	0.06	1	0.43
			40-49	21	28.57	0.52	0.86	3	1.52
			50-59	80	20.00	0.38	1.07	7	0.68
			60-69	45	15.56	0.24	0.64	5	0.28
			70-79	40	30.00	0.52	1.18	5	0.36
			80-89	29	31.03	0.34	0.31	2	0.16
			≥90	38	28.95	3.84	240.51	94	1.01
3Ps	18. northern St. Pierre Bank	Mar. 1985; Jan-	<30	10	10.00	0.20	0.40	2	2.74
		Mar. 1986; Jan-Mar. 1987	30-39	32	12.50	0.19	0.29	2	1.44
			40-49	42	14.29	0.24	0.43	3	0.91
			50-59	45	15.56	0.27	0.52	3	0.56
			60-69	36	16.67	0.50	3.06	10	0.70
			70.79	34	20.59	0.53	1.65	6	0.48
			80-89	19	10.53	0.16	0.25	2	0.09
			≥90	16	75.00	12.94	315.53	51	3.89
3Ps	19. Fortune Bay	Jan-Mar.-1986; Jan.-Mar. 1987	40-49	85	15.29	0.36	1.26	7	0.93
			50-59	451	24.17	0.75	5.90	25	1.20
			60-69	275	27.27	0.92	15.71	53	0.96
			70-79	88	21.59	0.75	5.73	17	0.52
3Ps	20. Burgeo Bank	Feb. 1987	30-39	13	0.00	0.00	0.00	0	0.00
			40-49	16	12.50	0.44	2.26	6	1.50
			50-59	17	5.88	0.06	0.06	1	0.11
			60-69	18	33.33	2.17	28.50	21	2.54
			70-79	12	41.67	1.00	4.00	7	0.74
			80-89	12	66.67	7.25	118.57	34	3.58
3Pn	21. Rose Blanche Bank	Feb.-Mar. 1986; Feb.-Mar. 1987	30-39	18	22.22	0.22	0.18	1	1.85
			40-49	155	29.68	0.62	3.37	17	1.80
			50-59	317	25.87	0.72	14.63	64	1.38
			60-69	94	31.91	0.71	1.84	8	0.88
			70-79	25	52.00	2.32	19.73	19	1.80
			80-89	19	63.16	7.89	547.77	103	3.99
			≥90	32	84.38	21.97	904.61	106	5.19

[a] Numbers refer to sampling areas in Fig. 1.

observed during 1947-53. When the sample sizes were adjusted using the heterogeneity factors (see Table 1) the differences were significant in 5 of the 15 comparisons and mainly for samples collected off the south coast of Newfoundland. In samples collected between Cape Race and Pass Island, abundances of nematodes in cod were two to three times higher than those reported during Templeman et al.'s (1957) survey. Differences in abundance were not tested statistically because no estimates of variance around the mean (= abundance) were provided by Templeman et al. (1957); however, in general trends in abundance were similar to those described above for prevalence. Templeman et al. (1957) also provided data on the proportions of *A. simplex* and *P.*

TABLE 3. Temporal trends in the prevalence and abundance of ascaridoid nematodes in the fillets of Atlantic cod, *Gadus morhua*, from various regions off Newfoundland and Labrador. Data for 1947-53 were obtained from tables VI, VII and VIII in Templeman et al. (1957). Differences in prevalence were compared using *G*-test after adjusting sample sizes with heterogeneity factors given in Table 1. * = $P < 0.05$, ** = $P < 0.01$, n.s. = not significant.

Sampling area	Cod Length class (cm)	Number of cod examined		Prevalence (% infected)		Probability by G-test	Abundance (×100)	
		1947-53	1985-87	1947-53	1985-87		1947-53	1985-87
Newfoundland east coast (inshore)	31-50	578	669	4	5.7	n.s.	8	8.4
	51-70	1647	772	4	6.0	n.s.	5	8.2
	71-150	556	80	3	8.8	*	3	11.3
Labrador (inshore and offshore)	31-50	597	672	3	3.9	n.s.	3	6.9
	51-70	1164	597	4	4.0	n.s.	4	5.7
	71-150	68	118	7	5.9	n.s.	12	7.6
Newfoundland south coast (Cape Race to Pass Island)	31-50	313	269	6	17.1	**	7	22.7
	51-70	490	847	13	24.2	**	17	66.5
	71-150	309	185	17	27.0	n.s.	31	76.8
St. Pierre Bank	31-50	299	114	6	14.9	n.s.	7	23.7
	51-70	371	214	17	15.9	n.s.	42	30.4
	71-150	192	161	24	25.5	n.s.	55	72.1
Newfoundland south coast (Pass Island to Cape Ray)	31-50	198	238	16	29.8	**	23	65.5
	51-70	652	407	29	35.1	n.s.	75	77.2
	71-150	248	106	38	53.8	*	187	238.7

TABLE 4. Proportions of *P. decipiens* in the fillets of Atlantic cod, *Gadus morhua*, collected off Newfoundland and Labrador during 1947-53 and 1985-87. All other nematodes in the flesh were *A. simplex*. Data for 1947-53 were obtained from fig. 12 in Templeman et al. (1957).

Sampling Area	Cod length group (cm)	Total number of nematodes		Proportion *P. decipiens*	
		1947-53	1985-87	1947-53	1985-87
St. John's (east coast Avalon Peninsula)	all sizes	31	31	0.84	0.90
South coast Newfoundland (Cape St. Mary's to Pass Island)	40-49		41		0.83
	50-59	97	320	0.97	0.92
	60-69		225		0.92
	>70		155		0.96
St. Pierre Bank (north of 46° 30') and Burgeo Bank	40-49		8		1.00
	50-59	109	12	0.92	0.92
	60-69		24		0.96
	>70		101		0.99
South coast Newfoundland (Pass Island to Cape Ray)	40-49		106		0.82
	50-59	362	269	0.97	0.74
	60-69		75		0.63
	>70		200		0.98

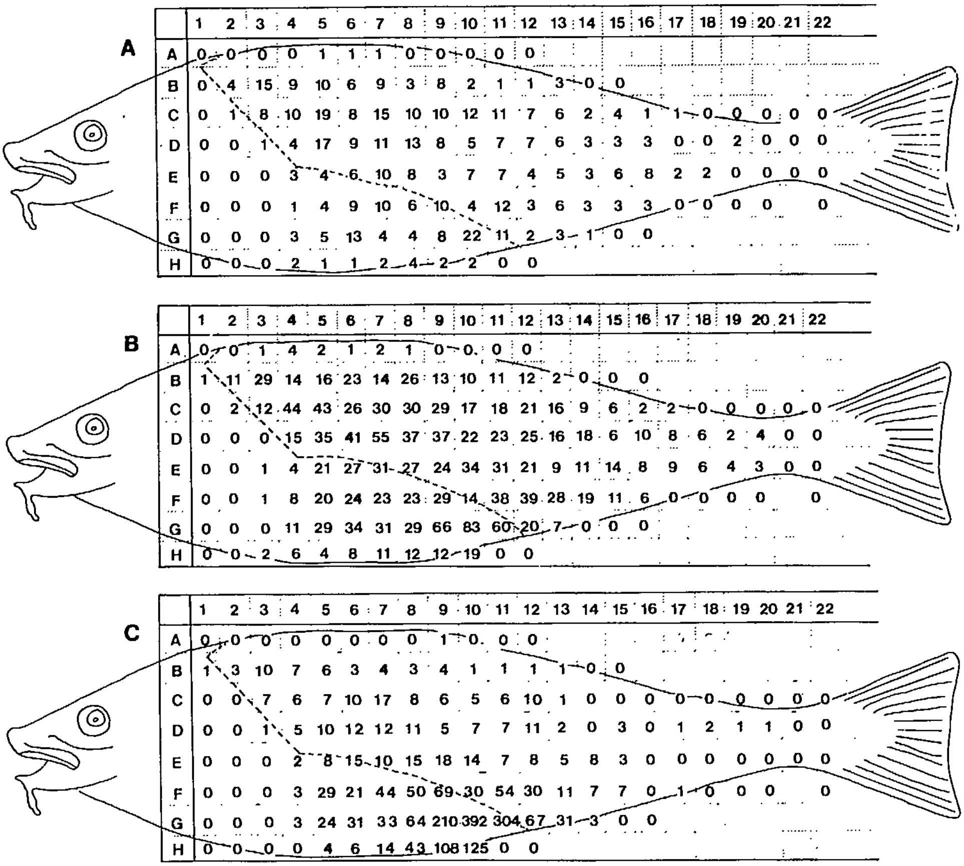
decipiens in the fillets of cod from various sampling regions. We compared the proportions of *P. decipiens* observed during 1947-53 with those observed during 1985-87 for four of the regions investigated by Templeman et al. (1957); for the remaining regions sample sizes provided by Templeman et al. were too small for meaningfull comparisons. Clearly, *P. decipiens* was the dominant nematode in the fillets of cod in all four regions during both surveys (Table 4). Although our data indicate some heterogeneity in the proportion of *P. decipiens* among cod size groups, the comparison suggests that the proportion of *A. simplex* has increased slightly among cod from Pass Island to Cape Ray. However, a slight increase in the proportion of *A. simplex* is insufficient to account for the overall increase in the total numbers of nematodes (see Table 3). Therefore, our findings suggest that the increase in the total numbers of nematodes in the fillets of cod off southern Newfoundland was due to sealworm, possibly with a relatively greater increase in the numbers of *A. simplex* for samples from Pass Island to Cape Ray.

Distribution in Cod Muscle

Larvae of *P. decipiens* were widely distributed in the nape and fillet of cod of a wide range of sizes (Fig. 3). Although there were generally more *P. decipiens* in the thicker portions of the fillet, in the largest fish most *P. decipiens* were found in the posterior part of the nape surrounding the vent (Grid squares G9 to G12). The numbers of sealworm were greater in the left than the right side for fillet and nape portions among cod of a wide range of sizes (Table 5). Small cod tended to have more sealworm in the fillet, but the percentage in the fillet decreased with cod length and most *P. decipiens* were found in the nape of large (>80 cm) cod.

Discussion

Our survey indicates that the numbers of sealworm in cod stocks off Labrador are similar to those reported by Templeman et al. (1957) but in stocks off Newfoundland, particularly those off the south coast, the numbers of sealworm appear to have increased. As McClelland et al. (1983a) have pointed out some caution should be used when comparing the results of these surveys because often there are sources of variation bet-



	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
A	0	0	0	0	1	1	1	0	0	0	0	0										
B	0	4	15	9	10	6	9	3	8	2	1	1	3	0	0							
C	0	1	8	10	19	8	15	10	10	12	11	7	6	2	4	1	1	0	0	0	0	0
D	0	0	1	4	17	9	11	13	8	5	7	7	6	3	3	3	0	0	2	0	0	0
E	0	0	0	3	4	6	10	8	3	7	7	4	5	3	6	8	2	2	0	0	0	0
F	0	0	0	1	4	9	10	6	10	4	12	3	6	3	3	3	0	0	0	0		0
G	0	0	0	3	5	13	4	4	8	22	11	2	3	1	0	0						
H	0	0	0	2	1	1	2	4	2	2	0	0										

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
A	0	0	1	4	2	1	2	1	0	0	0	0										
B	1	11	29	14	16	23	14	26	13	10	11	12	2	0	0	0						
C	0	2	12	44	43	26	30	30	29	17	18	21	16	9	6	2	2	0	0	0	0	0
D	0	0	0	15	35	41	55	37	37	22	23	25	16	18	6	10	8	6	2	4	0	0
E	0	0	1	4	21	27	31	27	24	34	31	21	9	11	14	8	9	6	4	3	0	0
F	0	0	1	8	20	24	23	23	29	14	38	39	28	19	11	6	0	0	0	0		0
G	0	0	0	11	29	34	31	29	66	83	60	20	7	0	0	0						
H	0	0	2	6	4	8	11	12	12	19	0	0										

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
A	0	0	0	0	0	0	0	0	1	0	0	0										
B	1	3	10	7	6	3	4	3	4	1	1	1	1	0	0							
C	0	0	7	6	7	10	17	8	6	5	6	10	1	0	0	0	0	0	0	0	0	0
D	0	0	1	5	10	12	12	11	5	7	7	11	2	0	3	0	1	2	1	1	0	0
E	0	0	0	2	8	15	10	15	18	14	7	8	5	8	3	0	0	0	0	0	0	0
F	0	0	0	3	29	21	44	50	69	30	54	30	11	7	7	0	1	0	0	0		0
G	0	0	0	3	24	31	33	64	210	392	304	67	31	3	0	0						
H	0	0	0	0	4	6	14	43	108	125	0	0										

FIG. 3. Numbers of larval sealworm, *P. decipiens*, in various regions of the musculature of three size groups of cod. A = ≤ 50 cm, *n* = 3 465; B = 51-70 cm, *n* = 7 416; C = ≥ 70 cm, *n* = 1 676 (where *n* = number of fish examined).

TABLE 5. Distribution of larval *P. decipiens* in the flesh (left and right fillet and nape) of various size classes of Atlantic cod collected off Newfoundland and Labrador during 1985-87.

Cod stock complex	Length class (cm)	Number of cod	Nape		Fillet		% of total *P. decipiens* in fillets
			Numbers of *P. decipiens*	% in left side	Number *P. decipiens*	% in left side	
2J, 3K and 3L	40-49	1936	53	58.5	118	62.5	69.0
	50-59	3559	176	61.4	324	50.0	64.8
	60-69	1446	74	62.2	87	57.7	54.0
	70-79	443	46	52.2	54	64.4	54.0
	80-89	163	19	63.2	16	75.9	45.7
	90-99	77	58	72.4	7	68.8	10.8
	100-109	54	24	54.2	5	85.8	17.3
3Pn, 3Ps	40-49	391	31	66.7	140	50.0	81.9
	50-59	1137	114	74.2	536	76.9	82.5
	60-69	670	154	65.8	295	55.0	65.7
	70-79	307	118	70.8	158	50.0	57.3
	80-89	112	198	71.2	122	60.7	38.1
	90-99	52	107	57.1	52	50.2	32.7
	100-109	29	161	65.4	53	70.5	24.8
	110-119	17	290	60.3	95	55.8	24.7

ween the studies that can influence the validity of the comparison. These include the methodology used during examination, timing and precise location of sampling, and size frequency distribution of samples. We minimized the influence of such differences by duplicating the methodology used previously, examining large numbers of fish with samples collected widely over each area, and by estimating the degree of heterogeneity in the proportion of infected fish within each region. Most surveys of parasites in fish are based on cluster rather than random sampling methods (i.e. trawls or gill nets) thereby violating the assumptions of many common statistical methods. We have attempted to eliminate this problem by estimating the degree of heterogeneity in the proportion of infected fish within each region and using the heterogeneity factor to adjust the sample size to the appropriate value needed for meaningful statistical tests. While the assumption of random sampling was reasonable for regions where the heterogeneity factor was close to 1.0, for other regions considerable adjustment of the sample size was necessary before quantitative comparisons of infection levels could be made. For small (31-50 cm) cod collected on St. Pierre Bank, the heterogeneity factor was 3.22; therefore, the effective sample size for statistical comparisons was less than one third of the number of fish examined. Clearly, erroneous conclusions could result from failure to recognize such within-region variability in the infection levels.

The increases in the numbers of sealworm in cod off southern Newfoundland are considerably less than those reported by McClelland et al. (1983a, b, 1985, 1987) for cod in the southern Gulf of St. Lawrence and on the Cape Breton and Scotian shelves where abundances of sealworm are approximately 10 times higher than those reported here. Parasitological surveys of cod in other areas indicate that high abundances (>1.0 per fish) of sealworm are not restricted to Canadian Atlantic stocks. Platt (1975) found that Icelandic cod collected during 1971-73 were often heavily infected with *P. decipiens* (0.8-8.4 per fish), Greenland stocks were lightly infected (0-0.06) and Arcto-Norwegian cod had abundances similar to those reported here (0.2-0.8 per fish). Young (1972) found that among cod collected around U.K. during 1968-70, abundances of sealworm were highest on the west coast of Scotland (3.20-4.36), in the Irish Sea (4.49-4.63), and off the northeast English coast (0.80-1.24).

Chandra and Khan (1988) also surveyed larval nematodes in the fillets of cod, collected off Newfoundland and Nova Scotia during 1984-85. They compared their findings with those of Templeman et al. (1957) and concluded "there has been a substantial increase of larval nematodes, especially *P. decipiens*, in the fillets of cod". However, close inspection of their Table 1, reveals that many of the comparisons made between this data and that of the earlier survey are invalid, particularly with respect to the portions of the musculature and geographic areas sampled. Furthermore, in light of the absence of information on sizes of fish examined and efficiency of their detection methods a more detailed comparison between the present study and that of Chandra and Khan (1988) is not justified.

This study shows that for cod off Newfoundland and Labrador larvae of *P. decipiens* are more common in the left side of the musculature and that the proportion of these nematodes in the nape increases with the size of cod. McClelland et al. (1983a, b, 1985) and Young (1972) reported similar distribution patterns for *P. decipiens* in the flesh of cod off Nova Scotia and the United Kingdom, respectively. McClelland et al. (1985) speculated that the greater numbers of sealworm in the left side was due to the liver lying on the right side of the stomach and intestine and therefore interfering with penetration of nematodes into that side. The reasons for the greater proportion of *P. decipiens* in the nape of large cod are unclear but may include the thicker lining of the peritoneum offering greater resistance to penetration of the musculature, and host immune responses.

Geographic differences in the abundance of *P. decipiens* can provide useful information for discriminating the stock complex of cod in the north Atlantic (Platt 1976). The similarity in abundance of *P. decipiens* among on-and off-shore samples of cod from northeast Newfoundland and the Labrador shelf is consistent with the findings of tagging studies which suggest that these fish form part of a common stock (Templeman 1974; Lear 1984). In contrast, samples of cod from the south coast of Newfoundland show much greater geographic variability in sealworm abundance, suggesting a more heterogeneous assemblage of stocks. Evidence from tagging studies suggests that cod from the eastern Gulf of St. Lawrence migrate south then eastward along the south coast of Newfoundland during January-March and mingle with other stocks (Templeman 1979). Since cod in the eastern Gulf of St. Lawrence are known to be heavily infected with sealworm (McClelland et al. 1985), and most of our samples from the south coast were collected during winter, we probably sampled a mixed stock complex which would explain the higher heterogeneity factors for these areas (see Table 1). This interpretion could be further substantiated if additional samples of cod collected off southern Newfoudland during summer were shown to have markedly different worm burdens from those collected from these areas during winter. The high abundances of sealworm in cod collected from Placentia Bay during summer are also of interest; they indicate that the sealworm problem off southern Newfoundland is not solely due to an influx of infected cod from the Gulf of St. Lawrence, as these cod do not normally migrate further east than Fortune Bay.

Our study showed that *P. decipiens* occurred in all surveyed cod stocks off Newfoundland and Labrador. Although there was considerable geographic variation in the prevalence and abundance of *P. decipiens*, in general the numbers of larval sealworm in cod appears to match the distribution of the principal definitive host, the grey seal. Information on grey seal abundance around Newfoundland and Labrador is largely anecdotal, but tag and bounty returns suggest that grey seals are more abundant off southern Labrador than on the east coast of Newfoundland and that grey seals occur in both these areas mainly during summer (Mansfield and Beck 1977; G. Stenson, Department of Fisheries and Oceans, St. John's, Newfoundland, pers. comm.). The absence of major grey seal breeding colonies off eastern Newfoundland and Labrador suggests, however, that grey seals are much less numerous in these areas compared to the Scotian Shelf and Gulf of St. Lawrence where several major breeding colonies have been reported (Mansfield and Beck 1977). The relativity low abundances of sealworm in cod off Labrador, eastern Newfoundland, and on the Grand Bank are, therefore, not unexpected. The large numbers of harp seals (*Phoca groenlandica*) which breed off southern Labrador and northeast Newfoundland during winter are rarely infected with mature adults of *P. decipiens* (Scott and Fisher 1958; Brattey and Ni, unpublished observations).

Cod from areas adjacent to the south coast off Newfoundland were clearly the most heavily infected with sealworm and these stocks are closest to the large concentrations of grey seals on Sable Island, the Cape Breton and Scotian shelves, and the southern Gulf of St. Lawrence (Mansfield and Beck 1977). Although to date no grey seal breeding colonies have been reported off southern or western Newfoundland, tag and bounty returns indicate that grey seals were not uncommon in the Port au Port area and in Hermitage Bay, Fortune Bay, and Placentia Bay during spring and summer in the 1970's (Mansfield and Beck 1977). Also, several grey seals have been observed during summer at Grand Barachois on the French island of Michelon off southern Newfoundland (Ling et al. 1974; Renouf et al. 1983). The higher abundances of sealworm in cod from these areas can therefore probably be attributed in part to migrant grey seals which move into waters off southern Newfoundland during summer.

Although grey seals generally have the largest numbers of adult *P. decipiens*, harbour seals also carry considerable sealworm burdens (Scott and Fisher 1958; Mansfield and Beck 1977; McClelland 1980). There is a large breeding colony of harbour seals on Miquelon (Renouf et al. 1983) and numerous smaller colonies along the Newfoundland coast (Templeman et al. 1957; Boulva and MacLaren 1979); therefore, harbour seals may also be an important source of *P. decipiens* infection for inshore cod stocks in the numerous bays off southern Newfoundland. However, without more detailed information on the numbers of grey and harbour seals in these areas and their respective sealworm burdens it remains difficult to determine what proportion of the sealworm infection in cod can be attributed to each of these seal species.

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Larval Anisakine Nematodes in Various Fish Species from Sable Island Bank and Vicinity

G. McClelland

Department of Fisheries and Oceans, Marine Fish Division,
Bedford Institute of Oceanography, P.O. Box 1006,
Dartmouth, N.S., Canada B2Y 4A2

R. K. Misra

Department of Fisheries and Oceans, Physical and Chemical Sciences Branch,
Halifax Fisheries Research Laboratory, P.O. Box 550,
Halifax, N.S., Canada B3J 2S7

and D. J. Martell

Department of Fisheries and Oceans, Marine Fish Division,
Bedford Institute of Oceanography, P.O. Box 1006,
Dartmouth, N.S., Canada B2Y 4A2

McCLELLAND, G., R. K. MISRA, AND D. J. MARTELL. 1990. Larval anisakine nematodes in various fish species from Sable Island Bank and vicinity, p. 83–118. *In* W. D. Bowen [ed.] Population biology of sealworm (*Pseudoterranova decipiens*) in relation to its intermediate and seal hosts. Can. Bull. Fish. Aquat. Sci. 222.

Larval anisakine infections were surveyed in 4 000 fish collected from waters surrounding Sable Island, Canada between May 1986 and February 1989. Sealworm (*Pseudoterranova decipiens*) was found in 26 of 32 fish species, 16 species being new host records for eastern Canada. Nineteen of 26 species infected with *Anisakis simplex* were also new eastern Canadian host records. *Contracaecum osculatum* occured in only two species. Levels of infection and distribution of the nematodes in fillets, napes and body cavity varied with host species and size. Sealworm, which has become increasingly abundant in groundfish from the Sable Island area in recent years, was most numerous in large demersal piscivores (*Lophius americanus, Brosme brosme, Gadus morhua* and *Hemitripterus americanus*) and in small benthophagous fish (*Macrozoarces americanus, Myoxocephalus octodecemspinosus, Scophthalmus aquosus* and *Hippoglossoides platessoides*). According to recently published data, *G. morhua, M. americanus* and *H. platessoides* are frequently consumed by eastern Canadian grey seals (*Halichoerus grypus*) and, hence, may play significant roles in the transmission of *P. decipiens* to its definitive seal hosts. Abundances of *A. simplex* larvae were greatest in piscivorous gadids (mature *B. brosme, G. morhua, Merluccius bilinearis* and *Pollachius virens*) but high densities of infection also occured in small pelagic feeders (*Clupea harengus, Argentina silus* and *Ammodytes dubius*).

La présence de larves de nématode «anisakidés» a été déterminée chez 4 000 poissons capturés entre mai 1986 et février 1989 dans les eaux baignant l'île de Sable (Canada). Le ver du phoque était présent chez 26 des 32 espèces étudiées dont 16 représentaient de nouveaux hôtes dans les eaux de l'est du Canada. De plus, 19 des 26 espèces parasitées par *Anisakis simplex* sont de nouvelles mentions d'hôtes dans cette région. Par contre, *Contracaecum osculatum* n'était présente que chez deux espèces. Les taux de parasitisme et la répartition des nématodes dans les filets, les parois abdominales et la cavité corporelle variaient selon l'hôte et sa taille. Le ver du phoque, de plus en plus abondant chez les poissons démersaux de la région de l'île de Sable au cours des dernières années, était plus abondant chez les piscivores démerseaux de grande taille (*Lophius americanus, Brosme brosme, Gadus morhu* et *Hemitripterus americanus*) et chez les benthophages de petite taille (*Macrozoarces americanus, Myoxocephalus octodecempsinosus, Scophthalmus aquosus* et *Hippoglossoides platessoides*). Selon de récentes données publiées, *G. morhua, M. americanus* et

H. platessoides sont fréquemment consommées par le phoque gris (*Halichoerus grypus*) et peuvent donc jouer un rôle important dans la propagation de *P. decipiens* à son hôte définitif, le phoque. L'abondance de larves de *A. simplex* était plus élevée chez les gadidés piscivores (individus matures de *B. brosme, G. morhua, Merluccius bilinearis* et *Pollachius virens*) quoiqu'on ait aussi noté des taux élevés de parasitisme chez des poissons pélagiques de petite taille (*Clupea harengus, Argentina silus* et *Ammodytes dubius*).

Introduction

Although larvae of the seal parasite, *Pseudoterranova* (*Phocanema*) *decipiens* (Nematoda: Anisakinae) have been identified in dozens of fish species from the North Atlantic (Appendix II), quantitative studies of the nematode have dealt primarily with infections in the flesh of Atlantic cod (*Gadus morhua*) (Scott and Martin 1957; Templeman et al. 1957; Young 1972; Platt 1975; Pälsson 1979; McClelland *et al.* 1983a, b; Hauksson 1984; Chandra and Khan 1988; Brattey *et al.* 1990). Moreover, fishermen, fish processors, laymen and some biologists, continue to refer to *P. decipiens* larvae as "codworm" while usage of "sealworm", a more appropriate common name for the parasite (McClelland et al. 1983a), has not been widely practiced. The preoccupation with larval *P. decipiens* infections in cod, however, reflects concern over a cosmetic nuisance and potential human pathogen in a commercially important fish species (Margolis 1977) and is not necessarily indicative of the relative significance of cod, among other fish hosts, as an intermediary in the sealworm life cycle. While sealworm larvae often occur in greatest abundance (mean numbers per fish) in mature cod, infections of higher density (nematodes per unit host weight) seem to be found in smaller fish such as smelt (*Osmerus mordax*) (Templeman *et al.* 1957) and young American plaice (*Hippoglossoides platessoides*) (McClelland et al. 1983b, 1985, 1987) which are perhaps more likely to be consumed by the definitive (seal) hosts of the parasite (SMRU 1984; Möller and Klatt 1988; Benoit and Bowen 1990a, b). Underutilized or unexploited species or age classes of fish which have not been surveyed could hold important reservoirs of larval sealworm.

Sealworm shares fish hosts with other species of larval anisakine, including the "herringworm" or "whaleworm", *Anisakis simplex* (Appendix II). While *A. simplex* larvae are most frequently found in the body cavity of fish, they also infect the flesh of many commercially important species and, like sealworm, present a cosmetic problem for fish processors and a potential health hazard for consumers (Smith and Wootten 1978; Smith 1984*b*). The viscera of pelagic fish, especially Altantic herring (*Clupea harengus*) (Khalil 1969; Parsons and Hodder 1971; Davey 1972; Van Banning and Becker 1978), salmon (*Salmo salar*) (Beverley-Burton and Pippy 1978) and mackerel (*Scomber scombrus*) (Eltink 1988) have been extensively surveyed for *A. simplex* larvae, but records of herringworm in cod and other demersal fishes are limited mainly to infections in the musculature (Templeman et al. 1957; Young 1972; Platt 1975; Wootten and Waddell 1977; Hauksson 1984; Chandra and Khan 1988), and, hence, greatly underestimate the abundance of this parasite (McClelland et al. 1983a). Although its definitive hosts are usually cetaceans (Smith and Wootten 1978), *A. simplex* may also infect and mature in Atlantic grey seals (*Halichoerus grypus*) (Young 1972).

In the present study we document and analyse levels of larval anisakine infection not only in commercially exploited fish species but also in underexploited fishes which may play important roles in the transmission of anisakines to their definitive marine mammal hosts. Our records include larval anisakines found on visceral organs and mesenteries and throughout the somatic musculature of fish hosts and variations in the distribution of the nematodes between body cavity and musculature are analysed. Sampling was confined to waters surrounding Sable Island, site of the largest and most rapidly growing grey seal colony in eastern Canada (Zwanenberg and Bowen 1990).

Materials and Methods

Fish samples were collected from the shoals and slopewaters of Sable Island and adjacent banks between May 1, 1986 and April 31, 1987 during Department of Fisheries and Oceans' groundfish surveys and dedicated cruises as well as from a commercial dragger. Most fish were taken from the shoals of Sable Island Bank, 30-60 km southwest of the island itself, but a few species, including argentine (*Argentina silus*), cusk (*Brosme brosme*), pollock (*Pollachius virens*), longfin hake (*Urophysis chesteri*) and roughhead grenadier (*Macrourus berglax*) were found in the deeper continental slopewaters along the southern edge of the bank (Fig. 1). All redfish (*Sebastes* sp.) ≤25 cm total length (TL) were caught at a depth of approximately 150 m in the channel separating Sable Island and Middle Banks and were assumed to be *S. fasciatus* while those ≥26 cm TL were from continental slopewaters at depths ≤615 m and may have been a mixture of *S. fasciatus* and *S. mentella* (Robins et al. 1986). Sandlance (*Ammodytes* sp.,

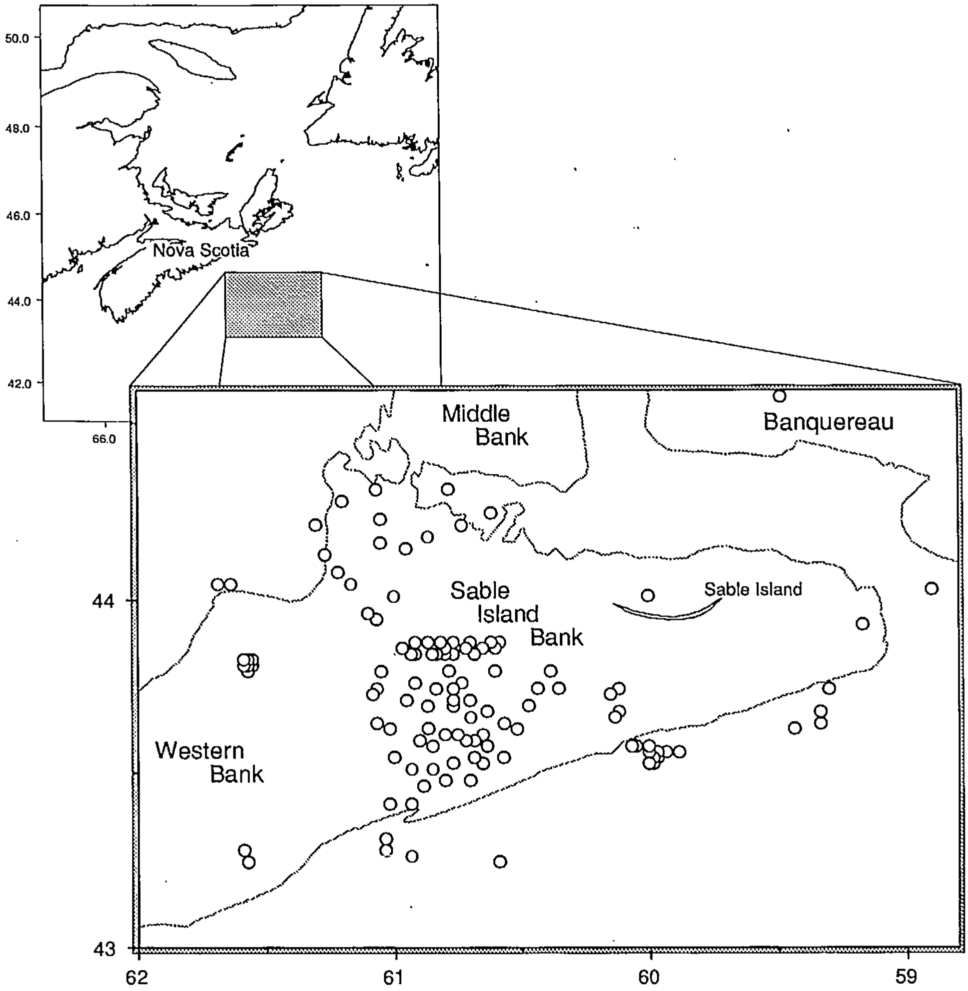


FIG. 1. Larval anisakines in fish from Sable Island Bank and vicinity: set locations (O) and 100 m depth contour (------).

presumably *A. dubius*) were taken from a single set on the western extremity of Banquereau, approximately 60 km north of Sable Island. Samples of species which were particularly abundant and varied in size, e.g. various gadids and flatfishes, were selected according to a forced orthogonal design in which the samples were stratified into 5 cm length groups containing equal numbers of fish (see McClelland et al. 1983a, 1985) and many of the samples conform to this design to some extent (Appendix I).

Fresh, iced samples collected from a commercial dragger were examined for larval anisakines immediately upon landing, while those frozen at sea or subsequent to landing were allowed to thaw for 18-24 h at room temperature (15-20°C) prior to examination. The length, weight and sex of each fish were recorded and the fillets and napes were removed and inspected for nematodes by systematic destruction of the flesh (Power 1961). The efficiency of destructive inspection of the flesh was tested in an earlier study (McClelland et al. 1983a) in which fillets and napes of cod (50-60 cm TL) ($n = 164$) were subjected to pepsin-HCL digestion following removal of all nematodes found during routine (destructive) examinations. Digestion of the flesh revealed that only 45 (13 %) of 339 *Pseudoterranova decipiens* larvae but 15 (68 %) of 22 *Anisakis simplex* larvae escaped detection by destructive examination.

Larval anisakines found on visceral organs and mesenteries, in napes and in fillets respectively, were identified and counted. Although some nematodes, particularly specimens from the body cavity, required microscopic examination, the great majority were identified by eye. Microscopic examinations of >3000 nematodes in our present and earlier surveys (McClelland et al. 1983a, b, 1985) have, in most cases (>98 %), confirmed identifications made with the unaided eye.

Quantitative terms such as prevalence (*P*), abundance (*A*); intensity (I*) and density (D*) are defined according to Margolis et al. (1982). Variations in prevalence and abundance of larval anisakines with host species and host length were analyzed in the gadid species Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), silver hake (*Merluccius bilinearis*) and white hake (*Urophysis tenuis*) and in the pleuronectids, grey sole (*Glyptocephalus cynoglossus*), American plaice (*Hippoglossoides platessoides*) and yellowtail flounder (*Limanda ferruginea*). Gadids were stratified into seven (≤30, 31-35, 36-40, 41-45, 46-50, 51-55 and ≥56 cm) and flatfishes into four (≤30, 31-35, 36-40 and ≥41 cm) length categories. In analyses of prevalence, individual fish were encoded in binary form, infected fish being assigned the value "1" and uninfected fish, the value "0" (Li 1964; Neter et al. 1985). To permit analyses of parasite abundance, the frequency distributions of worm counts, positively skewed to varying degrees (Fig. 2 and 3), were brought closer to normality by a $\log_{10}(n+1)$ transformation (Platt 1975). Two-way ANOVA's (SAS, GLM procedures) (SAS 1982) were then employed in the analysis of encoded prevalence data and transformed worm counts; Type III ANOVAs were used in the presence, Type II in the absence of interaction. Similar procedures were used to compare larval anisakine infections in 1986-87 samples of cod, grey sole, plaice and yellowtail flounder from Sable Island Bank with infections found in samples from the same area in 1982 (McClelland et al. 1983b). The validity of the log transformation and ANOVA procedures in analysis of abundance is discussed in an earlier report (McClelland et al. 1983a).

A binary approach was also used to examine variations in the proportion of nematodes in fillets (or tails) with host length. In this instance, individual nematodes in the fillets were assigned the value "1" while those found in the napes (hypaxial musculature of the abdomen) and body cavity were given the value "0". Variations in frequency were subsequently analyzed by one-way ANOVAs of nested design. Error terms were derived by pooling deviations from linear regression on host length strata with deviations among fish within length strata (Sokal and Rohlf 1969).

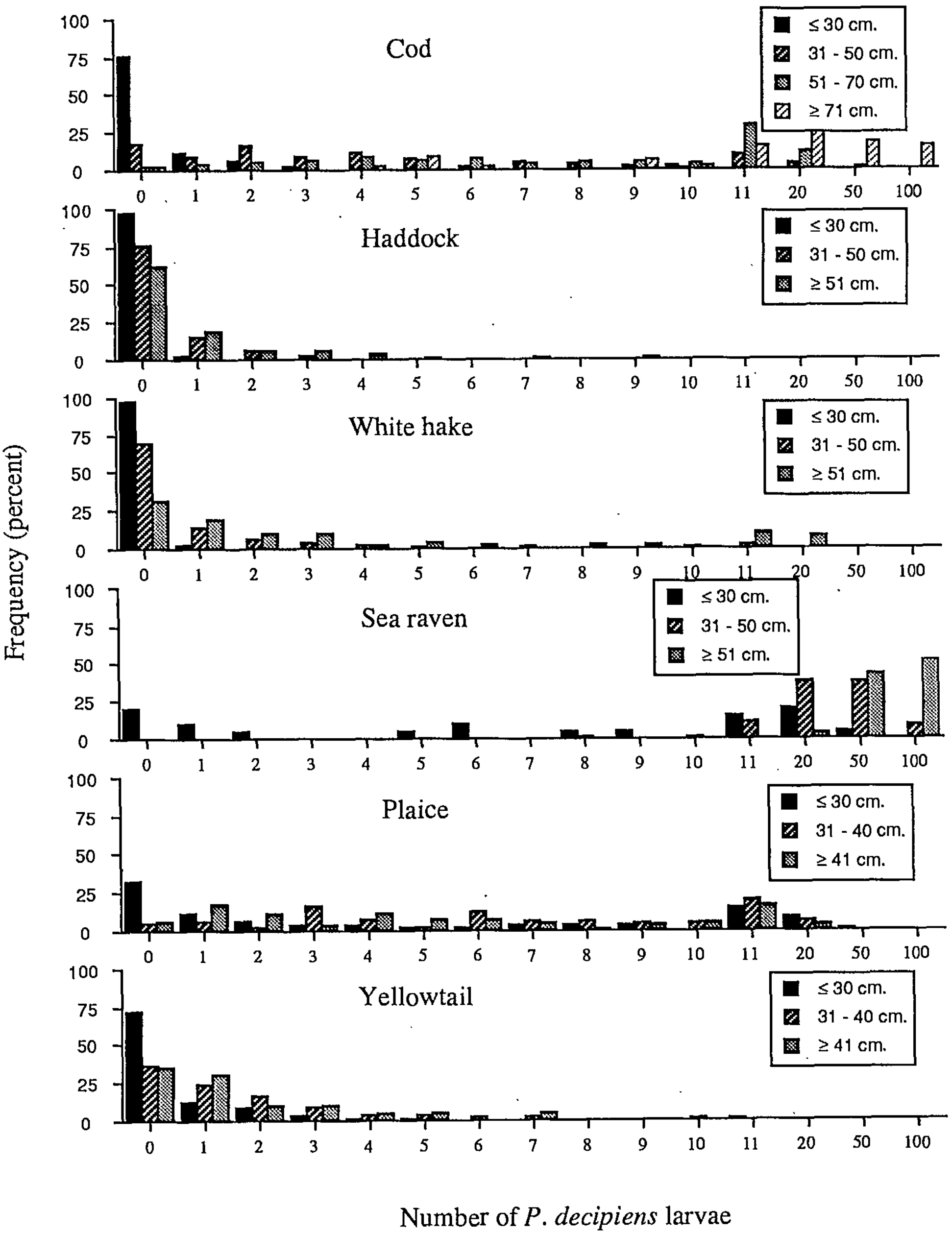


FIG. 2. Frequency distributions of *P. decipiens* larvae found in various fish species collected from Sable Island Bank in 1986-87.

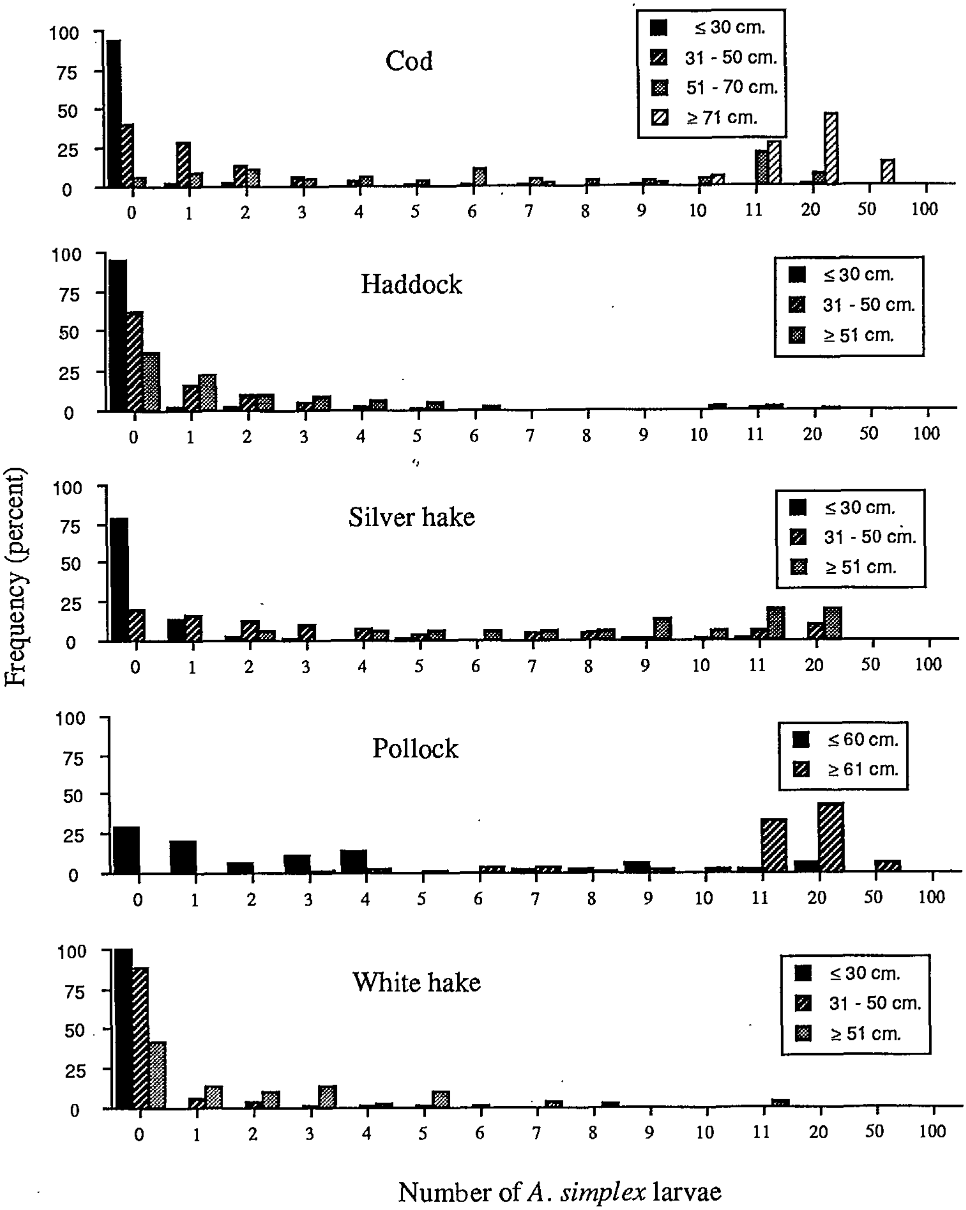


FIG. 3. Frequency distributions of *A. simplex* larvae in gadids collected from Sable Island Bank in 1986-87.

Results

Pseudoterranova decipiens

Larval *P. decipiens* occurred in 22 of 28 species collected in the vicinity of Sable Island in 1986-87 (Appendix I) and has subsequently been found in checker eelpout (*Lycodes vahlii*), alligatorfish (*Aspidophoroides monopterygius*), lumpfish (*Cyclopterus lumpus*) and spiny lumpsucker (*Eumicrotremus spinosus*) from the same area. Spiny dogfish (*Squalus acanthias*) (which, with the exception of one individual, were newborn specimens), herring (*Clupea harengus*), argentine, roughhead grenadier (juveniles), sand lance and mackerel (*Scomber scrombrus*) were the only fish in which sealworm was not detected.

Sealworm was most prevalent and abundant in demersal fishes, especially in monkfish (*Lophius americanus*) and various members of the cod, sculpin and flatfish families (Appendix I). While the infection of greatest intensity (*I*=488) occured in a 73 cm TL cod, sealworm abundances were generally greatest in monkfish and sea raven (*Hemitripterus americanus*). Infections in cod were also rivalled by those found in cusk (on the basis of six specimens examined) and American plaice. Pollock and winter flounder (*Pseudopleuronectes americanus*) were unique among gadids and pleuronectids respectively, in that they were seldom infected.

The smallest infected fish was a longhorn sculpin, 9 cm in length and weighing 7 g. The smallest infected windowpane (brill, *Scophthalmus aquosus*) and American plaice, flatfishes with relatively large mouths, were <15 mm TL. Among flatfishes with smaller mouths, such as grey sole, yellowtail flounder and winter flounder, however, the minimum lengths of infected specimens were 31, 20 and 44 cm, respectively. Prevalence and abundance of *P. decipiens* usually increased with host length (Fig. 4 and 5), but in American

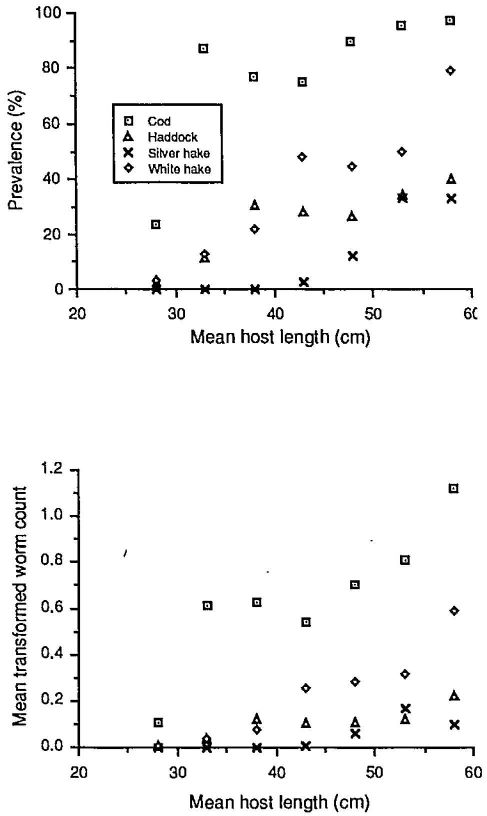


FIG. 4. Prevalences and mean transformed counts [$\log_{10}$ (n + 1)] of *P. decipiens* larvae in stratified samples of gadids from Sable Island Bank.

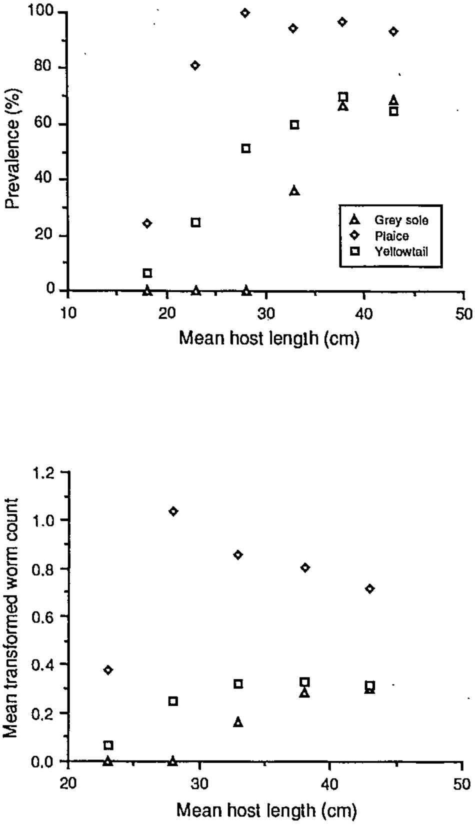


FIG. 5. Prevalences and mean trasformed counts [$\log_{10}$ (n + 1)] of *P. decipiens* larvae in stratified samples of flatfishes from Sable Island Bank.

TABLE 1. *P. decipiens* larvae in fish from the Sable Island area: distribution in host tissues and density of infection.

Host			Total number of *P. decipiens* recovered	Distribution (%) of *P. decipiens*			Density of infection	
Species	Length range (cm)	*n*		Body cavity	Napes	Fillets	In the round[a]	In fillets only[b]
Monkfish	≤30	13	3	0	0	100	1.82	6.38
	31-50	11	169	25.44	40.28	34.32	12.59	15.12
	51-60	16	743	29.21	43.88	26.92	16.78	15.81
	61-70	18	747	34.94	40.96	24.10	10.36	8.74
	≥71	7	278	33.81	42.45	23.74	5.16	4.29
Cusk	61-88	6	284	7.75	67.96	24.30	9.81	7.63
Cod	≤30	34	21	0	4.76	95.24	4.65	14.16
	31-40	64	338	0.59	2.66	96.75	13.78	42.67
	41-50	69	343	1.17	3.50	95.34	5.87	17.91
	51-60	57	490	0.82	7.14	92.04	5.09	14.99
	61-70	60	878	2.62	15.95	81.44	5.80	15.12
	≥71	33	1940	8.97	33.25	57.78	13.01	24.05
Haddock	≤40	162	39	0	0	100	0.63	2.00
	41-50	109	48	4.17	4.17	91.67	0.48	1.40
	51-60	110	67	4.48	8.96	86.57	0.37	1.02
	≥61	31	50	6.00	12.00	82.00	0.69	1.82
Silver hake	≥41	91	31	48.39	6.45	45.16	0.51	0.74
Longfin hake	26-36	40	4	0	25.00	75.00	0.67	1.60
Red hake	≤40	105	10	0	10.00	90.00	0.43	1.24
	≥41	20	19	5.26	31.58	63.16	1.88	3.79
White hake	≤40	117	20	0	10.00	90.00	0.69	2.00
	41-50	69	113	6.19	36.28	57.52	2.47	4.55
	51-60	33	101	3.96	39.60	56.43	2.09	3.78
	≥61	18	146	10.27	60.96	28.77	2.67	2.46
Ocean pout[c]	18-50	15	39	0	0	100	22.03	55.08
	51-76	11	28	0	0	100	1.78	4.44
Wolffish	69-95	6	35	—	17.14	82.96	1.00	2.89

TABLE 1. (Concluded.)

Host			Total number of *P. decipiens* recovered	Distribution (%) of *P. decipiens*			Density of infection	
Species	Length range (cm)	*n*		Body cavity	Napes	Fillets	In the round[a]	In fillets only[b]
Redfish	≤20	57	3	0	0	100	0.55	1.77
	21-35	142	47	0	2.13	97.87	0.87	2.80
	≥36	65	33	0	21.21	78.79	0.55	1.28
Sea raven[c]	≤30	20	245	9.80	12.24	77.96	61.63	168.13
	31-40	31	1327	13.26	20.42	66.31	57.83	134.23
	41-50	29	1945	21.59	28.89	49.51	37.31	64.66
	≥51	23	3095	21.10	34.77	44.14	42.40	65.50
Longhorn sculpin[c]	≤20	27	15	0	0	100	21.37	74.63
	21-30	110	390	0.77	0.51	98.72	22.67	80.40
	≥31	37	238	1.26	3.78	94.96	20.26	67.32
Windowpane	≤20	60	101	0	0	100	27.92	111.66
	21-25	47	115	0	0	100	23.09	92.37
	≥26	28	82	2.44	2.44	95.12	15.57	52.27
Gray sole	31-40	72	69	0	0	100	3.34	13.35
	41-50	56	76	1.32	0	98.68	2.21	8.71
	≥51	11	15	0	6.67	93.33	1.42	5.31
American plaice	≤20	37	54	0	0	100	52.63	210.53
	21-30	65	621	0.32	0	99.68	72.76	290.07
	31-40	66	517	0.77	0.58	98.65	22.38	88.31
	41-50	74	487	1.23	2.46	96.30	8.47	32.62
	≥51	36	208	0	4.33	95.67	3.48	13.33
Halibut	33-48	20	12	0	33.33	66.67	0.84	1.12
Yellowtail flounder	≤20	32	3	0	0	100	3.24	12.99
	21-30	67	61	0	0	100	7.13	28.50
	31-40	97	164	3.66	0.61	95.73	5.74	21.98
	≥41	20	32	0	0	100	3.07	12.30

[a] Number of *P. decipiens* kg^{-1} round weight.

[b] Number of *P. decipiens* in fillets kg^{-1}, fillet weight; fillet weights determined from conversions factors in STACAC Document No. 2, Revision No. 1: June 1984.

[c] Fillet weights were determined during parasitological examinations.

plaice, the abundance of the parasite peaked in the 26-30 cm length stratum and declined in larger fish.

In terms of the density of sealworm infection, the most heavily infected fish were, in descending order, sea raven, plaice ≤ 40 cm TL, ocean pout (*Macrozoarces americanus*) ≤ 50 cm TL, windowpane, longhorn sculpin, monkfish, cod, cusk, plaice ≥ 41 cm TL, yellowtail flounder, grey sole and white hake (Table 1). The individual infection of greatest density occurred in a 20 cm TL, 55 g plaice with 42 *P. decipiens* larvae in its fillets. Densities of infection in the fillets (or tail flesh) of 18 species, including haddock and redfish, exceeded the Canadian Fish Inspection standard for maximum density allowable (0.73 kg^{-1}) in processed fish. Sealworm densities in flatfish fillets and, in monkfish and sea raven tails declined with increasing host length but this trend was not evident in gadids.

While larval *P. decipiens* occurred most frequently in fillets, its distribution in the tissues of fish hosts varied dramatically with the species and size of the host (Table 1). In ocean pout, longhorn sculpin and all flatfish species with the exception of halibut, the parasite occurred almost exclusively (>95 %) in the fillets or tails. In monkfish, large cusk and white hake (≥ 61 cm TL), however, sealworm occupied the napes more frequently than the fillets. Sealworm were also numerous in the body cavities of many species, including monkfish, cusk, large cod (≥ 71 cm TL), silver hake, white hake (≥ 61 cm TL) and sea raven, where they were usually found encysted in the liver, stomach wall, pyloric caecae, gastro-intestinal mesenteries, gonads and peritoneum. Infections in thorny skate (*Raja radiata*) were confined to the body cavity, each of the four *P. decipiens* detected being encysted on the stomach wall. Some of the nematodes encysted on the visceral organs and mesenteries, particularly those found in silver hake and sea raven, were moribund and necrotic.

The proportion of *P. decipiens* larvae infecting fillets (number of sealworm in fillets as a proportion of total number in host) seemed to be inversely related to host length (Table 1). According to analyses of proportions, sealworm frequencies in the fillets of cod, haddock and white hake ($P<0.01$) and in the tails of monkfish ($P<0.05$) and sea raven ($P<0.01$) declined significantly with increasing host length.

Analyses of infections in gadids (Table 2; Fig. 4) indicated that prevalence and abundance of larval *P. decipiens* varied significantly with host species and host length and that species-length interactions were also highly significant. Evidently, much of the variance related to host length was, in each case, explained by a positive linear trend. As revealed in contrasts of samples, gadid species differed not only in respect to overall prevalence and abundance of the parasite but also in regard to linear trends of prevalence and abundance with host length; the differences were often highly significant. Sealworm was more prevalent and abundant in cod than it was in white hake while prevalence and abundance of the parasite in white hake were, in turn, greater than those found in haddock or silver hake. Infections in haddock and silver hake, however, did not differ in abundance or in respect to linear trends of prevalence and abundance on host length.

According to contrasts based on two-way type III ANOVA's (Table 3; Fig. 5), differences in the prevalence and abundance of *P. decipiens* in grey sole, plaice and yellowtail flounder were also highly significant. In spite of significant host species-host length interactions, the three flatfish species did not differ significantly in regard to linear trends of sealworm prevalence and abundance on host length.

Comparisons of sealworm infections in 1982 and 1986-87 samples of cod, grey sole, plaice and yellowtail flounder respectively (Table 4; Fig. 6), indicate that prevalences and abundances of *P. decipiens* were significantly greater ($P \leq 0.0054$) in the more recent samples; although '82 and '86 samples of *L. ferruginea* did not differ in respect to prevalence of sealworm ($P=0.0722$), the parasite was more abundant ($P=0.025$)

TABLE 2. Analyses of variations in prevalence and abundance of larval *P. decipiens* in gadids from Sable Island Bank.

Source of variation	*Pr* > *F* Prevalence	 Abundance
Two-way Type III ANOVA		
Hosts species	$\leq$0.0001	$\leq$0.0001
Host length	$\leq$0.0001	$\leq$0.0001
Species × length	$\leq$0.0001	$\leq$0.0001
Contrast		
All host species (means)	$\leq$0.0001	$\leq$0.0001
Cod vs. haddock (means)	$\leq$0.0001	$\leq$0.0001
Cod vs. silver hake (means)	$\leq$0.0001	$\leq$0.0001
Cod vs. white hake (means)	$\leq$0.0001	$\leq$0.0001
Haddock vs. silver hake (means)	0.0010	0.0764
Haddock vs. white hake (means)	$\leq$0.0001	$\leq$0.0001
Silver hake vs. white hake (means)	$\leq$0.0001	$\leq$0.0001
Length linear trend	$\leq$0.0001	$\leq$0.0001
Length quadratic trend	0.3751	0.2668
Cod vs. haddock (linear trend)	0.0115	$\leq$0.0001
Cod vs. silver hake (linear trend)	0.3080	$\leq$0.0001
Cod vs. white hake (linear trend)	0.1049	0.0024
Haddock vs. silver hake (linear trend)	0.7418	0.8900
Haddock vs. white hake (linear trend)	$\leq$0.0001	$\leq$0.0001
Silver hake vs. white take (linear trend)	0.0499	0.0020

TABLE 3. Analyses of variations in prevalence and abundance of larval *P. decipiens* in flatfish from Sable Island Bank.

Source of variation	*Pr* > *F* Prevalence	 Abundance
Two-way Type III ANOVA		
Host species	$\leq$0.0001	$\leq$0.0001
Host length	$\leq$0.0001	$\leq$0.0001
Species × length	$\leq$0.0001	$\leq$0.0001
Contrast		
All host species (means)	$\leq$0.0001	$\leq$0.0001
Grey sole vs. plaice (means)	$\leq$0.0001	$\leq$0.0001
Grey sole vs. yellowtail (means)	0.0051	0.0115
Plaice vs. yellowtail (means)	$\leq$0.0001	$\leq$0.0001
Length linear trend	$\leq$0.0001	$\leq$0.0001
Length quadratic trend	0.0071	$\leq$0.0001
Grey sole vs. plaice (linear trend)	0.1716	0.5332
Grey sole vs. yellowtail (linear trend)	0.3242	0.3567
plaice vs. yellowtail (linear trend)	0.5454	0.1480

in the '86 sample. As disparities in the prevalence and abundance of sealworm in the '82 and '86 cod samples occurred primarily in smaller fish ($\leq$40 cm TL), infections in these two samples also differed in regard to linear trends of parasite prevalence and abundance on host length. Recent and earlier samples of the respective flatfish species, however, did not vary significantly in respect to sealworm prevalence — or abundance — host length trends.

TABLE 4. Analyses of variations in prevalence and abundance of larval *P. decipiens* in 1982 and 1986 cod and flatfish from Sable Island Bank.

Host species	Source of variation	*Pr* >*F*	
		Prevalence	Abundance
Cod	*Two-way Type III ANOVA*		
	Sample (year)	≤0.0001	0.0054
	Host length	≤0.0001	≤0.0001
	Sample × length	≤0.0001	≤0.0001
	Contrast		
	Length linear trend	≤0.0001	≤0.0001
	Sample × length linear	≤0.0001	≤0.0001
Grey sole	*Two-way Type II ANOVA*		
	Sample (year)	≤0.0001	≤0.0001
	Host length	0.0186	0.0332
	Contrast		
	Length linear trend	0.0026	0.0036
Plaice	*Two-way Type II ANOVA*		
	Sample (year)	0.0004	≤0.0001
	Host length	0.1463	≤0.0001
	Contrast		
	Length linear trend		≤0.0001
Yellowtail founder	*Two-way Type II ANOVA*		
	Sample (year)	0.0722	0.0025
	Host length	0.0006	0.0006
	Contrast		
	Length linear trend	0.0020	0.0003

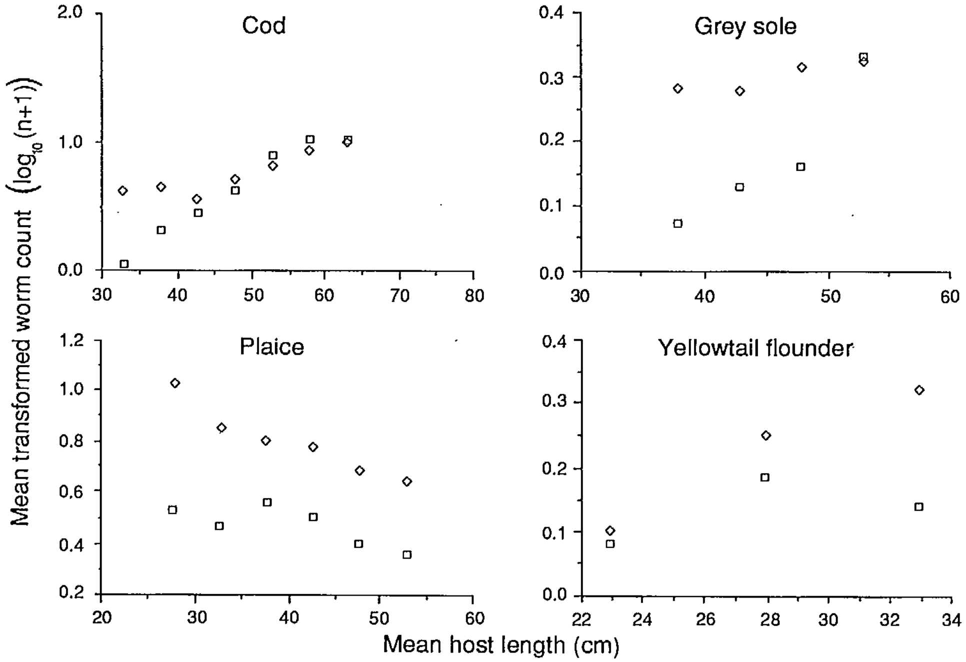
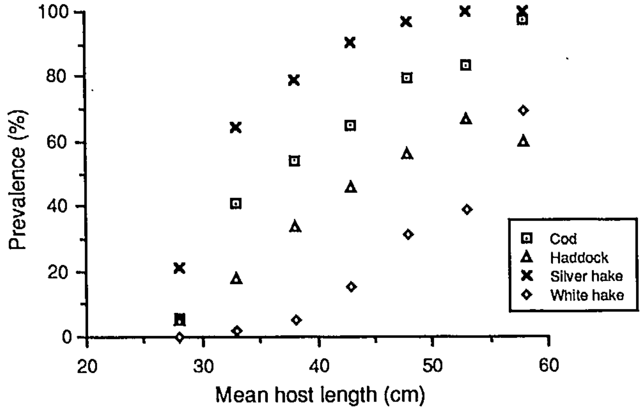


FIG. 6. Comparisons of mean transformed worm counts [$\log_{10}$ (n + 1)] of *P. decipiens* larvae in cod and flatfish samples collected from Sable Island Bank in 1982 (□) (McClelland et al. 1983b) and 1986 (◇).

Anisakis simplex

Larval *A. simplex* occurred in 25 of 28 species of fish collected near Sable Island in 1986-87 (Appendix I) and was subsequently identified in lumpfish during a more recent (1989) survey of the area. This parasite was not detected in roughhead grenadier (juveniles), checker eelpout, ocean pout, mature wolffish (*Anarhichas lupus*), alligatorfish and spiny lumpsucker. Prevalence and abundance of *A. simplex* invariably increased with host length (Fig. 7), the highest levels of infection being found in mature fish. The parasite was particularly abundant in mature gadids such as cusk, cod, silver hake and pollock but larger herring, monkfish, haddock, white hake and redfish were also heavily infected. The most intense infection (*I* = 100) occurred in the same 73 cm TL cod which hosted the heaviest *P. decipiens* infection (above). Herring and silver hake ($\geq$31 cm TL) had the greatest densities of *A. simplex* infection ($>$ 10 nematodes kg^{-1} round weight) Table 5); density of infection in large cod ($\geq$71 cm TL) and pollock ranged



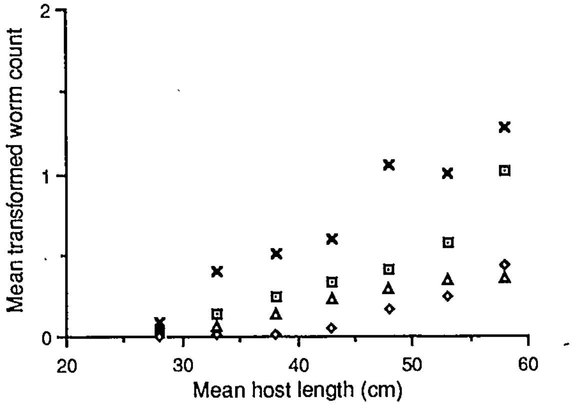


FIG. 7. Prevalences and mean transformed counts [$\log_{10}$ (n + 1)] of *A. simplex* larvae in stratified samples of gadids from Sable Island Bank.

TABLE 5. *A. simplex* larvae in fish from the Sable Island area: distribution in host tissues, prevalence of flesh infection, and density of infection in round fish.

Host			Total number of *A. simplex* recovered	Distribution (%) of *A. simplex*			Prevalence of flesh infection[a]	Density of infection in the round[b]
Species	Length range (cm)	*n*		Body cavity	Napes	Fillets		
Herring	≤26	44	15	86.67	0	13.33	6.25	2.16
	27-30	78	44	93.18	2.27	4.55	3.85	2.29
	≥31	14	58	91.38	3.45	5.17	28.57	11.69
Argentine	25-36	51	25	72.00	16.00	12.00	13.73	2.55
Monkfish	31-50	11	6	100	0	0	0	0.45
	51-60	16	18	100	0	0	0	0.41
	61-70	18	69	95.65	4.35	0	5.56	0.96
	≥71	7	27	100	0	0	0	0.50
Cusk	61-88	6	130	60.00	29.23	10.77	100	4.49
Cod	≤40	99	52	96.15	3.85	0	1.01	1.79
	41-50	58	131	92.05	7.95	0	14.49	2.58
	51-60	57	287	94.43	4.88	0.70	22.81	2.98
	61-70	60	667	94.60	4.50	0.90	38.33	4.41
	≥71	33	1049	93.23	6.20	0.57	63.64	7.03
Haddock	≤40	162	57	89.47	10.53	0	3.70	0.91
	41-50	109	155	96.77	2.58	0.65	4.59	1.55
	51-60	110	218	95.41	4.59	0	8.18	1.20
	≥61	31	85	92.94	7.06	0	19.35	1.18
Silver hake	26-30	55	51	96.08	1.96	1.96	3.64	6.14
	31-40	100	320	94.69	5.00	0.31	17.00	12.58
	41-50	76	732	93.99	4.37	1.64	32.89	16.38
	≥51	15	210	87.14	7.62	5.24	53.33	13.21
Pollock	≤30	17	30	93.33	3.33	3.33	5.88	6.82
	31-60	18	112	90.18	8.93	0.89	44.44	6.82
	61-70	65	1387	94.23	5.26	0.50	60.00	7.10
	≥71	28	729	96.02	3.84	0.14	57.14	5.84
Longfin hake	26-36	40	6	83.33	0	16.67	2.50	1.00
Red hake	31-40	74	40	95.00	2.50	2.50	2.70	2.01
	≥41	20	27	88.89	7.41	3.70	10.00	2.67
White hake	≤40	117	5	80.00	20.00	0	0.85	0.17
	41-50	69	33	69.70	27.27	3.03	8.70	0.72
	51-60	33	47	87.23	12.77	0	18.18	0.97
	≥61	18	76	77.63	22.37	0	33.33	1.39
Sand lance	16-28	144	18	72.22	—	27.78	3.47	4.01
Mackerel	27-38	53	25	88.00	8.00	4.00	5.66	1.37
Butterfish	10-23	102	7	71.43	14.29	14.29	1.96	0.80
Redfish	≤35	199	10	80.00	20.00	0	1.00	0.17
	≥36	65	92	82.61	17.39	0	12.31	1.37
Longhorn sculpin	≤31	37	37	89.19	10.81	0	8.11	3.15

[a] Number of fish with *A. simplex* in fish as a percentage of total number of fish in the sample.

[b] Number of *A. simplex* kg^{-1} round weight.

from 5-10 worms kg^{-1} while cusk, cod (41-70 cm TL) and smaller hosts including herring (≤ 30 cm TL), argentine, silver hake (≤ 30 cm TL), red hake (*Urophysis chuss*), sand lance and longhorn sculpin (31-33 cm TL) were infected with 2-5 *A. simplex* kg^{-1} round weight.

The majority (60-100 %) of *A. simplex* larvae were found in the body cavity (Table 5), encysted on the liver, stomach, pyloric caecae, mesenteries and peritoneum but the distribution of the parasite in fish tissues varied with host species. While most frequently associated with the liver and/or pyloric caecae in many of their hosts, *A. simplex* larvae occurred exclusively on the stomach wall in dogfish and skate. In silver hake, herringworm were often found in melanized capsules attached to the lower intestine, gonads, mesenteries and peritoneum in the posterior portion of the body cavity.

Infections in the flesh were primarily confined to the napes and belly flaps (hypaxial musculature surrounding the posterior end of the coelom), the latter having been included with the fillets in this study. Proportions of *A. simplex* larvae in the flesh (numbers of nematodes in flesh as a proportion of total numbers in host) while varying with host species, did not seem to be related to host length (Table 5); frequencies of flesh infection were greatest (15-40 %) in cusk and white hake and in smaller hosts such as argentine, sand lance and redfish. Prevalence of flesh infection (number of fish with *A. simplex* in flesh as a proportion of total number of fish in sample), on the other hand, usually increased with the length of a given host species.

In two-way type III ANOVAs (Table 6; Fig. 7 and 8), variations in prevalence (in whole fish and in flesh only) and abundance of *A. simplex* with species and length of various gadid hosts proved highly significant as did the interactions of host species and host length effects. In each case, much of the variance related to host length was explained by a positive linear trend. Contrasts revealed that infections in cod, haddock, silver hake

TABLE 6. Analyses of variations in prevalence and abundance of *A. simplex* larvae in gadids from Sable Island Bank.

Source of variation	$Pr \geq F$		
	Prevalence	Abundance	Prevalence[a] in flesh
Two-way Type III ANOVA			
Host species	≤0.0001	≤0.0001	≤0.0001
Host length	≤0.0001	≤0.0001	≤0.0001
Species × length	≤0.0001	≤0.0001	≤0.0001
Contrast			
All host species (means)	≤0.0001	≤0.0001	≤0.0001
Cod vs. haddock (means)	≤0.0001	≤0.0001	0.0039
Cod vs. silver hake (means)	0.0002	≤0.0001	≤0.0001
Cod vs. white hake (means)	≤0.0001	≤0.0001	0.2036
Haddock vs. silver hake (means)	≤0.0001	≤0.0001	≤0.0001
Haddock vs. white hake (means)	≤0.0001	0.0023	0.1659
Silver hake vs. white hake (means)	≤0.0001	≤0.0001	≤0.0001
Length linear trend	≤0.0001	≤0.0001	≤0.0001
Length quadratic trend	0.0.157	0.0134	0.0104
Cod vs. haddock (linear trend)	0.0182	≤0.0001	≤0.0001
Cod vs. silver hake (linear trend)	0.4623	0.0321	0.0943
Cod vs. white hake (linear trend)	0.1213	≤0.0001	0.2441
Haddock vs. silver hake (linear trend)	0.5969	≤0.0001	0.0002
Haddock vs. white hake (linear trend)	0.6073	0.5891	0.0228
Silver hake vs. white hake (linear trend)	0.8315	≤0.0001	0.0202

[a] Number of fish with *A. simplex* in flesh as a proportion of total number of fish in sample.

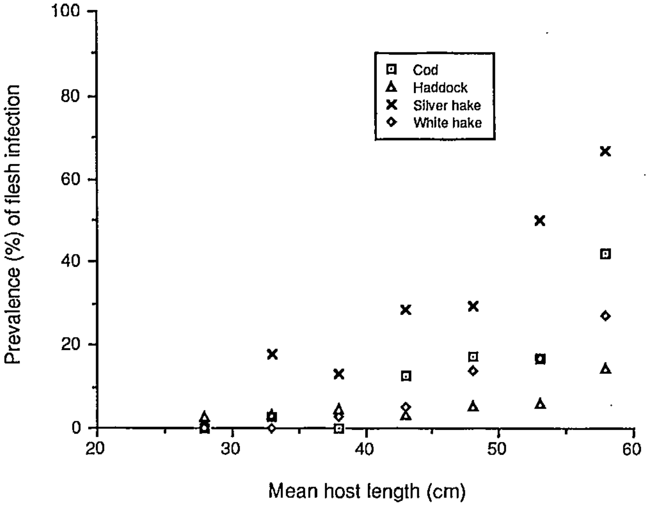


FIG. 8. Prevalences of *A. simplex* larvae in the flesh (fillets and napes) of gadids from Sable Island Bank.

and white hake differed not only in respect to prevalence and abundance of the parasite but often in regard to abundance - host length trends and means and linear trends for prevalence of flesh infection.

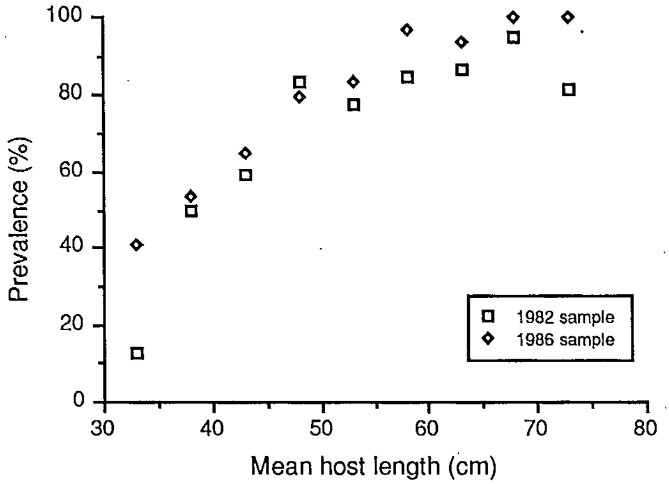
Comparisons of *A. simplex* infections in 1982 and 1986-87 samples of cod from Sable Island Bank show that the nematode was more prevalent and abundant in the more recent sample (Fig. 9). According to two-way ANOVAs (type II and type III), disparities in prevalence and abundance of the parasite in the two samples were highly significant ($P = 0.0078$ and ≤ 0.0001 for prevalence and abundance, respectively). Infections in these samples also differed significantly ($P \leq 0.0001$) in regard to the abundance - host length linear trends but not in respect to prevalence-length trends. Disparities in *A. simplex* abundance were greatest in large cod.

Contracaecum osculatum

A third species of larval anisakine, *C. osculatum*, occurred only in large (≥ 51 cm TL) cod and white hake, the prevalence of the infection being extremely low (< 5 %) in these hosts. *C. osculatum* larvae were usually encysted on the pyloric caecae and associated mesenteries.

Discussion

Larval *P. decipiens* and *A. simplex* infect a broad spectrum of marine and euryhaline fish species in the North Atlantic and adjacent waters (Appendix II). *Pseudoterranova decipiens* (*Phocanema, Terranova, Porrocaecum*) *decipiens* larvae and *Pseudoterranova* sp. larvae have been identified in 63 species belonging to 26 families, 10 orders and three classes of North Atlantic fishes while *A. simplex*, which has a somewhat wider distribution, infects 75 species from 32 families, 12 orders and three classes of fish; *A. simplex* is prevalent in many pelagic (clupeaform and salmoniform) and meso and bathypelagic species for which there are no records of *P. decipiens* infection. Infections



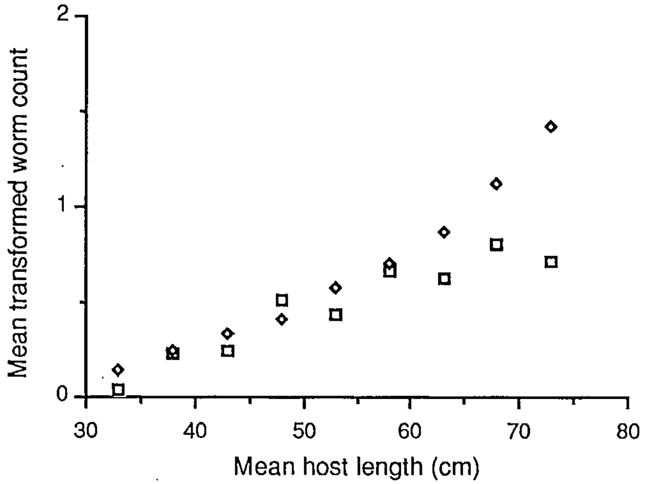


FIG. 9. Comparisons of prevalence and transformed counts [$\log_{10}$ (n + 1)] of *A. simplex* larvae in 1982 and 1986 cod samples from Sable Island Bank.

in thorny skate, monkfish, cusk, haddock, silver hake, pollock, longfin hake, red hake, checker eelpout, butterfish, redfish (*S. fasciatus* and *S. mentella*), alligatorfish, lumpfish, spiny lumpsucker, windowpane and halibut in the present study, are new host records for *P. decipiens* in eastern Canadian waters although *Pseudoterranova* (*Phocanema*, *Terranova*, *Porrocaecum*) sp. larvae have previously been reported in thorny skate, monkfish, haddock and windowpane; while identified as *S. marinus*, the redfish hosting *P. decipiens* larvae in an earlier study (Gaevskaya and Umnova 1977) may have in fact been *S. fasciatus* or *S. mentella*. New host records for *A. simplex* in eastern Canada include spiny dogfish, thorny skate, argentine, monkfish, cusk, haddock, pollock, longfin hake, red hake, white hake, butterfish, sea raven, longhorn sculpin, lumpfish,

TABLE 7. Densities of larval anisakine infections in various finfish species from Sable Island Bank and vicinity.

Host			Densities of larval anisakines[a]	
Species	Diet[b]	Length range (cm)	*P. decipiens*	*A. simplex*
Thorny skate	B, N[21,40,44,46]	≤40	–	–
		≥41	+ +	+ +
Atlantic herring	P[2,21,22,40,48]	≤30	–	+ + +
		≥31	–	+ + + +
Atlantic argentine	P[7,33,40,47]	25-36	–	+ + +
Monkfish	N[2,21,40,48]	≤30	+ +	–
		≥31	+ + + + +	+ +
Cusk	B[2,40], N (larger fish)[15,21]	61-88	+ + + +	+ + +
Atlantic cod	G, N (larger fish)[2,4,11,15,21,26,30,40,46,49]	≤30	+ + +	+ +
		31-50	+ + + +	+ + +
		51-70	+ + + +	+ + +
		≥71	+ + + + +	+ + + +
Haddock	B[2,4,11,15,21,40,48]	12-68	+	+ +
Silver hake	P[46,47], N (larger fish)[2,4,15,22,40,48]	≤30	–	+ +
		31-50	+	+ + + + +
		≥51	+ +	+ + + + +
Pollock	P, N (larger fish)[2,15,21,40,43,48]	25-67	+	+ + + +
Longfin hake	G[15,23,40,41,51]	26-36	+ +	+ +
Red hake	G[8,15,19,40,48]	≤30	+ +	–
		31-40	+	+ + +
		≥41	+ +	+ + +
White hake	G[9,46], N (larger fish)[15,40,48]	≤30	+	–
		31-50	+ +	+ +
		≥51	+ + +	+ +
Roughhead grenadier	G[2], B[32,40]	12-30	–	–
Ocean pout	B[2,15,40,46,48]	≤50	+ + + + + +	–
		≥51	+ +	–
Atlantic wolffish	B[1,2,3,40,45]	69-95	+ +	–
Northern sandlance	P[2,5,21,24,34,40]	16-28	–	+ + +
Mackerel	P[2,5,12,20,21,27,40,48]	27-38	–	+ +

TABLE 7. (Concluded.)

Host			Densities of larval anisakines[a]	
Species	Diet[b]	Length range (cm)	*P. decipiens*	*A. simplex*
Butterfish	P[2,21,40,48]	10-23	+	+ +
Redfish	P[2,13,21,40,42,48]	≤20	+ +	+
		21-35	+ +	+
		≥36	+ +	+ +
Sea raven	N[2,21,40,48]	14-68	+ + + + + +	+
Longhorn sculpin	B[2,21,40,48], G[46]	≤30	+ + + + + +	–
		≥31	+ + + + + +	+ + +
Windowpane	B, N (larger fish)[2,3,15,21]	≤20	+ + + + + +	+
		≥31	+ + +	+
Grey sole	B[2,15,21,38,40]	≤30	–	±
		≥31	+ + +	+
American plaice	B[2,15,21,25,31,35,36,40], N (regional)[6,28,29,46,48]	≤20	+ + + + + +	–
		21-30	+ + + + + +	–
		31-40	+ + + + + +	–
		41-50	+ + + +	+
		≥51	+ + +	+
Atlantic halibut	N, B (small fish)[2,10,21,40]	33-48	+ +	+
Yellowtail flounder	B[2,14,15,18,29,37,40]	≤20	+ + +	–
		21-30	+ + + +	+
		31-40	+ + + +	+
		≥41	+ + +	+
Winter flounder	B[2,15,16,17,21,39,40,48]	18-54	+	+

[a] Nematode density > <0.5(+), 0.5-2.0 (+ +), 2.1-5.0(+ + +), 5.1-10.0(+ + + +), 10.1-20.0(+ + + + +), and >20.0(+ + + + + +) kg^{-1} round weight.

[b] Primary food items: plankton (P), benthos (B), nekton (N), and general (G).

1. Albikovskaya (1983); 2. Bigelow and Schroeder (1953); 3. Bousfield and Leim (1959); 4. Bowman (1975); 5. Bowman et al. (1984); 6. De Groot (1969); 7. Emery and McCracken (1966); 8. Hacunda (1981); 9. Imrie and Daborn (1981); 10. Kohler (1967); 11. Kohler and Fitzgerald (1969); 12. Kulka and Stobo (1981); 13. Lambert (1960); 14. Langton (1983); 15. Langton and Bowman (1980); 16. (1981); 17. Levings (1974); 18. Libey and Cole (1979); 19. Luczkovich and Olla (1983); 20. MacKay (1979); 21. Mauer and Bowman (1975); 22. Messieh et al. (1979); 23. Methven and McKelvie (1986); 24. Meyer et al. (1979); 25. Minet (1973); 26. Minet and Perodou (1978); 27. Moores et al. (1975); 28. Pitt (1973); 29. (1975); 30. Powles (1958); 31. (1965); 32. Savvatimsky (1984); 33. Scott (1969); 34. (1973b); 35. (1975a); 36. (1975b); 37. (1975c); 38. (1975d); 39. (1976); 40. Scott and Scott (1988); 41. Sedberry and Musick (1978); 42. Steele (1957); 43. (1963); 44. Templeman (1982); 45. (1985), 46. Tyler (1972); 47. Vinogradov (1972); 48. (1984); 49. Waiwood et al. (1980); 50. Wells and Steele (1973); 51. Wenner (1983).

windowpane, grey sole, halibut, yellowtail flounder and winter flounder, there being prior records of *Anisakis* sp. larvae in but five of these species, spiny dogfish, thorny skate, haddock, pollock and grey sole. Previously unpublished records include the finding of sealworm larvae in the flesh of freshly ingested sand lance (possibly *A. americanus*) from the stomachs of young grey seals collected on the eastern Nova Scotia mainland and identification of both *P. decipiens* and *A. simplex* larvae in turbot (*Reinhardtius hippoglossoides*) taken incidentally with plaice samples during earlier surveys of the Gulf of St. Lawrence and Breton Shelf (McClelland et al. 1983a). Sealworm larvae have also been proven infective to gaspereau (*Alosa pseudoharengus*), Atlantic salmon, mummichog (Atheriniformes: *Fundulus heteroclitus*), Altantic silversides (Atheriniformes: *Menidia menidia*), three-spined stickleback (*Gasterosteideus aculeatus*), cunner (*Tautogolabrus adspersus*) and grubby (*Myoxocephalus aeneus*) in laboratory transmissions (McClelland, unpublished data). Anisakis larvae have been found in cultivated brown trout (*Salmo trutta*) and rainbow trout (*S. gairdneri*) (Wootten and Smith 1975), the source of infection in these latter cases presumably being the untreated marine fish offal provided as food.

Larvae of a third anisakine species, *Contracaecum osculatum*, while abundant in cod and American plaice from the Gulf of St. Lawrence and Newfoundland waters, rarely occur in fish from the Scotian Shelf (McClelland et al. 1985). In the present study, *C. osculatum* larvae were found only in large cod and white hake. The latter species was, however, a new host record for the nematode.

The distributions of *P. decipiens* and *A. simplex* larvae in marine fish species are clearly influenced by host feeding behavior. In the present study, densities of larval sealworm were greatest in benthophagous (ocean pout, longhorn sculpin, windowpane and American plaice) and piscivorous demersal fish (monkfish, sea raven and mature cusk and cod) while pelagic consumers, with the exception of large silver hake (≥51 cm TL) and redfish were seldom infected (Table 7). High densities of *A. simplex* larvae, however, often occured in pelagic feeders such as herring, argentine, silver hake, pollock and sand lance, although heavy infections were also found in demersal piscivores, e.g. large cusk and cod (≥71 cm TL), and in general consumers including scrod, market-sized cod (31-70 cm TL) and red hake. Herringworm were rare or lacking in benthophagous fish but haddock and large (≥31 cm TL) longhorn sculpin proved exceptions in that they had relatively high densities of *A. simplex*. Curiously, *A. simplex* larvae were more numerous than *P. decipiens* larvae in haddock. A third epibenthic species, American plaice, while lightly infected with *A. simplex* on Sable Island Bank herein, has high densities of infection in other parts of its range, especially in waters off southern and western Newfoundland (McClelland et al 1985).

The divergence in sealworm and herringworm distributions in North Atlantic fishes can be traced to the early development of the respective parasites. In the sealworm life cycle, the ensheathed free-living larvae which emerge from the eggs, adhere by their caudal extremities to the substrate and ultimately infect benthic and epibenthic meio- and macrofauna (McClelland 1982, 1990) (Fig. 10). The ensheathed larvae which emerge from *A. simplex* eggs, however, are free to swim or drift into the water column (Smith and Wootten 1978) and infect planktonic invertebrates (Smith 1983a, b).

The fact that sealworm occurred in greater density than *A. simplex* in small (≤25 cm TL) redfish from the Scotian Shelf in the present study, however, is surprising in light of evidence that redfish diets consist almost entirely of pelagic organisms (particularly krill) consumed at night when the fish move off bottom (Scott and Scott 1988). While conflicting with observations that redfish do not seem to feed during the day when they occur near bottom, our findings infer that these fish nevertheless consume the benthic or epibenthic precursor hosts of sealworm.

Winter flounder were remarkable among flatfishes and other benthic consumers from Sable Island Bank in that they are seldom infected with *P. decipiens*. Indeed, flatfish

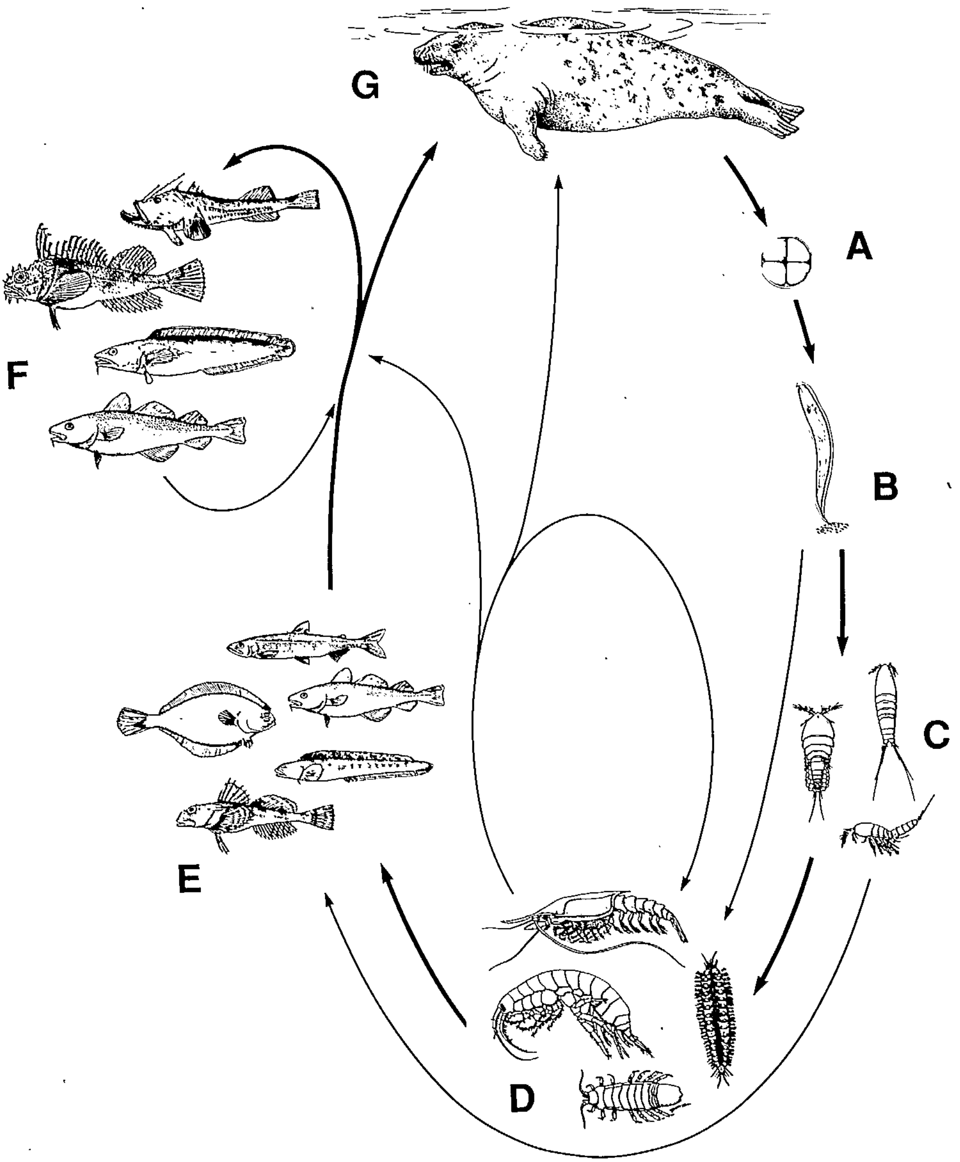


FIG. 10. Life cycle of sealworm (*Pseudoterranova decipiens*): A. partly embryonated ova passed in seawater with seal faeces; B. freshly-hatched, ensheathed L_2 (L_3?) larva, adhered to substrate by caudal extremity; C. early L_2 (L_3?) larvae in haemocoels of benthic harpacticoid and cyclopoid copepods; D. early to late L_2 with possible moult (M_2) to L_3 (or early L_3) in haemocoels of benthic macroinvertebrates (mysids, amphipods, isopods and errant polychaetes); E. early to late L_3 in body cavities and musculature of benthophagous fish eg. (clockwise from top) smelt, juvenile cod, ocean pout, longhorn sculpin and American plaice; F. late L_3 in body cavities and musculature of demersal piscivores including (top to bottom) monkfish, sea raven and mature cusk and cod; G. third (M_3) and fourth (M_4) moults and development to adult in stomach of a pinniped host; see text and McClelland (1990) for further discussion.

species surveyed here varied dramatically in regard to prevalence, abundance and density of sealworm although there appears to be considerable overlap in their diets (Scott 1975a, b, c, d; 1976; Langton and Bowman, 1981; Scott and Scott 1988). Evidently the distribution of *P. decipiens* in pleuronectiform fish is related, at least in part, to size of prey consumed as brill and American plaice, the species with the largest gapes, were also the most heavily infected flatfish. Detailed diet studies currently in progress, may explain disparities in sealworm abundance in the flatfishes of Sable Island Bank and identify important precursor hosts of sealworm among the benthic and epibenthic macroinvertebrates which these fish consume.

Demersal fishes evidently develop heavy *A. simplex* infections by consuming the parasite's pelagic intermediaries, many of which occur near bottom in the course of diurnal vertical migrations. Euphausiids, for example, are the predominant prey for young cod in the Gulf of St. Lawrence (Waiwood et al 1980) and are frequently consumed by cod and other gadids throughout the Northwest Atlantic (Langton and Bowman 1980; Scott and Scott 1988). Northwest Atlantic monkfish, gadids and cottids are known to prey upon a wide range of pelagic fishes (Bigelow and Schroeder 1953; Mauer and Bowman 1975; Langton and Bowman 1980; Grosslein et al. 1980; Vinogradov 1984; Scott and Scott 1988) including herring, silver hake and sand lance, species with high densities of *A. simplex* (Table 1). Sand lance, which bury themselves in the sediment during the day but emerge to feed pelagically at night (Scott 1973) must be a particularly important source of *A. simplex* infection in benthic consumers such as haddock and longhorn sculpin and a probable source of the heavy infections found in American plaice form Newfoundland waters (McClelland et al. 1985). According the Grosslein et al (1980), sand lance form a short link in the food web between the zooplankton and groundfish. Although primarily benthophagous, haddock, like redfish and cod, may undertake diurnal vertical migrations in pursuit of pelagic prey (Beamish 1966).

As evident in the present and earlier studies (Scott and Martin 1957; 1959; Templeman et al. 1957; Scott and Black 1960; Parsons and Hodder 1971; Young 1972; Platt 1975; Wootten and Waddell 1977; Wootten 1978; Pälsson 1979; McClelland et al. 1983 a, b; 1985; Hauksson 1984; Möller and Klatt 1988), prevalence and abundance of larval anisakines almost invariably increase with size or age of fish host. Mature fish incur heavier anisakine infections not only because they consume greater quantities of prey and, hence, greater numbers of infected precursor hosts but also because they consume larger, more heavily infected prey. Increases in the levels of *P. decipiens* and *A. simplex* infection in various gadids, for example, clearly correspond to the transition from a diet of benthic or planktonic invertebrates to predation on smaller fish. Larval anisakines are usually most numerous in piscivorous fish such as mature gadids, monkfish and sea raven.

As larval anisakines encyst in the body cavity and musculature of fish, emerging only on ingestion by a subsequent host, it is possible that they may persits indefinitely and become increasingly numerous through cumulative reinfections (Vooren and Tracey 1976; Wootten 1978). While larval anisakines are generally considered to be long-lived, their life spans in fish hosts are not known (Möller and Anders 1986). According to Smith's (1984c) studies of nematodes from captive herring, larval *A. simplex* were capable of excysting and infecting an experimental mammalian host after a minimum of 60-61 w and possibly >3 y in a fish host. By contrast, Moser et al. (1985) found that the majority of *Anisakis* sp. larvae died after a few weeks in the body cavities of Pacific striped bass (*Morone saxatiles*) although a few persisted for 31-33 w. Larval *P. decipiens* remained unencysted and vigorously active after a minimum of 40-50 w in captive smelt (McClelland, unpublished observations) but the presence of encapsulated necrotic specimens in the tissues of fish examined in the present study is evidence that sealworm infections in marine fish are also prone to attrition. Necrotic specimens of *P. decipiens* found encapsulated on the visceral organs and mesenteries of mature gadids and sea raven were probably from recent reinfections, as sealworm seldom occured in the body cavities of younger fish.

An apparent decline in the abundance of *P. decipiens* in American plaice >30 cm in length (Fig. 6) would seem to indicate loss of infection, but comparison of 1982 and 1986 plaice samples from Sable Island Bank reveals that parasites continued to accumulate within host cohorts (Fig. 7). In the 1982 sample, sealworm abundances were 3.22 ($n=18$), 2.64 ($n=36$) and 3.69 ($n=42$) in 7-8, 9-10 and 11-12 y-old plaice, respectively (age approximations according to age-length keys in Beacham 1982) while in 11-12, 13-14 and 15-16 y-old plaice sampled 4 yr later, the abundances of the nematode were 7.19 ($n=32$), 7.23 ($n=43$) and 5.68 ($n=31$). The negative sealworm abundance-host length trends in plaice from Sable Island Bank may be indicative of the growing abundance of the parasite in invertebrate precursor hosts such as crustaceans and polychaetes (Fig. 10) (McClelland 1990) which are more likely to be found in the diet of smaller plaice (Powles 1965; Minet 1973; Scott 1975b). Larger plaice feed primarily on echinoderms and molluscs.

Distributions of *P. decipiens* and *A. simplex* larvae in the musculature and body cavity of North Atlantic fish vary with species, size (age) and geographic origin of host. In the present study, sealworm larvae were mainly confined to the fillets of smaller (younger) fish but in larger (older) fish, the proportion of the total sealworm burden occupying the fillets declined as the parasite became increasingly abundant in the napes (hypaxial musculature surrounding the body cavity) and body cavity (Table 1). The proportion of the sealworm burden in the fillets of white hake, for example, fell from 90 % in hosts ≤ 40 cm TL to 29 % in hosts ≥ 61 cm TL. Sealworm in the napes of large (61 + cm TL) white hake and cusk outnumbered those in the fillets by more than two to one. In larger (51 + cm TL) monkfish, sealworm in the tailflesh were outnumbered not only by those in the napes but by those in the body cavity as well. Although most frequently found in the fillets of even the largest cod from Gulf of St. Lawrence and Nova Scotian waters (McClelland et al. 1983a, b, 1985, present study), sealworm larvae were most numerous in the napes of large (≥ 71 cm TL) Newfoundland cod (Brattey et al. 1990). However, densely infected hypaxial muscle lying posterior to the anus (sometimes referred to as "belly flaps" by Canadian processors) was processed with the fillets in the former (Gulf and Scotia-Fundy) series of surveys and with the napes in the latter (Newfoundland) study.

According to studies of cod from North Sea and British home waters (Young 1972; Wootten and Waddell 1977), *P. decipiens* larvae are more or less evenly distributed between the fillets and napes of smaller (younger) hosts but accumulate primarily in the napes (also referred to as "flaps") of hosts ≥ 2 yr old and 50 cm TL. The majority of sealworm larvae in large (≥ 71 cm TL) Icelandic cod also occur in the napes (Platt 1975). As the napes are the primary site of infection in larger fish, sealworm densities in the fillets of European cod decline with increasing length (age) of host. Young (1972) suggests that under these circumstances, selective fishing for larger cod, together with removal and separate processing of the napes (flaps), migth help alleviate the worm problem. While dismissing selective fishing as an uneconomical option, Platt (1975) endorses the separate processing of napes, noting that infections with *A. simplex* as well as sealworm are often concentrated in these tissues. Given that increases in sealworm abundance in the fillets of eastern Canadian cod (and other gadids) are often proportionate to or greater than increases in fillet weight and, consequently, that densities of infection in the fillets of larger fish rival those found in smaller fish (Scott and Martin 1957; Templeman et al. 1957; McClelland et al. 1983a, b, 1985, present study), it is unlikely that selective fishing would bring relief to the sealworm problem in eastern Canadian fisheries.

Smith (1984b) observed that *A. simplex* larvae are usually confined to the body cavities of plankton consumers such as Atlantic herring and mackerel but are more widely distributed in the tissues of piscivorous fish. Some species of piscivorous fish such as mature blue whiting (*Micromesistius poutassou*) from Scottish waters (Wootten and Waddell 1977; Smith 1984b), Atlantic salmon (Beverly-Burton and Pippy 1978) and cusk (herein) have a large portion (40-60 %) of their *A. simplex* burden in the flesh. In the present study, however, 17-30 % of the *A. simplex* larvae infecting plankton consumers such as argentine, sand lance, butterfish and redfish and only 0-13 % of those detected in piscivores, e.g. large monkfish, cod, silver hake and pollock, inhabited the musculature (Table 5).

The fact that *A. simplex* larvae occur primarily in the body cavities of fish is of little comfort to fish processors because heavy infections in the viscera could be a concern in the processing and marketing of products such as herring roe. Also, although only a small portion of the *A. simplex* burden may occupy the somatic musculature, the parasite may nevertheless be abundant in the flesh of heavily infected fish found in European (Young 1972; Platt 1975; Wootten and Waddell 1977; Smith 1984b), Newfoundland (McClelland et al. 1985; McGladdery 1986) and Scotian Shelf waters (present results): <7 % of the herringworm larvae infecting large (71+cm TL) cod from Sable Island Bank were found in the musculature, and yet prevalence of flesh infection was 64 % and abundance of the parasite in the flesh was 2.15 ($n=33$); 52 *A. simplex* larvae were found in the flesh of six large (61+cm TL) cusk from the same area. Futhermore, commercial candling procedures for the detection of nematodes in the flesh of fish are not very efficient (Power 1961) and even with a more efficient but industrially impractical destructive analyses like that performed in the present study, the majority of *A. simplex* larvae in fillets and napes may escape detection (McClelland et al. 1983a).

Commercial fishing practices may aggravate the *Anisakis* problem. When ungutted fish, particularly species with oily flesh such as herring and mackerel, are stored on ice for periods of more than a few hours, some *A. simplex* larvae migrate from the viscera to the flesh (Smith and Wootten 1975; Smith 1983b). Fresh evisceration of fish and disposal of heavily infected viscera at sea may, however, result in the increased abundance of the parasite in fish which feed on the discarded viscera. Cod which we collected from commercial draggers had often consumed the discarded viscera of fish caught in earlier tows.

Recent surveys (McClelland et al. 1983a, b, 1985, 1987; Malouf 1986; Brattey et al. 1990) show that *P. decipiens* larvae have become increasingly numerous in groundfish from southern Newfoundland, the Gulf of St. Lawrence and the Scotian and Breton Shelves over the past three decades as a possible consequence of the growth of the eastern Canadian grey seal population. The most dramatic increases in the parasite's abundance have occurred in fish from waters surrounding Sable Island, where the greatest densities of grey seals in the northwest Atlantic occur. As is evident from analyses presented here, sealworm prevalences and abundances in cod, grey sole, American plaice and yellowtail flounder from Sable Island Bank increased significantly between 1982 and 1986-87. Whereas haddock were lightly infected ($P=2$ %) ($n=121$) and redfish uninfected ($n=118$) in an earlier survey (Templeman et al. 1957) of the Sable Island area, our 1986 records indicate that 27 % ($n=415$) of the haddock and 23 % ($n=264$) of the redfish were infected with *P. decipiens* larvae. Although sealworm abundances appear to have remained unchanged in American plaice from eastern and northeastern Newfoundland (McClelland et al. 1985, 1987), Chandra and Khan (1988) report that cod from the Avalon peninsula and the northeast coast of the province have recently become more heavily infected. The validity of some of the comparisons in the latter study, however, have been questioned by Brattey et al. (1990).

It is not clear why disparities in prevalence and abundance of *P. decipiens* between our 1982 and 1986-87 samples of cod were confined to infections in smaller ($\leq$50 cm TL) fish. Possibly, it is because scrod, like the flatfish species above, are more likely to incur infections by feeding directly upon the invertebrate precursor hosts of the parasite. Moreover, the scrod examined here may have originated from local nursery stocks and, hence, have sealworm infections typical for the Sable Island area while the larger cod, which occurred on Sable Island Bank only during winter, were probably transient fish. As is evident from the annual movement of the southern Gulf of St. Lawrence population to the Breton (Shelf (Kohler 1975), cod may undertake extensive seasonal migrations.

The significance of apparent increases in the prevalence and abundance of *A. simplex* in cod from Sable Island Bank (Fig. 9) is also unclear, as supporting evidence on trends of *A. simplex* infection in Scotian Shelf fish is lacking. Although *A. simplex* abundances seem to have increased dramatically in fish from the Scottish (Smith and Wootten 1979) and Newfoundland waters (McClelland et al. 1985) in recent years, it is unlikely that cetacean (definitive host) populations, even those protected prior to the 1972 moratorium on whaling, have recovered sufficiently to have influenced such increases. Grey seal populations on the Scotian Shelf and throughout the North Atlantic have grown substantially over the last few decades (Zwanenburg and Bowen 1990) but few of the *A. simplex* ingested by seals survive to reproductive maturity (Young 1972; McClelland, unpublished data).

A summary of data on the diets of grey seals in eastern Canada (Benoit and Bowen 1990 a) reveals that cod are the most frequently consumed prey fish, being found in 18.5 % of the seal specimens in which fish remains were observed. Among other prey of possible significance in the transmission of *P. decipiens*, flatfishes (unspecified), pout and sculpins rank 4th, 15th and 23rd (frequencies of occurrrence 9.5, 1.6 and 0.7 %) in grey seal diets. In 1986-87 grey seal samples from Anticosti Island in the northern Gulf of St. Lawrence (Benoit and Bowen 1990b), cod ranked second to capelin (*Mallotus villosus*) in frequency of occurrence in the diet (29.3 %) and as a proportion of total numbers of fish consumed (15.6 %) while plaice, ocean pout and sculpins were 5th (10.9 %), 7th (4.3 %) and 9th (0.5 %) in frequency of occurrence and accounted for 4.5, 0.8 and $<$0.1 % (by numbers) of the fish consumed. The great majority of prey fish ($>$85 % of the cod and $>$90 % of the plaice) were $\leq$40 cm in length. As is evident from our data (Table 1, Appendix I), sealworm infections in juvenile cod (A=0.62-6.12; D=4.65-13.78 kg^{-1}) may not be as heavy as those found in small plaice (A=1.46-12.79; D=22.38-72.76 kg^{-1}), pout (A=2.60; D=22.03 kg^{-1}) and cottids (A=0.55-48.82; D=20.26-61.63 kg^{-1}). Given the frequencies (by species and length) of prey fish in grey seal diets described by Benoit and Bowen (1990b) and sealworm distributions in fish (by host species and length) in the present study however, cod appears to be the most important sealworm intermediary among fishes consumed by grey seals, with sealworm larvae transmitted to grey seals by cod outnumbering those transmitted by plaice by 1.5:1.

Despite an apparent preference for smaller prey, grey seals are nevertheless, capable of ingesting fish exceeding 70 cm in length and 3 kg in weight (SMRU 1984; Benoit and Bowen 1990b) and the significance of *P. decipiens* infecting infrequently consumed but (often) heavily infected larger fish cannot be ignored. With length frequencies of cod in grey seal diets according to Benoit and Bowen (1990b) and with sealworm distributions in cod (with host length) described herein, fish of commercial size ($\geq$40 cm TL) would account for only a small minority ($>$15 % by number) of the cod consumed but would carry the majority (54 %) of the sealworm larvae. A large portion (30 %) of the sealworm transmitted from cod to grey seals would come from fish $>$70 cm in length even though the latter comprise $<$2 % of the cod eaten. Of further relevance to this topic is anecdotal information from fishermen who have observed grey seals discarding the heads of larger prey. As species and size of prey are usually determined by analyses of otoliths found in the gastrointestinal tract or faeces of seals, occurrences of large decapitated prey, including heavily infected fish such as mature gadids, monkfish and sea raven may not be recorded.

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APPENDIX I. Prevalence and abundance of *P. decipiens* and *A. simplex* larvae in various fish species from Sable Island Bank and vicinity.

Host			Larval anisakines detected					
			P. decipiens			*A. simplex*		
Species	Length range	*n*	Prevalence[a]	Abundance[b]	Intensity range[c]	Prevalence	Abundance	Intensity range
Spiny dogfish (*Squalus acanthias*)	29-40	10	-	-	-	-	-	-
	67	1	-	-	-	100	1.00	1
Thorny skate (*Raja radiata*)	≤40	6	-	-	-	-	-	-
	≥41	8	38	0.50	1-2	25	0.38	1-2
Herring (*Clupea harengus*)	≤24	12	-	-	-	25	0.25	1
	25-26	32	-	-	-	25	0.38	1-2
	27-28	43	-	-	-	14	0.19	1-2
	29-30	35	-	-	-	46	1.03	1-6
	≥31	14	-	-	-	86	4,14	1-10
Argentine (*Argentina silus*)	25-36	51	-	-	-	27	0.49	1-6
Monkfish (*Lophius americanus*)	≤30	13	23	0.23	1	-	-	-
	31-50	11	91	18.55	2-33	27	0.55	1-3
	51-60	16	100	46.44	12-190	38	1.13	1-6
	61-70	18	100	41.50	3-152	72	3.83	1-7
	≥71	7	100	39.71	16-67	86	3.86	1-14
Cusk (*Brosme brosme*)	61-88	6	100	47.33	3-107	100	21.67	5-48
Cod (*Gadus morhua*)	≤30	34	24	0.62	1-10	6	0.09	1-2
	31-35	39	87	4.59	1-19	41	0.54	1-2
	36-40	26	77	6.12	1-25	54	1.08	1-4
	41-45	40	75	4.03	1-21	65	2.23	1-27
	46-50	29	90	6.28	1-26	79	2.14	1-9
	51-55	25	96	7.44	1-18	84	4.44	1-21
	56-60	32	97	9.50	1-27	97	5.47	1-23
	61-65	31	97	12.39	1-42	94	8.35	1-32
	66-70	29	100	17.03	2-52	100	14.07	1-37
	≥71	33	97	58.79	4-488	100	31.79	7-100
Haddock (*Melanogrammus aeglefinus*)	≤30	39	3	0.03	1	5	0.08	1-2
	31-35	61	11	0.15	1-2	18	0.28	1-4
	36-40	65	31	0.48	1-4	34	0.57	1-4
	41-45	57	28	0.42	1-3	46	1.11	1-7
	46-50	52	27	0.46	1-3	56	1.77	1-14
	51-55	64	34	0.48	1-5	67	2.03	1-23
	56-60	46	30	0.78	1-9	46	1.91	1-11
	≥61	31	55	1.61	1-7	81	2.74	1-14
Silver hake (*Merluccius bilinearis*)	≤20	18	-	-	-	-	-	-
	21-25	22	-	-	-	-	-	—
	26-30	55	-	-	-	38	0.93	1-13
	31-35	62	-	-	-	65	3.21	1-30
	36-40	38	-	-	-	79	3.18	1-14
	41-45	42	2	0.02	1	90	4.57	1-22
	46-50	34	12	0.38	1-7	97	15.88	1-42
	≥51	15	33	1.00	1-6	100	14.00	2-41
Pollock (*Pollachius virens*)	≤30	17	-	-	-	53	1.76	1-8
	31-60	18	6	0.06	1	89	6.22	1-33
	61-65	33	6	0.06	1	100	21.67	4-52
	66-70	32	6	0.06	1	100	21.00	4-62
	≥71	28	11	0.18	1-2	100	26.04	3-68
Longfin hake (*Uraphycis chesteri*)	≤25	14	-	-	-	-	-	-
	26-30	25	8	0.08	1	8	0.12	1-2
	≥31	15	13	0.13	1	20	0.20	1
Red hake (*Urophycis chuss*)	≤30	30	7	0.10	1-2	-	-	-
	31-35	43	9	0.09	1	12	0.30	1-8
	36-40	31	3	0.10	3	26	0.87	1-7
	≥41	20	40	0.95	1-7	40	1.35	1-15
White hake (*Urophycis tenuis*)	≤30	32	3	0.03	1	-	-	-
	31-35	47	13	0.13	1	4	0.06	1-2
	36-40	38	21	0.34	1-4	5	0.05	1
	41-45	40	48	1.35	1-12	15	0.23	1-6
	46-50	29	45	2.03	1-16	31	0.83	1-6
	51-55	18	50	3.33	1-36	39	1.33	1-5
	56-60	15	60	2.73	1-18	60	1.53	1-6
	≥61	18	94	8.11	1-27	78	4.22	1-17
Roughhead grenadier (*Macrourus berglax*)	12-30	47	-	-	-	-	-	-
Ocean pout (*Macrozoarces americanus*)	18-50	15	80	2.60	1-7	-	-	-
	51-82	11	91	2.55	1-11	-	-	-
Wolffish (*Anarhichas lupus*)	69-95	6	100	5.83	1-12	-	-	-
Sand lance (*Ammodytes dubius*)[d]	16-28	144	-	-	-	12	0.13	1-2
Mackerel (*Scomber scombrus*)	≤30	17	-	-	-	18	0.18	1
	≥31	36	-	-	-	42	0.61	1-3
Butterfish (*Peprilus triacanthus*)	10-23	102	1	0.01	1	7	0.07	1
Redfish (*Sebastes* spp.)[e]	≤20	57	5	0.05	1	4	0.04	1
	21-25	32	16	0.16	1	3	0.09	3
	26-30	58	24	0.29	1-3	2	0.02	1
	31-35	52	33	0.48	1-3	8	0.08	1
	36-40	39	26	0.33	1-2	26	0.49	1-4
	≥41	26	42	0.77	1-3	50	2.81	1-39

APPENDIX I. (Concluded.)

Host			Larval anisakines detected					
			P. decipiens			*A. simplex*		
Species	Length range	*n*	Prevalence[a]	Abundance[b]	Intensity range[c]	Prevalence	Abundance	Intensity range
Sea raven (*Hemitripterus americanus*)	≤25	11	64	4.09	1-20	-	-	-
	26-30	9	100	22.22	5-62	-	-	-
	31-35	14	100	35.50	10-73	21	0.43	1-4
	36-40	17	100	48.82	8-130	6	0.24	4
	41-45	13	100	53.92	20-92	15	0.31	1-3
	46-50	16	100	77.75	19-223	-	-	-
	51-55	13	100	95.85	56-175	15	0.23	1-2
	≥56	10	100	184.90	53-319	20	0.80	2-6
Longhorn sculpin (*Myoxocephalus octodecemspinosus*)	≤20	27	41	0.55	1-2	-	-	-
	21-55	*65*	*86*	*2.68*	*1-10*	-	-	-
	26-30	45	96	4.80	1-25	-	-	-
	≥31	37	95	6.43	1-31	41	1.00	1-6
Windowpane (*Scopthalmus aquasus*)	≤20	60	52	1.68	1-10	2	0.02	1
	21-25	47	57	2.45	1-18	-	-	-
	≥26	28	68	2.93	1-24	-	-	-
Gray sole (*Glyptacephalus cynoglossus*)	≤30	17	-	-	-	6	0.06	1
	31-35	33	36	0.70	1-4	6	0.06	1
	36-40	39	67	1.18	1-4	3	0.03	1
	41-45	31	65	1.26	1-5	-	-	-
	46-50	25	68	1.48	1-6	-	-	-
	≥51	11	82	1.36	1-4	18	0.18	1
American plaice (*Hippoglossaides platessaides*)	<20	37	24	1.46	1-42	-	-	-
	21-25	31	81	5.97	1-23	-	-	-
	26-30	34	100	12.79	1-36	-	-	-
	31-35	34	94	8.44	1-26	-	-	-
	36-40	32	97	7.19	1-33	-	-	-
	41-45	43	95	7.23	1-25	7	0.07	1
	46-50	31	94	5.68	1-32	3	0.03	1
	≥51	36	92	5.78	1-39	-	-	-
Halibut (*Hippoglassus hippoglossus*)	33-48	20	40	0.60	1-3	5	0.05	1
Yellowtail flounder (*Limanda ferruginea*)	≤20	32	6	0.09	1-2	-	-	-
	21-25	32	25	0.44	1-3	-	-	-
	26-30	35	51	1.34	1-13	17	0.17	1
	31-35	57	61	1.77	1-10	9	0.23	1-5
	36-40	40	68	1.58	1-7	15	0.15	1
	≥41	20	65	1.60	1-7	5	0.05	1
Winter flounder (*Pseudopleuronectes americanus*)	≤30	31	-	-	-	-	-	-
	31-35	35	-	-	-	3	0.03	1
	36-40	39	-	-	-	-	-	-
	41-45	31	3	0.03	1	-	-	-
	46-50	28	4	0.04	1	-	-	-
	≥51	10	-	-	-	-	-	-

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[a] Prevalence (P) = no. of infected fish / total number of fish (expressed as a percentage).

[b] Abundance (A) = total number of nematodes in sample / total number of fish in sample.

[c] Intensity (I) range = range of individual worm counts in infected fish.

[d] Sample taken on western extremity of Banquereau, approximately 57 km northeast of Sable Island, April 1987.

[e] All redfish, < 35 cm TL were collected at depths < 200 m and were, presumably, *S. fasciatus*; the majority of redfish ≥ 36 cm were collected from the continental slope at depths of 450-615 m and may be *S mentella*.

APPENDIX II. Fish host spectra of *P. decipiens* and *A. simplex* larvae in the North Atlantic and adjacent waters.

Host				Parasite records[a]	
Class Order Family	Species	Common name(s)	Location	*P. decipiens** or *Pseudaterranova*-type** larvae	*A. simplex** or *Anisakis*—type** larvae
Agnatha					
Petromyzontiformes					
Petromyzontiadae	*Lampetra japonica*	Arctic lamprey	White Sea	Shulman (1957)*	Shulman (1957)*
Chondrichthyes					
Squaliformes					
Squalidae	*Squalus ocanthias*	spiny dogfish	Canada	Threlfall (1969)**	Threlfall (1969)** present study*
Rajiformes					
Rajidae	*Raja laevis*	barndoor skate	Canada	Myers (1959)**	Myers (1959)**
	R. ocellata	winter skate	Canada	Threlfall (1969)**	Myers (1959)**
	R. radiata	thorny skate	Canada	present study*	Myers(1959)** present study*
			Barents Sea	—	Palyanskii (1966)**
Osteichthyes					
Anguilliformes					
Anguillidae	*Anguilla anguilla*	European eel	Germany	Möller and Schröder (1987)*	—
Serrivomeridae	*Serriuamer beani*	stout sawplate	USA	—	Gartner and Zwerner (1989)**
Clupeiformes					
Clupeidae	*Alasa pseudoharengus*	*alewife, gaspereau*	*Canada*	—	*Gaevskaya and Umnova (1977)**
	A. finta	twaite shad	France	—	Huang (1988)*
	Clupea harengus harengus	Atlantic herring	North Atlantic	—	Khalil 1969; Parsons and Holder 1971; Daveyt 1922; Beverley-Burton et al. (1977)*; Van Banning and Becker 1978**
			Iceland	Hauksson (pers. comm.)**	
	Sardina pilahardus	sardine	France	—	Huang (1988)*
Salmoniformes					
Salmonidae	*Salmo solar*	Atlantic salmon	North Atlantic	—	Beverley-Burton et al. (1977)*; Beverley-Burton and Pippy 1978*
	Salvelinus alpinus	Arctic char	Labrador	—	Hicks and Threlfall (1973)**
			Barents Sea	—	Polyanskii (1966)**
	S. fontinalis	brook trout	Canada	Pippy (pers. comm.)*[b]	Hicks and Threlfall (1973)**
Osmeridae	*mollotus villasus*	capelin	Canada	—	Pálsson and Beverley-Burton (1984)*
			Barents Sea	—	Polyanskii (1966)**
	O. mardan	European smelt	Germany	Kahl (1936)*, Möller and Klatt (1988)*	Möller and Klatt (1988)*
	Osmerus eperlanus	rainbow smelt	Canada	Scott and Black (1960)*, Templeman et al.(1957)**	Heller (1949)**
Argentinidae	*Argentina silus*	Atlantic argentine	Canada	—	present study*
			Barents Sea	—	Polyanskii (1966)**
Gonostomatidae	*Gonostoma elangatum*	longtooth anglemouth	USA	—	Gartner and Zwerner (1989)**
Sternoptychidae	*Sternoptyx diaphana*	transparent hatchetfish	USA	Gartner and Zwerner (1989)**	Gartner and Zwerner (1989)**
Chauliodontidae	*Chauliodus sloani*	Sloan's viperfish	USA	—	Gartner and Zwerner (1989)**
Stomiidae	*Stomias boa ferox*	boa dragonfish	USA	—	Gartner and Zwerner (1989)**
Alepocephalidae	*Alepocephalus agassizii*	Agassiz' smoothhead	USA	—	Campbell et al. (1980)*
Synodontidae	*Bathysaurus agassizi*	lizardfish	USA	—	Campbell et al. (1980)*
Myctophiformes					
Myctophidae	*Ceratocephalus maderensis*	horned lanternfish	USA	—	Gartner and Zwerner (1989)**
Lophiiformes					
Lophiidae	*Lophius americanus*	monkfish	Canada	Templeman et al.(1957)** present study*	present study*
	L. piscotorius	angler	Norway	Bjørge (pers. comm.)*[3]	—
			Germany	Kahl (1938a) *	—
Gadiformes					
Gadidae	*Brasme brasme*	cusk	Canada	present study*	present study*
		torsk	Barents Sea	—	Polyanskii (1966) **
			Norway	Bjørge (per. comm.)*[c]	—
			Germany	Möller (pers. comm.)**[d]	Möller (pers. comm.)**[d]
	Gadus marhua	Atlantic cod	Canada	Templeman et al. (1957)**; Scott and Martin (1957)*; McClelland et al. (1983a; 1985)*	Templeman et al. (1957)**; McClelland et al. (1983a; 1985)*
			Barents Sea	Kahl (1939)*; Polyanskii (1966)*; Platt (1975)*	Kahl (1939)**; Polyanskii (1966)**; Platt (1975)**
			Iceland	Kahl (1939)*; Platt (1975)*; Pálsson (1979)*; Hauksson (1984)*	Kahl (1939)**; Platt (1975)**; Pálsson (1979)*; Hauksson (1984)*
			Norway	Kahl (1939)*; Bjørge et al. (1981)*	Kahl (1939)**; Platt (1975)**
			Germany	Kahl (1938a; 1939)*	Kahl (1938b)**
			North Sea and British Isles	Young (1972)*; Platt (1975)*; Smith and Wootten (1979)**	Young (1972)**; Platt (1975)**; Smith and Wootten (1979)**

APPENDIX II. (Continued.)

	Host			Parasite records[a]	
Class Order Family	Species	Common name(s)	Location	*P. decipiens** or *Pseudoterranova*-type** larvae	*A. simplex** or *Anisakis*—type** larvae
	G. ogac	Greenland cod	Canada	Scott and Black (1960)*	—
	Melanogrammus aeglefinus	haddock	Canada	Templeman et al. (1957)**; present study*	Templeman et al. (1957)**; present study*
			Barents Sea	Polyanskii (1966)**	(1966)**
			Scotland	Wootten and Waddell (1977)*	Wootten (1978)**
	Merlangius merlangus	whiting	North Sea and Scotland	—	Wootten and Waddell (1977)**
			France	—	Huang (1988)*
	Merluccius bilinearus	silver hake	Canada	present study*	Gaevskaya and Umnova (1977)*; present study*
	M. merluccius	hake	France	Huang (1988)*	Huang (1988)*
	Microgadus tomcod	Atlantic tomcod	Canada	Templeman et al. (1957)**	Heller (1949)**
	Micromesistius poutassou	blue whiting	Barents Sea	—	Polyanskii (1966)**
			Scotland	—	Wootten and Smith (1976)**
	Molva molva	ling	Barents Sea	—	Polyanskii (1966)**
			Germany	Kahl (1938a)*	Möller (pers. comm.)**[d]
	M. byrkelange	blue ling	Germany	Kahl (1938a)*	Möller (pers. comm.)**[d]
	Pollachius virens	pollock	Canada	present study*	Templeman et al. (1957)**; present study*
		saithe	Barents Sea	—	Polyanskii (1966)**
			Iceland	—	Kahl (1939)**
			North Sea	—	Kahl (1939)**
	Trisopterus esmarkii	Norway pout	Scotland	—	Wootten (1978)**
	T. minutus	poor cod	Scotland	Wootten and Waddell (1977)	Wootten (1978)**
	Urophycis chesteri	longfin hake	Canada	present study*	present study*
	U. chuss	red hake	Canada	present study*	Heller (1949)**, present study*
	U. tenuis	white hake	Canada	Scott (1954)*	present study*
Macrouridae	*Coryphaenoides rupestris*	rock grenadier	USA	—	Campbell et al. (1980)*
	Macrourus berglax	roughhead grenadier	Newfoundland	—	Noble (1973)**
	Nezumia bairdi	marlin spike	Newfoundland	Zubchenko (1981)*	—
Gasterosteiformes					
Gasterosteidae	*Gasterosteus aculeatus*	three-spined stickleback	Barents Sea	—	Polyanskii (1966)**
Perciformes					
Carangidae	*Trachurus trachurus*	scad	France	—	Huang (1988)*
Labridae	*Tautogolabrus adspersus*	cunner	Canada	Sekhar and Threlfall (1970)**	Sekhar and Threlfall (1970)**
Zoarcidae	*Lycodes vahlii*	checker eelpout	Canada	present study*[f]	—
	Macrozoarces americanus	ocean pout	Canada	Scott and Black (1960)*	—
	Zoarces viviparus	eel pout	Barents Sea	Polyanskii (1966)*	
Stichaeidae	Lumpenus lumpretaeformis	snake blenny	Iceland	Hauksson (pers. comm.)*[e]	—
Pholidae	*Pholis gunnellus*	gunnel	Barents Sea	—	Polyanskii (1966)**
Ararhichadidae	*Anarhichas denticulatus*	norther wolffish	Barents Sea	—	Polyanskii (1966)**
	A. lupus	wolffish	Canada	Zubchenko (1980)*	—
		catfish	Barents Sea	Polyanskii (1966)**	—
			Iceland	Hauksson (pers. comm.)*[e]	—
			Germany	Kahl (1938a)*	—
Ammodytidae	*Ammodytes dubius*	northern sandlance	Canada	—	McClelland et al. (1985)*; present study
	Ammodytes sp.		Canada	present study*[g]	—
	A. hexapterus	Pacific sandlance	Barents Sea	—	Polyanskii (1966)**
Gobiidae	*Pomatoshistus* sp.	goby	Wadden Sea	Möller (pers. comm.)*[d]	—
Callionymidae	*Callionymus lyra*	dragonet	Scotland	Wootten and Waddell (1977)*	—
Scombriadae	*Scomber scombrus*	Atlantic mackerel	Canada	—	Gaevskaya and Umnova (1977)*; present study*
			North sea, British Isles and France	—	Eltink 1988** Huang (1988)*
Stromateidae	*Peprilus triacanthus*	butterfish	Canada	present study*	present study*
Scorpaenidae	*Sebastes fasciatus*	Acadian redfish	Canada	present study*	Bourgeois and Ni (1984)*; present study*
	S. marinus	golden redfish	Canada	Gaevskaya and Umnova (1977)*	Templeman et al. (1957)*; Bourgeois and Ni (1984)*
			Barents Sea	—	Kahl (1939)**
			Iceland	Kahl (1939)*	Kahl (1939)**
			Norway	Kahl (1939)*	(1939)**
			North Sea	—	Kahl (1939)**
			France	Huang (1988)**	Huang (1988)**
	S. mentella	deepwater redfish	Canada	present study*	Bougeois and Ni (1984)*; present study*
Triglidae	*Aspitrigla cuculus*	red gumard	France	Huang (1988)*	Huang (1988)*
	Eutrigla gurnardus	grey gurnard	France	—	Huang (1988)*
Cottidae	*Gymnocanthus tricuspis*	Arctic staghorn sculpin	Barents Sea	Polyanskii (1966)*	Polyanskii (1966)**
	Hemitripterus	sea raven	Canada	Scott and Black (1960)*;	present study*

APPENDIX II. (Concluded.)

Host				Parasite records*	
Class Order Family	Species	Common name(s)	Location	*P. decipiens** or *Pseudaterranava*-type** larvae	*A. simplex** or *Anisakis*—type** larvae
Agonidae	*Aspidapharoides monopterygius*	alligatorfish	Canada	present study*	—
Cyclapteridae	*Cyclapterus lumpus*	lumpfish	Canada	present study[f]	present study**
			Barents Sea	—	Polyanskii (1966)**
	Eumicrotremus spinosus	spiny lumpsucker	Canada	present study*	—
	Liparis liparis	seasnail	Barents Sea	Polyanskli (1966)*	Polyanskii (1966)**
Pleuronectoformes					
Bothidae	*Scophthalmus aquosus*	windowpane	Canada	Ronald (1963)**; present study*	present study*
Pleuronectidae	*Glyptocephalus cynoglassus*	grey sole	Canada	Templeman et al. (1957)**; Myers (1960)*; McClelland et al. (1985)*	Templeman et al. (1957)**; present study*
		witch	Scotland	Wootten and Waddell (1977)*	—
			Iceland	Hauksson (pers. comm.)*[e]	—
	Hippoglossaides platessoides	American plaice	Canada	Scott (1954)*; Templeman et al. (1957)**; McClelland et al. (1985)*	Templeman et al. (1957)**; McClelland et al. (1985)*
	Hippoglossus hippoglassus	Atlantic halibut	Canada	Ronaid (1963)**; present study*	present study*
	Limanda limanda	dab	Barents Sea	—	Polyanskii (1966)**
	L. ferruginea	yellowtail flounder	Canada	Scott and Black (1960)*; Gaevskaya and Umnova (1977)*; McClelland et al. (1985)*	present study*
	Lyopsetta putnami	smooth flounder	Canada	Ronald (1963)**	—
	Platichtys flesus	flounder	Barents Sea	—	Polyanskii (1966)**
			Germany	Möller and Klatt (1988)*	—
	Pseudopleuronectes americanus	winter flounder	Canada	Scott (1954)*; Ronald (1963)**	present study*
	Reinhardtius hippoglassoides	turbot	Canada	present study*[h]	present study*[h]
		Greenland halibut	Barents Sea	—	Polyanskii (1966)**

[a] Original generic and specific records of parasites and major surveys cited.

[b] J. Pippy, Dept. of Fisheries and Oceans, St. John's Newloundland: larval sealworm found in sea run brook trout.

[c] A. Bjbrge, Ministry of the Environment, Oslo, Norway.

[d] H. Mölier, Institut für Meerskund, Keii, Germany: nematodes belonging ta the *Anisakis-Pseudaterranava* species complex in fillets of German market fish (industrial sources).

[e] Unplublished data, J. Pálsson and E. Haukssan, Marine Research Institute, Reykjavik, Iceland.

[f] Infected 12 cm TL specimen collected by D. J. Marcogliese with an epibenthic sled at lat. 44°22'N, long. 61°31'W on June 5, 1989; no prior record of *L. vohlii* south of lat. 44°58'N (Scott and Scott 1988).

[g] Larval *P. decipiens* found encysted in flesh of freshly ingested sand lance (possibly *A. americanus*) form the stomachs af grey seals collected off the Eastern Nova Scotia mainland.

[h] Heavily infected turbot found among commercial samples of American plaice during survey af the southern Gulf of St. Lawrence and the Breton Shelf (McClelland et al. 1983a).

Abundance of Sealworm (*Pseudoterranova decipiens*) in Rainbow Smelt (*Osmerus mordax*) from the southwestern Gulf of St. Lawrence

T. Landry and G. M. Hare[1]

Department of Fisheries and Oceans, Science Branch,
P.O. Box 5030, Moncton, N.B., Canada E1C 9B6

LANDRY, T., AND G. M. HARE. 1990. Abundance of sealworm (*Pseudoterranova decipiens*) in rainbow smelt (*Osmerus mordax*) from the southwestern Gulf of St. Lawrence, p. 119-127. *In* W. D. Bowen [ed.] Population biology of sealworm (*Pseudoterranova decipiens*) in relation to its intermediate and seal hosts. Can. Bull. Fish. Aquat. Sci. 222.

Larval sealworm (*Pseudoterranova decipiens*) infestation levels in anadromous American smelt (*Osmerus mordax*) may serve as an index of sealworm abundance in inshore areas. Twenty eight hundred smelt from five locations in the southwestern Gulf of St. Lawrence were examined for anisakines over a 4-yr period (1984-87). Significant heterogeneity in sealworm abundance was detected among host size groups and geographical locations. Temporal changes in sealworm abundance were not apparent in smelt from four of the locations. These results are not consistent with evidence of increasing sealworm abundance in American plaice (*Hippoglossoides platessoides*) from offshore areas.

Les niveaux d'infestation de larves de vers de phoque (*Pseudoterranova decipiens*) chez l'éperlan d'amérique (*Osmerus mordax*) peuvent servir comme un indice d'abondance du vers de phoque pour les régions côtières. Deux mille huit cents éperlans échantillonnés sur cinq sites dans la partie sud-ouest du golfe du Saint-Laurent ont été examinés pour la présence de vers anisakinés, sur une période de 4 ans (1984-1987). L'abondance de vers de phoque est significativement hétérogène parmis les groupes de taille des hôtes et les sites géographiques. Des variations temporelles chez l'abondance de vers de phoque ne sont pas évidentes chez les éperlans de quatres des sites géographiques. Ces résultats ne sont pas consitent avec l'indiction d'augmentation de l'abondance de vers de phoque chez la plie canadienne (*Hippoglossoides platessoides*) de régions hauturière.

Introduction

The relationship between increasing trends in the abundance (mean number of parasites per host) of sealworm larvae (*Pseudoterranova decipiens*) in fish and the increasing number of grey seals (*Halichoerus grypus*) (the primary definitive hosts) in eastern Canada is not completely understood. Increases in the abundance of *P. decipiens* in groundfish throughout the northwestern Atlantic have been documented by McClelland et al. (1987) as have increases in the numbers of grey seals (Zwanenburg and Bowen 1990). Sealworm abundance in offshore areas of eastern Canada is monitored using infestation levels in groundfish as an index. McClelland et al. (1983) concluded that the American plaice (*Hippoglossoides platessoides*) was the most suitable host indicator of sealworm abundance partly due to its relatively sedentary nature. In a attempt to establish a similar abundance index for inshore areas, a survey of sealworm infestations in anadromous rainbow smelt (*Osmerus mordax*) was initiated in 1984.

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[1] Present address: Fisheries Environmental Consultants
Consultants en Pêches et Environnement.
P.O./C.P. 1027
Moncton, N.B. Canada
E1C 8P2

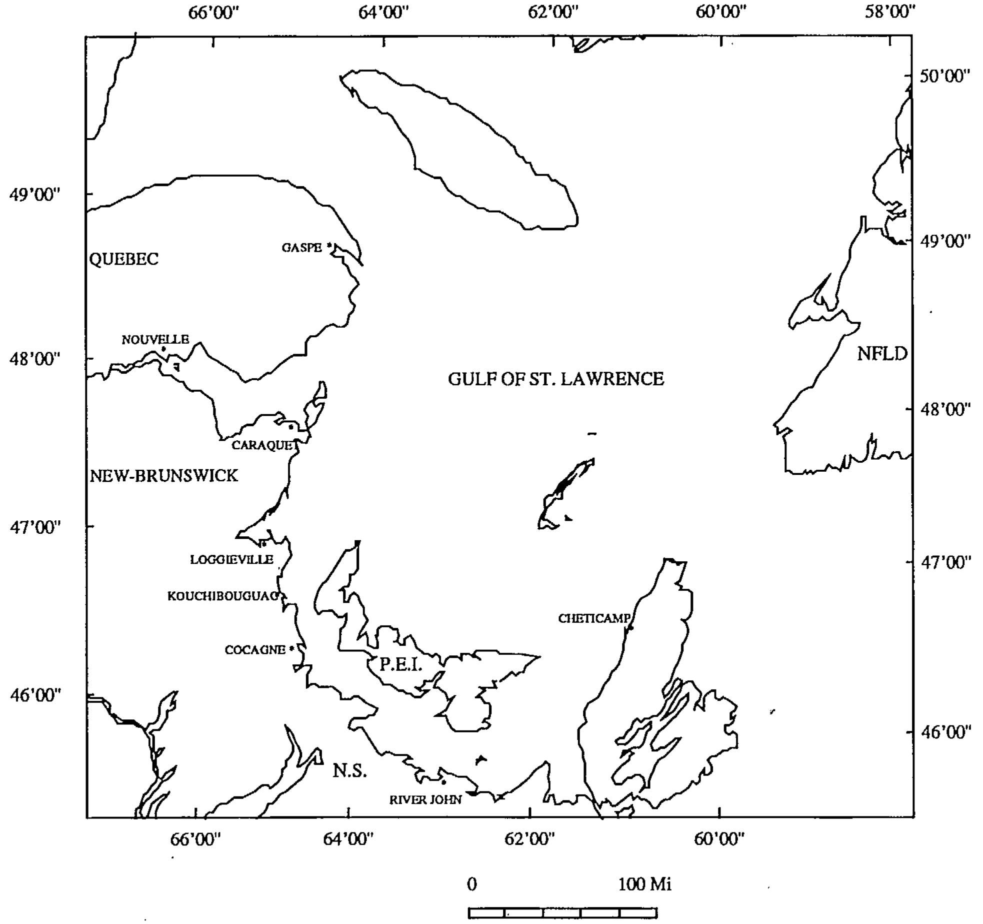

FIG. 1. Sampling locations in the Gulf of St. Lawrence.

In the western Atlantic, rainbow smelt is found from New Jersey to Labrador. The most extensive review of its life history and fishery was conducted by McKenzie (1964) on smelt from the Miramichi River, New Brunswick. Anadromous smelt are sedentary in nature being restricted to relatively small geographical areas, however, it is unlikely that they possess a strong homing instinct for their spawning river (McKenzie 1964; Fréchet et al. 1983). Male and female smelt reach sexual maturaty at age 2 with an average length of 135 and 139 mm, respectively. The majority (up to 95 %) of spawners are 2-3-yr-old fish (McKenzie 1964).

Pseudoterranova decepiens infestation in smelt from eastern Canada have been reported by Templeman et al. (1957), Scott (1950, 1953, 1954), Scott and Black (1960), and Fréchet et al. (1983). Templeman et al. (1957) concluded that smelt was one of the fish species with the greatest density (number of parasites per weight of host) of sealworm larvae, thus smelt may play an important role in the life cycle and population dynamics of *P. decipiens*. Furthermore, smelt are found in coastal areas where seals and commercially important piscivorous fish such as Atlantic cod (*Gadus morhua*) commonly feed. Abundance of sealworm in smelt may be indicative of current abundance of sealworm in specific inshore areas due to the short life span of the host, and of future infestation levels in commercially important groundfish.

TABLE 1. Results of the Kruskall-Wallis test for comparison of sealworm counts among four size groups of smelts.

Location	Date	Value of *H*
Caraquet	1985	4.52*
Caraquet	1987	0.56
Cocagne	1984	10.85*
Cocagne	1985	4.75
Cocagne	1987	0.82
Kouchibouguac	1984	24.33*
Kouchibouguac	1985	3.19
Kouchibouguac	1987	10.60*
Loggieville	1984	0.45
Loggieville	1985	12.33*
Loggieville	1987	8.70*
Nouvelle	1984	3.00
Nouvelle	1985	199.00*
Nouvelle	1987	1.88

* indicates significant ($P < 0.05$) heterogeneity among size groups.

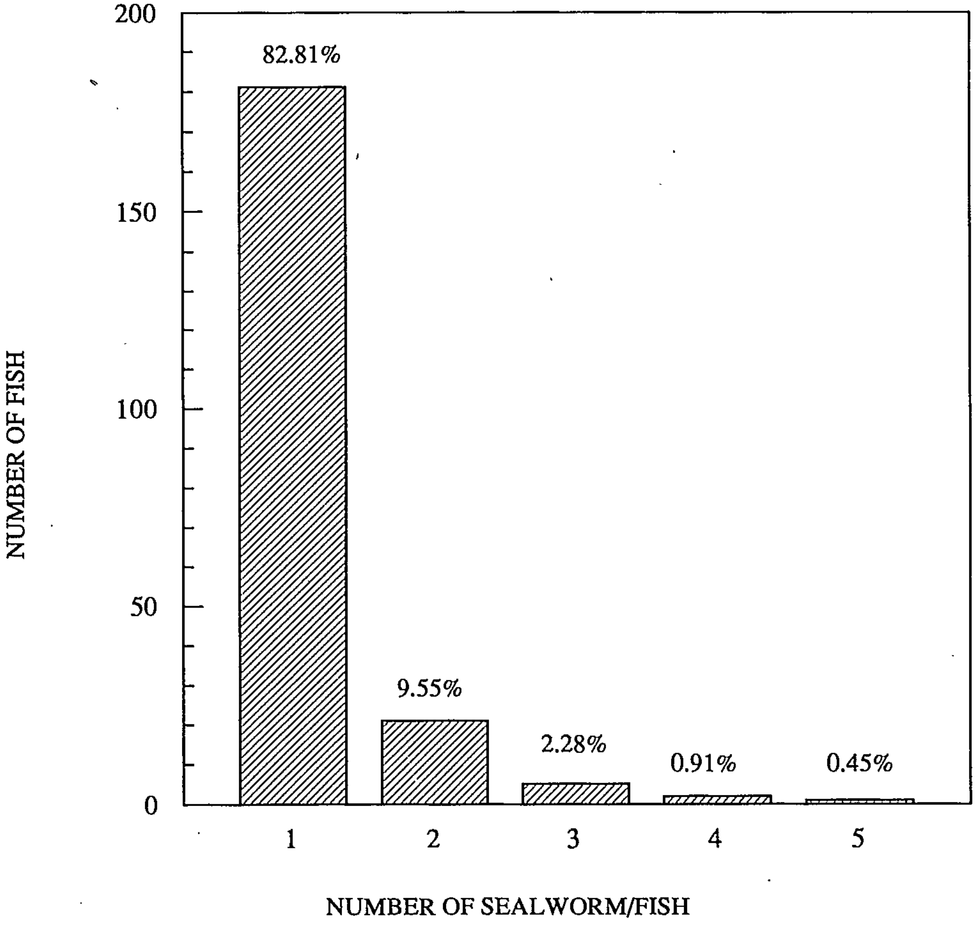

FIG. 2. Frequency distribution of sealworm larvae in smelt examined from 1984 to 1987 containing one or more parasites.

Methods

Samples of smelt were collected from five locations along the southwestern coast of the Gulf of St. Lawrence during late January and early February of 1984, 1985 and 1987 (Fig. 1, Table 1). Samples were obtained from the commercial box net fishery and stored at −10 to −13°C.

Two hundred smelt were randomly selected from each sample and examined for the presence of sealworm. Fork length, weight, and sex were recorded for each smelt examined. The effect of host size on the level of sealworm infestation in smelt was evaluated by selecting 4 size groups, approximating year-classes 1-2 (length (l) $\leq$16,0 cm), 3 (16.0 cm $<l\geq$ 17.5 cm), 4 (17.5 cm $<l\geq$ 19.0 cm) and 5 and older ($l>$ 19.0 cm). The head and skin of the smelt were removed and the musculature was examined under low (6 x -12 x) magnification following systematic destruction (examination technique described by Wiles 1968). The digestive tract was examined separately under low (6 x) and high (25 x -50 x) magnifications. The infestation sites of sealworms were recorded wherever possible. All sealworms recovered were preserved in 70 % ethanol.

Statistical analyses of the survey data were restricted to non-parametric techniques (Siegel 1956) due to the low infestation levels (Arthur 1978).

Results

Two hundred and eleven (7.5 %) of 2800 smelt examined were infected with at least one sealworm. The sealworm count frequency distribution was negatively skewed with 86.26 % of the infested fish with one sealworm (Fig. 2). Ninety six percent of the 252 sealworm recovered were found in the musculature (Fig. 3).

All other larval anisakines recovered from smelt were tentatively identified as *Hysterothylacium* sp. and were usually found in the digestive tract. *Anisakis* sp. larvae were not detected.

Prevalence (percentage of infected fish in a sample) and abundance of sealworm from all the smelt examined, increased with host size whereas density decreased (Fig. 4). The examination of each individual sample, however, revealed significant differences ($P < 0.05$) in sealworm counts among size groups, when tested with the Kruskal-Wallis test (Fig. 5, Table 1).

Yearly variations in prevalence, abundance and density of sealworm infestation in smelt were not consistent at the five locations surveyed (Fig. 6). A Kruskal-Wallis test was used to evaluate the temporal variation in sealworm counts from one size group ($l<$ 16.0 cm) of smelt for all five locations. The only significant difference ($P < 0.05$)

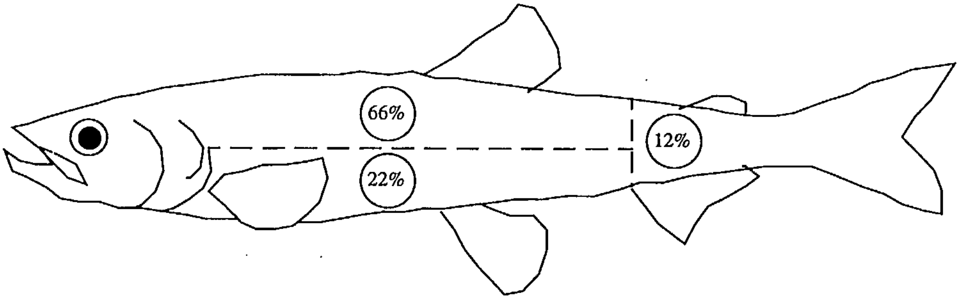

FIG. 3. Distribution of *Pseudoterranova decipiens* recovered from the musculature of smelt.

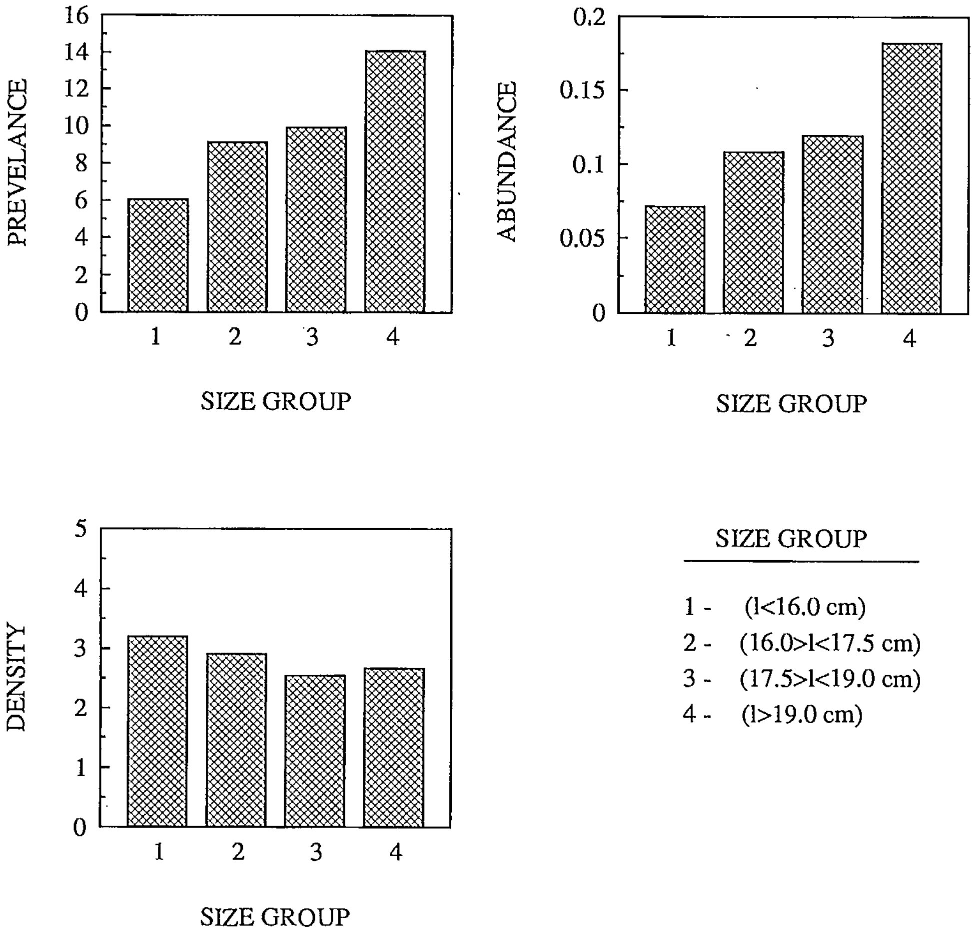

FIG. 4. Prevalence, abundance and density of sealworm infestation in the four size groups of smelt from all samples combined.

was found between the 1985 and 1987 Caraquet subsamples where prevalence, abundance and density increased over four fold in the 2-yr period, 1985-87.

Geographical variation in sealworm prevalence, abundance and density was more pronounced in 1984 than in 1985 and 1987 (Fig. 7). Differences in sealworm counts from one size group of smelt (length < 16.0 cm) between areas, however, were significant ($P < 0.05$) for all years of collection, when analysed with the Kruskal-Wallis test.

Discussion

Prevalences of *P. decipiens* in smelt from this survey are within the range of those reported in smelt from Newfoundland by Templeman et al. (1957), but relatively low compared to those found in cod or flattfish (Templeman et al. 1957; McClelland et al. 1983). This is expected considering the different age structure of the smelt examined (predominantly 2-yr-old) and that of cod or plaice from these previous reports (usually 4-yr-old and older). The differences in diets among these hosts is an another important factor contributing to the differences in sealworm prevalences, as smelt are predominantly

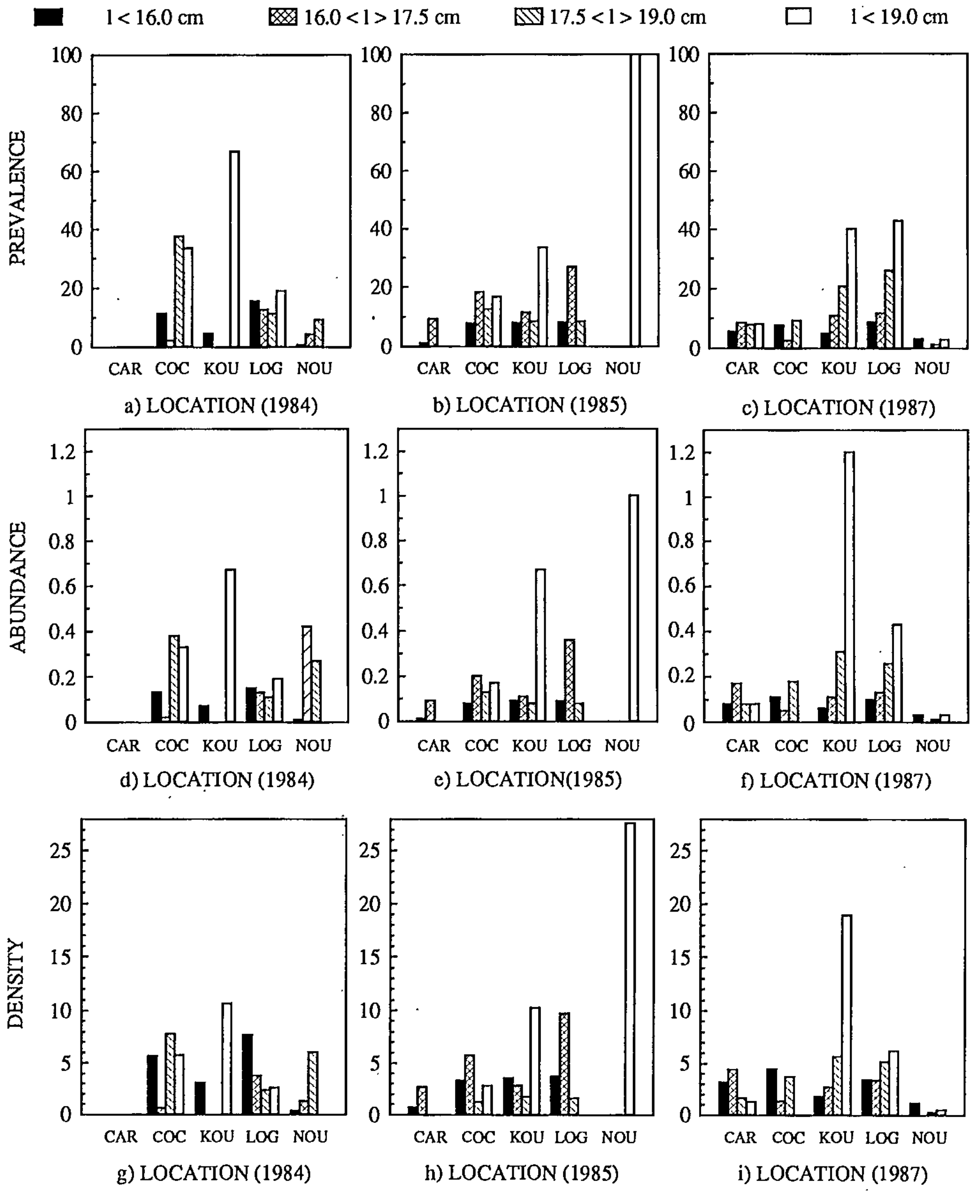

FIG. 5. Prevalence, abundance and density of sealworm in 1984, 1985 and 1987 in four size groups of smelt from Caraquet (CAR), Cocagne (COC), Kouchibouguac (KOU), Loggieville (LOG) and Nouvelle (NOU).

invertebrate feeders whereas cod and plaice also feed on fish that may serve as sealworm hosts.

The significant variation in sealworm counts among the four size groups likely reflects differences in the age/size composition of the smelt populations at different sites as well as differences in the abundance of the parasite in smelt prey and diet of smelt. The low sample size of the older smelt also contributes to this variation. Therefore, the evaluation of temporal and geographical variations in sealworm counts were restricted

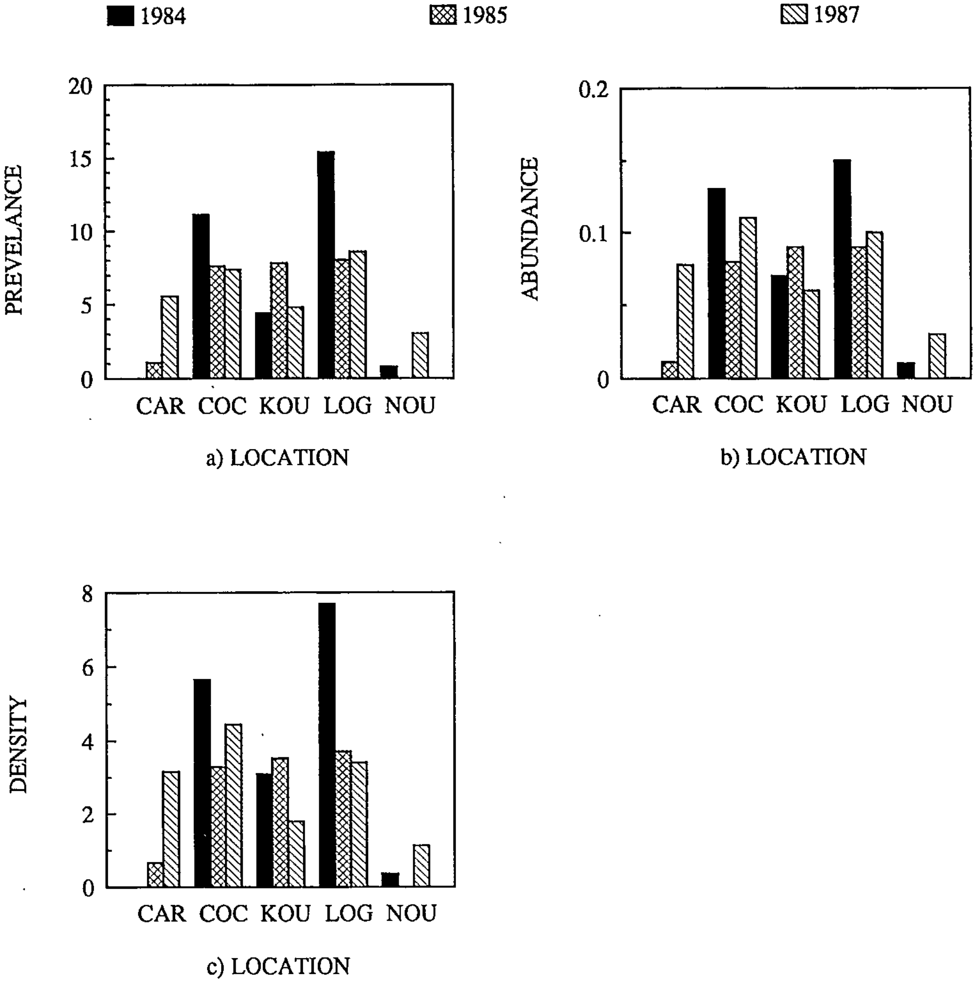

FIG. 6. Interannual variation of prevalence (a), abundance (b) and density (c) of sealworm infestation in smelt (length <16.0 cm) from Caraquet (CAR), Cocagne (COC), Kouchibouguac (KOU), Loggieville (LOG) and Nouvelle (NOU).

to smelt from the first size group, 1-2-yr-old, which comprised over 63 % of all fish examined. Furthermore, the sealworm counts from the selected smelt did not differ significantly from that of the total smelt from their respective samples, when tested with the Mann-Whitney *U*-Test.

The results of this survey indicate relatively stable sealworm abundances in inshore areas between 1984-87, with the possible exception of Caraquet, N.B. The reason for a significant difference in sealworm counts between the 1985 and the 1987 smelt samples from Caraquet, may be due to sampling error, as the 1985 sample was obtain via a fish wholesaler. The size structure of the 1985 sample was also very different from that of the 1987 sample, suggesting a possible different source. McClelland et al. (1985) reported a similar stability in sealworm infestation in American plaice from 1980 to 1983 in the Gulf of St. Lawrence, however, the results from their 1985 survey revealed a "surprising" increase from most locations investigated from the Gulf (McClelland et al. 1987).

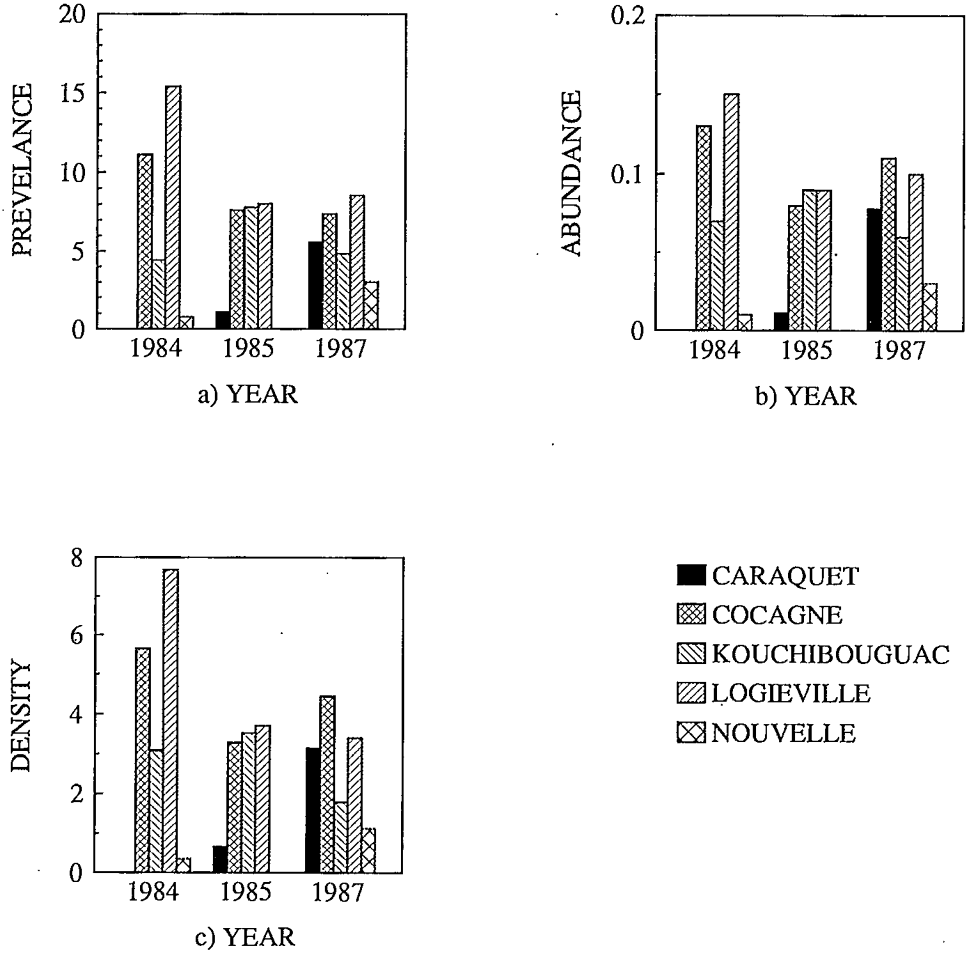

FIG. 7. Geographical variation of prevalence (a), abundance (b) and density (c) of sealworm infestation in smelt (length <16.0 cm).

The only common sampling location for the smelt survey (inshore) and the American plaice survey (offshore) is the Miramichi Bay area. Density of infection is considered to be the most accurate parameter for inter-specific comparaison of sealworm infestation levels. The average sealworm density in smelt from the Miramichi Bay area (Loggieville), 4.51/kg, is similar to that of American plaice in 1980-1981, 4.42/kg, and 1983, 6.41/kg from the same area (Escuminac). However, the sealworm density in plaice collected from 1985 has increased five fold from that of 1980-81 and the average sealworm density in smelt. In the proximity of the Chaleur Bay, smelt samples were collected from Caraquet, N.B. and American plaice samples were collected from the Gaspé, P.Q. area. Here, the sealworm density in smelt from 1987, 2.75/kg, is similar to that of American plaice from 1983, 2.70, but is lower by a factor of five than the 1985 observation of 9.97/kg in plaice. Theoretically, any significant changes in the sealworm abundance within a short time period should be more pronounced in smelt than American plaice, due to the different age (size) structure of the samples of the two host species examined. The age structure of American plaice (31-40 cm in length) examined by McClelland et al. (1987) is estimated at 7-15-yr-old (older for males) whereas the smelt used in this analysis are 1-2-yr-old (Tallman and Sinclair 1988). The reason for a stable sealworm infestation rate in smelt (inshore) vs an increasing rate in American plaice (offshore) is unclear, but may simply reflect differences in their diets and/or the geographical and temporal distribution of these prey in relation to seal hosts.

Acknowledgements

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Smelt as Host of the Sealworm (*Pseudoterranova decipiens*) in the Elbe Estuary

H. Möller and S. Klatt

Institut für Meereskunde an der Universität, D-2300 Kiel, Germany

MÖLLER, H., AND S. KLATT. 1990. Smelt as host of the sealworm (*Pseudoterranova decipiens*) in the Elbe estuary, p. 129–138. *In* W. D. Bowen [ed.] Population biology of sealworm (*Pseudoterranova decipiens*) in relation to its intermediate and seal hosts. Can. Bull. Fish. Aquat. Sci. 222.

In the Elbe estuary, the smelt is an important intermediate host of the muscle-inhabiting nematode *Pseudoterranova decipiens*, which matures in the stomach of harbour seals. As an anadromous species, juvenile smelt become infected in summer after migration from their freshwater spawning place towards the estuary. At the end of the year, 10 % of the 0-group, 36 % of the I-group and 73 % of the adult smelt were infected in 1985. Both the frequency of multiple infection and the average length of the parasites increase with host age. Ten percent of the adult smelt harbour degenerating nematodes in their flesh. The condition factor of host fishes is lowered, indicating severe pathogenic effects of the parasite. Some evidence suggests that the abundance of the parasite might have increased during recent years.

Dans l'estuaire de l'Elbe, l'éperlan est le principal hôte intermédiaire du nématode *Pseudoterranova decipiens* qui s'enkyste dans les muscles et parvient à maturité dans l'estomac du phoque commun. Poissons anadromes, les éperlans juvéniles sont parasités en été, apès la fraye dans les eaux douces et la migration vers l'estuaire. À la fin de 1985, 10 % du groupe d'âge 0, 36 % du groupe d'âge 1 et 73 % des adultes étaient infestés. La fréquence d'infestation multiple et la longueur moyenne des parasites augmentent en fonction de l'âge de l'hôte. Dix pour cent des éperlans adultes sont infestés de nématodes dégénérescents. Le coefficient de condition des poissons hôtes est plus bas, ce qui témoigne des graves effets pathogènes du parasite. Certains indices donnent à penser que le parasite a proliféré au cours des dernières années.

During a survey on fish stocks and fish diseases in the lower Elbe River, carried out in 1981–86, smelt (*Osmerus eperlanus,* L.) were the most abundant fish species between the North Sea and the city of Hamburg (Fig. 1) (Möller 1988). Most adult smelt are supposed to use feeding grounds along the open coast, congregating in large shoals in winter in the estuaries and migrating upstream for spawning in March (Möller 1987). After spawning in freshwater (Dieckwisch 1987), the survivors return to sea. Young smelt feed mainly on copepods and amphipods which are the dominant groups in the Elbe plankton (Fiedler 1990). Larger smelt (>6 cm) also take fish and become cannibalistic. Elbe smelt carry a variety of diseases, some of which occur at high prevalences (Anders 1988; Anders and Möller 1987). Smelt is also heavily infected with the nematode *Pseudoterranova decipiens* and therefore may be a significant vector of this parasite to the definite host, which in the area of the Elbe estuary is the harbour seal, *Phoca vitulina*. Purpose of this study was to quantify the occurrence of sealworm in smelt over an annual cycle.

The occurrence of nematodes in the flesh of fish may cause problems for the fishing industry. Following a short report on this topic on German television in July 1987, the fish consumption in the country fell markedly during the following weeks. Similar problems have repeatedly occurred since the beginning of this century (Kahl 1939). A chronicle from the city of Cologne, written in 1582, also shows that this problem is not new (Jütte 1987).

Materials and Methods

Up to 17 stations on the lower Elbe River between Cuxhaven and Hamburg harbour were sampled monthly between October 1984 and July 1985. Sampling was interrupted in January and February due to ice conditions. Samples were taken with a 7 mm mesh size anchor net operated from a commercial vessel. In October, samples from stations 4-8 were taken from a commercial shrimp trawler (Fig. 1). Altogether 4845 smelt from the 1985 year-class, 14 299 smelt from the 1984 year-class, 583 adult smelt were examined (Table 1).

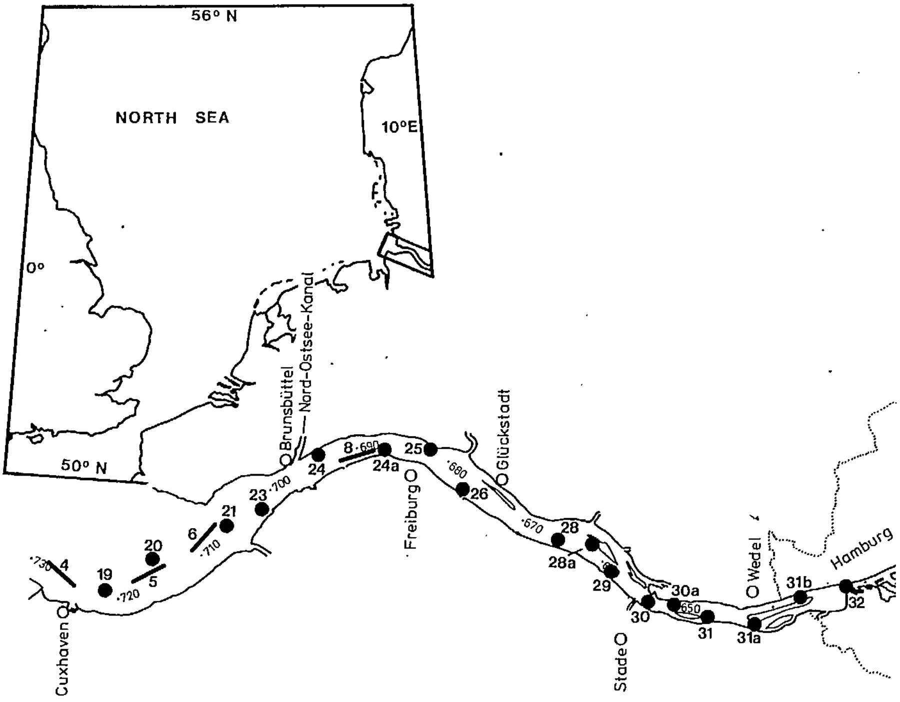

FIG. 1. Station locations on the Elbe River with kilometre-marks.

TABLE 1. Number and age of smelt examined.

Year-class	1985				1984						1983 and older			
Sampling date	Apr. 1985	May	June	July	Oct. 1984	Nov.	Dec.	Mar. 1985	Apr.	May	Oct. 1984	Nov.	Dec.	May 1985
Station														
19(*4)	30	100	0	0	124*	225	298	237	171	190	24*	0	0	0
20(*5)	58	100	0	300	43*	244	400	237	234	126	13*	0	0	0
21(*6)	0	0	0	300	30*	245	300	223	151	140	14*	48	40	50
23	65	0	77	300	0	0	233	356	190	11	86*	52	39	0
24(*8)	88	0	202	300	310*	335	123	330	223	160	0	46	39	0
24a	88	0	0	300	0	220	0	235	212	170	0	47	0	0
25	0	0	0	300	0	174	123	302	281	110	0	45	40	0
26	0	0	0	300	0	265	144	311	228	160	0	0	0	0
28	0	0	0	300	0	243	119	188	179	0	0	0	0	0
28a	0	0	0	300	0	324	155	321	270	0	0	0	0	0
29	0	0	137	300	0	284	123	55	267	105	0	0	0	0
30	0	0	0	300	0	356	150	77	252	0	0	0	0	0
30a	0	0	0	300	0	0	0	63	107	0	0	0	0	0
31	0	0	0	0	0	0	151	0	0	0	0	0	0	0
31a	0	0	0	300	0	259	135	19	245	85	0	0	0	0
31b	0	0	0	0	0	235	137	0	251	0	0	0	0	0
32	0	0	0	0	0	0	0	0	0	220	0	0	0	0
Total	329	200	416	3900	507	3409	2591	2954	3261	1577	137	238	158	50

Smelt were assigned to the 1984 and 1985 year-classes based on body length (Möller 1984). The age of the adult smelt was determined by reading the left otolith (sagitta). The condition factor was expressed as c = (weight in g)/(length in mm $\cdot$ $10)^3 \times 100$. Weight refers to ungutted juvenile and to gutted adult fresh smelt.

Only the flesh was examined for nematodes. With the exception of November samples, which were stored on ice for 1-3 d, all fish were examined within 3 h of capture. Nematodes were located using candling table with a 30 × 35 cm milk-glass screen and 24 or 220 V neon tubes. Juvenile smelt are transparent for several hours after death and therefore can be candled without being filleted. Adult smelt were filleted and the skin removed before candling.

Nematodes were removed from the muscle with a hook needle, transferred to physiological saline (0.9 % NaCl) and kept at about 6°C. Live parasites were identified and measured within 4 d of removal. Dead nematodes from frozen samples were cleared in glycerin-ethanol (Berland 1961). Nematodes were measured to 0.1 mm in a 7 cm long plate with 3 grooves of 0.5, 1.0, and 1.25 mm width, filled with ethanol.

Results

Most nematodes removed from smelt were identified as *Pseudoterranova decipiens*. Only in November samples was the muscle of 0.9 % of the smelt examined also infected by *Anisakis simplex*. However, these nematodes seem to have migrated from the body cavity to the muscle after death of the hosts as this was the only sample which was not examined immediately after capture.

Smelt muscle was divided into three parts to examine the distribution of *P. decipiens* within the host. The caudal part was defined as that portion posterior to a vertical line drawn from the anal fin. The belly flaps were the muscle portions which cover the body cavity below the vertabral column. The rest was defined as dorsal muscle.

Of 581 nematodes found in 1945 juvenile and 396 adult smelts, 70 % occurred in the dorsal muscle, in many cases being visible through the skin, 26 % were found in the caudal muscle, and 4 % were located in the belly flaps. This distribution was similar in all age-groups (Table 2).

TABLE 2. Distribution of *P. decipiens* in the muscle of smelt of different age-groups.

Age (yr)	Total number of nematodes	Distribution (%) of nematodes in		
		Dorsal muscle	Caudal muscle	Belly flaps
0	235	64	31	5
1	23	70	30	0
2	125	78	20	2
3	129	74	22	5
4+	69	65	30	4
Total/Average	581	70	26	4

Smelt hatched in spring 1985 were free of *P. decipiens* until June of that year. The first parasites were found in July 1985 in fish caught at station 28 and downstream. The prevalence increased towards the estuary from 0.7 % at station 28a to 3.3 % at station 20. On average over the period November 1984 to May 1985, the prevalence in the 1984 year-class nearly doubled from the freshwater area to the oligohaline area and again towards the mesohaline area (Table 3). During this period the prevalence on estuarine stations increased while it decreased further upstream. The smallest differences between the three biotopes were found in March 1985.

TABLE 3. Prevalence of *P. decipiens* in smelt of the 1984 year-class. Arithmetric means of station data. For sample size see Table 1.

	Mesohaline Stats. 19-23	Oligohaline Stats. 24-26	Freshwater Stats. 28-32
Nov. 1984	10.0	8.5	4.3
Dec.	11.0	8.2	5.0
Mar. 1985	10.6	7.4	6.8
Apr.	17.7	6.5	1.6
May	13.7	4.1	1.1
Average	12.6	6.9	3.8

The nematode prevalence increased with increasing fish age until age 2, but stayed constant in older fish. From November/December 1984 to May 1985 an increase of 4 % was noted in age-group 0 and 28 % in age-group 1 (Table 4).

TABLE 4. Nematode prevalence in smelt of different age in November/December 1984 and May 1985. Age 0 from stations 19-32, other ages from stations 19-23.

	Nov. + Dec. 1984		May 1985	
Age (yr)	Number examined	Prevalence in %	Number examined	Prevalence in %
0	1945	10	567	14
1	99	36	50	64
2	120	69	0	
3	114	76	0	
4+	60	73	0	

Smelt caught in November and December 1984 at stations 19-23 were examined for multiple infection. Among 1945 0-group smelts, 194 carried one and only 12 carried two *P. decipiens*. The rate of multiple infection increased to 14 % in 1-yr-old and to 49-54 % in older fish (Table 5). In one 21 cm smelt 13 nematodes were found.

TABLE 5. Multiple infection (in % of fish examined) of smelt from the Elbe (November + December 1984) with *P. decipiens*. 0-group collected in the estuary (stations 19-23), older fish from stations 19-31b.

Age (yr)	Number of smelt examined	Number of nematodes per fish					
		0	1	2	3	4	5+
0	1945	89	10	1	0	0	0
1	99	64	22	11	2	1	0
2	120	30	20	21	18	8	3
3	114	23	23	24	14	8	8
4+	60	27	22	20	15	3	13

Figure 2 shows that the intensity of infection (mean number of nematodes per fish examined) increased in the 10-16 cm length groups and then decreased from 2.33 in the 20-21 cm group to 1.35 in the 24-27 cm group.

Thirty-one of 396 infected smelts contained degenerating nematodes while nine carried encapsulated nematodes (Table 6). In degenerating nematodes, the cuticula at the posterior end was affected, and all died within less than 48 h in physiological saline at 6°C. Encapsulated stages were defined under the microscope without using

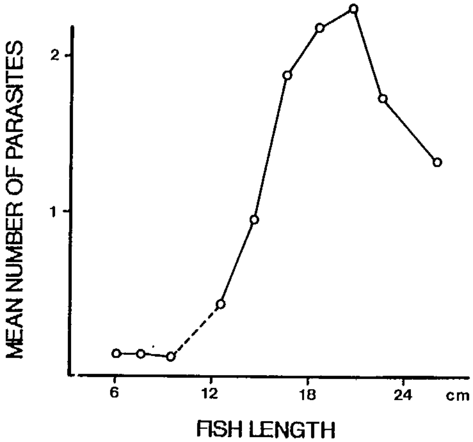

FIG. 2. Mean number of *P. decipiens* per smelt in November and December 1984 in relation to fish length (2-cm-groups, except 24–27 cm).

histological techniques. Dead nematodes were not found in fresh smelt. Only one degenerating and no encapsulated parasites were found in 1-yr-old smelt. Comparing older age-groups, no clear differences were evident in the percentage of infected fish carrying degenerated (8–14 %) or encapsulated (2.6–3.3 %) nematodes.

TABLE 6. Occurence of degeneration (death within 48 h after transfer to physiological saline at approx. 6°C) and encapsulated *P. decipiens* in smelt.

Age (yr)	Number of infected smelt examined	Number of smelt with degenerating nematodes	Number of smelt with encapsulated nematodes
1	99	1	0
2	121	12	4
3	114	9	3
4+	62	9	2

Infection with *P. decipiens* reduces the condition factor of its host fish (Fig. 3). The difference between non-infected and infected smelt is slight in smelt up to an age of 2 yr, but evident in older fish.

The size of 655 *P. decipiens*, measured in November 1984, varied between 6.7 and 44.7 mm. Although nematodes up to 30 mm were found in juvenile smelt of only 6 cm length, the average length of parasites increased with host age. In November 1984 the average nematode length was 23.0 mm in the youngest age-group and 33.0 mm in smelt of 4 yr and older (Fig. 4). From November 1984 to May 1985 the average nematode length increased significantly (*t*-test, $P < 0.05$) by 1.5 mm in the 0-group and by 4.0 mm in the I-group. No significant regional differences were found for the average length of nematodes in I-group smelt in November 1984.

Discussion

The smelt is considered to be an important fish intermediate host of *P. decipiens* in the Elbe estuary and probably also in neighbouring coastal waters of the Wadden

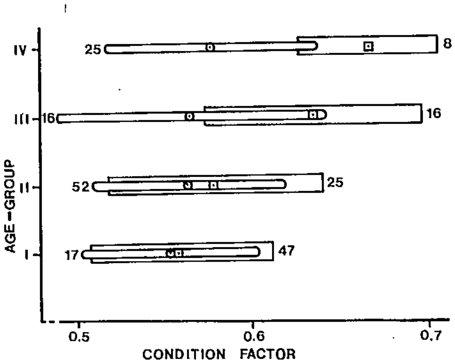

FIG. 3. Reduction of condition factor due to infection with *P. decipiens* of different age-groups of smelt in November 1984 (stations 26-31b). Circles: infected fish, squares: non-infected fish. Number of fish examined, average, and standard deviation.

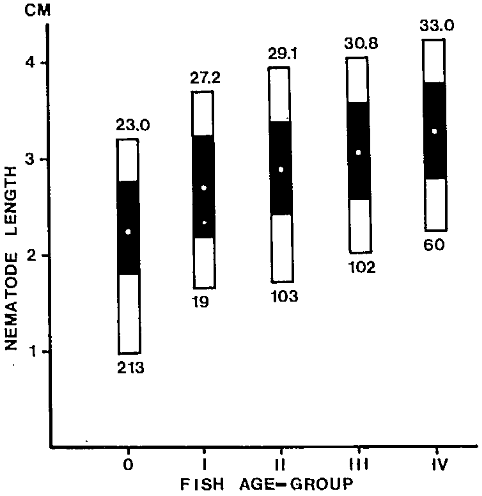

FIG. 4. Growth increment of *P. decipiens* in smelt of different age-groups, caught in November 1984 (average, standard deviation, and minimum/maximum length). Average length (top) and number of nematods measured (bottom).

Sea. Also the closely related rainbow smelt (*Osmerus mordax*) in waters around Newfoundland (Templeman et al. 1957) and in the Gulf of St. Lawrence (Landry and Hare 1990) is known to be sometimes heavily infected by this parasite. Recent pilot investigations have shown that in the Elbe estuary the sea scorpion (*Taurulus bubalis*) (33 %), flounder (16 %), cod (*Gadus morhua*) (19 %), and eel (9 %) are also infected (Möller and Schröder 1987). No parasites were found in trout (*Salmo trutta*) and in two freshwater species. The crustacean intermediate hosts are unknown. No *P. decipiens* was discovered in 603 *Gammarus zaddachi* from the lower Elbe, nor in 1417 gammarids of 6 different species examined recently from other coastal waters in Germany (Voigt 1987).

Although data are lacking, it is supposed that the 7 100 harbour seals (*Phoca vitulina*) present in 1985 served as the local final host for sealworm in the southeastern North Sea. Only a small colony of about 30 grey seals (*Halichoerus grypus*) inhabits the Wadden Sea which includes the shallow coastal water zone of southwest Denmark, northwest Germany, and the east of the Netherlands (Haaften 1983).

It is assumed that regional differences in the prevalence of *P. decipiens* in fish are correlated with the local occurrence of seals (Björge 1985; McClelland et al. 1985; Platt 1976; Scott and Martin 1959). Accordingly, it can be speculated that a temporal increase in local seal population will lead to a temporal increase in nematode prevalence in fish from that locality as well. This correlation was supposed by the studies of McClelland et al. (1985, 1986), Rae (1963), and Hauksson (1984) who found increasing prevalences of *P. decipiens* in groundfish from east Canadian, Icelandic, and Scottish waters, where the stocks of several seal species were shown or supposed to have increased in size the years before (Hickling 1957).

Until 1940, population estimates of seals in the Wadden Sea were based entirely on bounty statistics. During the following years, they were supplemented by boat counts. Since 1960, aerial censuses are carried out, counting seals in summer on sand banks during low tide. According to these data, the population size of the harbour seal was estimated to be 5 500 in 1960. It then decreased to 3 600 in 1974, and has since shown a constant recovery. In 1985, a record high of 7 100 seals were counted (Reijnders et al. 1983; Heidemann, Forschungsstelle Wildbiologie, Univ. Kiel, Germany, pers. comm.). The recovery is most likely due to reduced seal hunting (Reijnders 1983).

It would not be surprising, therefore, that the increase in seal numbers would lead to an increase in worm burden of Wadden Sea fish. However, few historical data are available on the occurrence of *P. decipiens* in Elbe smelt. Martin (1921) reported a prevalence of 3.5-7.5 %, Mann (1962) reported 30-40 %. However, they did not report on the size, age and number of fish examined. Jarling (1982) found 14 % of 64 smelt of different age-groups to be infected. Kahl (1936) investigated 448 Elbe smelt of three different age-groups for muscle nematodes, but did not record the date and place of capture. Based on a comparison of Kahl's data and those in this study, the nematode prevalence has increased from 16 to 36 % in 1-yr-old smelt, from 22 to 69 % in those 2-yr-old, and from 54 to 76 % in older fish.

Records from a local fish processor indicate an increase in nematode prevalence during the early 1980's in the dominant commercial fish species landed at Bremerhaven fish market. The nematodes were preserved, but not identified. According to their large size, most of them seem to belong to *Pseudoterranova*. The fish studied came from fishing grounds all over the North Atlantic (Möller and Schröder 1987).

Due to its commercial importance, most quantitative studies on the occurrence of sealworm have focussed on cod (McClelland et al. 1983, 1985; Platt 1975; Rae 1963; Scott and Martin 1957, 1959; Wootten and Waddell 1977). In the southwestern North Sea it is unlikely that cod of commercial size are an important link in the development of the parasite. Food analysis of harbour seal from the Wadden Sea revealed that this mammal mainly feeds on fish of 14-20 cm in total length. Havinga (1933) in Dutch coastal waters as well as Behrends (1985) and Sievers (1985) in German coastal waters reported flatfish, especially flounder, to form the dominant part of the seals' diet. Cod and smelt contributed 4 and 2 % to the stomach content weight according to Havinga and 5 and 6 % according to Sievers.

Due to the high prevalence of *P. decipiens* in smelt it is postulated that this species nevertheless is one of the most important transmitters of the nematode to the final host. The average smelt of 16-18 cm length harbours two *Pseudoterranova* in its flesh (Fig. 3). One kilogram smelt of this length group thus contains 73 *P. decipiens*. For each 1 kg food eaten, of which 4 % is smelt, 18 *P. decipiens* are ingested. Assuming a daily food uptake of 4-8 kg (Behrends, Sievers, Kiel Aquarium; pers. comm.), a seal in the Elbe estuary ingests 12-24 *P. decipiens* per day via smelt only. Comparative calculations for other fish species at the moment are not possible, but it is unlikely that the prevalence of nematode infection in any other local fish species is as high as it is in smelt.

The fact that an infection of smelt with *Pseudoterranova* reduces the condition factor of the host is biologically significant as it may make the host more susceptible to predation by marine mammals. On the other hand, no reduction of the hosts' condition factor has been found by Pálsson et al. (1985) studying parasitized adult cod.

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Group Report 2: Infection of Definitive Hosts

J. Brattey and W. T. Stobo (*Rapporteurs*), A. Bjþrge, M. D. B. Burt, S. des Clers, L. P. Fanning, E. Hauksson, L. Jarecka, T. Landry, A. Mansfield, G. McClelland, R. Mohn, H. Möller, R. A. Myers, I. H. Ni, J. Pálsson, J. W. Smith, D. Thompson, and R. Wootten.

Abundance of Sealworm in Seals

Published records of sealworm (*Pseudoterranova decipiens*) in seals from the North Atlantic are summarized in the References section. Table 1 summarizes quantitative information on the numbers of adult and larval sealworms in the stomach or gastrointestinal tract of seals from the North Atlantic. Adults of *P. decipiens* have been found mainly in grey (*Halichoerus grypus*), harbour (*Phoca vitulina*) and harp seals (*Phoca groenlandia*). Most published accounts give the mean numbers of adults and larvae of *P. decipiens*; however, these values may in some instances be misleading due to the highly skewed distribution of worm counts. Nonetheless, grey seals are clearly the most heavily infected, with stomachs containing on average approximately 100-150 adult worms and even larger numbers of larvae. Harbour seals typically carry much lower sealworm burdens, and harp seals are rarely infected (Table 1).

Recruitment of Worms and Pathogenic Reactions

At the present time, McClelland's (1980) experimental work with captive seals forms the basis for our understanding of recruitment of sealworm larvae to seals. Experimental studies have shown that the sealworm parasite is more easily established in grey seals than in harbour seals (McClelland 1980). At least 50 % of larvae fed to captive grey seals established residence in the stomach. The transmission efficiency may be even higher in free ranging animals where exposure to the parasite may be more gradual. Successful establishment of sealworm larvae in harbour seals was low because captive seals commonly regurgitated larvae. Available data also suggest that the parasite may be more pathogenic in harbour seals. Infection experiments with captive animals showed secondary infection to be less successful than the initial exposure to the parasite. However, this result may have been an artifact produced by the high initial dose given to experimental animals.

Larvae of P. decipiens commonly penetrated the mucosa and submusosa of the stomach of harbour seals and their anterior extremities were encapsulated in an amorphous eosinophilic substance. The stomachs of infected harbour seals often become hyperaemic and oedematous. Raised inflammatory areas or ulcerative lesions were also observed in harbour seals infected with fourth stage larvae and adult worms. Similar but less severe pathology was observed in experimentally infected grey seals.

Sex Ratio and Maturity of Sealworms

Based on experimental work (McClelland 1980), the sex ratio of infections is near 1:1, but with a slight bias towards females, possibly due to the selection of larger larvae from fish hosts for use in these experiments. Stobo et al. (1990) found an equal sex ratio of sealworms in the stomachs of both grey and harbour seal collected from Sable Island. Additional work is needed to determine if the density of sealworm in grey seal stomachs might affect sex ratio.

Based on data from a number of sources (Table 1) the proportion of mature sealworms in grey seals generally ranged from 30 % to 50 %. However, data from Sable Island showed strong seasonal variation in the proportion mature. In harbour seals, available

TABLE 1. Mean number of *P. decipiens* in stomach or gastro-intestinal tract of seals from the North Atlantic.

			Mean no./Seal		
Location	Periods	No. of seals	Adult	Immat.	Ref.
Grey Seal					
Northwest Atlantic					
Sable Island	Jan.-Feb. 1983-84	64	93	541	1
	Mar.-June 1983-84	85[a]	427	1071	1
	Aug. 1983-84	28	505	474	1
	Sept.-Oct. 1983-84	29[a]	413	601	1
	Nov.-Dec. 1983-84	29	510	1428	1
	1949-56	3	48	35	2
Ecum Secum, N.S.	Jan.-Feb. 1975-78	19	76	461	3
	Apr.-June 1975-78	6	196	521	3
	Sept.-Oct. 1975-78	5	483	601	3
Eastern Shore	Mar.-Nov. 1984-87	136	223	359	9
Amet Island, N.S.	June 1975-78	5	1	197	3
Amet Island and Malagash, N.S.	Dec.-Jan. 1985-87	22	180	1179	9
Camp Island	Dec.-Jan. 1985-87	17	124	616	9
E Northumberland Strait	Sept.-Oct. 1975-78	9	389	351	3
Port Hood and Antigonish	Dec.-Jan. 1985-87	20	195	513	9
Northumberland Strait	N/A	49	212	640	4
Anticosti	Mar.-Nov. 1984-87	130	69	159	9
E. Cape Breton Island, N.S.	N/A	18	172	378	4
Grand Manan	Mar.-Nov. 1982-84	52	305	451	9
Miramichi Estuary, N.B.	1949-56	29	187	84	2
Bras d'Or Lakes, N.S.	1949-56	3	169	2727	2
NE Nova Scotia	1949-56	17	60	99	2
Northeast Atlantic					
N North Sea	1964	6	38	—	5
Orkney Islands, Scotland	Oct.-Nov. 1966	8	179	556	6
W Isles, Scotland	Sept.-Oct. 1966-68	9	38	97	6
	Mar. 1969	2	4	17	6
Farne Islands, UK	N/A	10	167	235	12
Shetland Islands, Scotland	Feb.-Apr. 1969	10	8	17	6
E Anglia, England	Feb.-May 1968	7	2	3	6
Iceland	1975-77	6	188	507	7
Harbour Seal					
Northwest Atlantic					
Sable Island, N.S.	1983, 1985	39	42	181	1
	1949-56	2	9	2	2
Ecum Secum, N.S.	June-July 1975-78	5	2	79	3
Northumberland Strait	1949-56	5	6	10	2
Magdalen Islands	1949-56	8[a]	8	88	2
Bras d'Or Lakes, N.S.	1949-56	4	43	308	2
NE Nova Scotia	1949-56	8	21	31	2
SW Nova Scotia	1949-56	1	11	63	2
	Mar.-Nov. 1984-87	60	32	63	9
Lower Bay of Fundy, N.B.	1949-56	76	13	34	2
Grand Manan	Mar.-Nov. 1984-87	68	51	158	9

TABLE 1. (Concluded.)

Location	Periods	No. of seals	Mean no./Seal Adult	Mean no./Seal Immat.	Ref.
Northeast Atlantic					
N North Sea	1970	1	0	45	5
Orkney Islands, Scotland	Oct. 1966	1	17	28	6
W Isles, Scotland	Mar. 1969	11	1	12	6
Shetland Islands, Scotland	Feb. 1969	1	50	5	6
E Anglia, England	Arp.-May 1968-69	6	0.8	1	6
Iceland	Jan.-Feb. 1975-77	5	74	175	7
	Mar. 1975-77	8	45	68	7
	Apr.-May 1975-77	15	12	42	7
	June-July 1975-77	3	6	12	7
	Nov. 1975-77	5	30	23	7
Norway	Sept.-Nov. 1976	12	1087	817	11
Harp Seal					
Magdalen Islands	Mar.-May 1956	195	0.4	4	8
	Mar.-Apr. 1954-56	61	0.03	5	2
	Apr.-May 1952-56	237	5	10	2
Port Hood, N.S.	Feb. 1950	4	110	140	2
Blanc Sablon, P.Q.	June 1953-55	274	0.2	0.1	2
E Coast NF/LB	May-May 1949-51	43	0	0.3	2
	Mar.-Apr. 1958	68	0	0	2
La Tabatière, P.Q.	Jan. 1950	21	0	0	2
Placentia Bay and St. Mary's Bay, NF	June-July 1987	84	0.01	0.2	10
NE Newfoundland and Labrador	1983-86	402	0	0.2	10

References: 1. Stobo et al. (1990); 2. Scott and Fisher (1958a); 3. McClelland (1980); 4. Mansfield and Beck (1977); 5. van Banning and Becker (1978); 6. Young (1972); 7. Palsson (1977); 8. Myers (1957); 9. McClelland (unpublished); 10. Brattey and Ni (unpublished); 11. Benjaminsen et al. (1977); 12. Prime (1973).

[a] one highly parasitized seal not included.
N/A not available.

data suggest that the proportion mature is more variable, ranging from 4 % to 87 % at Grand Manan and from 25 % to 30 % at Iceland (G. McClelland pers. comm., J. Palsson pers. comm.). The relationship between total sealworm numbers and the proportion mature remains unknown, but should be investigated for evidence of density-dependence.

Residence Time in the Seal

The sealworm has a prepatency period of about 2-3 weeks and a patency period averaging 2-3 weeks, with a maximum of 6 weeks, in captive grey seals (McClelland 1980). About 56 % of the worms have reached early patency 20-30 days after ingestion and midpatency after 35-50 days. Some 50 % of the larvae reaching patency survived to the 6th week in the primary infection. Much lower survival was observed in the secondary infections of these captive animals.

In harbour seals the parasite has a prepatency period of 3 weeks and a patency period of 2-6 weeks. Less than 50 % reached patency and only 10 % survived to the 6th week of the experiment. The success of these challenge infections to harbour seals was highly variable.

In wild grey seals, the high worm burdens and the high proportion of immature worms in some animals suggest that the prepatency period and the overall duration of natural infections may be longer than in captivity. For example, one animal collected on Sable island during March 1983 had 12 680 worms, of which 12 561 (99.9 %) were immature

(Stobo et al. 1990). Assuming that all these larvae were ingested within the previous 3 weeks implies an unrealistically high ingestion rate of at least 598 larval worms per day.

Sealworm Fecundity

The relationship between number of eggs in the uterus and worm body length is expotential in sealworms from both grey or harbour seals (McClelland 1980). Harbour seals generally support smaller adult sealworms than do grey seals. In both species female sealworms continue to grow during the patency period and fecundity increases. Mean fecundity of sealworms in grey seals was 366 000 eggs/female, and 156 000 eggs/female in harbour seals held in captivity. Daily egg production/female in experiments on grey seals ranged from 1 000 to 68 000 ($n = 7$) during the patency period. In harbour seals fecundity was much lower at an average of 100-11 000 ($n = 4$) eggs/female/day. Recent work suggests that approximately 85-95 % of sealworm eggs are viable.

Concern was expressed by many participants at the workshop about the lack of reliable estimates of sealworm fecundity. Uterine egg counts give only a point estimate of fecundity and give no information on numbers of eggs already laid or eggs still to be produced during continued growth of female worms throughout the patency period. Egg counts from faecal sampling of live animals also provides a point estimate of egg output; however, unless all faeces shed during the patency period can be collected, an estimate of total egg output becomes difficult. Also, even with controlled doses of worms the numbers which establish, mature, and produce eggs during the course of an infection remains unknown. Clearly, egg output per female worm remains difficult to assess, but more effort should be directed toward gaining realistic estimates of egg production. Monitoring egg output by gravid worms cultured *in vitro* could provide useful information on daily egg output per worm; however, difficulties may arise in extrapolating these results to the situation *in vivo*.

Sealworm Mortality

Work by McClelland (1980) suggests daily loss of worms of all sizes from the seal stomach over the experimental period. Actual estimates of mortality based on egg production are confounded by changes in fecundity per individual over the patency period. Data from grey seals taken from Sable Island indicate seasonal changes in total sealworm abundance and the proportion mature (Stobo et al. 1990). These data also indicate that mortality during the seal breeding season is largely restricted to adult worms. However, studies on ice-breeding grey seals in the Gulf of St. Lawrence indicate that unlike those on Sable Island, some breeding adults continue to feed during the pupping season and these animals do not exhibit a reduction in the proportion of mature worms (G. McClelland pers. comm.).

Trends in Sealworm Abundance in Seals

Time series on trends in sealworm abundance in grey seals are scant (Table 1). The earliest quantitative data in eastern Canada are from the 1950's from animals collected in the Gulf of St. Lawrence by Scott and Fisher (1958a). Data from the eastern shore of Nova Scotia are available for 1970 and recent years (G. McClelland pers. comm.) and from Grand Manan in recent years (Table 1). In the United Kingdom, Young (1972) gives estimates of the numbers of sealworms in grey seals for the late 1960's and early 1970's. Some data from Iceland are available for 1975-77, and for the 1980's (E. Hauksson pers. comm.), but too few samples were examined to provide detailed information on temporal trends.

Even fewer data are available on trends in sealworm abundance in harbour seals. It is believed that some data may have been collected by Scott and Fisher in the Grand Manan area in the 1950's. G. McClelland has collected data in this area recently, but again insufficient numbers of samples are available to determine trends.

The group noted that the lack of time series data provides a serious obstacle toward understanding the population dynamics of sealworms. The information summarized in Table 1 indicates that sampling in all localities has been highly inconsistent. Clearly, repeated sampling over time should be conducted at specific localities to provide accurate information on temporal trends in sealworm numbers in seals.

Seasonal Changes in Sealworm Numbers in Seals

Data on seasonal changes are largely from eastern Canada for both grey and harbour seals. The most extensive work has been done on Sable Island by Stobo et al. (1990). In grey seals, seasonal changes in sealworm numbers were strongly influenced by the host feeding pattern and body size. Breeding adults had their lowest burdens in January and exhibited a substantial increase during the next few months. By June sealworm burdens were declining and the worm burden for the summer period reached its lowest level in August. Highest sealworm numbers were found in grey seals sampled in November. In contrast to adults, having once established a worm burden, pups did not show seasonal variation in sealworm numbers. The proportion of mature sealworms in seals varied seasonally. Mature worms were found throughout the year with the greatest proportion occuring in August (75 %). Individual sealworm burdens depended, to a great degree, on the feeding behaviour of the host. During a period of fasting in grey seals, i.e. breeding and moulting periods, there was a slight reduction in sealworm abundance in the stomach. B. Beck and W. Stobo (pers. comm.) have data suggesting that the increase in the proportion of mature worms during the summer reflects a change in diet to fishes such as silver hake (*Merluccius bilinearis*) and sand lance (*Ammodytes americanus*) which carry few sealworm larvae.

The only data on seasonal changes in sealworm numbers in harbour seals are from animals collected on Sable Island during the 1980's (Stobo, Beck and Fanning pers. comm.). Harbour seals were infected throughout the year, but infections exhibited some seasonality with highest burdens in winter. Harbour seals showed only a slight increase in sealworm burdens beyond age 1, and consistently had fewer sealworms then grey seals of comparable size. J. Palsson (pers. comm.) also noted that harbour seals in Iceland show little trend in sealworm abundance beyond age 1.

Competitive Effects

Based on a preliminary multivariate analysis be G. McClelland et al. (pers. comm.), there is little evidence of intra- or interspecific parasite competition in seal hosts. However, given the potential importance of density-dependent processes to the dynamics of the parasite most participants agreed that further analysis of available data was warranted. The possibility of competitive effects between sealworms and *Contracaecum osculatum* should be investigated, in addition to intra-specific effects.

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STOBO, W. T., B. BECK, AND L. P. FANNING. 1990. Seasonal sealworm (*Pseudoterranova decipiens*) abundance in grey seals (*Halichoerus grypus*), p. 147-162. *In* W. D. Bowen [ed.] Population biology of sealworm (*Pseudoterranova decipiens*) in relation to its intermediate and seal hosts. Can. Bull. Fish. Aquat. Sci. 222.

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Seasonal Sealworm (*Pseudoterranova decipiens*) Abundance in Grey Seals (*Halichoerus grypus*)

Wayne T. Stobo, Brian Beck, and L. Paul Fanning

Department of Fisheries and Oceans, Marine Fish Division,
Bedford Institute of Oceanography, P.O. Box 10006,
Dartmouth, N.S., Canada B2Y 4A2

STOBO, W. T., B. BECK, AND L. P. FANNING. 1990. Seasonal sealworm (*Pseudoterranova decipiens*) abundance in grey seals (*Halichoerus grypus*), p. 147–162. *In* W. D. D. Bowen [ed.] Population biology of sealworm (*Pseudoterranova decipiens*) in relation to its intermediate and seal hosts. Can. Bull. Fish. Aquat. Sci. 222.

The *P. decipiens* burdens in the stomachs of 244 grey seals (aged 0–38 years) collected between January 1983 and January 1984 on Sable Island ranged from 4 to 12 680 worms. Sexually mature worms were found in pups within 3 mo of commencement of independent feeding. Seal size (length) was the most important single effect in determining total burden; consequently, due to the sexual dimorphism in growth, adult males generally carried the highest burdens.

Substantial seasonal variation occured both in total worm burden and the proportion of sexually mature worms, but these burdens were not substantially eliminated at any time during the year. A decline in total burdens observed in adult seals during the breeding season is probably due to the breeding season fast, since worm burden levels are acquired and maintained by ingesting immature worms from finfish prey. A second decline in late summer in all age groups (adults, immatures, and pups), we suggest is due to a change in seal diet from primarily highly infected fish species to less infected ones. The proportion of mature worms increased during reductions in total worm burdens due to the lack of immature worms being ingested and the progressive development of the existing immature worms into sexually mature adults.

As a management consideration, we suggest that a vermicide applied on the breeding grounds could substantially reduce the overall annual worm egg production by eliminating the larvae carried by adult grey seals. Alternatively, if a cull were undertaken, elimination of the largest seals would have the greatest impact on egg production in subsequent years.

La charge en *P. decipiens* relevés dans l'estomac de 244 phoques gris âgés de 0 à 38 ans, recueillis entre janvier 1983 et janvier 1984 à l'île de Sable, allait de 4 à 12 680 vers. On a trouvé des vers sexuellement mûrs chez des petits phoques qui ne se nourissaient de façon indépendante que depuis trois mois. La taille des phoques (longueur) était le premier facteur qui déteminait la charge totale; en conséquence, du fait du dimorphisme sexuel dans la croissance, c'étaient généralement les mâles adultes qui portaient la charge la plus forte.

Des variations saisonnières importantes ont été relevées tant dans la charge totale en vers que dans la proportion de vers sexuellement mûrs, mais à aucune période de l'année les charges ne disparaissaient de façon substantielle. La baisse des charges totales observée pendant la saison des amours est probablement due au jeûne caractéristique de cette période, car les charges en parasites se constituent et se maintiennent par ingestion de vers immatures présents dans les poissons dont se nourissent les phoques; une deuxième baisse observée à la fin de l'été chez tous les groupes d'âge (adultes, immatures et petits) nous semble liée à une modification du régime alimentaire des phoques, qui abandonnent les espèces très infestées au profit de poissons qui le sont moins. La proportion de vers sexuellement mûrs augmente pendant les phases de réduction de la charge totale, du fait qu'un nombre moins grand de vers immatures est ingéré et que ces vers immatures se développent et atteignent la maturité sexuelle.

Sur le plan de la gestion, nous proposons d'appliquer un vermicide dans les zones de reproduction, ce qui pourrait réduire fortement la production globale annuelle d'oeufs de vers en éliminant les larves portées par les phoques gris adultes. Par ailleurs, si on procédait à un abattage sélectif, c'est l'élimination des phoques de grande taille qui aurait l'impact le plus fort sur la production d'oeufs les années suivantes.

Introduction

Marine mammals are the final hosts of a number of anisakine nematodes whose life cycles include commercially important finfish species as intermediate hosts (Templeman et al. 1957; Young 1972; Platt 1975; Margolis and Arthur 1979). Grey seals (*Halichoerus grypus*) are a final host to several of these parasitic nematodes, *Pseudoterranova decipiens* (formerly *Phocanema*, see Gibson 1983), *Anisakis* spp., *Contracaecum osculatum*, and *Phocascaris* spp. (Scott and Fisher 1958; Young 1972; Dailey 1975), and several reports suggest that they are the prime vector of sealworm, *P. decipiens*, in the North Atlantic (Scott and Fisher 1958; Young 1972; Mansfield and Beck 1977; Bjørge 1984; Stobo and Beck 1985).

The harbor seal (*Phoca vitulina*) and the harp seal (*Phoca groenlandica*), overlap in their distribution range with the grey seal and are also suitable hosts for this parasite, however, they appear to be of minor importance as a vector of sealworm in the Northwest Atlantic. In the case of harbor seals, this is probably due to small population size (Boulva and McLaren 1979) and low individual *P. decipiens* burdens (McClelland 1980a). The eastern Canadian harp seal population is numerically much larger (Bowen and Sergeant 1983) than the grey seal population, but individual harp seals rarely have burdens of more than a few *P. decipiens* larvae (Scott and Fisher 1958; Mansfield and Beck 1977). Harp seals are generally found in colder more northerly waters than grey seals; consequently, only a portion of the harp seal population is exposed, during the limited period of the annual southern migration, to intermediate hosts with a high prevalence of *P. decipiens*. The low *P. decipiens* burdens in harp seals, and their finfish prey (Templeman et al. 1957; Wells et al. 1985) may also be due to lower survival of eggs (McClelland and Ronald 1970; Myers 1960) and retarded development of larvae at temperatures less than 4-5°C (McClelland 1982).

The life cycle of the sealworm is well described (McClelland et al. 1983a). The ova, shed in the faeces of the seal host, settle to the bottom where they hatch. Young larvae anchor themselves to the substrate until consumed by harpacticoid or cyclopoid copepods (McClelland 1982), the first intermediate hosts. A sequence of various benthic macroinvertebrates and finfish act as intermediate hosts before larval *P. decipiens* are ingested by seals (Myers 1960).

The occurrence of sealworm in the flesh of groundfish species has been a long standing and well documented condition for Northwest Atlantic fisheries (Templeman et al. 1957; Scott and Martin 1957). More recent studies on Atlantic cod (*Gadus morhua*), American plaice (*Hippoglossoides platessoides*), and witch flounder (*Glyptocephalus cynoglossus*), indicate substantial increases in the level of sealworm infestation over the whole of the Scotian Shelf and most of the Gulf of St. Lawrence (McClelland et al. 1983a, b, 1985). The greatest increases were found in the vicinity of Sable Island, one of the two primary breeding areas of grey seals in the Northwest Atlantic. The one sample of cod and American plaice from the southwestern Grand Banks which McClelland examined also showed a substantial increase in sealworm infestation. Wells et al. (1985) however, conducted much more intensive sampling on the southern Grand Banks and noted no significant differences in cod fillet infestation rates from those of Templeman et al. (1957).

The increase in sealworm abundance in fish is coincident with an increase in the size of the Northwest Atlantic grey seal population (Zwanenburg et al. 1985; Zwanenburg and Bowen 1990) and has supported the view that seals are responsible for the increase in the abundance of the parasite. While this may be true, little is known about the dynamics of the relationship between this parasite and the grey seal. The present study was undertaken to examine seasonal variation in the abundance of *P. decipiens* in the grey seal, its primary definitive host, as a step in understanding the population dynamics of this parasite.

Materials and Methods

Two hundred and forty-four adult and juvenile grey seals were collected during eight trips to Sable Island, Nova Scotia in 1983 and 1984. Information on standard length, axillary girth, blubber thickness (excluding skin) (Anon. 1967), and sex was complete for 234 animals and only these specimens were used in the present analysis (Table 1).

TABLE 1. Numbers, age and sex of seals sampled during each trip to Sable Island.

		Trip								
		1	2	3	4	5	6	7	8	
Age-group	Sex	10 Jan. 9 Feb.	16-21 Mar.	7-11 May	31 May 7 June	2-7 Aug.	29 Sept. 5 Oct	23 Nov. 1 Dec.	10-31 Jan	Total
0	M	0	3	4	4	2	5	5	0	23
	F	0	5	2	1	5	1	3	0	17
1-3	M	4	2	3	1	1	2	0	4	17
	F	5	3	1	0	0	3	2	6	20
4-8	M	0	3	2	4	4	2	2	0	17
	F	9	0	2	0	2	3	3	3	22
9+	M	14	7	8	12	4	3	10	0	58
	F	12	4	3	8	9	12	5	7	60
Total	M	18	15	17	21	11	12	17	4	115
	F	26	12	8	9	16	19	13	16	119

The sample was partitioned into four age-groups (Table 1) for descriptive purposes. The pups were treated as a separate group since they do not develop nematode burdens until they begin independent feeding; for this reason, no pups were taken during the two January trips (trips 1 and 8). The other age-groups were based on the onset of reproduction; 4 yr is the age of sexual maturity for most females and 9 yr is the age of social maturity for most males. In this paper we refer to female seals of ages 1-3 and male seals of ages 1-8 as immatures. The oldest observed ages were 38 yr for females (2 specimens) and 33 yr for males.

The lower jaw was removed for subsequent age determination. The stomach was ligated at the oeophagus and near the pyloric sphincter before removal to prevent loss of parasites. In most cases, the nematodes were removed alive from the stomach within 1-2 days of collection, washed in a solution of saline and placed in a hot mixture of 95 % ethanol and glycerine (70:30 ratio) to relax and fix the animals. Within 2 wk, the initial ethanol-glycerine mixture was replaced with a 50:50 mixture to clear the specimens and facilitate microscopic identification. In a few instances, 10 % formalin was used to initially preserve the nematodes. These were subsequently cleared by boiling in a 50:50 mixture of ethanol-glycerine.

The nematodes in each stomach were sorted by species and enumerated. Only adults were enumerated by sex since the sex of immatures is not discernible by simple microscopy. Although three species of nematodes were found in the stomach, only the data on *P. decipiens* will be presented here.

Box and whisker plots (Tukey 1977) have been used to summarize the data. These plots consist of three components: the box including the two central quartiles of the data separated by the median; the whiskers indicating the range of the data on either side of the median consistent with the central group; and points, indicating outliers.

Three characteristics of the *P. decipiens* burden, sex ratio, total worm burden, and proportion mature worms, were examined in relation to the grey seal host. Generalized linear models (McCullagh and Nelder 1983) were used to investigate the relationship between worm burden and the length, age and sex of the seal host using the GLIM program (Payne 1986) on a personal computer. Explanatory variables were fitted to the data and tested for inclusion in a linear model according to the amount of deviance explained. The theory of Generalized Linear Models refers to deviance as the measure of discrepancy between the observed and fitted values (McCullagh and Nelder 1983) and the form of this measure is specific to the error distribution being used. We have presented the results of model fitting in Analysis of Deviance tables, where the significance of the amount of deviance accounted for by the inclusion of each covariate is tested with a χ^2 statistic. Significance levels of $P \leq 0.05$ have been used throughout. Initially the Poisson distribution was examined since it is generally held to be the appropriate error distribution for count data (McCullagh and Nelder 1983). The resulting GLIM models all had very large deviances, indicating that the model was inadequate; in particular, the data were overdispersed, with respect to the Poisson distribution. A log transformation made the data more symmetrical however, and the transformed data were then analysed with a series of GLIM models using the Normal distribution and identity link.

Since the dynamics of worm burdens could be strongly affected by the seals undergoing non-feeding (fasting) periods, we also examined changes in worm burdens as a function of the duration of fasting during the breeding (late December-early February) and moulting (early May-mid June) periods. Since we lacked information on the duration of the fast for lactating females, we linked advancing pup pelage stage to decreases in their mother's blubber thickness as an indication of the duration of the breeding fast. Subsequently we used pup pelage stage as a proxy for duration of the fast, and related it to the female worm burdens. Duration of pup pelage stages has been described for Northeast Atlantic seals by Kovacs and Lavigne (1986), and our Sable Island observations (unpubl. data) indicate stages of similar duration. Stage 0 was defined as a full term foetus while the approximate durations of pelage stages 1 to 4 are 2, 3, 7, and 5 d, respectively. For samples from the moulting season we related the degree of moult completed by the adults to their worm burdens.

Results

Sex Ratio

The proportion of adult male *P. decipiens* was 0.51 and did not differ significantly from 0.5 ($t= 1.679$, $df= 231$, $P= 0.095$), consistent with a 1:1 sex ratio among adults. This finding is similar to McClelland (1980a) and consequently the two sexes were combined in further analyses.

Abundance

The total worm burden was highly variable with individual burdens ranging from 4 to 12 680 worms. The largest worm burden observed was in a 31 yr-old female taken in March 1983, with 12 680 *P. decipiens*. The distribution of individual burdens in our sample was positively skewed (Fig. 1) for both male and female seals, but generally, male seals had higher worm burdens than females. This could be due to the sexual dimorphism in growth, evident even in young grey seals (Fig. 2). The analysis of deviance (Table 2) associated with the various generalized linear models, indicated that

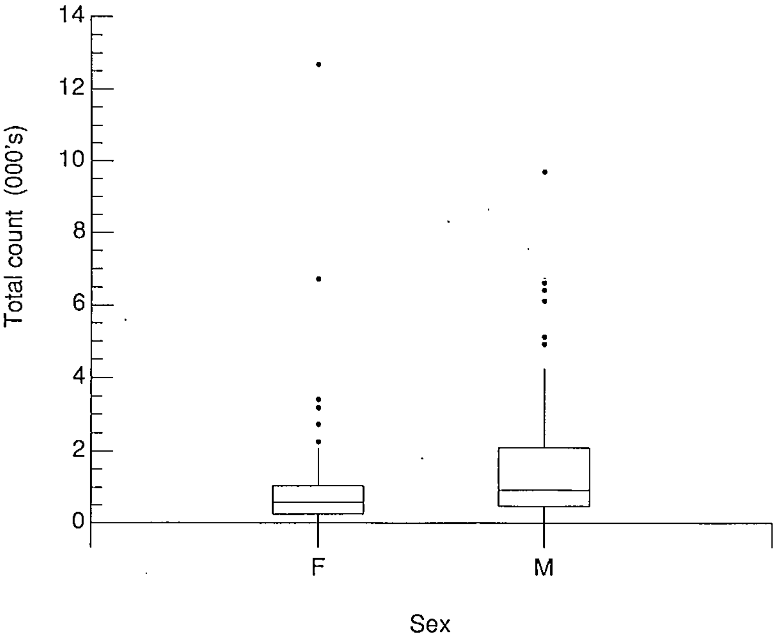

FIG. 1. Total *P. decipiens* burdens of female (F) and male (M) seal specimens collected on eight trips to Sable Island.

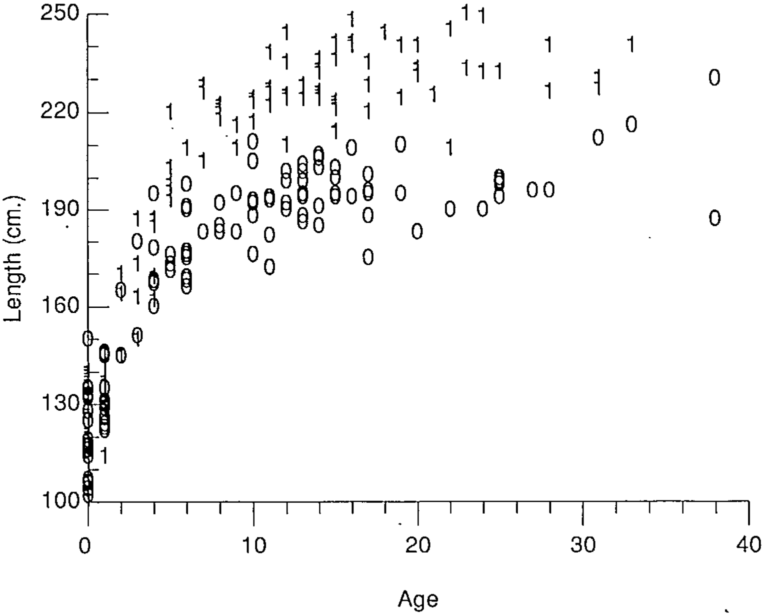

FIG. 2. Length at age of female (0) and male (1) grey seals sampled.

length (model LENGTH) was the most important single effect, accounting for 99.0 units of the deviance from the Mean model and neither age nor sex were significant factors when entered subsequent to length. An alternative model of age nested in sex (model SEX.AGE) was almost as good as model LENGTH, explaining 95.0 units of deviance. The parameter estimates for both models (Table 3) indicated that the larger seals had larger worm burdens. In model LENGTH, the parameter estimate for length was significantly greater than zero (its absolute value is greater than 2 times its S.E.). In model SEX.AGE, the parameter estimate for age in males (the larger sex; Fig. 2) was more than double that in females. The residuals from model LENGTH indicate no apparent trends, non-linearity or heteroscedasticity. The residuals from model SEX.AGE suggested generally lower worm burdens, that is more negative residuals, in pups (age 0) of both sexes than in older seals. Both sexes had worm burdens higher than predicted by the model, that is more positive residuals, prior to the onset of reproductive activity.

TABLE 2. Analysis of deviance of all possible models of AGE, SEX and LENGTH to explain variability of log worm burden. All models use identity link and Normal error. Deviance explained is the amount of deviance explained by factor B given factor A is already in the model as indicated by R(B|A). SEX.AGE indicates AGE is nested in the factor SEX.

Model	Factors	d.f.[a]	Deviance	Reduction in d.f.[a]	Deviance explained[b]	R(.|.)
MEAN		233	337.5			M
LENGTH		232	238.4	1	99.0	L|M
	+SEX	231	236.2	1	2.2 n.s.	S|M,L
	+AGE	231	236.2	1	2.2 n.s.	A|M,L
SEX.AGE		231	242.5	2	95.0	S.A|M
SEX		232	321.3	1	16.2	S|M
	+AGE	231	248.1	1	73.2	A|M,S
	+LENGTH	230	231.9	1	16.2	L|M,S,A
	+LENGTH	231	236.2	1	85.0	L|M,S
	+AGE	230	231.9	1	4.3	A|M,S,L
AGE		232	264.1	1	73.4	A|M
	+SEX	231	248.1	1	16.0	S|M,A
	+LENGTH	230	231.9	1	16.2	L|M,A,S
	+LENGTH	231	236.2	1	27.9	L|M,A
	+SEX	230	231.9	1	4.3	S|M,A,L

[a] d.f. refers to degrees of freedom.

[b] All values are significant ($P \leq 0.05$) except those followed by n.s.

TABLE 3. Parameter estimates from GLIM for the two models of log worm burden. Both use an identity link and Normal error model.

Model	Parameter	Estimate	Standard Error
LENGTH	mean	3.629	0.3016
	length	0.016	0.0016
SEX.AGE	mean	5.895	0.0999
	female.age	0.042	0.0093
	male.age	0.089	0.0094

Worm burden varied with the time of year (Fig. 3), with two apparent peaks. The seasonal pattern of worm burden in adult seals (Fig. 4) is more clearly defined than that for the total sample (Fig. 3), with substantially less variation in any given trip. Much

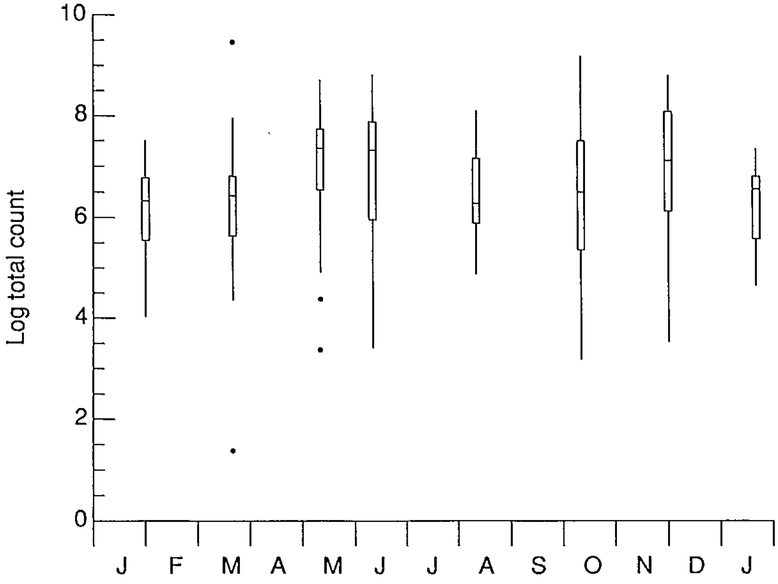

FIG. 3. Total *P. decipiens* burdens in grey seals (all ages) sampled during eight field trips to Sable Island between January 1983 and 1984.

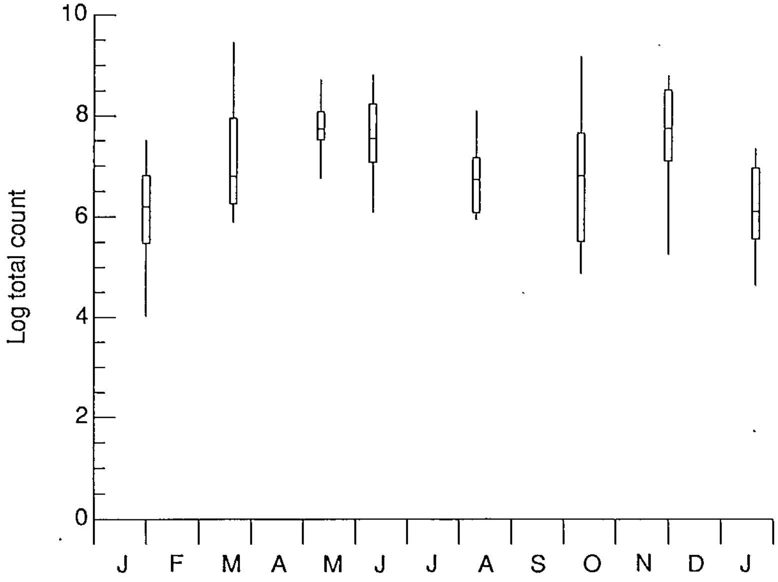

FIG. 4. Total *P. decipiens* burdens in the adult grey seal samples.

of this within trip variability is due to pups, except for the two January trips when no pups were collected. Both the 1983 and 1984 January samples indicated that mature seals had their lowest burdens during the breeding season. A substantial increase was exhibited during the next few months, and by June their burdens had peaked. The worm burden declined throughout the summer, but peaked again in late November. The seasonal worm burden patterns for pups and immature seals varied considerably from that of adults over the course of the year. Worm burdens in immature seals appeared to lack any discernible seasonal changes. Pups however exhibited a rapid increase in worm burden until March and then a more gradual increase during the remainder of the year.

The seasonal patterns shown were preserved in the residuals from both the LENGTH and SEX.AGE models even after the systematic factors associated with the length or age of the individuals had been removed. Thus the apparent seasonal pattern is not an artifact of the length or age of the sampled seals.

Maturity in Worms

Due to the different behavioral cycles of mature and immature seals, the worm maturity, defined as the proportion of mature worms in each seal, was examined separately for adults and pups. In breeding adults (Fig. 5a) there appeared to be two annual peaks in the median worm maturity, with a weak peak in March and a much stronger peak in August. The pattern of worm maturity in immatures was very similar to that of the adults. In contrast, the median worm maturity in pups (Fig. 5b) was lowest in March, corresponding to the minor peak in adults, however in August there was a similar peak to that observed in the adults.

Fasting Periods

To examine potential changes in worm burdens during the breeding season fast, we first compared the median worm maturity in mature seals in the pre-breeding sample (Nov.-Dec.) with the two January breeding seal samples. The lowest median worm maturity in adult seals was less than 5 %, observed in the January 1983 sample (Fig. 5a). In contrast, the January 1984 median worm maturity was over 20 %, similar to the Nov.-Dec. sample. This may be due to differences in the dates of collection between the 2 years. Since the majority of specimens in the 1984 sample were collected earlier in the breeding season than the 1983 sample, we examined the changes in worm burden within the breeding season using the lactating females with pups in our samples.

We found a highly significant decrease in the thickness of the female blubber layer with the pelage stage of their pups (Fig. 6). This supports the current view of maternal fasting during the breeding period and also indicates that pup stage can be considered an indicator of the duration of the females' fast prior to sampling. Examination of the worm burden in these same females, as a function of pup pelage stage, revealed declines in both total worm burden (Fig. 7) and in worm maturity (Fig. 8). Although the regression slopes were non-significant, median worm maturity had declined from above 20 % to less than 5 % by pup pelage stage 4, the end of the lactation period. These values are comparable respectively to the median maturity levels found in the January 1983 and 1984 samples (Fig. 5a), and provide an explanation for the difference between the two January samples.

Grey seals moult during a period of about 4 wk from May to mid-June on Sable Island. Our observations indicate a period of reduced feeding by grey seals during this period. Therefore, changes in worm burden during this period were examined by relating total worm burden and worm maturity to the duration of the fasting, measured as the degree to which moulting had progressed. This analysis indicated a marginally significant (P= 0.04) decline in worm burden and a non-significant decline in the worm maturity.

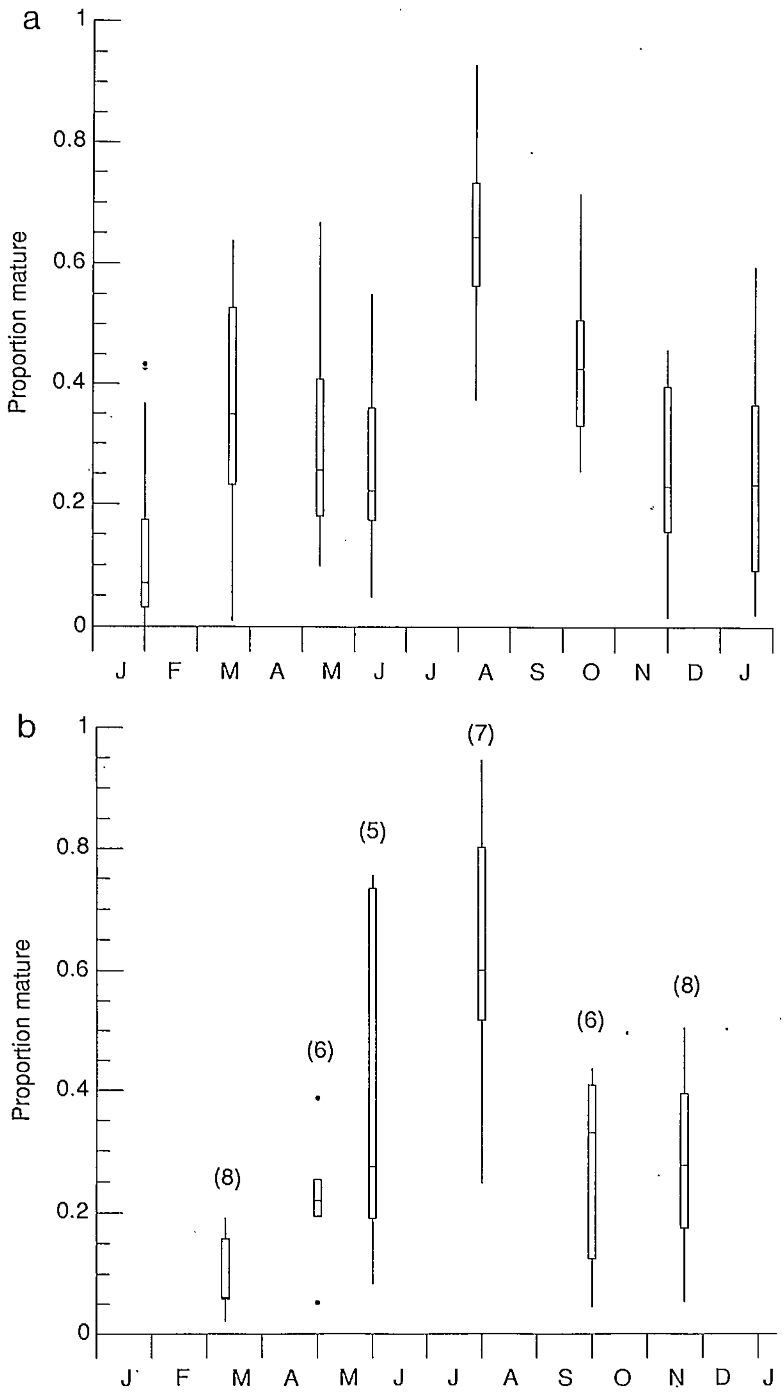

FIG. 5. (a) Proportion of sexually mature *P. decipiens* in the burdens of adult grey seals (females 4+ ; males 9+) between January 1983 and 1984; (b) Proportion of sexually mature *P. decipiens* in the burdens of grey seal pups between January 1983 and 1984.

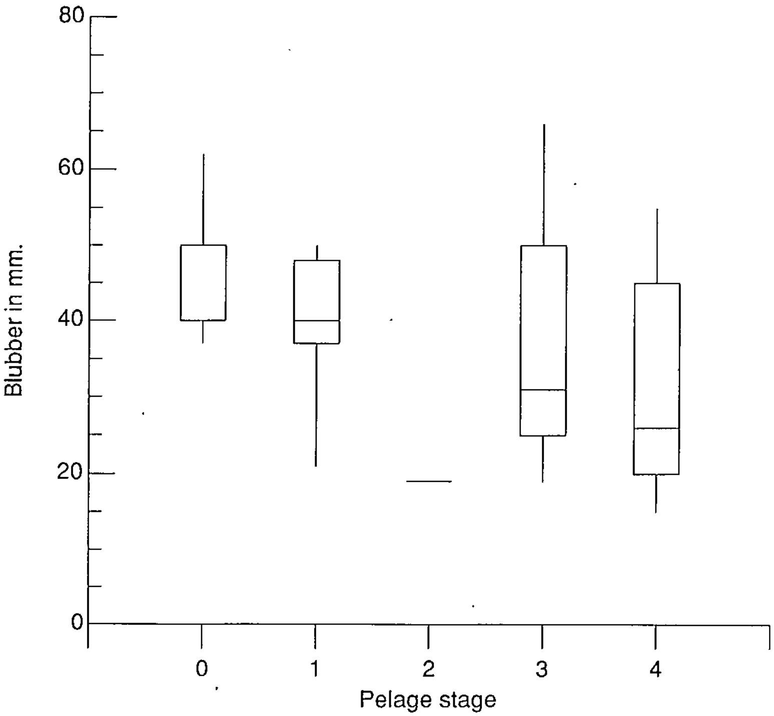

FIG. 6. Change in blubber thickness of female grey seals in relation to development of their pups (pelage stage is an index of pupage).

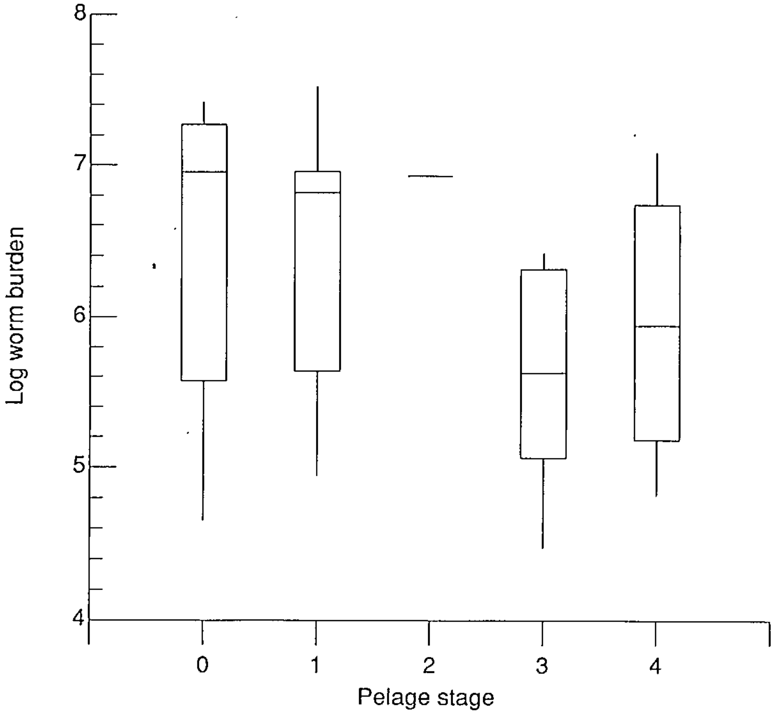

FIG. 7. Changes in total *P. decipiens* burdens in female grey seals in relation to development of their pups (pelage stage is an index of pupage).

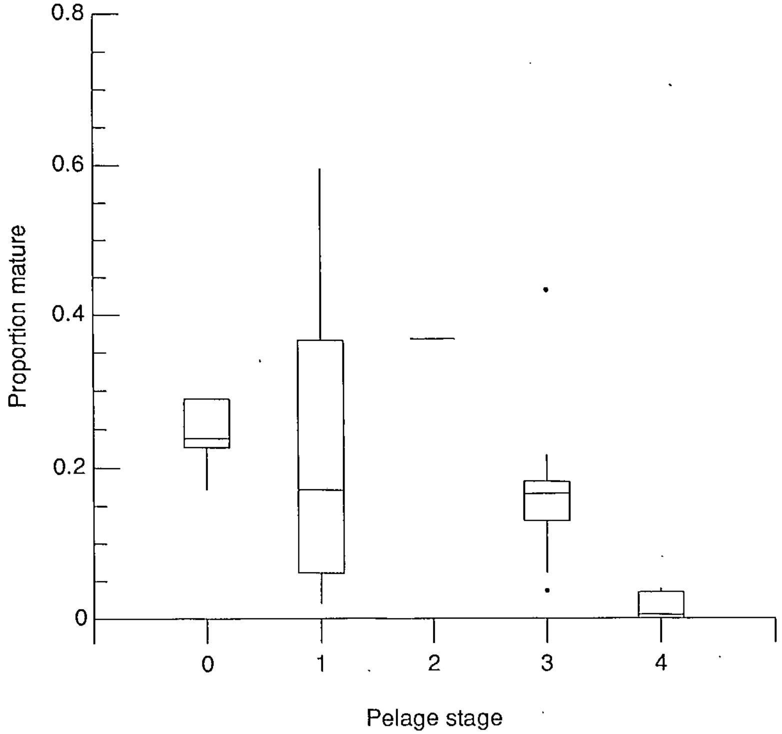

FIG. 8. Proportion of sexually mature *P. decipiens* in the burdens of female grey seals in relation to development of their pups (pelage stage is an index of pupage).

Discussion

Our analysis indicated that size was the single most important factor in determining the magnitude of individual total worm burdens. Age nested in sex (model SEX.AGE) as a primary factor was almost as good as length (model LENGTH) in explaining variation in total worm burden. However, both of these models are essentially proxies for size. Since seals obtain their worm burdens from the fish which they consume, and food consumption is a function of seal size, it is not surprising that larger seals develop larger total worm burdens. While probably most closely related to weight, it is apparent that food consumption is also closely related to length. The good fit observed with age nested in sex as the explanatory factor is consistent with the increase in size with age due to growth and the observed sexual dimorphism in size. The fact that age alone (model AGE) explains considerably less of the variation than age nested in sex indicates that variation is more likely due to size than age.

There is substantial variation in worm burden at length, age, and sex, during the year. Some of the differences between samples from different trips may be due to unequal sampling of age groups; for example, the differences between the January 1983 and 1984 samples are probably due to the greater proportion of immature seals taken in 1984. However, differences in the behaviour patterns of certain age groups are probably also responsible for some of this variation. Pups have generally lower than expected total worm burdens, as indicated by the residuals of the model SEX.AGE. Pups do not begin feeding independently until late February, a few weeks after the end of the breeding season and increase their worm burden during the remainder of the year

(Prime 1973; Stobo and Beck 1985). Their lower total worm burdens are probably due to this later commencement of feeding and initially lower success rate in capturing fish prey (unpubl. data). Residuals from the model SEX.AGE indicate that immature seals (up to age 4 for females, and age 9 for males) tend to have generally higher total worm burdens than expected for their size. Since the only discernible behavioral differences between the immature and adult seals are the breeding season activities, this difference suggests that the breeding season has an impact on an individual seal's total worm burden.

The seasonal patterns in the total worm burden and worm maturity indicate a population that undergoes two annual cycles of development. A schematic of the hypothesized patterns for all age groups and the relationship between adult seal food consumption and the proportion of infected fish consumed is given in Fig. 9. (The intent of this

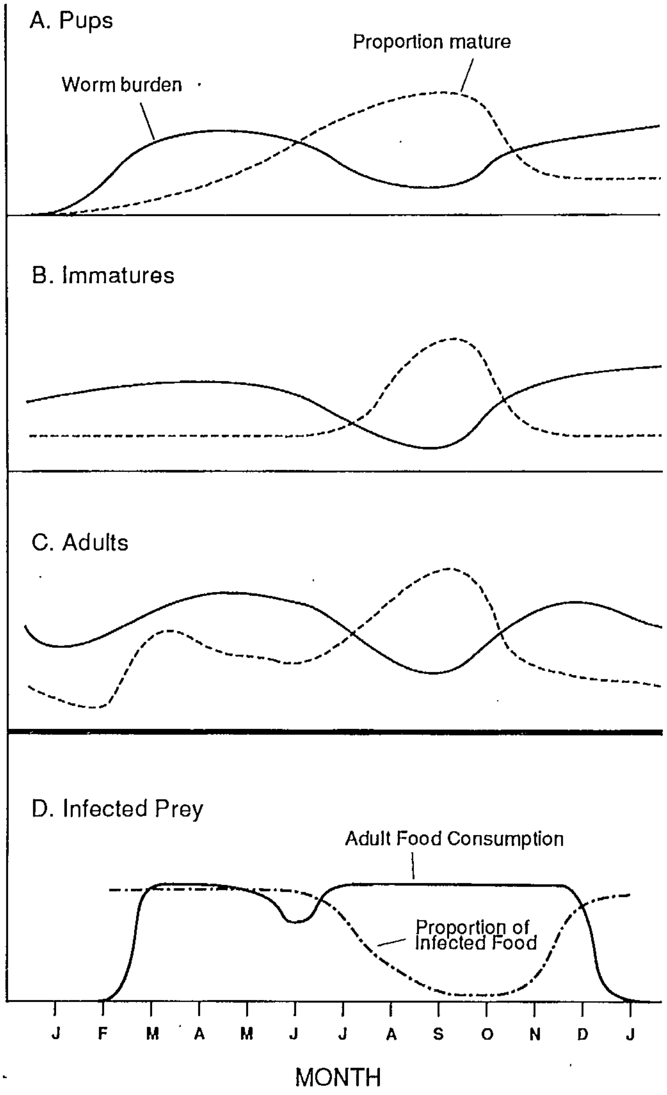

FIG. 9. Schematic of the hypothesized cycles of sealworm (total burden and proportion sexually mature) in grey seal (A) pups, (B) immatures, and (C) adults, and the associated relationship between adult seal food consumption and the proportion of infected fish consumed (D).

representation is only to demonstrate the timing of the increases and decreases of worm burdens, worm maturity, food consumption and proportion of infected food relative to each other, not the magnitude of the changes, thus we have not scaled the y-axis.) Since the host acquires new infections of worms while feeding on infected fish, the rate of growth of the total worm burden in a seal at any given time, will depend on the difference in the rate of ingestion of larval worms and the rate of shedding of mature and immature worms in the faeces of the seal. The rate of ingestion of larval worms will depend on the rate of feeding, as well as on the species composition of the prey. When the seals are feeding on highly infected fish, the rate of ingestion of *P. decipiens* larvae will exceed the rate of shedding of worms and hence the total worm burden will increase. If the seal reduces its intake of highly infected fish, either by fasting or by changing the prey composition, then the rate of shedding will exceed the ingestion of new larvae and the total worm burden will decrease.

The worm maturity cycle should exhibit a somewhat different seasonal pattern than that for total worm burden, reflecting the time lag associated with development from the larval to reproductive adult stage. McClelland (1980a,b) has reported that *P. decipiens* reach sexual maturity only in the stomach of the host seal, requires a mean maturity development time of 19d, and has a reproductive period of 20-60d. We assume that once ingested, almost all of the worms will complete their life cycle before being shed, and that they actively feed, and thus mature, only when the host seal is actively feeding. While there are some suggestions that nematodes feed on the gastric lining of the host (Schell 1952; Gier and Ameel 1959), the worms are generally considered to feed on the food bolus in the stomach (Gray and Anderson 1982; Lincoln and Anderson 1973). Consequently, when the host seal begins fasting, the immature worms would suspend development at a pre-mature stage. Those that have already moulted into the adult stage may be committed to completing their life cycle and are subsequently shed from the host. Alternatively, since some of the adult worms found in the intestines of the seals are still fecund (G. McClelland, pers. comm.), adult worms with their higher nutritional requirements, may be unable to survive prolonged periods of food deprivation. This is similar to behaviour described for nematode parasites in skunks (Cawthorn and Anderson 1976).

Adult grey seals undergo and extended fast on the breeding grounds (Anderson et al. 1975; Boness and James 1979). During the grey seals' breeding season fast therefore, the reduction in total worm burden (Fig. 4) should be due to the loss of adult worms, the larvae having suspended development. This can be illustrated by comparison of the worm maturity in adult seals in the pre-breeding period (Nov.-Dec.) of over 20 % to the 1983 breeding period (Jan.-Feb.) of less than 5 % (Fig. 5a). The comparison cannot be extended to the January 1984 sample since in that year, the adult seals (all female) were taken between January 11-14, early in the breeding season. It is clear that none of these females had undergone prolonged fasting since 3 were still pregnant and the remaining 7 had newborn pups. This decline in worm maturity during the breeding season can be demonstrated by using the pup pelage stage as an indicator of fast duration (Fig. 8). In this instance the 1984 collection was included although the pups were all stages 0 (in utero) and 1 (newborn). It is apparent that the worm populations can undergo substantial changes in composition in periods as short as 3 wk, the approximate interval from pelage stage 1 to stage 4 in pups.

The resumption of feeding in February initiates the subsequent increase in total worm burden (Fig. 4), which peaks in May-June.

The dramatic increase in worm maturity observed in the March sample (Fig. 5a) reflects the completion of development of those larvae which remmained in the mature seals' stomach during breeding season. Their rate of maturation obviously exceeds the rate of ingestion of new larvae by the actively feeding host seal. The eventual shedding of these adult worms and the rebuilding of the seal's worm burden, due to sustained ingestion of new larvae, causes the subsequent decline in worm maturity.

The fact that immature seals did not exhibit a discernible reduction in worm maturity during the breeding season, nor a discernible increase in worm maturity in the March sample, supports the cause and effect relationship of the breeding season, given above for mature grey seals.

Mature and immature grey seals undergo a moult in May–June. We found only a marginally significant decline in worm burden and a non-significant decline in worm maturity during the moult. Thus grey seals do not rid themselves of substantial numbers of worms during this period. Thus the subsequent decline in worm abundance (Fig. 4) and concurrent increase in worm maturity in August (Fig. 5a), is not caused by reduced feeding during the moult. Our observations on the food of grey seals are limited due to the difficulty of obtaining stomachs with identifiable remains. However they do suggest that grey seals around Sable Island change their diet in summer from species heavily infected with *P. decipiens*, such as cod and flatfish (McClelland et al. 1983), to less infected species such as small silver hake, billfish and sand launce. We suggest this change in prey species causes a decline in the rate of ingestion of new larvae and thus worm burden (Fig. 3); the continued consumption of food by both adult and immature grey seals allows the *P. decipiens* larvae already in the host seals' stomach to complete their development, and thus worm maturity increases (Fig. 5a). The subsequent increase in worm burden (Fig. 3), and the concurrent decrease in worm maturity (Fig. 5a) is a result of the seals switching back to the more highly infected fish prey.

Pups do not exhibit a decline in worm burdens during the summer, thus the observed increase in worm maturity in pups (Fig. 5b) cannot be explained by a decrease in the ingestion of new larvae. However, pup worm burdens increase rapidly during the first part of the year, and more gradually during the remainder of the year. This change in the rate of ingestion of new larvae may be a consequence of a change of diet. Further, given the lag in worm maturation, this reduction in the ingestion rate would explain the increase in worm maturity in August.

Although an immunological response by the seals could also expain some of our observations, McClelland (1980a) suggested that grey seals do not develop any significant immunity to *P. decipiens*. Our data indicate that whatever immunological response occurs, it is insufficient to prevent grey seals from acquiring and retaining substantial *P. decipiens* burdens throughout the year. Our conclusions regarding mechanisms of seasonality in the worm burdens and proportions mature depend on the seasonal changes in prey species and amount taken by the host grey seals. Currently available data on these two aspects are scanty and do not permit quantitative estimates of worm ingestion rates. This is the area most needing examination to confirm our interpretation of the dynamics of these worms in stomachs of grey seals.

Implications for Management

In our interpretation of the seasonal pattern of *P. decipiens* burdens in grey seals there are some aspects relevant to the management of this problem. Grey seals do not substantially eliminate their worm burdens at any time during the year. Those worms which mature on the Sable Island breeding grounds will contribute nothing to the worm population since their eggs will be shed on land. In spite of this, control of the worm burdens in actively breeding seals could be an effective control method. The pattern of feeding throughout the year results in seals developing their heaviest worm burdens just prior to the breeding season; most of the immature worms in the seals' stomach at that time will remain viable and become reproductive when the seals resume feeding. Consequently, the successful application of a vermicide on the breeding grounds could substantially reduce the overall annual worm egg production by eliminating the larvae carried by adult grey seals. Since the worms are not feeding during the seal breeding season fast, they may not be susceptible to vermicides until the seal resumes feeding. In that case, only vermicides with a potency period of two months or more would be effective. Alternatively, since these are long-lived animals, a cull of the largest seals could be expected to have the greatest impact on worm egg production in the subsequent years.

Acknowledgements

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Group Report 3: Seal Ecology

D. Thompson and A. W. Mansfield (Rapporteurs), B. Beck, A. Bjørge, D. Bowen, M. Hammill, E. Hauksson, R. Myers, I-Hsun Ni, and K. Zwanenburg.

As the definitive host of the parasite, three aspects of seal ecology are of particular interest in understanding the dynamics of *Pseudoterranova decipiens*: population size, distribution, and diet.

Population Size

Available data on trends in abundance of grey seals (*Halichoerus grypus*) and harbour seals (*Phoca vitulina*) in the North Atlantic are summarized in Table 1. At present, the harp seal (*Phoca groenlaundica*) is not considered an important vector of sealworm. However, its importance as a vector may increase in the future owing to the recent increase in numbers of harp seals summering in Newfoundland waters, with consequent exposure to prey infected with sealworm.

Grey Seals

It is generally not possible to estimate total population size directly. However, the annual pup production is relatively easy to estimate and some form of population model is used to derive total population size from a time series of pup production estimates (eg. Zwanenburg and Bowen 1990; Harwood and Prime 1978).

There are two main breeding areas of grey seals in eastern Canada: Sable Island and the ice and small islands in the southern Gulf of St. Lawrence (Mansfield and Beck 1977). At Sable Island, a time series of pup production estimates is available from 1962 to the present (Stobo and Zwanenburg 1990). In recent years, production has been fully censused by tagging all live pups and recording the number of pups that die between birth and weaning. Prior to 1969 there is evidence that production was underestimated (Zwanenburg and Bowen 1990). Pup production has increased exponentially at a rate of 12.6 % per annum to a level of 9712 pups in 1989 (Stobo and Zwanenburg 1990).

Few data are available on grey seal pup production in the Gulf of St. Lawrence, Canada. Estimates ranging from about 6 000 to 11 000 pups were obtained from mark recapture studies between 1982 and 1986 (Stobo and Zwanenburg 1990). These estimates, combined with cull and bounty data, a rough pup production estimate for 1962 and vital rate parameter estimates from the populations in the United Kingdom have been used to produce a range of possible population trajectories. These suggest that the population may have increased by between 2 and 5 times since 1962 compared with the 20-fold increase at Sable Island (Zwanenburg and Bowen 1990).

Age-specific pregnancy rates for grey seals sampled in the Gulf of St. Lawrence and the age structures from Department of Fisheries and Oceans culls in the Gulf of St. Lawrence and bounty returns from both the Gulf and Sable Island have been used to reconstruct total population trends (Zwanenburg and Bowen 1990). The 1987 total population estimate was about 50 000 at Sable Island and between 30 000 and 60 000 in the Gulf of St. Lawrence. No confidence interval has been derived for the total population estimate.

The most recently published all-age population estimate for grey seals in the United Kingdom is 99 500, but revision of the pup production estimation model will reduce this figure. Long time-series of pup production estimates are available for most breeding colonies. Pup production is estimated either by direct enumeration as at Sable Island, or more generally by converting serial survey counts of the numbers of pups ashore to total production using one of a number of models (Ward et al. 1987). These estimates, together with independent estimates of age-specific fecundity, are used in a modified Leslie matrix model to provide estimates of age-specific survival rates and thus produce an age structure for the female component and an estimate of the female population size for each stock. At the Farne Islands, where pup production is measured exactly, the parameter values obtained are maximum likelihood estimates and the likelihood ratio method has been used to produce confidence intervals. If the model assumptions hold the confidence interval for the 1972 population was 3 100 to 5 600 (A. R. Hiby, unpubl. data). Management culls in 1972 and 1975 at the Farne Islands and in 1977 in the Outer Hebrides perturbed the age structure in an unknown way and, as a result, fitted age structures after the cull dates are less reliable.

United Kingdom colonies are growing at variable rates: North Rona is reasonably stable, the Farne Islands population is increasing after a period of decline due to management culls and the Orkney and Hebridean populations are generally increasing. One component of the Hebridean stock, the Monach Isles group, is increasing at a similar rate to the Sable Island population and currently produces about 6 000 pups annually. Overall the United Kingdom population has increased at around 5 % per annum over the past 25 years.

In Norway, the current total population estimate of 3 100 is a minimum value based on a combination of pup production estimates and counts of seals at haul-out sites (Wiig 1986). There is little information available on trends. A time-series of pup production estimates in the Froan Nature reserve indicates an increasing trend over the period 1977 to 1987. However, the status of seal protection within the reserve is different to that applying to the coast in general. The population trend in the reserve should therefore not be taken as an indication of the trend in the overall Norwegian grey seal population.

In 1986, the all-age population estimate for grey seals in Iceland was 14 500. Quantitative data on trends in grey seal numbers are limited to point estimates on the northwest coast in 1940 and the west coast in 1960 and recent studies between 1982 and 1986 along the whole coast. In addition there are estimates, for some colonies, of population size in 1978 based on pup hunting statistics.

In general, estimates of vital rate parameters are available for the United Kingdom and Canadian grey seal populations from seals taken in breeding colony culls, from seals shot outside the breeding season, from branding programmes and from the fitting of population models to long time-series of pup production estimates (Harwood and Prime 1978; NERC 1984; Mansfield and Beck 1977; Zwanenburg and Bowen 1990).

Harbour Seals

Information on trends in harbour seal numbers is almost uniformly scant for the North Atlantic (Table 1). In general, harbour seal populations are censused by counting the number of seals of all ages hauled out. At best these counts are standardised by counting at the same time each year and in similar conditions. The number obtained is always an unknown and potentially variable proportion of the total population and thus must be taken as simply a minimum estimate. Only at Sable Island is there a time-series of pup production figures comparable to the grey seal data (W. Stobo and B. Beck, unpubl. data).

No current all-age population estimate is available for eastern Canada. Pup production on Sable Island has increased from 313 in 1978 to 621 in 1989 (W. Stobo and B. Beck, unpubl. data). No recent data are available to identify trends in the rest of Eastern Canada.

TABLE 1. Data on pup production and trends of grey and harbour seal populations in the North Atlantic.

	Country	Locality	First survey	Last survey	1987 Pup production	Trend	Age structure known	Comments
Grey seal								
	Canada	Sable Island	1962	1987	7 400	+ 0.126	Yes	
		Non-Sable	1966	1986	5.5-11 000 (1984-86)	increase	No	
	Britain	Farne Islands & Isle of May	1956	1987	1 800	increase	Yes	
		North Rona &	1961	1987			Yes	
		Inner Hebrides & Outer Hebrides &		1987	23 600	+ 0.1	Yes	
		Orkney	1969	1987			Yes	
		Wales	—	1982	800-900	?	No	
		Shetland	—	1983	1 000	?	No	
	Iceland		1972	1986	2 918	+ 0.09	Yes	
	Faroes	No information				?	No	
	Norway		1977	1986	?	?	No	
Harbour seal								
	Canada	Sable Island	1967	1986		increase	No	Pup production
		Non-Sable	1949	1973		decline	No	
	Britain	Wash	71/72*	1981		increase (?)	No	* Point estimate — mark/recapture
		Orkney	1982	1986		increase	No	* Probably results from improvement in census techniques
		Shetland	1975	1984		increase	No	* Boat survey of haul out numbers every third year
		Hebrides	1970s			?	No	* Point estimates
		E. Scotland	1985*			?	No	* Point estimates
	Iceland		1972	1985*		increase	(82-84 hunt)	* Point estimates 72, 76, 80, 85
	Norway		1977	1986		?		Point estimates
	Wadden Sea		1960	1986		from 1964 increase	No	

In the United Kingdom, the current all-age population estimate is 24 000 animals but this is generally regarded as an underestimate (NERC 1987). A recent aerial survey count of the Wash and triennial boat surveys in Shetland indicate some increase since the mid-1970's but elsewhere in the United Kingdom only point estimates are available (D. Thompson, pers. comm.).

The current all-age population estimate of harbour seals along the Norwegian coast is 4 200 (plus 300-500 at Svalbard). This again is a minimum estimate. Comparison of recent surveys with one from the mid-1960s indicates a stable total population, although local changes have been observed. A time series of estimates is available for Oslofjord which seems to indicate an increase in the last 10 years (A. Bjørge, pers. comm.).

In Iceland, the 1985 minimum all-age population estimate was 12 300 harbour seals. Point estimates for different sections of the coast were obtained between 1973 and 1980 and a complete census was carried out in 1985. Comparison of these two data sets shows a range of trends from an 8 % increase to a 10 % decrease (E. Haukkson, pers. comm.).

In the WaddenSee, the current minimum all-age population estimate is 7 100 based on aerial survey counts. A time-series of counts showed the population declining from 5 500 in 1960 to a minimum of 3 600 in 1974, since then it has increased steadily (H. Moller, this meeting).

During the spring and summer of 1988 a major viral epidemic has been observed throughout the Skaggerak, Waddensee, southern Norwegian and United Kingdom harbour seal populations, causing heavy mortality (Dietz et al. 1989). In the light of this epidemic, the estimates of most Eastern Atlantic populations will need revision.

Distribution and Movements

Grey Seals

In Canada there is evidençe from tag and brand recoveries of large-scale movements of all ages between eastern Nova Scotia, including Sable Island, and the Gulf of St. Lawrence (Stobo et al. 1990). Although these data cannot be corrected for resighting effort, and hence cannot be used quantitatively, they do provide considerable insight into the large-scale seasonal movements of grey seals. Pups from both areas disperse widely throughout Eastern Canada. Pups born at Sable Island appear to remain in the vicinity of the Island until June. They appear in significant numbers along the south coast of Newfoundland in July and also begin to appear in the Gulf of St. Lawrence in July, reaching peak numbers in August. Some Gulf-born pups are carried out of the Gulf of St. Lawrence on drifting ice and are observed on and around Sable Island up to the end of June. There are few recoveries of older animals but they suggest that adults undergo similar seasonal movements. Sable Island seals appear to move offshore during the period from September to December.

In the United Kingdom, tag recoveries have shown a similar wide dispersal of pups with animals from the Farne Islands being recovered throughout the North Sea basin as far north as 67° on the Norwegian coast. Tag recoveries of the 0+ age class from five main tagging sites have been used to calculate migration rates between five recovery areas around the United Kingdom (McConnell et al. 1984a). The majority of seals stayed in the sea adjacent to their natal area but extensive migrations occur between adjacent recovery areas with consequent mixing of pups of different breeding stocks.

In both the United Kingdom and Canada significant numbers of tagged young seals have been recovered from offshore waters, mostly from fishing gear. This suggests that at least some juveniles have a pelagic phase. Telemetry studies of adult seals in the

United Kingdom have shown some animals travelling distances of up to 270 km in a week, while others make only very local feeding forays around inshore haul-out sites (D. Thompson, pers. comm.).

There is little quantitative data on grey seal movements in either Norway or Iceland but the general pattern is of seals spreading out from breeding sites to most parts of the coast. As in the United Kingdom there are usually concentrations around breeding areas throughout the year.

Harbour Seals

Pups tagged shortly after birth on Sable Island disperse widely during their first year of life with recoveries coming from Newfoundland to New Jersey (W. Stobo and B. Beck, pers. comm.). There are few recoveries of older age classes, but adult seals (tagged as pups on Sable Island) have been found on the mainland. A north-south movement of harbour seals between the Bay of Fundy and the northeastern USA has been reported by Rosenfeld et al. (1988). There is very little information on the movements of harbour seals in the rest of Eastern Canada.

Some pups from United Kingdom colonies also disperse widely, with pups from Orkney recovered as far away as southwestern Norway and Wash pups recovered in Holland (D. Thompson, pers. comm.). From telemetry studies in the summer months it appears that adults are much more sedentary, remaining within a few tens of kilometres of particular haul-out sites. Different patterns occur in winter with wider dispersal, although seals frequently return to their summer sites.

Norwegian studies suggest that harbour seals show a high level of site fidelity at least in the summer. In the Froan area there is anecdotal evidence of movement to more sheltered inshore areas during the winter (A. Bjørge, pers. comm.).

In Iceland the little information available suggests that, in the north, seal distribution may be affected by the ice conditions.

Feeding

A compilation of information on grey seal diets in Eastern Canada collected between 1950 and 1987 indicated significant seasonal and geographic variation in the frequency of occurrence of different prey species (Benoit and Bowen 1990a). Unfortunately, these data do not provide an accurate picture of the caloric contribution of different species to the energy requirements of the population.

The first attempt to estimate the size composition and relative importance of prey, on wet weight basis, in the diet of grey seals in Canada comes from work conducted at Anticosti Island in 1986 and 1987 (Benoit and Bowen 1990b). Based on otolith-fish length regressions, fish eaten by grey seals ranged in length from 7 to 80 cm, with approximately 88 % of prey being <30 cm. The mean length of prey (about 25–30 cm) eaten by grey seals was similar for a number of species despite differences in the size range of these species suggesting that grey seals feed mainly on young, schooling or aggregated species. Cod, capelin, lumpfish (*Cyclopterus lumpus*) and ocean pout (*Macrozoarces americanus*) accounted for about 79 % of the biomass of fish eaten in the summer diet.

A great deal of effort has been put into defining the diet of grey seals in United Kingdom waters. Studies in the 1960's and 1970's produced frequency of occurrence data from seals around the Scottish coast (Rae 1968, 1973). However these data are mainly from fishing gear and not surprisingly are heavily biased towards the target species of the particular fishery. Recent studies (Prime and Hammond 1987; McConnell et al. 1984b) have concentrated on quantifying the species composition of the diet in terms of percentage by weight. These data are obtained by identifying and measuring otoliths

TABLE 2. Data on grey and harbour seal diets from Norway and Iceland.

			Grey Seal		Harbour seal	
AREA: PERIOD METHOD: SOURCE:			NORWAY[a] 1977-80 % vol Faeces	ICELAND 1979-82 % vol Stomach	NORWAY[a] 1978-81 % vol Stomach	ICELAND 1979-82 % wt Stomach
Gadoid	Cod	*Gadus morhua*	14.2	20.1	7.7	24.3
	Haddock	*Melanogrammus aeglefinus*	14.9	4.7	—	
	Saithe	*Pollachius virens*	7.1	18.3	4.1	33.4
	Whiting	*Merlangius merlangus*	—		—	5.9
(Other Hake)	Unid. Gadoid				11.8	2.0
Flatfish	Plaice	*Pleuronectes platessa*		1.0		1.9
	DAB (yellowfin)	*Limanda limanda*		0.6		3.5
	Unid. Flatfish				1.2	2.9
	Halibut	*Hippoglossus hippoglossus*	2.9	8.6		2.2
	Sandeel	*Ammodytes* sp.	1.1	5.4	—	9.9
Pelagics	Herring	*Clupea harengus*	0.8	5.9		2.4
	Capelin	*Mallotus*		1.0		2.7
Other Fish	Unidentified		25.0	4.1	2.9	
	Sebates		7.4		13.3	
	Catfish	*Anarhichas lupus*	16.8	11.4		5.1
	Scorpion			13.1		3.2
	Lumpfish	*Cyclopterus lumpus*	1.5	12.4		
	Skate		4.5	0.1		
	Squid			5.0	8.0	
	Inverts		3.4	1.3	1.0	2.0

[a] A. Bjørge (unpubl. data).

found in seal faeces. Appropriate digestion coefficients and fish to otolith size relationships are then applied. Knowledge of the energetic requirements of seals and energy content of different fish is used to estimate total consumption of each species. These methods also produce size frequency distributions of the fish eaten. Again there are marked geographical and seasonal variations in the observed diets (Hammond and Prime 1990). The most striking feature of the data from the United Kingdom is the importance of the sand eel (*Ammodytes marinus*) in the diet at the two main seal concentrations in Orkney and the Hebrides.

Similar data, expressed as percentage by weight, are available from both Norway and Iceland (Table 2) but these data are based on stomach contents, not on faeces. Icelandic data also show seasonal and geographic variation in diet composition (Hauksson 1984, unpubl. data).

Although it is frequently suggested that grey seals are opportunistic feeders, this description is little more than an acknowledgement that the diets of seals vary in space and time. In fact, the foraging ecology of grey and harbour seals remains poorly understood. However, efforts to quantify the size and species composition of diets using otoliths and other hard parts and advances in the use of telemetry and stable isotopes promise to significantly increase our understanding of the foraging ecology of these species.

A striking feature of current information on diets is the lack of consistent time series on the size and biomass of prey eaten by either species. Given the dynamic nature of seal diet composition and the variation in the abundance of sealworm in the different fish species eaten by seals, this lack of a time series represents a serious obstacle to our understanding of the role of seals in the transmission of the parasite.

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Grey Seal (*Halichoerus grypus*) Pup Production on Sable Island and Estimates of Recent Production in the Northwest Atlantic

Wayne T. Stobo and Kees C. T. Zwanenburg

Department of Fisheries and Oceans, Marine Fish Division, Bedford Institute of Oceanography, Dartmouth, N.S., Canada B2Y 4A2

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Grey seal pup production on Sable Island in the Northwest Atlantic was enumerated from 1977 to 1989 by complete cohort marking. During that period, pup production increased exponentially from 2 181 to 9 712 pups, a rate of 12.6 % annually. Pup mortality on the pupping grounds ranged from 2.8 to 15.6 %, but did not exhibit any temporal trends. Concurrent with this population growth was an expansion of existing, and the development of new, pupping colonies on the Island. Given the opportunity for further expansion of the pupping areas, it is unlikely that density-dependent pup mortality due to crowding will moderate growth in the near future. Mark-recapture estimates of non-Sable (NSI) pup production in the Northwest Atlantic for the years 1984-86, were made using tag recoveries at Sable Island, the Eastern Shore of Nova Scotia, and Anticosti Island in the Gulf of St. Lawrence. There was considerable variation in these estimates of pup production, attributable in part to heterogeneous mixing of tagged and untagged seals. However, this range likely brackets the actual production in this area during those years. These estimates, plus the direct marking counts, indicate that total pup production in the Northwest Atlantic for the period 1984-86 was between 9 000 and 20 000 pups.

La production de jeunes phoques gris sur l'île de Sable, dans l'Atlantique nord-ouest, a été dénombrée entre 1977 et 1989 par marquage complet de cohorte. Pendant cette période, la production de petits a augmenté de façon exponentielle, passant de 2 181 à 9 712, soit un taux de 12,6% par an. La mortalité des petits sur les aires de mise bas variait entre 2,8 et 15,6%, sans montrer toutefois de tendance temporelle. Parallèlement à cette croissance démographique, on a noté l'expansion des colonies de mise bas existantes et la création de nouvelles colonies sur l'île. Étant donné les possibilités d'expension des aires de mise bas, il est peu vraisemblable que la croissance soit, dans un proche avenir, modérée par une mortalité des petits dépendante de la densité et causée par le surpeuplement. Des estimations de la production de petits à l'extérieur de l'île de Sable dans l'Atlantique nord-ouest, de 1984 à 1986, ont été effectuées grâce à des opérations de marquage avec recapture à l'île de Sable, sur la côte est de la Nouvelle-Écosse et à l'île d'Anticosti, dans le golfe du Saint-Laurent. Ces chiffres présentaient des variations considérables, attribuables en partie au mélange de phoques marqués et non marqués. Cette fourchette couvre probablement la production réelle de la région pendant cette période. Ces estimations, auxquelles s'ajoutent les dénombrements du marquage, indiquent que la production totale de petits phoques dans l'Atlantique nord-ouest de 1984 à 1986 se situe entre 9 000 et 20 000 individus.

Introduction

Altough grey seals were identified in eastern Canadian waters as early as the 1600's (Gilpin 1874), formal research began in the 1950's, mainly because of their role in the sealworm *Pseudoterranova decipiens* (Gibson 1983) life cycle. Seals are the definitive host of *P. decipiens*, and in the Northwest Atlantic, the grey seal is the most important host (Scott 1953; Scott and Fisher 1958; Mansfield and Beck 1977; Stobo et. al. 1990a). Finfish are one of several intermediate hosts of this parasite (Margolis and Arthur 1979). Consequently, the increasing abundance and prevalence of *P. decipiens* in the flesh of commercially important fish and by association, the population status of the grey seal, are of continuing concern to the fishing industry of Canada's east coast (Malouf 1986; McClelland et. al. 1983a,b).

Sable Island and the southern Gulf of St. Lawrence (Fig. 1) are the two major breeding areas in the Northwest Atlantic (Mansfield and Beck 1977). In the southern Gulf of St. Lawrence grey seals breed both on isolated islands and pack ice, while on the Scotian Shelf breeding is restricted to a few small islands (Mansfield 1966).

Pupping on Sable Island, located approximately 150 km southeast of Halifax (Fig. 1), begins in late December and lasts until mid-February (Boness and James 1979; Mansfield 1966). The females are gregarious (Boness and James 1979; Anderson et al. 1975) and congregate in large groups to whelp. Lactation lasts about 17 d and mating commences soon after (Boness and James 1979). Since the pups do not begin to swim for 20-30 d after birth and become highly aggregated after weaning (Davies 1949; Boyd and Campbell 1971; Coulson and Hickling 1964; Mansfield 1966), they can be censused over an extended period.

Whelping in the southern Gulf of St. Lawrence, the only other known major breeding ground for grey seals in the Northwest Atlantic, starts in late December. However, observations in late February 1982 (Stobo unpubl.) suggest that the temporal distribution of births in the Gulf is more protracted than that observed on Sable Island. From

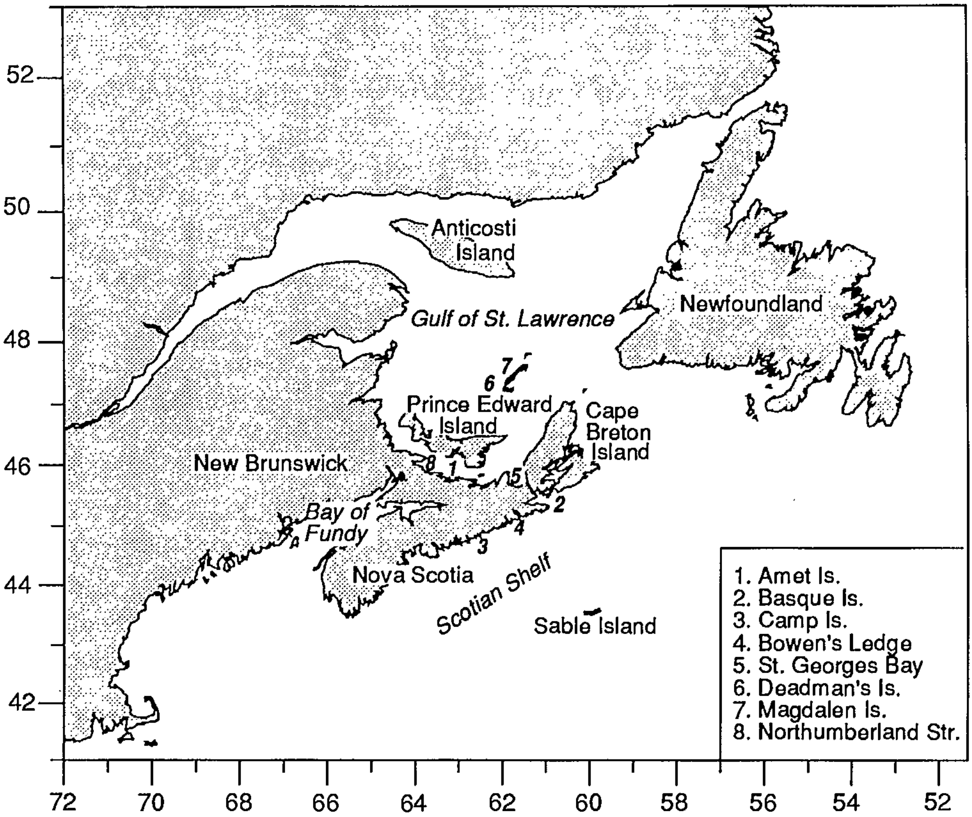

FIG. 1. The Northwest Atlantic showing place names mentioned in the text.

December to February ice forms and gathers in a 5 500 km^2 area between Prince Edward Island and the west coast of Cape Breton Island (Fig. 1). The ice cover is variable between years, but generally consists of shore fast ice in St. Georges Bay and along the Cape Breton coast, plus extensive areas of adjacent floe ice. Grey seals give birth on both ice types as well as on two small islands, Amet Island at the western end of this area, and Deadman's Island near the Magdalen Island. Pups born on these two Gulf Islands are concentrated and thus easily censused, but seals whelping on the ice are sparsely distributed. Residual ocean currents in the southern Gulf cause floe ice to move slowly in a clockwise gyre with a net export along the Cape Breton coast and out of the Gulf onto the Scotian Shelf. There have been numerous observations of grey seal pups drifting out of the Gulf on floe ice onto the Scotian Shelf in February. This continuous export and the annual variability in ice cover makes these pups difficult to count.

Prior to 1975, research on the population biology of Northwest Atlantic grey seals was limited (Mansfield and Beck 1977; Gray and Beck 1979). Monitoring of annual grey seal pup production on Sable Island began in 1962 and, with the exception of 1966 and 1975, has continued to the present. Between 1962 and 1976, the pup censuses were based on a combination of aerial and ground surveys during the breeding season (Mansfield 1966; Mansfield and Beck 1977); since 1977, each cohort has been counted and tagged. Assessments of population status, conducted after 1980, have relied heavily on the results of this tagging work (Zwanenburg et. al. 1981; Zwanenburg 1984; Zwanenburg et. al. 1985; Zwanenburg and Bowen 1990). This paper documents current trends in pup production on Sable Island and provides estimates of total Northwest Atlantic pup production for the period 1984 to 1986.

Materials and Methods

Sable Pup Counts

Sable Island is a crescent-shaped sandbar, approximately 40 km long, up to 2 km wide, and about 30 % is vegetated (Fig. 2). The first grey seal pups are born as early as the last week of December and the first mating activity commences about 17 d later, when these pups are weaned (Boness and James 1979). Most births occur during the second and third weeks of January, with whelping being essentially complete by the first week of February. However, few pups are weaned prior to the second week of January and none have left the Island by then. Each year since 1977, investigators have been on the Island from the first week in January until the second week of February to ensure that all pups were tagged.

All pupping areas were divided into sections using prominent landmarks and, once weaned pups were observed, designated sections of the pupping areas were searched daily. By moving between sections in rotation, all sections were searched several times during the 6-wk field trip. All dead pups were counted and paint-marked to prevent recounting. All live pups were tagged in the webbing of the hind flipper using uniquely numbered, colour-coded cattle ear tags[1] (Table 1). Since tags are not readily visible, in 1977 and 1978 we also applied a dye or paint mark to their coats to reduce the need to re-examine previously tagged pups. Since 1979 a highly visible, 15 cm long piece of flag material[2] was attached to each tag. In 1977 pups of all ages (whether suckling or weaned) were tagged by a team of two people. The pup was captured or removed from the mother, a hole was punched in the flipper, the tag applied and the pup released. Punching a hole in the flipper prior to tag application, and the two-person

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[1] Dalton Supplies Ltd., Nettlebed, RG9 5AB, Henley-on-Thames, England.

[2] Safety Flag Co., P.O. Box 1005, Pawtucket, Rhode Island, USA, 02862.

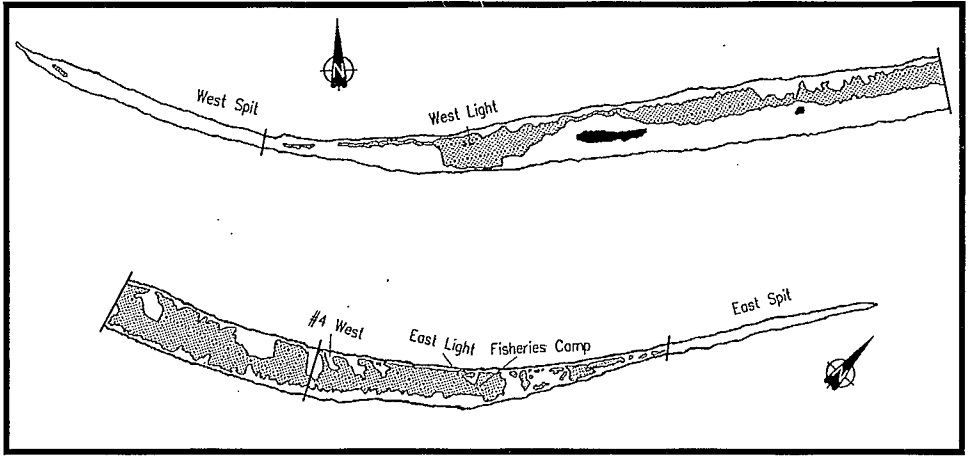

FIG. 2. Sable Island indicating geographic locations, vegetated areas (grey shading), and saline ponds (black shading). The lines transecting the Island at the west and east ends delineate the areas of major pupping and breeding.

tagging team, were discontinued in 1979 and 1980, respectively, in order to increase tagging rate. Since 1980, pups were generally not tagged during lactation, as pups could be handled more safely and efficiently after weaning when their mothers had left the colony.

TABLE 1. Annual pup production on Sable Island from 1977 to 1989. Only live pups were tagged. All pups which died prior to being tagged were counted; in 1988 and 1989, counts were also made of pups which died after being tagged. The percentage dead is of total production; for 1988-89 the values in parentheses include untagged and tagged dead.

Year	No. tagged	Untagged dead	Tagged dead	Total count	Percent dead
1977	1 968	213		2 181	9.8
1978	2 268	419		2 687	15.6
1979	2 712	221		2 933	7.5
1980	3 250	94		3 344	2.8
1981	2 843	300		3 143	9.6
1982	4 140	349		4 489	7.8
1983	4 738	697		5 435	12.8
1984	5 189	667		5 856	11.4
1985	4 857	749		5 606	13.4
1986	5 800	501		6 301	8.0
1987	6 931	460		7 391	6.2
1988	7 855	738	130	8 593	8.6 (10.1)
1989	9 117	595	62	9 712	6.1 (6.8)

Non-Sable Pup Production

Tagging trips were conducted in the southern Gulf of St. Lawrence between 18 January and 9 February, 1984-86 (Table 2). Pups produced on the only other documented grey seal breeding areas, Camp Is., Basque Island, and Bowen's Ledge, along the eastern coast of Nova Scotia (Eastern Shore) were also enumerated during these three years. In 1984, the last year of an annual breeding season cull program, most pups produced on the Eastern Shore were killed. In 1985 and 1986 all pups found in this area were tagged, but tagging effort was restricted to a one day trip in late January.

TABLE 2. Number of grey seal pups tagged in 1984-86 in the Northwest Atlantic.

Year	Sable Island	Gulf of St. Lawrence	Eastern Shore
1984	5189	1386	13
1985	4757	1993	125
1986	5800	1630	144

Recapture samples of grey seals were taken at three locations in the Northwest Atlantic: Sable Island, the Eastern Shore, and Anticosti Island. Between March and October, 1984-86, we made 14 field trips to Sable Island to collect information on the ratio of Sable Island to NSI pups. Using all-terrain vehicles, as many as 622 pups per trip were live captured, examined for tags or tag loss, and released (Table 3). For all pups examined, tag number was recorded to determine tag origin. By August of each year, pups were no longer segregated from the aggregations of older seals, therefore subsequent samples were obtained by shooting the specimens. We took less than 55 animals on any of these late season trips. We also collected a sample of 61 yearlings (1985 cohort) in January/February 1986.

TABLE 3. Counts of grey seal pups examined on Sable Island for tags between 1984-86.

		Pup count				
Year	Date	Sable Island[a]	Gulf of St. Lawrence[b]	Untagged[c]	Eastern Shore[d]	Ratio: Sable/Total
1984	2-5 Mar.	202	1	5	—	0.97
	3-5 Apr.	230	5	25	—	0.88
	3-6 May	220	8	20	2	0.88
	1-5 June	181(6)	10	48	—	0.76
	4-12 Oct.	37(10)	1	5	—	0.89
1985	26-31 Mar.	356	1	64	1	0.84
	4-8 May	450	27	139	3	0.73
	4-12 June	279	22	112	3	0.67
	10-17 Sept.	26	2	12	1	0.72
1986[e]	Jan./Feb.	41	7	12	1	0.72
1986	13-19 Mar.	247	1	—	—	0.99
	3-9 May	388	27	151	4	0.69
	26 May-1 June	404	17	130	6	0.73
	10-17 Sept.	29	2	9	—	0.73

[a] Pups bearing a mark applied on Sable Island; the value in parentheses indicate cases of tag loss which were assigned to a Sable Island origin.
[b] Pups bearing a mark applied in the Gulf of St. Lawrence.
[c] Untagged pups assumed to originate from areas other than Sable Island.
[d] Pups bearing tags applied at Camp or Basque Islands.
[e] Sample of yearlings.

Throughout 1985, contracted hunters collected grey seals from the Eastern Shore, the majority being taken in May and September-October. All animals were examined for tags; only the data on pups taken during these two time periods (Table 4) were used to estimate cohort size. In 1986 and 1987, contracted hunters, accompanied by a biological technician, collected grey seals from Anticosti Island in the northern Gulf of St. Lawrence. Since tags had been applied to the 1984-86 Gulf cohorts, all specimens were examined for tags or tag loss. We estimated the sizes of the 1984-86 Gulf cohorts using the data on pups, yearlings, and two-year olds in these samples (Table 5).

TABLE 4. Counts of grey seal pups collected along the Eastern Shore of Nova Scotia during the spring and fall of 1985.

	Pup count			
Season	Sable Island[a]	Gulf of St. Lawrence[b]	Untagged[c]	Eastern Shore[d]
Spring	6	6	10	
Fall	13	2	13	1
Total	19	8	23	1

[a] Pups bearing a mark applied on Sable Island.

[b] Pups bearing a mark applied in the Gulf of St. Lawrence.

[c] Untagged pups assumed to originate from areas other than Sable Island.

[d] Pups bearing tags applied at Camp or Basque Islands, or Bowen's Ledge.

TABLE 5. Numbers of juvenile grey seals sampled during July-August, 1986 and 1987, from the 1984-86 cohorts at Anticosti Island in the Gulf of St. Lawrence.

Cohort	1986		1985		1984
Specimen Age	0	1	1	2	2
Untagged	39	13	21	14	31
Gulf tags	16	5	13	4	10
Total	55	18	34	18	41

In estimating non-Sable production we assumed that all live pups produced on Sable Island, Camp and Basques Islands, and Bowen's Ledge had been tagged, and therefore all untagged pups were of southern Gulf of St. Lawrence origin. Since all recoveries on Sable and Anticosti Island were made by scientific personnel, and since a permanent hole remains in the flipper when a tag is lost, all instances of tag loss were easily detected and recorded. We assumed that the tag loss rate was the same for both locations, then apportioned the number of animals which had lost their tags in direct proportion to the relative numbers of Sable and NSI pups observed. We then estimated Gulf pup production using the model of Chapman (1951):

$$N^* = \frac{(M + 1)(n + 1)}{(m + 1)} - 1 \tag{1}$$

where: M = number of pups marked in the Gulf
n = total pups observed
m = total Gulf marked pups observed (corrected for tag loss)
N^* = number of Gulf pups produced

An estimate of the variance and 95 % confidence limits of N^* were derived by Seber (1973) as:

(2) $$\mathrm{Var}(N^*) = \frac{(M+1)(n+1)(M-m)(n-m)}{(m+1)^2(m+2)}$$

(3) and $$N^* \pm 1.96\sqrt{\mathrm{Var}(N^*)}$$

Results

Sable Island Pup Production

The counts on Sable Island indicate an increase in pup production from 2 181 pups in 1977 to 9 712 in 1989 (Table 1). However, as the degree of underestimation cannot be quantified for any year, these values must be considered minimum estimates of annual production. Although it is difficult to ensure that all live pups were tagged, it is likely that very few pups were missed due to the extensive coverage of all pupping areas. This is corroborated by the fact that in spite of continuing extensive searches of all pupping areas, few if any untagged pups could be found by the end of each field trip. The enumeration of dead pups is less reliable. In 1980, 1981, 1985, and 1987 several severe winter storms buried an undetermined number of dead pups under sand and snow. As a result, total production may have been underestimated in those years. In other years, conditions were such that few dead pups were missed.

From 1977 to 1989 pup production on Sable Island (Fig. 3) increased at an exponential rate of 12.6 % per year ($y = 2033.19e^{0.120x}$; $r^2 = 0.97$, $SE = \pm 0.079$). Deviations of observed numbers from that predicted were less than 16 % for any year. At this rate of growth, pup production will double every 6–7 yr.

Pre-weaning pup mortality varied substantially between years but there was no trend of increasing mortality despite an almost 5-fold increase in pup production between 1977 and 1989 (Table 1). From 1977 to 1987, a number of operational factors could have biased the count of dead pups downwards. First, some of the dead were lost due to winter storms. Second, prior to 1988 some members of the tagging team did not con-

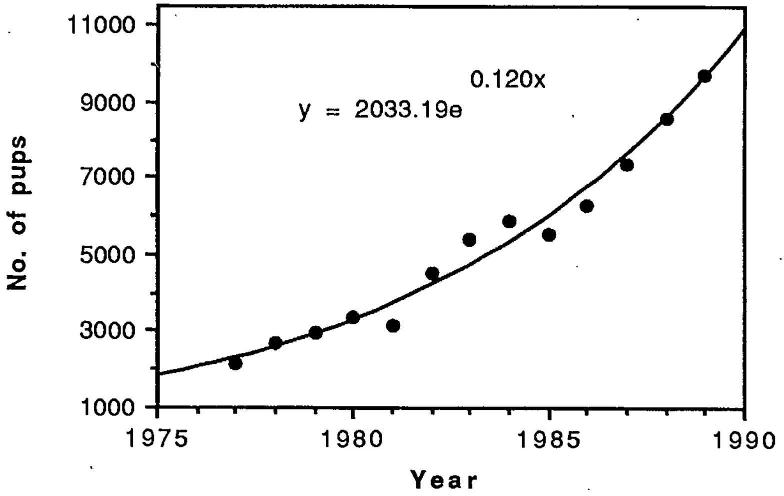

FIG. 3 Total grey seal pup production observed on Sable Island between 1977 and 1989.

sistently include in the total dead counts, pups which died after tagging. As a result, the mortality estimates for 1977-87 are minimum values. Although the degree of underestimation for these earlier estimates cannot be strictly quantified, in 1988 and 1989 mortality of tagged (and thus weaned) pups was 15 and 9.4 %, respectively, of total recorded mortality and only 1-2 % of total production (Table 1). These data suggest any underestimate of total mortality in earlier years would have been minimal.

The largest concentration of pups on Sable Island has traditionally been found in a 5 km^2 area about 5 km from the eastern tip, stretching continuously from the north to the south beach. Fifty percent of this area is vegetated and sufficiently elevated to protect the mothers and their pups from flooding during winter storms. The remainder of the area utilized by lactating females is low lying and subject to storm surges, such that in any given year portions are under water for varying periods of time. The low lying area east of the main colony is used only sporadically. Pupping at the west end of the Island traditionally occurs on the last 5 km of the low lying western tip. This area is frequently buffeted by storm surges and portions are flooded for prolonged periods.

Both the number and area of pup concentrations has grown with the increase in pup production in recent years. Between 1977-89, there was an expansion of the pupping and breeding areas at the east and west ends of the Island (Fig. 4). Generally this involved established historical locations with extensions along the beaches and increased movement into the vegetated portions of the Island. Pregnant females, plus attendant males, now often use vegetated dunes up to 10 m high which can be up to 0.75 km inland. One new colony developed, in 1983 at #4 West (Fig. 4) on the north side of the Island, and has since expanded rapidly.

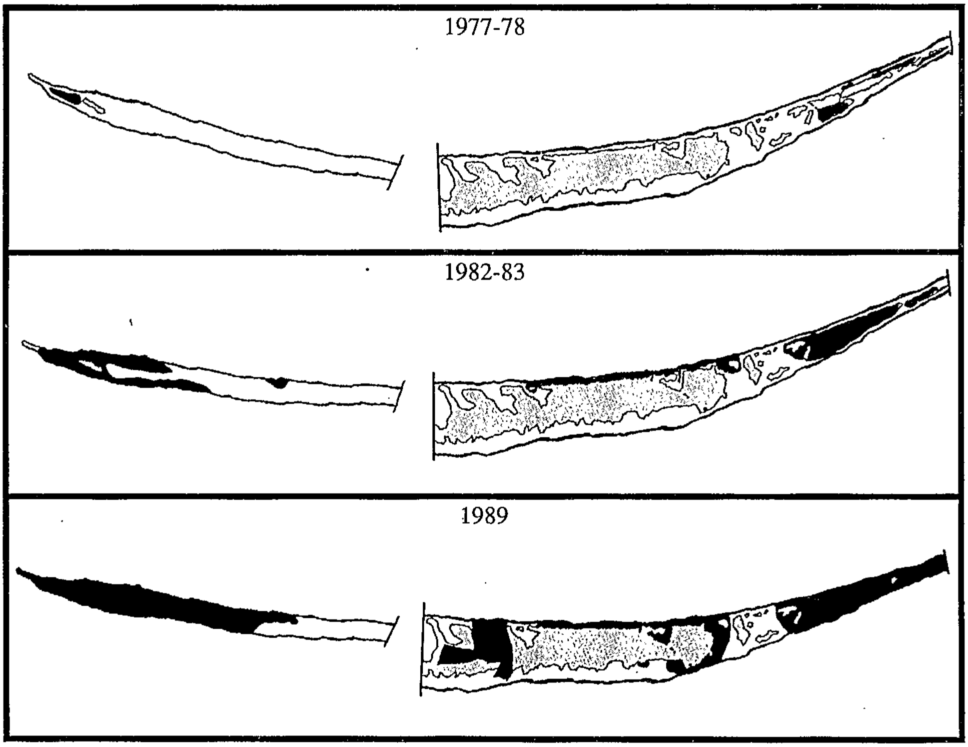

FIG. 4 Composite maps of the west and east ends of Sable Island showing the expansion of pupping areas (black shading) over beach (unshaded) and vegetated (grey shading) areas between 1977 and 1989.

From 1985 to 1989, total pup production increased by over 70 %, from 5 606 to 9 712 pups. The number of pups born in each of the three areas also increased, but the extent of the increase was inversely related to initial size (Table 6). Pup production at #4 West, the newest colony, increased by 159 %. West End production increased by 89 %, while the largest colony, the East End, experienced the smallest increase (69 %).

TABLE 6. Sable Island grey seal pup production partitioned into three distinct pupping areas, with percent of total production in parentheses. Percent increase from 1985 is also given.

Year	West End		#4 West		East End	
	Pup No.	Increase	Pup No.	Increase	Pup No.	Increase
1985	629(11.2)		116(2.1)		4 861(86.7)	
1986	744(11.8)	18.3	196(3.1)	69.0	5 361(85.1)	10.3
1988	1 339(15.6)	112.9	184(2.1)	58.0	7 070(82.3)	45.4
1989	1 188(12.2)	88.9	300(3.1)	158.6	8 224(84.7)	69.2

Estimates of NSI Pup Production

From Sable Island Recoveries

In 1984 single tags were used at all release sites. In subsequent surveys of this cohort, 16 out of 1025 recaptured pups had lost tags, 6 in June and 10 in October. Since the expected recoveries of Sable pups in June and October represented 0.95 and 0.97, respectively, of the observed total recoveries of tagged pups, all 16 animals were counted as Sable pups (Table 3).

In 1985 most Sable Island and NSI born pups were tagged in both hind flippers. During subsequent Sable surveys of this cohort, no tags were lost by the 240 recaptured seals (pups and yearlings) originally tagged with a single tag; only 5 out of the 1325 recaptured double tagged seals lost tags. In each case only one tag was lost, thus still allowing all pups to be accurately assigned to site of origin.

In 1986, all NSI pups were tagged in both flippers, while only single tags were applied to Sable born pups. During surveys of this cohort, no tags had been lost by the 347 recaptured double tagged seals, and a total of 12 of the 1 068 recaptured single tagged seals lost tags. Since only Sable born pups carried single tags, all were of Sable origin.

In all surveys of Sable Island, the proportion of Sable born pups dominated the censuses (Table 3). Generally few NSI pups arrive on Sable before the end of February, but the timing of their arrival, and their total numbers appears to be influenced by the amount of ice drifting out of the Gulf of St. Lawrence. In 1984 when little ice drifted out of the Gulf, the proportion of NSI pups on Sable remained low throughout the year. Conversely, in 1985 when heavy ice drifted within 32 km of Sable the numbers of NSI pups was high during the March survey relative to that observed in 1984. The variability between years in numbers of NSI pups observed on Sable during the March surveys was high, probably as a result of differences in the time of first arrival. Due to that variation and the low ratio of NSI to Sable born pups relative to the summer and fall surveys, they were not considered to be representative of the annual ratios. The March data were therefore not used in estimating cohort size.

From March to May 1985, the proportion of the NSI pups on Sable increased and then stabilized at about 0.30 during the May to September surveys. The proportion of NSI animals in the January/February 1986 sample of yearlings was 0.28, similar to that observed in the previous three surveys. A chi-square test of homogeneity between the four surveys (May, June, Sept, and Jan./Feb.) of the 1985 cohort (χ^2 = 5.36; d.f.

= 3; $P>0.10$) indicated no significant differences, thus the observations for all trips were combined. The similarity in the proportions of NSI animals in the samples of pups and yearlings further suggests that after the initial dispersal from the pupping grounds, the proportion of NSI grey seals on the Scotian Shelf remains fairly constant throughout the first year of life. No significant differences were found between the successive April-October surveys for 1984 (χ^2 = 1.82; d.f. = 3; $P>0.50$), or the successive May-September 1986 surveys (χ^2 = 1.08; d.f. = 2; $P>0.90$), thus these observations were also combined by year. The estimated sizes of the 1984, 1985, and 1986 NSI cohorts using the Sable survey data were 6823 ± 2321, 11287 ± 2553, and 11694 ± 3024, respectively.

Eastern Shore and Anticosti Recoveries

A total of 51 pups were collected along the eastern shore of Nova Scotia in 1985 (Table 4). In contrast to the situation observed on Sable, the proportion of NSI born pups in this sample was 0.63. There are two potential biases in these data. First, the samples were taken in the Camp-Basque Islands, Bowen's Ledge areas where tagging was restricted to a single day. If the total production in this area had not been tagged, then the untagged portion, which we have assumed comes from the Gulf, may have been biased upwards. Secondly, the hunters may not have noted the presence of a tagging hole in the flipper of a pup which had lost a tag, again causing the untagged portion to be overestimated. However, our observations on Sable indicate that a very small percentage of tags were lost by the 1985 cohort (0.3 %), and because of double tagging, the origin of most animals could still be established. Consequently we have made no adjustments for potential tag loss. A chi-square test of homogeneity indicated no significant differences (χ^2 = 0.02; d.f. = 1; $P > 0.75$) between the spring and fall sample. The data were therefore combined and resulted in an estimated 1985 NSI cohort size of 7089 ± 3717.

The Anticosti samples, consisting of several age-groups, were taken in 1986 and 1987 (Table 5). Forty-eight animals with Gulf tags and 118 untagged animals from the 1984, 1985, and 1986 cohorts were taken. Seven Sable (6 pups, 1 yearling) and 2 Camp-Basque Islands-Bowen's Ledge (1 pup, 1 yearling) animals were also collected. Chi-square tests of homogeneity indicated no significant differences between the samples for either the 1985 (χ^2 = 1.50; d.f. = 1; $P > 0.10$) or the 1986 (χ^2 = 0.02; d.f. = 1; $P > 0.75$) cohorts, thus the data were combined for each cohort. The resultant estimates of the 1984, 1985, and 1986 NSI cohort sizes were 5295 ± 2564, 5870 ± 2135, and 5485 ± 1867, respectively.

Discussion

Sable Pup Production

The 12.6 % annual rate of increase on Sable Island has been consistent from 1977 to 1989. Since these pup production values (Table 1) are based on the robust method of blanket marking, they are reliable at least as minimum estimates and, due to the intensity of tagging effort, are close to actual production. The annual variations must be due to currently unquantified effects such as immigration, emigration, and undetected mortality on the pupping grounds.

Given the proximity of the other major breeding areas, substantial immigration of breeding adults could inflate the natural rate of increase of the Sable population, either in a sustained manner or in certain years. Pups born in the Gulf of St. Lawrence and Eastern Shore areas have been found on the Scotian Shelf at various ages (Mansfield and Beck 1977; Stobo et al. 1990b), and on Sable Island throughout the year

(Table 3). We have also observed adults, branded as pups in the Gulf and on Eastern Shore breeding grounds, consistently breeding on Sable. Thus immigration does occur. But the number of identifiable NSI adults breeding on Sable Island are fewer than 5 annually out of 360 branded as pups in the Gulf and along the Eastern Shore. Assuming a mortality rate of approximately 25 % for pups and less than 10 % annually for older animals, 5 breeding animals on Sable represents a very low immigration rate (see also Zwanenburg and Bowen 1990). We also have a 10 yr time series of unpublished resighting data on adults, branded as pups on Sable Island, consistently breeding there. These data suggest that most grey seals return to the same breeding grounds in successive years. Emigration from Sable Island has also been documented. Pups tagged and branded on Sable Island were taken in the 1986-87 Anticosti samples as pups and yearlings. Sable born grey seals have also been observed in the other areas at all ages (Mansfield and Beck 1977; Stobo et al. 1990b) and as breeding adults in the southern Gulf of St. Lawrence (unpubl.). Thus the available data suggest that transfer between breeding grounds is low.

Mansfield and Beck (1977) calculated the annual rate of increase for Sable Island pup production from 1962 to 1976 to be 11.3 %. In some years, their annual estimate of pup production was based on a single aerial survey or short-duration field trip and thus required substantial extrapolation. They estimated cohort size in the early 1960's (Mansfield 1967) to be less than 300 pups. The pup production curve derived from our 1977-89 data predicted a 1962 cohort size of 379 pups. This suggests that Mansfield's estimate of the size of the 1960's breeding population on Sable Island was essentially correct, and that the population has been increasing exponentially since that time (see Zwanenburg and Bowen, 1990, for a detailed discussion).

There are a variety of historical references to annual winter seal hunts on Sable Island (St. John 1921; Patterson 1894; Gilpin 1874; Christie 1980). Although largely anecdotal, these references suggest extensive sealing on Sable in the 1600-1700's, being reduced to a yield of a few hundred seals annually by the late 1800's. Thus a relatively large population of grey seals may have once inhabited Sable Island. It is not known when sealing on Sable was terminated. But there is documentation that the human population on the Island was substantially above current levels well into the 1900's, due to the life saving and lighthouse maintenance operations. It wasn't until the 1950's that the lighthouses became automated. It is possible that the activities of the Island residents reduced the attractiveness of the Island as a pupping ground, or directly controlled pup production, thus explaining the small numbers of pups observed in the 1960's (Mansfield 1967).

The annual rate of increase of 12.6 % derived from data collected on Sable Island since the 1960's is, to our knowledge, the longest time series of information on population growth for grey seals. The rate is higher than the 3-8 % observed for European grey seals (Summers et al. 1975; Bonner and Hickling 1971; Summers 1978; Anon. 1985), and is among the highest recorded rate of increase for Phocids. Some colonies of northern elephant seals (*Mirounga angustirostris*) in California have experienced much higher rates of pup production during re-establishment after a period of near extinction. But *M. angustirostris* pup production on San Miguel, San Nicolas, and Ano Nuevo Islands, since the end of an initial establishment phase, has increased at nearly uniform exponential rates of 13.6, 16.5 and 15.8 %, respectively, over a 12-21 yr period (Cooper and Stewart 1983). The rate of increase for Sable Island grey seals is only slightly less than these. It is also slightly less than that observed for Otariids; Payne (1977) recorded a mean annual rate of increase of 16.8 % for the fur seal (*Arctocephalus gazella*) over a 14 yr period.

Mansfield (1967) observed that most Sable Island grey seal pups were born at the eastern end of the Island in a fairly confined area. During the 1977-89 period most of the pupping continued to occur at the eastern end. As the breeding population increased however, the smaller West End and the new #4 West (Table 6) colonies appear to have expanded at a higher rate. The expansion in the size of the pupping areas, the development of new breeding colonies, and the extensive areas of presently unutilized beach suggest crowding on the breeding grounds will not occur in the foreseeable future. This expansion, coupled with no apparent increase in pup mortality, despite an almost 5-fold increase in pup production, suggests that density dependent mortality on the pupping grounds due to crowding will not likely limit population growth on Sable Island.

Non-Sable Estimates

The bounty for grey seals, implemented in 1967, has provided samples of grey seals from most of the coastal areas of eastern Canada. However, Zwanenburg (1984) noted a number of problems associated with the recognition and reporting of tags by fishermen which would bias the returns from the bounty kill. Potentially the most serious problem was the non-reporting of tag loss and the extent to which individuals might preferentially return either tags or jaws. As a result, we used only data collected as part of directed scientific studies, for which the data collection techniques are clearly defined.

The estimates of total NSI pup production from Sable Island are the highest of all three sampling locations. The 1985 and 1986 estimates from Sable are at least 40 % higher than the 1984 estimate. This difference may be due to the larger sample sizes taken in 1985 and 1986, making the latter the more reliable of the estimates. The 1985 and 1986 estimates derived from Sable Island are more than double that obtained from the Anticosti samples. The sample taken on the Eastern Shore is intermediate between Sable and Anticosti, both geographically and in the pup production estimate.

Since the estimates of NSI production differ substantially depending on sampling location, the model assumptions are violated at some, or all, sampling locations. The Gulf tagging effort was not distributed over the entire pupping period, therefore tagged and untagged pups may not have become randomly mixed. A movement of ice out of the Gulf may have exported pups produced before mid-January to the Scotian Shelf prior to tagging operations. The relatively large ratio of untagged to tagged pups observed on Sable in March 1985 compared to 1984 and 1986 (Table 3), suggests uneven distribution at least in that year. The 1985 Eastern Shore samples may suffer from the same problem. A net export of early born pups would also inflate the number of tagged pups left in the Gulf, resulting in an under-representation of untagged pups on Anticosti Island. We cannot quantify the effects of these phenomena nor determine if they might persist for yearlings and 2 yr olds, but we suggest that pup production estimates derived from sampling on Sable Island may have overestimated, and those from Anticosti Island may have underestimated, NSI production due to their geographic positions relative to the release site. The reliability of any of these estimates cannot be substantiated, and although the true value could lie outside of these estimates, we believe that they cover the range of probable values. Adding this range for NSI pup production, to the recorded production of pups for Sable Island and the Eastern Shore, the range of grey seal production in the Northwest Atlantic between 1984 and 1986 was probably in the order of 9 000 to 20 000 pups.

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Population Trends of the Grey Seal (*Halichoerus grypus*) in Eastern Canada

K. C. T. Zwanenburg and W. D. Bowen

Department of Fisheries and Oceans, Marine Fish Division, Biological
Sciences Branch, Bedford Institute of Oceanography, Dartmouth,
N. S., Canada B2Y 4A2

ZWANENBURG, K. C. T., AND W. D. BOWEN. 1990. Population trends of the grey seal (*Halichoerus grypus*) in Eastern Canada, p. 185-197. *In* W. D. Bowen [ed.] Population biology of sealworm (*Pseudoterranova decipiens*) in relation to its intermediate and seal hosts. Can. Bull. Fish. Aquat. Sci. 222.

The trends in grey seal (*Halichoerus grypus*) numbers in Eastern Canada between the early 1960's and 1988 are reconstructed using estimates of pup production, vital rates from shot samples and published sources, and reported kills in a Leslie matrix model. Our analysis indicates different trends in pup production and hence in population trajectories for the Sable Island breeding component and other breeding areas, the largest of which is located in the southern Gulf of St. Lawrence. This difference is likely the result of an annual cull of grey seals that was carried out in the breeding colonies on Amet Island and on the ice in the southern Gulf between 1967 and 1983. Non-Sable pup production in 1966 must have been 3 to 4 times greater than previous estimates if current (1984-86) estimates of production from mark-recapture are reliable. Since the early 1960's, the Sable Island component has been increasing exponentially at 12.6 %/year, representing a more than 20 fold increase to 1988. The trend in non-Sable pup production is less certain but it is unlikely to have more than doubled up to the mid-1980's. With the cessation of the Gulf cull, both components are likely increasing exponentially, however, the overall rate of increase is unknown.

Les tendances démographiques du phoque gris (*Halichoerus grypus*) dans l'est du Canada, du début des années 60 à 1988, sont reconstituées d'après le nombre estimatif des naissances, le taux de mortalité à partir des spécimens abattus et des sources publiées, et le nombre de prises enregistrées, à l'aide d'un modèle matriciel de Leslie. L'analyse montre des tendances différentes dans les naissances et les effectifs reproducteurs de l'île de Sable et d'autres colonies de reproduction, dont la plus vaste se trouve dans le sud du golfe du Saint-Laurent. Cette différence résulte probablement de l'abattage sélectif annuel des phoques gris dans les colonies reproductrices de l'île Amet et sur la banquise dans le sud du golfe, entre 1967 et 1983. Des naissances en 1966 devraient être de 3 à 4 plus nombreuses que prévu dans les secteurs autres que l'île de Sable remettent en question la fiabilité des estimations de la production actuelles (1984-1986) établies d'après des expériences du marquage-recapture. Depuis le début des années 60, la population de l'île de Sable a augmenté à un rythme exponentiel de 12,6 % par année, soit une hausse supérieure de plus de vingt fois à celle de 1988. La tendance est moins nette dans les autres régions, mais les naissances n'ont sans doute guère dépassé le double de celles enregistrées au milieu des années 80. Après l'abolition du programme d'abattage sélectif dans le golfe, les deux populations ont probablement connu une croissance exponentielle; cependant, le taux d'accroissement global est inconnu.

The grey seal (*Halichoerus grypus*) inhabits temperate and sub-arctic waters on both sides of the North Atlantic (Mansfield and Beck 1977; Summers 1979; Davies 1957). It is a sexually dimorphic species which gathers in large concentrations during the breeding season and during the annual moult. Most pups are born at land-based rookeries, although ice breeding populations are found in the Gulf of St. Lawrence (Mansfield and Beck 1977) and in the Baltic Sea (Curry-Lindahl 1975). Grey seals have been reported in Canadian waters since at least the mid-1800s (Gilpin 1870, 1874), however, rough estimates of total pup production and population size were first made only in 1966 (Mansfield 1966). Since then efforts have been made to locate and estimate the size of all breeding colonies (Mansfield and Beck 1976). Despite numerous aerial surveys which have attempted to find other colonies (B. Beck, D. Clay, D. Sergeant unpublished data), we now know that Sable Island and the ice in the southern Gulf of St. Lawrence (including Amet Island) comprise the major breeding colonies in eastern Canada, accounting for over 90 % of the 12 000–13 000 pups born in 1984 (Zwanenburg et al. 1985).

Although not the only mammalian host (Rhode 1984), grey seals (*Halichoerus grypus*) are thought to be the most important definitive host of the sealworm (*Pseudoterranova decipiens*) because of the high numbers carried by individual seals (Stobo et al. 1990a; McClelland et al. 1983) and their wide geographic distribution (Mansfield and Beck 1976; Stobo et al. 1990b). The sealworm is one of the most important parasitic nematodes in Canadian Atlantic waters and indeed in the North Atlantic. The larvae of this species are found in the flesh of fish, many of which are of commercial importance, making fillets unsightly and unappealing to consumers. The presence of the larvae reduces the market value of fish products and their removal increases the cost of processing (Fisheries Council of Canada 1985; Malouf 1986).

The sealworm has a complex life-cycle which is indirect and entirely marine (McClelland et al. 1983). The grey seal enters the life cycle as the definitive host, i.e. the host where the parasite matures and reproduces. Sealworm ova are released in the stomach of the seal, are shed in the seal's faeces, and then sink to the ocean floor where they hatch. The post-hatch larvae are eaten by benthic invertebrates which are in turn eaten by fish. Infected fish are consumed by larger fish or by seals thus completing the life cycle. Thus it is clear that changes in the number of mammalian hosts, particularly grey seals, are of considerable interest in attempting to understand trends in the abundance of sealworm in the flesh of commercially harvested fishes.

Accurate censuses of the number of grey seal pups born on Sable Island since 1977 show an annual rate of increase of nearly 13 % (Stobo and Zwanenburg 1990). Unfortunately, a consistent time series of pup production estimates is not available for the other major colony. In this paper, we examine the evidence for trends in the abundance of grey seals in eastern Canadian waters over the last 25 yr. A knowledge of changes in grey seal numbers during this period is critical to understanding increases in the abundance of sealworm larvae in fish in eastern Canada during the last decade (McClelland et al. 1983, 1985, 1987).

Materials and Methods

Data Sources

Grey seal pup production estimates on Sable Island were derived from counts conducted during the whelping season. The length of the period of enumeration increased from a single day's observation in 1962 to periods which represent a significant proportion of the breeding season in the mid 1960's and through the mid 1970's (Mansfield and Beck 1977, A.W. Mansfield, Arctic Biological Station, St. Anne de Bellevue, Quebec, pers. comm.). Since 1977, as a result of a total cohort tagging program (Stobo and Zwanenburg 1990), a census has been conducted over the entire breeding season with the exception of 1981 where observations were restricted to 9 d. There are no annual estimates of pup production for the non-Sable Island (NSI) portion of the Northwest Atlantic grey seal population. Pertinent data in this case are restricted to a relatively coarse aerial survey estimate of pup production in 1966 in the order of 1 500 (Mansfield

1966; Mansfield and Beck 1977), and a range of mean estimates of between 6 000 and 11 000 for the period 1984-86, based on mark-recapture methods (Zwanenburg et al. 1985; Stobo and Zwanenburg 1990).

In addition to estimates of pup production, there is information on the numbers of seals killed in the annual cull conducted by Department of Fisheries and Oceans (DFO) personnel between 1967 and 1984 at breeding colonies in the Gulf of St. Lawrence (Table 1). For each year, the kill is broken down into total pup and adult removals. Since the present simulation model requires that the sex and age for all removals be known, total adult kills were apportioned between sexes based on the average ratio of males to females observed in all years for which these data were collected. Since all culls were conducted on the breeding grounds, and juvenile animals are rarely observed at whelping sites, we assumed that all non-pup kills in the cull were mature animals. In addition to the cull, DFO has also paid a bounty on grey seals since 1976. Since this bounty is paid for grey seals from all areas, only those kills which could be positively attributed to the NSI component of the population were included in the total NSI

TABLE 1. Summary of Departmental culls of grey seals along the east coast of Canada. The cull commeced in 1967 and was terminated in the Gulf of St. Lawrence after the 1983 breeding season; it was terminated on Bowen's Ledge and Camp and Basque Islands in 1984. Prepared in March, 1987, from annual trip reports of the Departmental cull teams.

	Bowen Ledge				Camp Island				Basque Island			
Year	Adult	F	M	Pups	Adult	F	M	Pups	Adult	F	M	Pups
1967										14	3	212
1968										2	16	134
1969									9	19	3	104
1970					100			350	25			100
1971					52			250	25			132
1972				18		20	10	261		15	7	129
1973					25			311	11			120
1974						35	5	348		8	3	134
1975						53	12	330		18	4	170 (12)
1976						47	7	325 (27)		20	6	103 (11)
1977						11	7	251 (15) (3)		4	12	92 (12)
1978		5	1	13		1 (45)	(20)	114		7	11	159 (4)
1979						18	9	139 (7)		12	6	111 (12)
1980	211[2]			115[2]								
1981						9	2	91 (12)		14	10	91 (3)
1982						22		136 (12)		18	2	108 (20)
1983						19	6	75 (12)		18	2	57 (8)
1984						12		50		22		30

	Amet Island				Gulf Ice				Dead-Mans	
Year	Adult	F	M	Pups	Adult	F	M	Pups	Pups	Totals
1967										229
1968										152
1969					74	73	12	485		779
1970				70						645
1971	45			361						865
1972						75	5	191		731
1973	4			67	35			60		633
1974		16	4	136		50	5	424		1168
1975		54	6	296		355	32	942		2284
1976		16		76 (3)						641
1977				31		177	131	642		1388
1978		10	15	232		20	12	35		704
1979									215	529
1980				186				485	135	1132
1981		19 (1)	14 (1)	81 (11)		234	91	923		1607
1982		36	16	128 (15)		502	122	637 (83)		1857
1983		5	4	267 (25)		485	124	1268		2375
1984										114

( ) = Indicates adults or pups found dead or removed live for scientific purposes.

[2] 115 pups and 211 adults (46 males and 165 females) culled in total for Basque and Camp islands and for Bowen Ledge. Data on number of pups and adults culled at each of these locations is unavailable.

removals (Table 2). This was done by including removals only from those cohorts for which the total Sable Island production had been tagged so that all Sable Island seals could be excluded from the bounty totals. This applies to the 1977-87 cohorts and ensures that the totals given on Table 2 are minimum NSI removals.

TABLE 2. Minimum non-Sable Island removals by both the DFO cull and bounty systems. All animals included in these removals were of non-Sable Island origin. See text for details of calculations.

Year	Females	Males	Juveniles (Males & Females)	Pups (Males & Females)
1967	14	3	—	212
1968	2	16	—	134
1969	157	33	—	589
1970	97	28	—	520
1971	95	27	—	743
1972	110	22	—	599
1973	58	17	—	558
1974	109	17	—	1042
1975	480	54	—	1750
1976	83	13	—	545
1977	192	150	—	1229
1978	88	59	58	882
1979	30	15	146	875
1980	165	46	164	1298
1981	279	118	182	1535
1982	591	140	149	1230
1983	546	136	168	1886
1984	41	0	35	128
1985	14	0	92	108

Population Reconstruction

I. *Sable Island*

In reconstructing the dynamics of the Sable Island population, we assumed that: (1) the Sable Island component is a closed population generating an intrinsic rate of increase of 12.6 % per annum, and (2) the population had a stable age distribution in the early 1960's. We reconstructed the historical dynamics of grey seals on Sable Island by modifying initial estimates of survivorship and age-specific pregnancy rates (Mansfield and Beck 1977) to define a transition matrix (Leslie 1945) which generated the observed annual rate of increase in pup production of 12.6 %. The transition matrix was of the form:

$$(1) \qquad M = \begin{bmatrix} f_0 & f_1 & f_2 & f_3 & \dots & f_{k-1} & f_k \\ S_0 & 0 & 0 & 0 & \dots & 0 & 0 \\ 0 & S_1 & 0 & 0 & \dots & 0 & 0 \\ 0 & 0 & S_2 & 0 & \dots & 0 & 0 \\ \cdot & \cdot & \cdot & \cdot & \dots & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \dots & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \dots & \cdot & \cdot \\ 0 & 0 & 0 & 0 & \dots & S_{k-1} & 0 \end{bmatrix}$$

where, f is the pregnancy rate at age, and S is the survival rate at age for ages 0 through k, where k is the maximum age in the population. Maximum age was assumed to be 34 yr. Even though older seals have been observed, the number of survivors at ages 34 and older is less than 1 % in the assumed stable age distribution, so that their contribution to pup production would be minimal. To determine the stable age distribution, the model was initiated with a starting population of 1 000 pups which were then allowed to grow according to the parameters of the transition matrix for 100 yr. A further 50 yr did not result in any changes in proportional age distributions within the population, indicating stability. The actual reconstruction of the population was initialized by using the Sable Island pup production model for the period 1977-87 to predict a value of pup production for 1961. This was then used to estimate total numbers present at each age in the population by:

$$(2) \qquad N_i = (N_0 \times P_0^{-1}) \times P_i$$

where N_i is the number of seals at age i, N_0 is the number of pups predicted by the pup production model, and P_0 and P_i are the proportions of pups and seals at age i estimated to be in the population according to the stable age distribution. The resulting values of N_i were cast as a column vector and used as starting inputs to the Leslie matrix model.

II. *Non-Sable Island*

As in the case of the Sable Island population, we made the simplifying assumption of a stable age distribution for the NSI population in the early 1960's prior to the inception of the DFO cull. The intrinsic rate of population growth for this component of the population is not known; however, a rate lower than that observed for the Sable Island component seems probable given both the nature of the whelping habitats (crowded islands and shifting ice) and the potentially unpredictable distribution of weaned pups in relation to suitable prey which might cause higher pup mortality. In the absence of data permitting estimation of a rate of increase it was assumed that the population was increasing at a rate of about 7 % per annum as has been observed for the British populations (Summers 1978). The actual rate used was 7.5 % due to somewhat higher estimates of fecundity (Mansfield and Beck 1977). The stable age distribution of this component of the population was determined in the same way as the Sable Island component, and was used to estimate numbers at age in the population for 1967. These population numbers were in turn used as input to a Leslie matrix model modified to permit the simulation of both age - and sex - specific annual hunts. The number of NSI seals killed between 1967 and 1985 are given in Table 2.

Results

Pup censuses on Sable Island for the period 1977-87 indicate an exponential increase in production of 12.6 % per year (Fig. 1 see also Stobo ans Zwanenburg 1990). To examine the reliability of earlier incomplete censuses in estimating pup production, we used the exponential model given in Fig. 1 to predict pup production on Sable Island for the period 1962-76. In Fig. 2 we see that censuses in this earlier period consistently fall below the predicted values. A plot of the standardized residuals of the model show a clear trend over the period 1962-76 (Fig. 3) which is consistent with our hypothesis that early pup censuses significantly underestimated total Sable Island production. This conclusion is supported by the observation that a model fit to the 1962-76 data implies a rate of increase in pup production of 19.5 % per annum which is inconsistent with reasonable estimates of grey seal vital rates (Mansfield and Beck 1977; Harwood

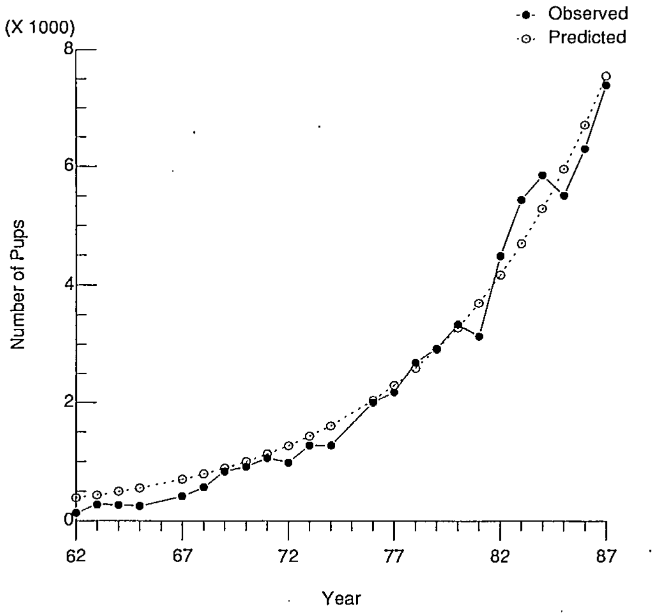

FIG. 1. Observed and predicted pup production for the Sable Island grey seal colony. Predicted values for all years were derived from complete annual census data collected between 1977 and 1987.

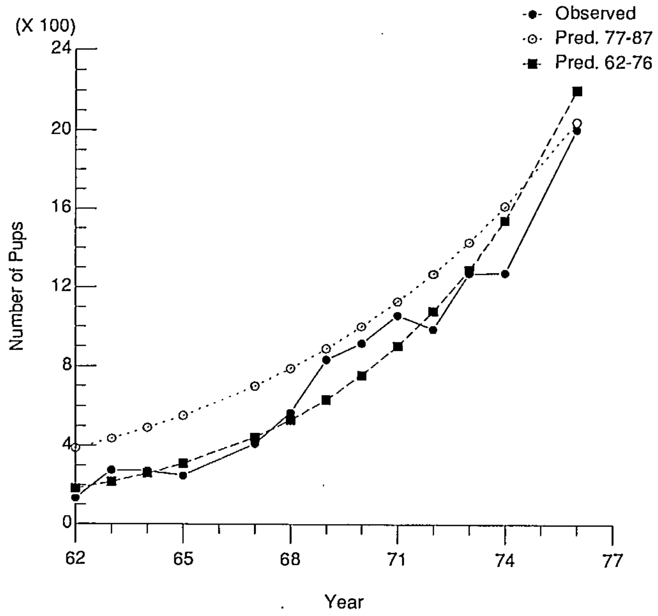

FIG. 2. Observed and predicted pup production for the Sable Island grey seal colony between 1962 and 1976. Predicted values shown are derived from the incomplete census data collected between 1962 and 1976, or from the complete censuses conducted since 1977.

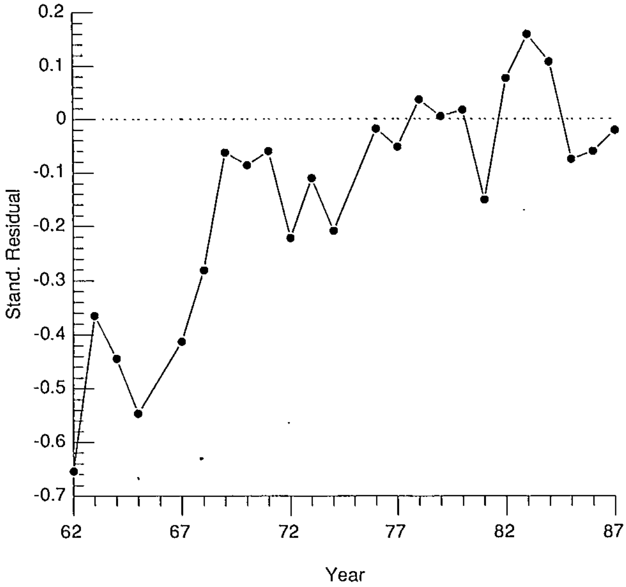

FIG. 3. Standardized residuals of the relationship between pup production and year as defined by the complete censuses of the Sable Island grey seal colony conducted since 1977. Residuals were calculated as (obs.-pred.)/pred.

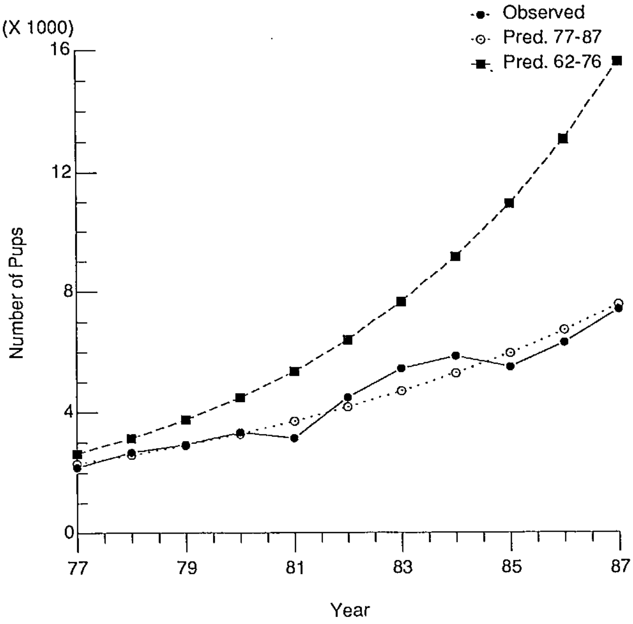

FIG. 4. Observed and predicted pup production for the Sable Island grey seal colony between 1977 and 1987. Predicted values shown are derived from the incomplete census data collected between 1962 and 1976, or from the complete censuses conducted since 1977.

and Prime 1978; Summers 1978), and predicts pup production estimates in recent years substantially larger than those observed (Fig. 4).

The parameters of the transition matrix resulting in a 12.6 % annual rate of increase in pup production were pregnancy rates (*f*) of 0.16, 0.71, and 0.91 at ages 4, 5 and 6+ respectively, a juvenile survival rate (S_0) rate of 0.787 and an adult survival ($S_{k\text{-}1}$) of 0.96. The stable age distribution for a population with these vital rates (Table 3) comprises 17.5 % pups. Given a predicted pup production value of 387 for 1962, this implies a total Sable Island population size of 2 213. At the rate of increase defined above this results in 7 554 pups produced in 1987, translating into a total 0+ population size of 43 173. The actual Sable Island pup production in observed 1987 was 7 391 animals implying a slightly lower total population size of approximately 42 242.

TABLE 3. Stable age distribution estimated for Sable Island and NSI components of the Northwest Atlantic grey seal populations using a Leslie matrix based growth model. Vital parameters and details of calculations are given in the text.

	Percent at Age	
Age	Sable Island	Non-Sable Island
0	17.50	18.14
1	12.23	11.13
2	10.42	9.63
3	8.88	8.33
4	7.57	7.20
5	6.46	6.23
6	5.50	5.39
7	4.69	4.66
8	4.00	4.03
9	3.41	3.49
10	2.91	3.02
11	2.48	2.61
12	2.11	2.26
13	1.80	1.95
14	1.53	1.69
15+	8.50	10.22

For the NSI population, the parameters of the transition matrix giving a rate of population increase of 7.5 % per annum were $f=$ 0.16, 0.71, and 0.85 at ages 4, 5 and 6+ respectively, $S_0 = 0.66$ and $S_{k\text{-}1} = 0.93$. In this case pups comprised 18.1 % of the total population (Table 3). Given 1 500 pups in 1966 (Mansfield 1966), the transition matrix defined above, and removing animals at the levels given on Table 2, the resulting NSI population trajectory is shown in Fig. 5. This simulation shows that pup production fluctuates between 1 500 and 2 000 animals from 1967 to 1980 and declines thereafter, reaching a low of just over 350 pups in 1985. This pattern is not consistent with the estimated pup production of between 6 000 and 11 000 derived from mark-recapture results or the actual numbers of pups tagged in each year between 1984 and 1986. To simulate the estimated numbers of pups produced over the period 1984-86 requires a 1966 pup production of 3 000-4 000. A pup production of 3 000 in 1966 would have required a total population of about 16 500. This results in a 1987 population of approximately 42 000, comprising 7 500 pups, consistent with the lower bound of the mark-recapture estimate (Fig 6). The higher estimate of pup production would have required a 1966 population of about 22 000 seals (4 000 pups) and produced a total 1987 population of 67 000 comprising about 12 000 pups (Fig. 6).

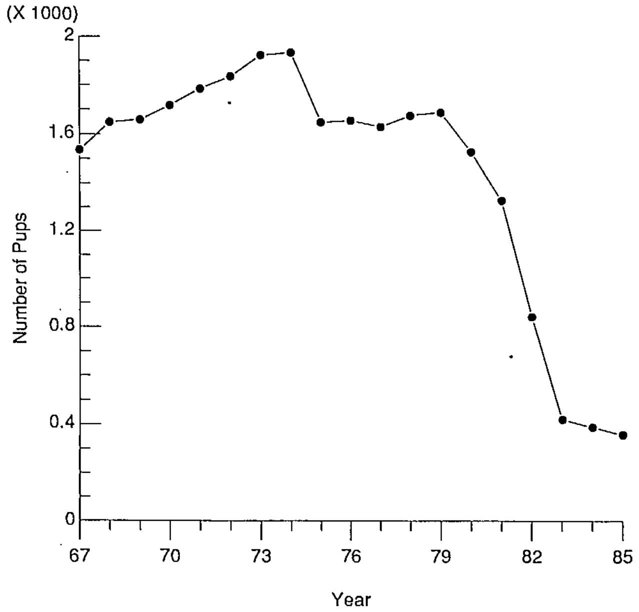

FIG. 5. Simulated annual estimates of NSI grey seal pup production obtained from a Leslie matrix based population growth model with vital parameters as given in the text, a 1966 pup production estimate of approximately 1 500, and incorporating hunting removals as listed on Table 2.

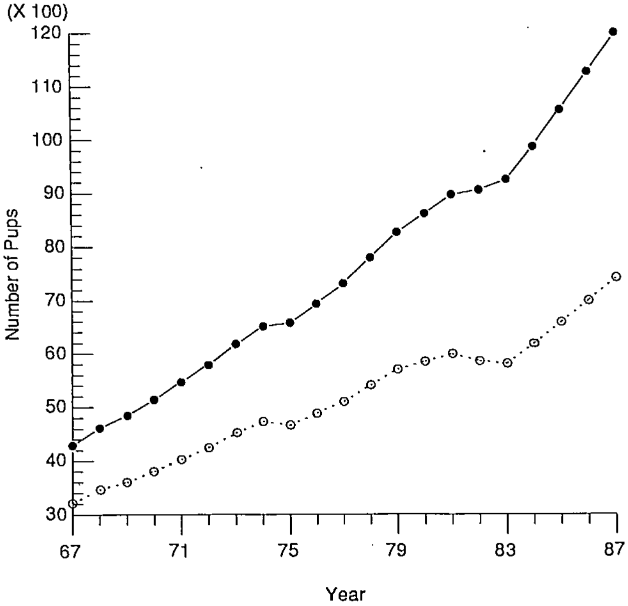

FIG. 6. Simulated annual estimates of NSI grey seal pup production obtained from a Leslie matrix based population growth model with vital parameters as given in the text, a 1966 pup production estimate of approximately 3 000 (open circle), or 4 000 (closed circle), and incorporating hunting removals as listed on Table 2.

Discussion

Our analysis indicates that estimates of pup production on Sable Island from 1962 to 1976 are negatively biased as had been suspected by Mansfield and Beck (1977). This finding is not unexpected given the relatively brief time over which these early counts were made. The pre-1977 pup counts could have been used to better estimate total pup production had we known both the shape of the birthing-ogive and the proportional distribution of pup age-classes during each of the early trips. Although Mansfield (1967) presents an estimate of the whelping-ogive for 1963, we have no information on the ages of pups observed in other years. In the absence of these data no suitable correction could be applied. Attempts to fit a model to the observations made during this earlier period (1962–76) results in an estimated rate of increase in pup production (19.5 % per annum) which is inconsistent with reasonable vital rates in that it implies an adult survival rate ($S_{k\text{-}1}$) of greater than 0.96. However, this rate of increase might be achieved with more reasonable vital rates if there were significant immigration of NSI breeding adults to Sable Island.

The only direct evidence of immigration to Sable Island comes from two sources: (1) pups tagged in the Gulf of St. Lawrence oberved on Sable Island later in the year, and (2) pups branded in the Gulf of St. Lawrence and subsequently observed on Sable Island as breeding adults. As shown in Stobo and Zwanenburg (1990) between April and September approximately 10–30 % of the pups oberved on Sable Island come from NSI colonies. From these observations, it seems clear that immigration to Sable Island may be common. However, of 360 pups branded in the Gulf of St. Lawrence in 1971 only two to four have been observed each year at the Sable Island breeding colony as adults since 1981. If the mortality schedule assumed for this population is reasonable it would imply a survival of approximately 123 of the tagged seals to 1981. Since only two to four have been seen as breeding adults it implies an immigration rate of less than 5 %. It is therefore more likely that the 19.5 % estimate of annual increase is spurious resulting from a combination of a real increase in annual pup production and an increase in counting efficiency. Using only the data from 1977 to 1987, the estimated rate of increase in pup production on Sable Island (12.6 % per annum) is still the highest reported for grey seals.

Data on emigration of Sable Island seals to the Gulf of St. Lawrence is equally sparse but clearly does occur at apparently low rates (W. T. Stobo and B. Beck, Bedford Institute of Oceanography, pers. comm.). A detailed analysis of brand re-sighting data on Sable Island may provide further insight on site fidelity patterns in adults. For the present, available data suggest that we can usefully think of the Northwest Atlantic grey seal population as being comprised of a Sable Island and a non-Sable Island component which over the past 25 yr have experienced different population trends as a result of different patterns of exploitation (cull and bounty) since 1967. Of recorded kills, the large majority have been taken from the NSI component. This is true of the bounty kills and especially so in the case of the culls on the breeding grounds (Table 1).

If mark-recapture estimates of NSI pup production between 1984 and 1986 of between 6 000 and 11 000 (Zwanenburg et al. 1985; Stobo and Zwanenburg 1990) are correct in identifying the range of recent production, then the number of pups born in 1966 should have been approximately 3 to 4 times that estimated by Mansfield (1966), given vital rates producing a 7.5 % annual increase and the minimum observed removals of NSI seals. Even assuming more optimistic, but unlikely, vital rates (i.e. those implied for the Sable Island colony) pup production in 1966 would need to have been near 2 000 for the population to have grown to a level consistent with present estimates. Our analysis therefore suggests that while pup production on Sable Island has increased more than twenty-fold since 1962, the NSI population may only have increased by two to five-fold since 1966.

Our conclusion about the trend in pup production and population size of NSI seals assumes that: (1) the initial population age structure can be adequately approximated by a stable age distribution, (2) this component of the population has vital rates which are constant in the absence of hunting and generate a 7.5 % annual rate of increase in population size, and (3) the mark-recapture estimates for the period 1984-86 are reliable. The first assumption is likely reasonable given that apart from incidental hunting there was no commercial hunt or bounty on grey seals for a number of years prior to 1966. This should have led to an condition of equilibrium and a stable age distribution. The specific stable age distribution estimated for the NSI component of the population is also dependent on the vital rates assumed to apply to the unexploited population. A different set of vital rates used as a transition matrix would have resulted in a different estimate of the proportions at age in the population. More serious is the lack of data which could be used to estimate the reliably of the vital rates used to project trends in population numbers over the period. However, we do know that pre-weaning pup mortality on small near-shore islands, such as Amet Island can reach 30 %, a level considerably higher than that recorded on Sable Island over the last 10 yr (Stobo and Zwanenburg 1990). It seems likely that pre-weaning mortality on the unstable floe ice in the southern Gulf of St. Lawrence, where most of the NSI pups are born, would also be higher than that observed on Sable Island. Since no estimate of pup mortality during the first year is available, we used the value calculated by Harwood and Prime (1978) for the Farne Island grey seal colony in the United Kingdom. Similarly, we felt it prudent to use the lower estimate of adult survival from the British study rather than the value used for Sable Island which may be somewhat inflated by immigration from the NSI component of the population.

The population trajectory of the NSI component is affected most by the uncertainty in adult survival rate, followed next by juvenile survivorship and finally by age-specific birth rate. This conclusion is based on the work by Eberhardt and Siniff (1977) and Harwood and Prime (1978) which concluded that the rate of population change is less sensitive to changes in fecundity and juvenile survival than to changes in adult survival.

Regarding the third assumption, the analysis by Stobo ans Zwanenburg (1990) suggests that the mark-recapture estimates should be viewed only as a rough approximation of NSI pup production. However, even with this level of uncertainty it is unlikely that between 1984 and 1986 NSI production was less than 5 000 pups.

Thus with the exception of trends in pup production on Sable Island, available data are insufficient to permit firm conclusions to be made about overall trends in the numbers of grey seals in eastern Canada. However, even given these limited data, some tentative conclusions can be usefully made. First, the Sable Island and NSI components of the grey seal population in eastern Canada have experienced quite different trends over the last 25 years. While pup production on Sable Island has increased 20 fold, production in NSI colonies has likely increased only 2-5 fold since 1966. Total population size in 1987 was likely in the range of 84 000 to 110 000 individuals, including 15 000 to 19 000 pups. Second, the number of pups born in NSI colonies in 1966 was likely 3-4 times that previously believed. And finally, the observed rate of increase in pup production on Sable Island is the highest reported for this species. In Great Britain, where more than half of the world population is found, the overall grey seal population has been increasing for some time, and at the time of the last survey in 1985 about 23 000 pups were born. Although some colonies have been relatively stable in numbers for the past 20 yr, others have increased by 3-8 % annually (NERC 1985).

Taken together these conclusions may help to explain the observed differences in the trends of sealworm larvae in cod and American plaice on the Scotian Shelf and the Gulf of St. Lawrence. The relatively higher infestation rates in the Gulf of St. Lawrence found by McClelland et al. (1983, 1985, 1987) may in part reflect the larger number of grey seals that have been present in this area historically.

Acknowledgments

We wish to thank Mr. Brian Beck for aging all of the bounty samples, his meticulous data collection habits, and especially his untiring efforts in running the Sable Island field camp. We also wish to thank Dr. W. T. Stobo for his work on the Sable Island census and marking programs, Dr. A. W. Mansfield for his kind permission to use his detailed records of observations collected on Sable Island in the early 1960's, and all other staff who have participated in the Sable Island field program over the years. Comments by an anonymous reviewer were greatly appreciated.

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Seasonal Movements of Grey Seals (*Halichoerus grypus*) in the Northwest Atlantic

Wayne T. Stobo, Brian Beck, and John K. Horne

Department of Fisheries and Oceans, Marine Fish Division,
Bedford Institute of Oceanography,
P.O. Box 1006, Dartmouth, N.S. Canada B2Y 4A2

STOBO, W. T., B. BECK, AND J. K. HORNE. 1990. Seasonal movements of grey seals (*Halichoerus grypus*) in the Northwest Atlantic, p. 199–213. *In* W. D. Bowen [ed.] Population biology of sealworm (*Pseudoterranova decipiens*) in relation to its intermediate and seal hosts. Can. Bull. Fish. Aquat. Sci. 222.

The geographic range and seasonal distribution of grey seals (*Halichoerus grypus*) were examined through the use of bounty and tag recoveries of the 1977–87 cohorts. The data included 2 736 bounty returns, 2 139 tag recoveries from the 1977–87 Sable Island cohorts, and 210 tag recoveries from the 1979, 1980, and 1982 Gulf of St. Lawrence cohorts. Comparison of the geographic distribution of bounty returns and tag recoveries indicate no differential movement between tagged and untagged seals. Sable Island seals appear to have a post-breeding pelagic phase (Jan.-Apr.) during which time they disperse, followed by a spring moulting phase (May-June), a summer movement northward (July- Sept.), and finally a return toward the Sable Island breeding area (Oct.-Dec.). The more restricted distribution of Gulf of St. Lawrence seals suggested by the data may be an artifact of resighting effort, with the exception of their virtual exclusion from the Gulf of Maine and Bay of Fundy. Although the breeding areas in the Gulf of St. Lawrence and Sable Island are spatially separated, extensive distributional overlap occurs throughout the year. Direct evidence of transfer of breeding adults between the two populations is presented, but the extent is unquantifiable at this time.

Nous avons examiné la dispersion géographique et la répartition saisonnière du phoque gris (*Halichoerus grypus*) à partir des résultats des captures avec primes et des récupérations d'individus marqués portant sur les cohortes 1977–1987. Les données concernaient 2 736 captures avec primes, 2 139 individus marqués des cohortes 1977–1987 de l'île de Sable, et 210 individus marqués des cohortes 1979, 1980 et 1982 du golfe du Saint-Laurent. La comparaison de la distribution géographique des captures avec primes et des individus marqués ne révèle aucune différence dans le déplacement selon que les phoques sont marqués ou non. Les phoques de l'île de Sable semblent présenter une phase pélagique post-reproduction (janv.-avril), pendant laquelle ils se dispersent, puis une phase de mue printanière (mai-juin), un déplacement estival vers le nord (juillet- sept.) puis un retour vers l'aire de reproduction de l'île de Sable (oct.-déc.). La répartition plus restreinte des phoques du Saint-Laurent que semblent indiquer les données peut être un artefact lié à l'effort de réobservation, à l'exception de leur exclusion virtuelle du golfe du Maine et de la baie de Fundy. Bien que les aires de reproduction de l'île de Sable et du golfe du Saint-Laurent soient géographiquement séparées, les aires de répartition se recouvrent nettement tout au long de l'année. Nous présentons des données montrant le transfert de géniteurs entre les populations, mais ce phénomène n'est pas quantifiable à l'heure actuelle.

Introduction

Historical accounts of the presence of grey seals (*Halichoerus grypus*) in the north western Atlantic have been published on numerous occasions (Gilpin 1870, 1874; Allen 1880; Saint-Cyr 1886; Millais 1904; Comeau 1909; Newsom 1937). To date, the most extensive work on their life history is that of Mansfield and Beck (1977). However, published information on the dispersal from breeding colonies, seasonal movement, and distribution is limited. The earliest marking studies were initiated in 1954 and 1955 in the southern Gulf of St. Lawrence when 218 pups were tagged at Amet Island (Fisher and Mackenzie, 1955). Between 1963 and 1974, a total of 1974 pups were tagged in the southern Gulf of St. Lawrence, on the Basque Islands and Sable Island. Hot-iron branding has also been used to study the movement of 433 and 2 805 grey seal pups branded in the southern Gulf of St. Lawrence and on Sable Island, respectively. The results of these studies indicate that pups disperse from the southern Gulf of St. Lawrence to the Scotian Shelf (including Sable Island), southern Newfoundland, throughout the Gulf of St. Lawrence, and along the Labrador coast. Pups marked on Sable Island exhibit a distribution similar to those marked in the southern Gulf, but also move as far south as Cape Cod and along the east coast of Newfoundland.

The purpose of this paper is to document the distributional range of northwest Atlantic grey seals, and to investigate the seasonal movements of young-of-the-year, juveniles and adults.

Methods and Analysis

Study Area

The study area extends from the coastal waters of southern Labrador to the Gulf of Maine (Fig. 1). The two primary grey seal colonies are located in the Gulf of St. Lawrence and on Sable Island. In the Gulf, breeding is concentrated in the area

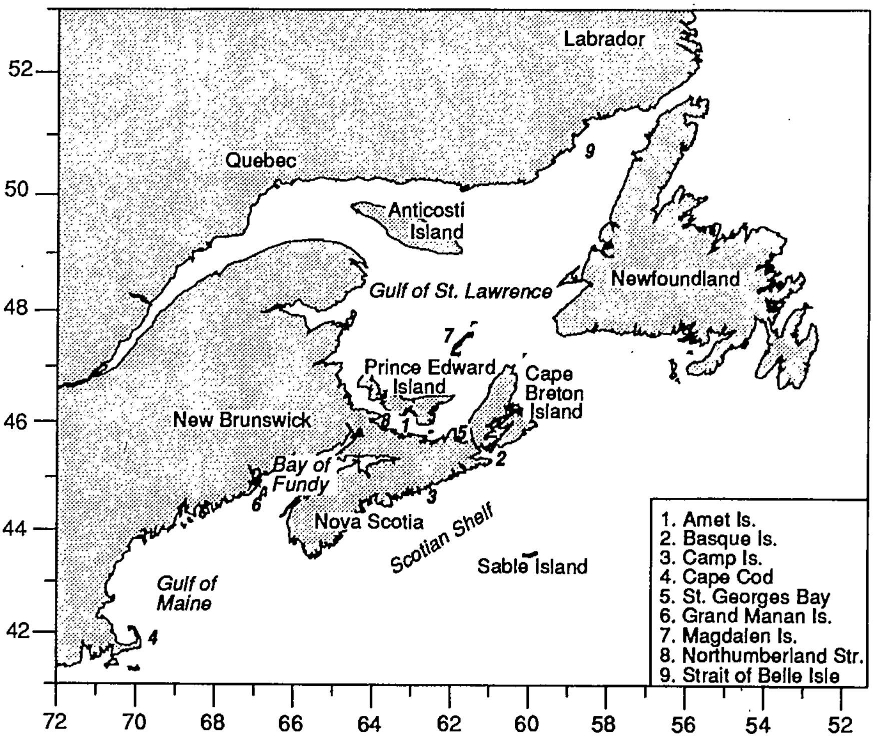

FIG. 1. Study area and place names referred to in the text.

between the eastern end of Prince Edward Island and Cape Breton Island, primarily on Amet Island and on the ice in St. Georges Bay. Breeding colonies also occur at Camp Island and the Basque Islands on the east coast of Nova Scotia. During the moulting period in May and throughout the summer, grey seals are also observed on Anticosti Island (Mansfield and Beck 1977). Sable Island is located approximately 140 km from the Nova Scotia mainland, close to the edge of the continental shelf. The island is a slender crescent shaped sand bar, 40 km long and approximately 1.5 km at its widest point. Grey seals use the broad sandy beaches of the western tip and eastern third of the island as pupping sites in winter. During the moulting season, up to 15 000 (Stobo and Beck unpubl. data) haul out, usually in dense aggregations on the eastern and western tips.

Methods

From 1977 to 1987, all grey seal pups born on Sable Island during the December to February pupping season were censused (see Stobo and Zwanenburg 1990). All live newly-weaned pups were tagged with uniquely numbered cattle ear tags (Jumbo Rototags, Dalton Supplies Ltd., Henley-on-Thames, Oxen, England) applied to the webbing of the hind flipper with tagging pliers. All tags were colour coded by year to simplify identification on recapture. As part of other studies, over 2 500 of these pups were also marked with hot-iron brands. Studies in the Gulf of St. Lawrence were conducted on a more limited scale during 1979, 1980, and 1982, and only tags were applied. The numbers of tags applied on Sable Island and in the Gulf of St. Lawrence are summarized in Table 1. In total, 44 665 seals were tagged on Sable Island and 1 273 in the Gulf. Since 1963 when the first tags were applied, a reward has been paid for the return of the tag with information on the date and location of capture, and cause of death.

TABLE 1. Number of tags applied to grey seal (*Halichoerus grypus*) pups by year.

Location	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	Total
Sable Island	1 968	2 268	2 712	3 250	2 843	4 140	4 738	5 189	4 857	5 800	6 900	44 665
Gulf of St. Lawrence	—	—	460	160	—	653	—	—	—	—	—	1 273

Coincident with the tagging program, a bounty was placed on grey seals in the Scotian Shelf area in 1977 and extended to include the Gulf of St. Lawrence and Newfoundland in 1978. The bounty was paid to commercial fisherman for returning the lower jaw of adult or juvenile seals with information on the location and date of capture and cause of death. Additional rewards for a tag or branding marks were also paid. The bounty program in the three regions has continued in this form through 1987. However, due to a lack of publicity, knowledge of the bounty program in Newfoundland did not become well known until 1985.

The age of individual animals was determined by counting annual layers in the cementum of the canine teeth (Hewer 1964). The age of tagged or branded seals was known by the tag number and colour combination of the male and female sides of the tag or the brand number, but was also verified through the examination of the teeth. If a seal jaw submitted for bounty was accompanied by a tag or brand, the animal was used in the bounty as well as the tag return data sets.

Tag and bounty recovery data can not be corrected for effort, as such data are not available. However, it is likely that effort was not spread eveny throughout the study area, nor throughout the year. Fishing seasons, sea ice coverage, and human population centers all exert an influence on the number of tags returned, as do the location and duration of the bounty hunt.

Analysis

There are two primary steps in the analysis. The bounty and tag recovery data are aggregated geographically by one degree squares and plotted to establish the distributional range and to highlight dense concentrations of recoveries. The Sable and Gulf tag recovery data have been aggregated into three age-groups (pups, juveniles, and adults) by season in distinct regions along the Scotian Shelf and in the Gulf of St. Lawrence. The boundaries of these regions are linked to readily identifiable geographic locations. The division between juvenile (ages 1,2,3) and adult seals is based on the onset of sexual maturity. Females are 100 % sexually mature and 70 % pregnant at age 4 (Mansfield and Beck 1977; Mansfield 1978). Males also mature at age 4 (Mansfield 1978), although they are not socially dominant until at least 8 yr of age (Mansfield 1978; Stobo and Beck personal observations). The division of seasons is associated with our perception of grey seal annual activities from personal observation on Sable Island and elsewhere, and preliminary analysis of the data. For Sable Island and the Scotian Shelf, four periods have been defined to represent post-breeding dispersal, moulting, northward dispersal, and return to the breeding areas: January-April, May-June, July-September, and October-December, respectively. Only two time periods, January-June and July-December, are used in the analysis of the Gulf of St. Lawrence data due to the limited number of tags applied.

Results

Total Recoveries

In this analysis, we have used the data from all tag and bounty recoveries of the 1977 to 1987 cohorts received to the end of 1987. Altogether 2 137 seals marked on Sable Island and 210 seals marked in the Gulf of St. Lawrence have been recovered. Tags and brands have been taken from seals that have drowned in various types of gear used in commercial fishing operations, and from seals shot for the bounty program; a few tags, lost from seals, have also been recovered from fishing nets. In the seasonal distributional maps, the total tag returns were reduced to 1 843 Sable and 179 Gulf returns because of insufficient information on the date of recovery. In the bounty program no restrictions are placed on the number of animals shot annually, but all grey seals are protected on the breeding grounds from January 1 to the end of February. The bounty data consisting, of 2 736 records of both tagged and untagged seals has been restricted to the 1977-87 cohorts to match the tag recovery data. The bounty kill, and the Sable Island and Gulf tag recoveries for each year are summarized in Table 2. The Sable Island and Gulf of St. Lawrence tag recoveries during the study period amounted to 4.8 and 16.5 %, respectively, of the total tags applied. Unusually large bounty hunts conducted in the Gulf during 1979 and 1980 accounted for the high number of bounty and Gulf tag returns during those years. As an example, 18 % of Gulf of St. Lawrence tags applied in 1979 were returned during the first year.

TABLE 2. Annual grey seal (Halichoerus grypus) bounty returns and Sable Island and Gulf of St. Lawrence tag recoveries for the 1977-87 cohorts.

Location	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	Total
Bounty	23	52	735	593	189	155	231	163	98	319	178	2 736
Sable Island	70	104	251	173	194	151	225	256	218	314	181	2 137
Gulf of St. Lawrence	—	—	84	44	11	39	19	4	4	2	3	210

Overall Distribution

The range and areas of concentration of bounty returns from the 1977–87 cohorts are shown in Fig. 2a. The bulk of the returns originate form the eastern half of the Nova Scotian mainland (an area known as the Eastern Shore) to Cape Breton Island. Offshore incidental captures were spread evenly over the Scotian Shelf with the exception of localized returns from the entrance to the Bay of Fundy. In the Gulf of St. Lawrence, large numbers of seals were taken at Anticosti Island, the Magdalen Islands, and in the eastern half of Northumberland Strait. Returns from Newfoundland were restricted to the southern Strait of Belle Isle and the southeastern coastal areas.

Recoveries of pups tagged in the Gulf of St. Lawrence (Fig. 2b), were concentrated around Anticosti Island, the Magdalen Islands, and the southeastern portion of the Gulf of St. Lawrence. The range of these recoveries appears restricted to the Gulf of St. Lawrence area with a few animals being recovered outside of the Gulf along the eastern shore of Nova Scotia. These data do not indicate an extension into the southern and outer portions of the Scotian Shelf or Gulf of Maine, except for a single return received from Grand Manan Island in the Bay of Fundy. However the distribution of pups produced in the Gulf may not be restricted to the Gulf of St. Lawrence since many unmarked pups have been observed at Sable Island. They cannot have been part of the Sable Island production since virtually all pups born there since 1977 have been tagged.

Recoveries of pups tagged at Sable Island (Fig. 2c) extensively overlap the patterns observed in both bounty returns and Gulf tag recoveries. The Sable returns are distributed throughout the entire region, with highest concentrations along the eastern shore of Nova Scotia, the southeastern shore of Newfoundland, and in the Anticosti Island area in the Gulf of St. Lawrence. Offshore recoveries are almost entirely accidental recoveries in fishing gear. The large number of tag recoveries from the coastal regions of Newfoundland and Labrador are attributed to a greater awareness of the reward program for tag recoveries, compared to awareness of the bounty program. In the Gulf of St. Lawrence, the larger number of Sable tag returns compared to Gulf tag returns, simply reflects the larger number of tags applied on Sable Island.

Seasonal Distribution of Tag Returns by Age-Group

Recoveries from the Sable Island and Gulf of St. Lawrence tagging programs indicate a shift in the seasonal distribution patterns for each age group in the two tagging areas. The percentage of pup (69 %), juvenile (25 %), and adult (5 %) tag recoveries are virtually identical for Sable Island and the Gulf of St. Lawrence. About 85 % of recoveries from each tagging site had sufficient data to be included in the seasonal distribution maps.

Sable Island Pups

On Sable Island, pups are born between December 23 (Boness and James 1979) and February 8. Pups are weaned after approximately 17 d. They begin to disperse after an additional 10 d fasting period during which the lanugo is moulted. During January to April (Fig. 3a) the majority of recoveries were made on the Scotian Shelf. The main tag recovery locations extend southwest from Sable Island along the Scotian Shelf to the Gulf of Maine. A second, smaller group of tags was received from southeastern Newfoundland.

During May and June, recoveries shifted north and east. Tag returns east of Halifax (the Eastern Shore) were more numerous than those along the southwestern coastal inshore area and fewer were recovered in the Gulf of Maine. Recoveries also increased in the Gulf of St. Lawrence and along the southeastern and east coasts of Newfoundland, although numbers were less than those from eastern Nova Scotia.

The inshore and northeastern dispersal continued during July through September. Large numbers of tags were returned from the Eastern Shore area. Substantial increases in

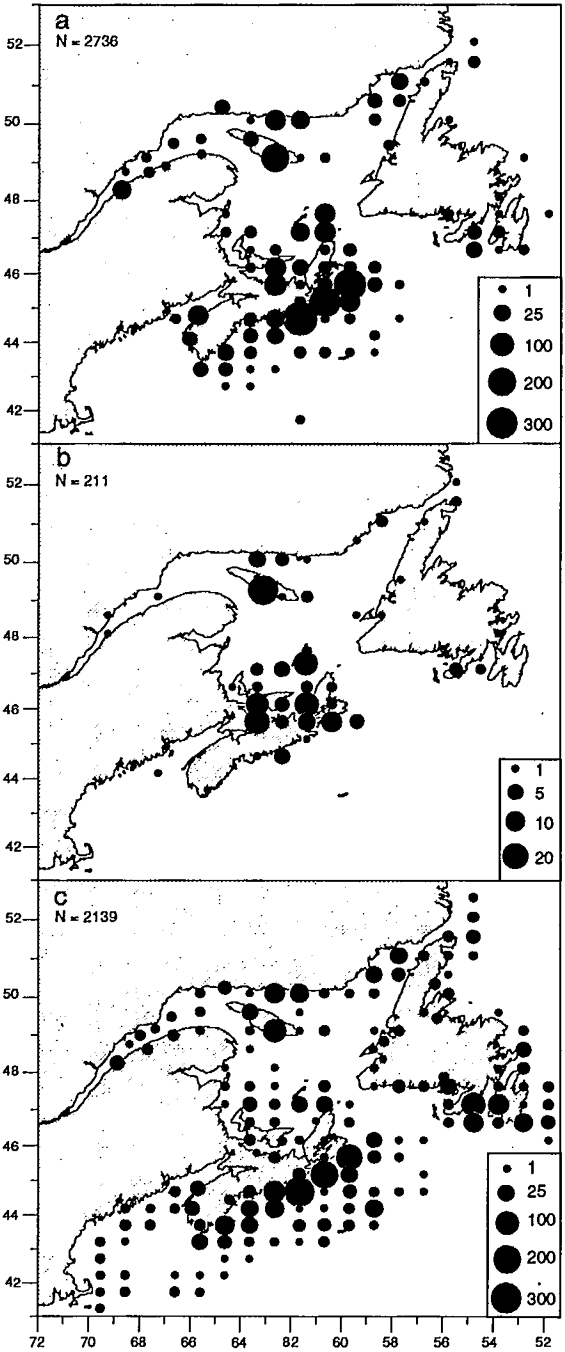

FIG. 2. Bounty kill returns of grey seals during 1977-87 (a), recoveries of Gulf of St. Lawrence tags (b), and of Sable Island tags (c) for the same period. *N* indicates the number of returns used in each figure.

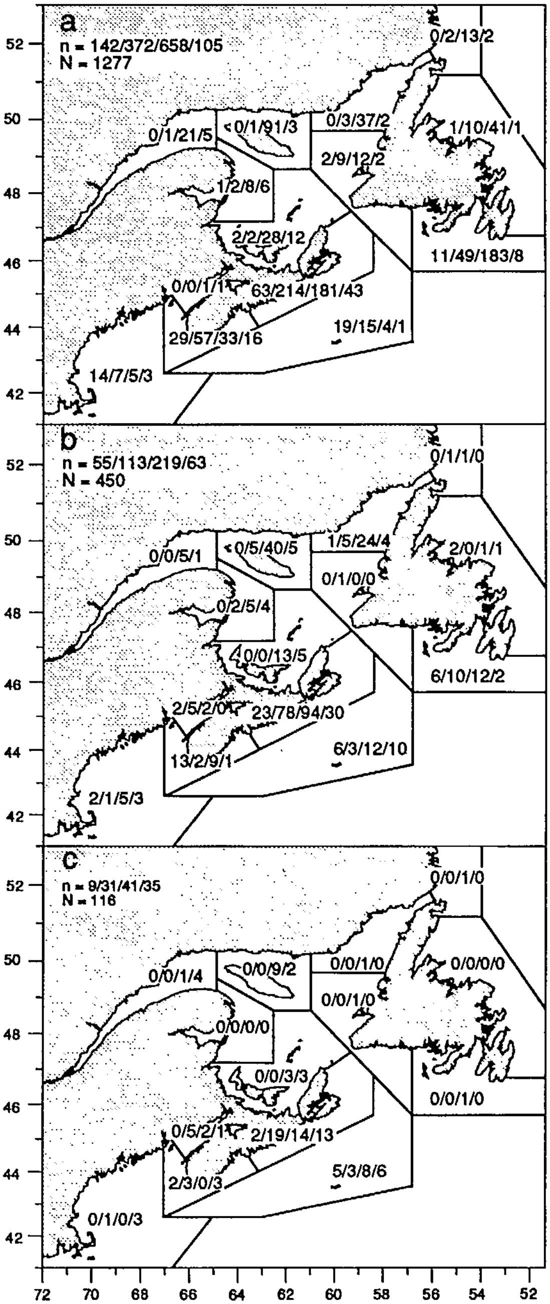

FIG. 3. Recoveries of grey seal pups (a), juveniles (b), and adults (c) marked on Sable Island 1977-87. Recoveries are presented sequentially (separated by slashes) by season: Jan.-Apr., May-June, July-Sept., Oct.-Dec. Seasonal totals (*n*) and overall totals (*N*) are provided.

recoveries were also observed throughout the Gulf of St. Lawrence, especially from the North Shore, and from the southeastern and east coasts of Newfoundland and the coast of Labrador.

During October to December, fewer recoveries were made than at any other period of the annual cycle. These were primarily from the southern half of the Gulf, and along the coasts of Cape Breton Island and the Eastern Shore.

Sable Island Juveniles

Recoveries of tagged juvenile grey seals from January to April (Fig. 3b) were concentrated along the coast of Nova Scotia, with a few from the Bay of Fundy. Juveniles were also taken relatively frequently on the Scotian Shelf and along the southeastern coast of Newfoundland. Fewer juvenile grey seals were recovered than expected from the overall tag and bounty returns (see Table 2). This suggests that juveniles spend more time offshore living pelagically, than either adults or pups. After the first year of life, the number of juvenile grey seals recovered from fishing gear is greatly reduced. This is probably a result of young seals gaining experience with different types of gear and increasing their strength, which allows older and stronger animals to escape more easily from gill nets and otter trawls.

During May and June a larger number of juvenile grey seals were taken inshore. The area with the largest number of recoveries remains the Eastern Shore, with reduced numbers from southwestern Nova Scotia and offshore on the Scotian Shelf. Recoveries of juveniles continued in the Bay of Fundy and Gulf of Maine areas, while returns increased in the northern Gulf of St. Lawrence and in coastal waters of southeastern Newfoundland.

From July through September the total number of juveniles recovered increased substantially over the previous two periods in most areas. Large numbers were recovered from the Eastern Shore and increases were observed along southwestern Nova Scotia and offshore on the Scotian Shelf. Recoveries in the Gulf of St. Lawrence increased dramatically in the northern areas, with concentrations around Anticosti Island and in the Strait of Belle Isle. Recoveries from the southern Gulf also increased substantially, an event that had not been previously observed.

Through October to December the number of recoveries in almost all areas declined, most dramatically in the Gulf of St. Lawrence. Substantial declines were observed along the coast of Nova Scotia while the number of recoveries from the offshore Scotian Shelf remained consistent.

Sable Island Adults

Since adults grey seals give birth and breed on Sable Island from late December until early February, their distributional range is necessarily constrained. During the January to April period (Fig. 3c), recoveries were restricted to the offshore Scotian Shelf and the two inshore regions of Nova Scotia. No tag returns were received from the Gulf of Maine, Bay of Fundy, the Gulf of St. Lawrence, or the coast of Newfoundland during this season.

May and June is the annual moulting period for adult grey seals. Large numbers of adult seals can be found on Sable Island and Anticosti Island, and smaller numbers at isolated haulout sites along the Atlantic coast. Recoveries during this period were again limited to the Scotian Shelf with larger numbers being received from the Eastern Shore.

During the July to September period, tagged adults were recovered from the offshore and eastern areas of Nova Scotia. Anticosti Island appeared to be the main area of concentration of adult seals in the Gulf, with small numbers of returns from other localities throughout the Gulf of St. Lawrence.

From October to December, the majority of adult tag recoveries shifted from the Gulf of St. Lawrence to the Scotian Shelf. Small numbers of tags were returned from Anticosti Island and the southern Gulf, but the Scotian Shelf was the primary return area.

Gulf of St. Lawrence Pups

The smaller number of tags applied in the Gulf of St. Lawrence during the study period precluded examining the distribution of this group using the four previously defined recovery seasons.

Between January and June (Fig. 4a), the majority of pup recoveries were made in the southern Gulf of St. Lawrence in the vicinity of Prince Edward Island, the Magdalen Islands, and the northwestern coast of Cape Breton Island. A smaller number of pups were recovered outside the Gulf along the Eastern Shore, extending up the eastern coast of Cape Breton Island.

During the July to December period the movement of pups appeared largely restricted to the Gulf of St. Lawrence. Recoveries remained high in the southern Gulf, and a substantial increase occurred at Anticosti Island. A smaller number of animals were taken along the Eastern Shore and along the southeastern coast of Newfoundland.

Gulf of St. Lawrence Juveniles

Recoveries of juveniles from January to June (Fig. 4b) from pups tagged in the Gulf of St. Lawrence were very limited. In the Gulf, seals were recovered from Anticosti Island, the Strait of Belle Isle, and in the southern Gulf between Prince Edward Island and the west coast of Cape Breton Island. The greatest number of tags was returned from the eastern coast of Nova Scotia.

From July to December the distribution of juvenile grey seal recoveries was not greatly altered. Numbers from Anticosti Island and the southern Gulf increased and some juveniles were returned from the coastal region of Labrador. The numbers recovered in eastern Nova Scotia remained constant, while single recoveries were made in southeastern Newfoundland and southwestern Nova Scotia.

Gulf of St. Lawrence Adults

Only four Gulf tags from adult grey seals were returned during the January to June period (Fig. 4c), one from Anticosti Island, two from the southern Gulf, and one from eastern Nova Scotia.

The July to December adult recoveries were equally limited. All tags received were from within the Gulf of St. Lawrence and were comparable in number to the January to June period.

Discussion

A number of caveats must be placed on the interpretation of seal distributions from bounty returns and tag information. First, the majority of tag and bounty recoveries are made by the same groups of fisherman, and the observed focal points of recovery usually coincide with the geographic area surrounding a fisherman's home port. Furthermore, the amount and type of fishing effort has varied over the years in response to fluctuating resource allocations, gear restrictions, and fishing area closures. Effort data are available for a number of finfish species, but seal captures in fishing gear are accidental occurrences and thus it would be extremely difficult to quantify this non-directed fluctuating effort. In addition, the majority of tags have been recovered from seals which were shot opportunistically from fishing vessels, making fishing effort irrelevant. A large proportion of these recoveries are either pups or sexually immature animals. Since the naïveté of young seals is well known, their predominance in the recoveries is not indicative of the proportion of these age-groups in the population. To further complicate attempts to quantify recovery information, the bounty program in Newfoundland was not promoted until the mid 1980's, which accounts for the low number of bounty returns compared to the tag recoveries in that area (see

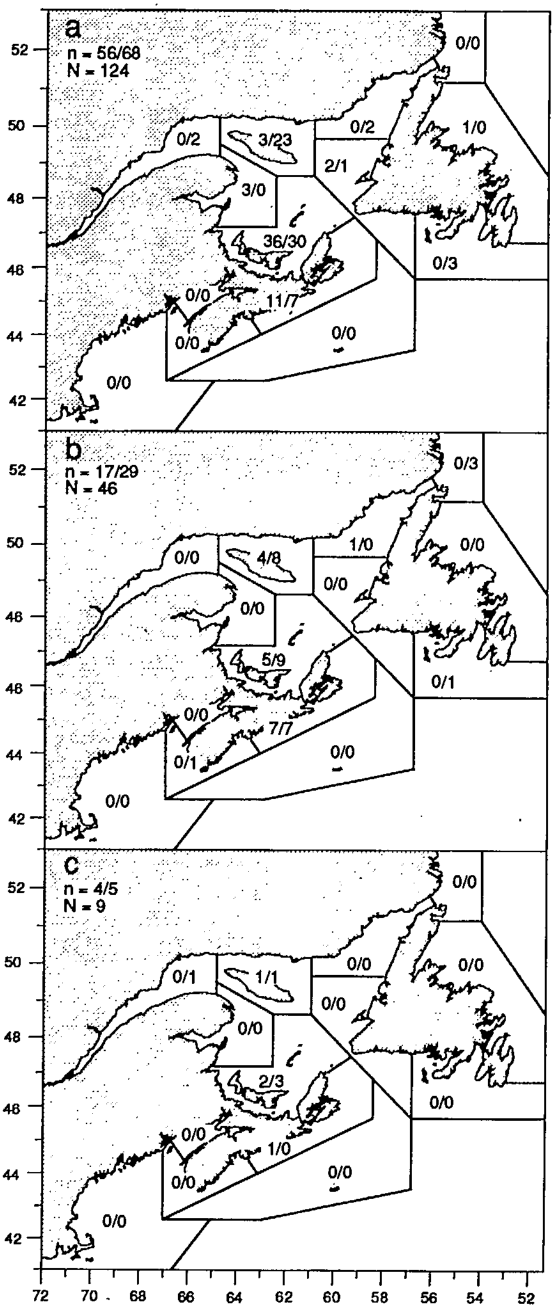

FIG. 4. Recoveries of grey seal pups (a), juveniles (b), and adults (c) marked in the Gulf of St. Lawrence 1977-87. Recoveries are presented sequentially (separated by slashes) by season: Jan.-June, July-Dec. Seasonal totals (*n*) and overall totals (*N*) are provided.

Fig. 2a and c). The lack of recoveries along the coast of the United States is probably a direct result of the *Marine Mammal Protection Act (1972)* which prohibits the killing of marine mammals.

Bounty effort in the Gulf of St. Lawrence, and around Newfoundland and Labrador, is also restricted by the annual formation and movement of sea ice. Ice first forms in the St. Lawrence River estuary and along the coastal areas of the western Gulf of St. Lawrence during the latter part of December. The ice spreads and drifts to the east and southeast through the action of prevailing winds and water currents. Sea ice expands seaward from the Gulf of St. Lawrence through Cabot Strait from the end of January until the end of April during a normal year. In the north, the Strait of Belle Isle is closed to marine traffic during winter and spring months because of sea ice. This restricts recovery effort but not necessarily movement of the seals. Along the east coast of Newfoundland, the Labrador Current carries icebergs and sea ice southward to the Grand Banks. The southward extension of this ice is dependent on the severity of the winter and prevailing wind direction. Sea ice reaches the southern tip of Newfoundland (approximate latitude 46°40' N) as early as the middle of January but this southern extension is considered normal in March. Retreat of sea ice begins in late March and by the end of April the southern edge of the ice has shifted north to the approximate latitude 49°15' N (Anon. 1985a, 1985b, 1986). Thus ice cover restricts the amount of hunting effort during winter and early spring, and more profitable fishing activity diverts effort from a directed grey seal bounty hunt as the year progresses.

In view of these sources of potential bias, it has not been possible to devise a suitable correction for hunting effort. Thus the data can only be used to indicate the presence of seals in a given area at the time of recovery.

General Movements

Using the overall distribution maps, seasonal distribution maps, and anecdotal observations, we have summarized the seasonal distribution patterns of grey seals in the Northwest Atlantic.

Comparison of the bounty returns with tag recoveries of the 1977-87 cohorts (Fig. 2a, b, c) illustrates the problems associated with using bounty data in isolation to describe movements of grey seals in this area. The bounty data also show that untagged animals of these cohorts match the range and areas of concentration of tagged animals. The primary purpose of comparing the two data sets was to determine if untagged animals had a different distribution than tagged animals. The comparison indicates a similar inshore and offshore geographic range in the Canadian zone of the Northwest Atlantic, as well as concentrations around Anticosti Island and along the eastern shore of Nova Scotia. Thus, there do not appear to be any areas with large concentrations of seals which might be missed by examining only the tag recovery data. The bounty data can not indicate dispersal into the Gulf of Maine due to the prohibition of killing marine mammals in the United States. Similarly, the lack of advertising of the bounty program in Newfoundland has resulted in little data being obtained from that area. The greater number of tag recoveries than bounty returns (Table 2) in some years and the more extensive recovery locations (see Fig. 1a, c) indicate that only the tag reward is being claimed for many tagged grey seals recaptured throughout the Northwest Atlantic.

From these data and a wide range of associated field operations we consider the January to April period to be a dispersal phase. Adult and juvenile grey seals arrive on Sable Island from late December to early February (Mansfield 1977; Mansfield and Beck 1977; Boness and James 1979; Stobo and Zwanenburg 1990). The earliest observed pupping date is December 23. Peak pupping occurs between January 12 to 15 and the latest birth is February 8. Pups on Sable Island are weaned in 2-3 wk (Mansfield 1977), after which the adults mate and leave the Island. Some pups depart with the adults, but the majority remain on Sable Island for a further 2-3 wk before departing. The breeding adults and the majority of the pups have left the Island by the end of the first week in February. Despite an increase in pup production of 12 % per year since 1977 (Stobo and Zwanenburg 1990), the duration of the breeding period has not changed. Juveniles and subdominant young adult males occupying the tips of the Island during the breeding period, probably use the adult and pup departures as visual clues to also leave the Island. All age-groups appear to remain largely pelagic during the post-breeding dispersal season. Tag recoveries indicate a substantial pup movement towards the southwest, while a smaller movement occurs to the south coast of Newfoundland. Juvenile and adult seals recovered for bounty or tag rewards at this time are primarily from the Scotian Shelf waters.

Most animals evidently remain offshore during this period. The most important indication of a pelagic life-style from January to April is the comparative lack of recoveries inshore despite an active fishery relative to the May and June period. Observations on Sable Island during March and April also support the idea of a pelagic life-style. During favourable weather conditions an estimated 2 000-6 000 seals of all ages haul out on the eastern and western ends of the Island, but during the more typical cold spells and gales at this time of year, relatively few animals are observed over the entire Island. These animals appear to be taking advantage of short spans of good weather and would be unlikely to travel any great distance to do so; thus the likelihood of seals staying in the offshore area, in the vicinity of Sable Island, is strong. The absence of juvenile or adult seals caught in offshore fishing gear does not preclude them from being in the area since animals older than one year appear to have sufficient experience and strength to avoid being caught in fishing gear.

May and June form the annual moulting period for juvenile and adult seals. Large numbers of these age groups haul out on Sable Island at this time. Pups do not moult during the first year, but large numbers of pups from Sable Island and the Gulf of St. Lawrence haul out on Sable Island (see Stobo and Zwanenburg 1990). Observations on Sable suggest that adult grey seals complete the moult in a relatively short period, probably a few weeks. Counts from photographs taken during an aerial survey of Sable Island in May 1983 indicate that at least 10 000 adults were in the area. However it has not been possible to estimate the total number of seals moulting on the island during the entire moulting period. At the conclusion of the moult most of the seals leave Sable Island and migrate inshore. Large numbers of pup tag returns are received from the Eastern Shore region of Nova Scotia and the southwestern coast of Cape Breton Island. At this time pups and juveniles begin to arrive in the Gulf of St. Lawrence and along the east coast of Newfoundland in increasing numbers.

July through September appears to be a time of northward and eastward dispersion. Large numbers of pups are still being taken along the Eastern Shore and the southeastern coastal areas of Newfoundland. All age groups, most notably pups and juveniles, have spread throughout the Gulf of St. Lawrence, Labrador, and the east coast of Newfoundland. However, the sustained recoveries of adults on the Scotian Shelf suggests that many remain in this offshore area for a prolonged period.

During the October to December period, grey seals appear to migrate offshore onto the Scotian Shelf. The decline in adult recoveries in all locations except coastal Nova Scotia and the Scotian Shelf suggests that the adults move southward from the Gulf of St. Lawrence onto the Scotian Shelf and then move towards Sable Island in anticipation of the approaching breeding season. Resightings of individually branded adults returning annually to Sable Island for the breeding season (Stobo and Beck unpubl. data) confirm this return movement by adults. Major declines in pup and juvenile recoveries in all areas also suggest an offshore southward movement, with a relatively greater magnitude of decline in the northern and eastern areas than in coastal Nova Scotia and on the Scotian Shelf. Since pups and juveniles are sexually immature, this southward movement is unlikely to result from a reproductive drive, but nevertheless the recovery data suggest that the movement does occur. Further, observations on Sable Island during the breeding season (Stobo and Beck unpubl. data) confirm the presence of tagged and branded yearlings among breeding aggregations, and among the groups of juveniles hauled out at the tips of the Island. The numbers of these yearlings and juveniles greatly exceeds those observed on Sable Island during the July-September period, thus confirming the southward movement of Sable Island progeny during the latter part of the year.

The limited data on Gulf of St. Lawrence tag recoveries indicate an annual distribution of Gulf seals restricted to the southern Gulf and Eastern Shore areas. Grey seal adults are known to pup and breed on the landfast ice surrounding Amet Island in late December, spreading more widely on the sea ice through January and into February (Mansfield and Beck 1977; Clay and Nielson 1985). Grey seals could be excluded from the northern and western Gulf during January and February due to ice, but since harp seals (*Phoca groenlandica*) move freely into this area to breed in February-March (Sergeant 1976), it is unlikely that the ice cover is heavy enough to impede grey seal movements. The tag returns indicate that only small numbers disperse into the northern Gulf during the first half of the year, but in the 1983 May-June moult period, approximately 2 000 moulting adults were counted during an aerial survey of Anticosti Island (Clay and Nielson 1985). Clay and Nielson (1985) found no other large concentrations of moulting juvenile or adults grey seals at any other locations in the Gulf of St. Lawrence.

Numerous incidental observations indicate that near the end of the grey seal breeding season, adults and pups either find open water or are carried on drift ice out of the Gulf of St. Lawrence. Under the influence of prevailing winds and the Laurentian Current they are carried onto the Scotian Shelf. Data collected in recent studies confirm this movement. From 1984 to 1986, between one and two thousand pups were tagged annually in the southern Gulf of St. Lawrence. During the March to June period in each of those years, between 972 and 1 463 pups hauled out on Sable Island were captured and examined for Gulf tags (see Stobo and Zwanenburg 1990). The results of this work indicate that substantial numbers of seals born in the Gulf can be found on Sable Island at this time. In the second half of the year tagging recoveries indicate wider dispersal, predominately by pups, throughout all regions but primarily into the northern Gulf of St. Lawrence. Additional observations conducted in September and October indicate dramatic reductions in the number of seals on Sable Island, thus supporting the suggestion of general movement off the Scotian Shelf, including Gulf seals.

In summary, the distribution of Gulf of St. Lawrence seals is largely restricted during January to April to the southern Gulf of St. Lawrence and the eastern Scotian Shelf by ice coverage and breeding activity. North and eastward dispersal probably occurs as the ice front retreats, while the southward dispersal is facilitated by movement of ice out of the Gulf. During the latter half of the year, their distribution is similar to that of Sable Island seals with the exception of their absence in southwestern Nova Scotia, the Bay of Fundy, and the Gulf of Maine.

Population Structure

Two primary breeding areas have been identified for Northwest Atlantic grey seals. Although these areas are spatially separated, there is direct evidence of transfer of animals between them and a mixing of the two groups over most of the range. Two samples of pups were marked with cohort brands in the Gulf of St. Lawrence in 1971 and 1972 (360 pups marked G1 and 124 pups marked G2, respectively) and larger numbers (2 867 pups) were branded on Sable Island between 1963 and 1974. Pups and juveniles originally tagged in the Gulf have been observed throughout the year on Sable Island, and small numbers of surviving adults from these Gulf cohorts have been observed breeding on Sable Island through the entire study period. Unfortunately the non-specificity of these cohort brands and the impossibility in efficiently and accurately reading the tag numbers on active adults, have prevented any quantitative data being obtained from these observations. Animals branded at Sable Island have also been observed breeding in the Gulf, but due to the lack of a sustained research effort in that area, the extent of this transfer is not known.

Sable Island seals, through brand or tag resightings have in fact, been observed as breeding adults at all known grey seal colonies in the Northwest Atlantic. These colonies include the Gulf of St. Lawrence, Grand Manan Island, Bowens Ledge, and the Nantucket Shoal area. The range of Sable Island seals does not appear to be restricted in any way in the Northwest Atlantic.

In conclusion, extensive overlap of the two groups occurs throughout the geographic range considered, except for the southern area. Adults are known to move between breeding colonies in the Northwest Atlantic, and although the extent is unquantifiable at this time, the limited data suggest that the exchange between breeding colonies is small. Our findings confirm observations that grey seal pups disperse widely from the breeding grounds and travel great distances in the Northwest Atlantic (Mansfield and Beck 1977). Similar behaviour has been reported in the northeast Atlantic (Boyd and Campbell 1971; Bonner 1972). Boyd and Campbell (1971) reported a 640 km journey by a grey seal pup from North Rona. The Northwest Atlantic grey seals may travel even greater distances. Mansfield and Beck (1977) reported a pup travelling 1 200 km from Sable Island to New Jersey and in our current study a Sable Island pup moved a distance of 1 500 km to Virginia.

Early studies of the Northwest Atlantic grey seal were largely confined to pups and suggested no set patterns of movement. Our analysis expands the dynamics of the distribution. We have found that all age groups disperse throughout the geographic range and live pelagically for extended periods when not at the breeding colonies. This dispersal is one of directed movement with a seasonal pattern. We hypothesize that a seasonal cycle is a general characteristic of all grey seal populations. Although the pattern can exhibit inter-annual variation, the breeding grounds remain the focus of the annual cycle for each population. The degree of dispersion from the breeding grounds is effected by the sexual maturity of the individual.

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Seasonal and Geographic Variation in the Diet of Grey Seals (*Halichoerus grypus*) in Eastern Canada

D. Benoit and W. D. Bowen[1]

Biology Department, Dalhousie University, Halifax, N.S., Canada B3H 4J1

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Between 1950 and 1987, 682 food-containing stomachs of grey seals were collected in Eastern Canada. The frequency of occurence of different species groups in grey seal diets differed among four broad geographic areas, with groundfish being most frequently observed in all areas except the Atlantic coast of Nova Scotia, where pelagic fishes occurred more frequently. In the Upper Gulf of St. Lawrence, capelin (*Mallotus villosus*), Atlantic cod (*Gadus morhua*), Atlantic herring (*Clupea harengus harengus*), lumpfish (*Cyclopterus lumpus*) and flatfishes (Pleuronectidae) accounted for 71.1 % of all food items, whereas in the Lower Gulf of St. Lawrence, skates (*Raja* spp.), flatfishes, herring, cod and rainbow smelt (*Osmerus mordax*) accounted for over 70 % of food items. Herring, Atlantic mackerel (*Scomber scombrus*), squid, cod and crabs comprised 67.6 % of food items along the Nova Scotia coast. At Sable Island, cod, haddock (*Melanogrammus aeglefinus*), silver hake (*Merluocious bilinearis*), and sand lance (*Ammodytes americanus*) accounted for the majority (63.6 %) of items identified from stomachs. Seasonal variation in the frequency of different food was evident for the Nova Scotia coast area, with spring feeding mainly on herring and mackerel being replaced by an increase in groundfish later in the year. Insufficient data exists in the other areas to examine seasonal variation.

Entre 1950 et 1987, 682 estomacs de phoques gris contenant de la nourriture ont été prélevés dans l'est du Canada. La fréquence d'apparition de différents groupes d'espèces dans le régime alimentaire du phoque différait selon quatre grandes régions géographiques, le poisson de fond étant l'espèce la plus fréquemment observée dans toutes les régions, sauf sur la côte Atlantique de la Nouvelle-Écosse, où les espèces pélagiques dominent. Dans le cours supérieur du golfe Saint-Laurent, le capelan (*Mallotus villosus*), la morue (*Gadus morhua*), le hareng (*Clupea harengus harengus*), la lompe (*Cyclopterus lumpus*) et les poissons plats (Pleuronectidés) représentaient 71.1 % de tous les aliments, tandis que dans le cours inférieur du golfe, les raies (*Raja* spp.), les poissons plats, le hareng, la morue et l'éperlan (*Osmesu mordax*) représentaient plus de 70 % des aliments. Le hareng, le maquereau (*Scomber scombus*), le calmar, la morue et les crabes constituaient 67.6 % des aliments le long de la côte de la Nouvelle-Écosse. À l'île Sable, la morue, l'aiglefin (*Melanogrammus aeglefinus*), le merlu argenté (*Merluocious bilinearis*) et le lançon d'Amérique (*Ammodytes americanus*) constifuaient la majorité (63.6 %) des aliments trouvés dans les estomacs. Des variations saisonnières dans la fréquence d'apparition des différents aliments étaient évidentes sur la côte de Nouvelle-Écosse, les aliments consommés au printemps étant constitués surtout de harengs et de maquereaux, la proportion de poissons de fond augmentant plus tard dans l'année. Les données pour les autres régions sont insuffisantes pour permettre d'établir des variations saisonnières.

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[1] Present address: Department of Fisheries and Oceans, Marine Fish Division, Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, N.S., Canada B2Y 4A2.
Reprint requests to W.D.B.

Introduction

Grey seals (*Halichoerus grypus*) are found in coastal and offshore waters on both sides of the North Atlantic including the Baltic Sea (Bonner 1985). In eastern Canada, grey seals give birth and mate from late December to February mainly on Sable Island and on the ice floes in the southern Gulf of St. Lawrence (Mansfield and Beck 1977). After the breeding season, the population disperses to both inshore and offshore feeding areas primarly on the Scotian Shelf, in the Gulf of St Lawrence, and off southern Newfoundland (Stobo et al. 1990a). In these feeding areas, grey seals may directly or indirectly interact with commercial fisheries in three ways: (a) by damaging fishing gear and disrupting fishing operations, (b) by competing with fishermen for fish or invertebrate resources, or (c) by serving as a definitive host of the sealworm parasite (*Pseudoterranova decipiens*).

The sealworm is one of the most important nematode parasites in the North Atlantic. Its larvae are found in the flesh of many species of commercially important fish, making the fillets unsightly and unappealling to consumers. The presence of the larvae reduces the market value of fish products and their removal increases the cost of processing (Fisheries Council of Canada 1985; Malouf 1986). Grey seals complete the life cycle of this parasite by feeding on fish that have been infected with sealworm larvae (McClelland et al. 1983a). Studies by McClelland et al. (1983 a, 1985, 1987, 1990) show that the prevalence and intensity of sealworm infestation varies considerably in different species of fish, in different populations of the same species, and as a function of host age. Given this variation, it is clear that information on seasonal and geographic variation in the species composition of grey seal diets is fundamental to understanding the population dynamics of the sealworm. However, relatively little has been written about the foods eaten by grey seals in eastern Canada (Fisher and Mackenzie 1955; Mansfield 1965; Mansfield and Beck 1977).

In this paper, we compile all available data on the composition of grey seal diets in eastern Canada to serve as input to a model synthesis of sealworm population dynamics (Mohn 1990) and to provide a basis upon which to plan future quantitative studies.

Materials and Methods

Sources of Data

Data from 1878 seal stomachs were available for study. Samples were collected from the St. Lawrence estuary to Grand Manan Island (Fig. 1), and include all previously published and unpublished information, plus new field collections. The new collections of 231 and 288 stomachs were taken during the summers of 1986 and 1987, respectively, at Anticosti Island in the Gulf of St. Lawrence. A reference number, the date and location of collection, and the sex and age of the seal were recorded for the Anticosti Island samples. A sample of 199 formalin-preserved stomachs from seals killed between 1968 and 1971 in the Gulf of St. Lawrence and along the shores of Nova Scotia was also analyzed.

In addition to these field collections, published and unpublished data were re-examined and, except for those of Fisher and Mackenzie (1955), the original raw data were used. The sources of data are as follows: (i) 248 seals from the coastal areas of the Maritimes, 1984-87. (G. McClelland unpubl. data); (ii) 223 seals from Sable Island, 1983-84 (B. Beck and W. T. Stobo unpubl. data); (iii) 60 seals from Anticosti Island, 1983 (D. Murie unpubl. data); (iv) 166 seals from Anticosti Island, 1982 (D. E. Sergeant unpubl. data); and (v) 463 seals from eastern Canada, 1969-71 (Mansfield and Beck 1977), which included data from 44 seals collected between 1950 and 1954 (Fisher and Mackenzie 1955). Date and location of collection were available for all of these samples.

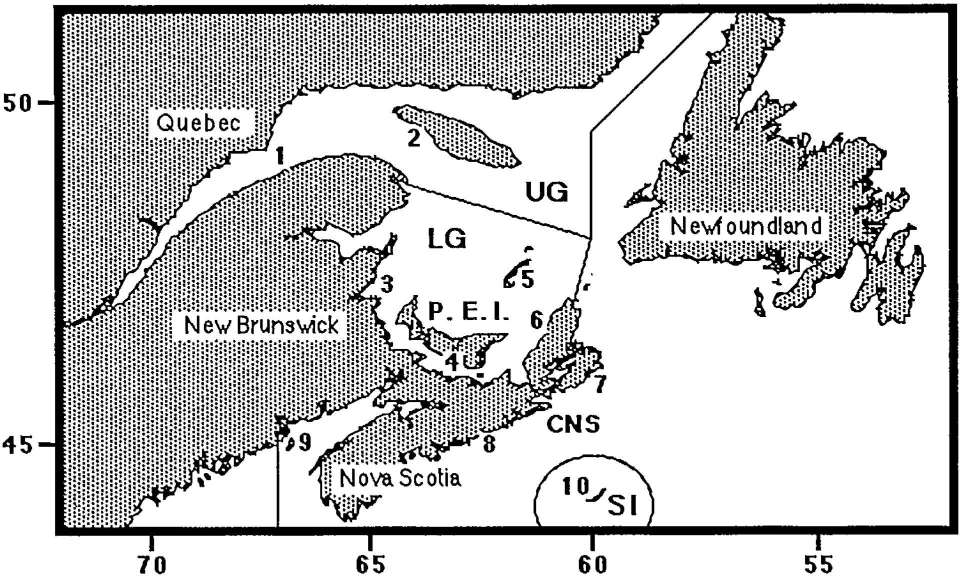

FIG. 1. Geographical subdivision of the feeding range of grey seals in eastern Canada (**UG**, Upper Gulf of St. Lawrence; **LG**, Lower Gulf of St. Lawrence; **CNS**, Coastal Nova Scotia; and **SI**, Sable Island). Collection sites; **1**, St. Lawrence estuary; **2**, Anticosti Island; **3** Miramichi Bay; **4**, Northumberland Strait; **5**, Magdalen Island; **6**, western Cape Breton Island; **7**, eastern Cape Breton Island; **8**, coastal Nova Scotia; **9**, Grand Manan Island; and **10**, Sable Island.

Stomach Content Analysis

In the laboratory, stomachs were opened longitudinally along the greater curvature. Contents were manually sorted into the following categories: fish, invertebrates, seaweed and substrate. A stomach was operationally defined as containing food when any remant of food, otoliths, invertebrate hard parts, or other bony material was recovered.

All undigested food items were identified from visual keys (Liem and Scott 1966) and measured (fish; standard length; Crustacea: carapace width). Hard parts and otoliths from stomach contents were recovered to reconstruct species composition of food eaten using the recovery technique developed by Murie and Lavigne (1985). Recovered material was preserved in 70 % ethanol. Otoliths were identified using Härkönen's (1986) key and reference material collected in eastern Canada (J. Hunt, St. Andrews Biological Station, St. Andrews, New Brunswick, pers. comm.)

Because the diet information obtained from published and unpublished sources is expressed only in terms of frequency of occurence, data from new collections are also expressed in this way. Frequency of occurence is the number of stomachs that contained at least one individual of the *ith* prey taxon expressed as a percentage of the total number of food-containing stomachs examined (e.g., George-Nascimento et al. 1985).

Analysis of Data

Prey species were classified into the following "species-groups" (NAFO 1985): groundfish, pelagic fish, other finfish, unidentified fish and invertebrate. To examine the diets of grey seals for evidence of geographical and seasonal variation, we statistically compared the frequency distributions of species-groups observed in stomachs using a χ^2 test ($P<0.05$) in a two-way table (SYSTAT statistical package, Wilkinson 1986). The feeding range of grey seals in eastern Canada was divided into four areas (Fig. 1) based on the location of collection sites: (1) Upper Gulf of St. Lawrence including the St. Lawrence estuary and Anticosti Island, (2) Lower Gulf of St. Lawrence including Miramichi Bay, the Northumberland Strait, the Magdalen Islands and western Cape Breton Island, (3) coastal Nova Scotia from eastern Cape Breton Island to the Grand Manon Island and (4) Sable Island. The annual cycle of the northwest Atlantic population was divided into the following three periods to examine seasonal variation within a geographical area: (1) breeding season (December 21-February 28), (2) dispersal and moulting season (March 1-June 30), and (3) feeding season (July 1-December 20).

Results

The prey items found in grey seal stomachs during the period 1950 to 1987 are summarized in Table 1. During the 38-yr period, only 682 (36.3 %) of the 1878 stomachs examined contained food. Of the 40 prey items found in these stomachs, the most frequent were Atlantic cod (*Gadus morhua*), Atlantic herring (*Clupea harengus harengus*) and capelin (*Mallotus villosus*) which together with the next seven most frequent items accounted for 78.8 % of prey items identified. Among the 1019 items, fish were the predominate prey. We consider algae to have been incidently ingested.

Geographical Variation

The frequency of occurence of different species-groups in grey seal diets differed ($\chi^2 = 126.388$, df = 12, $P<0.05$) among the four areas (Table 2). The 10 items occurring most frequently in the diet by area are illustrated in Fig. 2. In the Upper Gulf of St. Lawrence groundfish, pelagic and other finfish accounted for 35.9, 15.5 and 25.0 %, respectively, of species-group occurrences. Prey diversity was higher in the Upper Gulf region with 29 items identified (18 fishes; 8 invertebrates; 3 others). The top three items accounted for over 55.0 % of identifiable occurrences. Seal stomachs from the Lower Gulf of St Lawrence contained fewer items (10 fishes; 8 invertebrates; 2 others). Demersal fish species again predominated with 29.1 % of the occurrences. Grey seals collected from the coastal waters of Nova Scotia ate 24 items (16 fishes; 7 invertebrates; 1 other). Pelagic and demersal fish species occured in approximately 29.6 % and 22.9 % of the stomachs, respectively. Relatively more invertebrates (21.0 %) occurred in the diets of seals from the Atlantic coast region. This was due to a greater intake of squid (15.0 %). Also, more stomachs from the Atlantic coast region contained unidentified fish species because of the poorly preserved stomach contents, some kept for many years, and this might have produced and apparently greater invertebrate contribution to the diet. Most stomachs with unidentified fish remains came from a sample of seals collected between 1968 and 1971. On Sable Island only 47 stomachs (19.0 %) had food remains, within which 17 items (9 fishes; 6 invertebrates; 2 others) were found. Gadoids (39.3 %) appeared to be the dominant prey in that area, making up most of the demersal fishes (54.1 %). The algal material recovered from seals in some areas, consisted mostly of pieces of kelp (*Laminaria* spp.) or other small algal species, and would have contributed little to the diet.

In the Upper Gulf of St. Lawrence, the most frequent species were capelin, cod, herring, lumpfish (*Cyclopterus lumpus*) and flatfishes (Pleuronectidae) accounting for 71.7 % of all food items, excluding the unidentifield fish group. In the Lower Gulf of St. Lawrence, skate (*Raja* spp.), flatfishes, herring, cod, and rainbow smelt (*Osmerus mordax*) accounted for 70.7 %, whereas along coastal Noval Scotia herring, Atlantic mackerel (*Scomber scombus*), squid, cod and crabs comprised 67.6 % of the diet. At Sable Island cod, haddock (*Melanogrammus aeglefinus*), silver hake (*Merluccius bilinearis*), sand lance (*Ammodytes americanus*) and gastropod species accounted for 63.6 % of prey items identified from stomach contents (Table 2).

TABLE 1. Number of occurrences, frequency of occurrence and rank of different prey items found in grey seal stomachs in eastern Canada, 1950-87 (*n* = 1878; empty stomachs = 1196; food-containing stomachs = 682).

	Occurence		
	no.	%	Rank
Fish	830	(81.4)	
Cod, *Gadus morhua*	126	18.5	1
Herring, *Clupea harengus harengus*	125	18.3	2
Capelin, *Mallotus villosus*	117	17.2	3
Flatfishes, Pleuronectidae	65	9.5	4
Mackerel, *Scomber scombus*	55	8.1	5
Lumpfish, *Cyclopterus lumpus*	54	7.9	6
Skate, *Raja* spp.	31	4.5	9
Skate eggs	9	1.3	17.5
Hake, *Merlcuccius bilinearis*	24	3.5	12.5
Sand lance, *Ammodytes americanus*	11	1.6	15
Haddock, *Melanogrammus aeglefinus*	11	1.6	15
Ocean pout, *Macrozoarces americanus*	11	1.6	15
Gaspereau/shad., *Alosa* spp.	9	1.3	17.5
Smelt, *Osmerus mordax*	7	1.0	19
Salmon, *Salmo salar*	6	0.9	20.5
Salmon eggs	1	0.1	36.5
Wolffish, *Anarhichas lupus*	5	0.7	23
Sculpin, Cottidae	5	0.7	23
Pollock, *Pollachius virens*	4	0.6	25
Lamprey, *Petromyzon marinus*	2	0.3	29
Tomcod, *Microgadus tomcod*	2	0.3	29
Cunner, *Tautogolabrus adspersus*	2	0.3	29
Saury, *Scomberesox saurus*	2	0.3	29
Hagfish, *Myxine glutinosa*	1	0.1	36.5
Dogfish, *Squalus acanthas*	1	0.1	36.5
Cusk, *Brosme brosme*	1	0.1	36.5
Prickleback, Stichaeidae	1	0.1	36.5
Unidentified fish	142	20.8	—
Invertebrates	162	(16.0)	
Squid, Cephalopoda	51	7.5	7
Crab spp.	40	5.9	8
Shrimp spp.	27	4.0	10.5
Gastropoda	24	3.5	12.5
Clam, Pelecypoda	6	0.1	20.5
Polychaeta	5	0.7	23
Sipunculida	2	0.3	29
Euphausiacea	2	0.3	29
Lobster, *Homarus americanus*	2	0.3	29
Mussel, Pelecypoda	1	0.1	36.5
Sea urchin, Echinoidea	1	0.1	36.5
Sponge	1	0.1	36.5
Seaweed, algea	27	4.0	10.5
Substrata	20	1.1	—
Species-groups			
Groundfish	321	47.1	1
Pelagic	182	27.7	2
Other finfish	175	25.7	3
Invertebrate	162	23.8	4
Unidentified fish	142	20.8	—

TABLE 2. Number of occurrences and frequency of occurrence of different prey items found in grey seal stomachs by geographical region.

	Upper Gulf of St. Lawrence		Lower Gulf of St. Lawrence		Coastal Nova Scotia		Sable Island	
	no.	%	no.	%	no.	%	no.	%
Fish	422	(84.7)	124	(84.9)	211	(75.0)	48	(72.7)
Cod	72	22.8	12	13.5	29	13.6	10	21.3
Herring	59	18.7	19	21.5	42	19.7	1	2.1
Capelin	117	37.0	0	—	0	—	0	—
Flatfishes	28	8.9	24	27.0	4	1.9	3	6.4
Mackerel	16	5.1	1	1.1	37	17.4	1	2.1
Lumpfish	45	14.2	0	—	9	4.2	0	—
Skate spp.	2	0.6	27	30.3	0	—	2	4.2
Skate eggs	1	0.3	4	4.5	0	—	4	8.5
Hake	2	0.6	3	3.4	7	3.3	9	19.1
Sand lance	2	0.6	0	—	3	1.4	6	12.8
Haddock	3	0.9	0	—	3	1.4	5	10.6
Ocean pout	11	3.4	0	—	0	—	0	—
Gaspereau/shad	1	0.3	2	2.2	6	2.8	0	—
Smelt	0	—	5	5.6	2	0.9	0	—
Salmon	1	0.3	2	2.2	0	—	0	—
Salmon eggs	1	0.3	0	—	0	—	0	—
Wolffish	1	0.3	0	—	4	1.9	0	—
Sculpin	3	0.9	2	2.2	0	—	0	—
Pollock	3	0.9	0	—	1	0.5	0	—
Lamprey	0	—	0	—	2	0.9	0	—
Tomcod	2	0.6	0	—	0	—	0	—
Cunner	2	0.6	0	—	0	—	0	—
Saury	0	—	0	—	0	—	2	4.2
Hagfish	0	—	0	—	1	0.5	0	—
Cusk	0	—	0	—	1	0.5	0	—
Prickleback	0	—	0	—	1	0.5	0	—
Unidentified fish	50	15.8	23	25.8	59	27.7	5	10.6
Invertebrates	65	(13.1)	21	(14.1)	56	(19.9)	17	(25.8)
Squid	13	4.1	4	4.5	32	15.0	2	4.2
Crab spp.	21	6.6	7	7.9	10	4.7	2	4.2
Shrimp spp.	14	4.4	4	4.5	4	1.9	2	4.2
Gastropoda	12	3.8	0	—	5	2.3	7	14.9
Clam	1	0.3	2	2.2	1	0.5	2	4.2
Polychaeta	0	—	0	—	3	1.4	2	4.2
Sipunculida	0	—	2	2.2	0	—	0	—
Euphausiacea	2	0.6	0	—	0	—	0	—
Lobster	1	0.3	1	1.1	0	—	0	—
Mussel	0	—	1	1.1	0	—	0	—
Sea urchin	0	—	0	—	1	0.5	0	—
Sponge	1	0.3	0	—	0	—	0	—
Seaweed, algae	11	3.5	1	1.1	14	4.7	1	2.1
Species-groups								
Groundfish	174	35.9	41	29.1	61	22.9	33	54.1
Pelagic	75	15.5	20	14.2	79	29.6	4	6.6
Other finfish	121	25.0	36	25.5	12	4.5	2	3.3
Invertebrate	65	13.4	21	14.9	56	21.0	17	27.9
Unidentified fish	50	10.3	23	16.3	59	22.1	5	8.2
no. stomachs:	782		194		606		247	
empty stomachs:	466		105		393		200	
food-containing:	316		89		213		47	

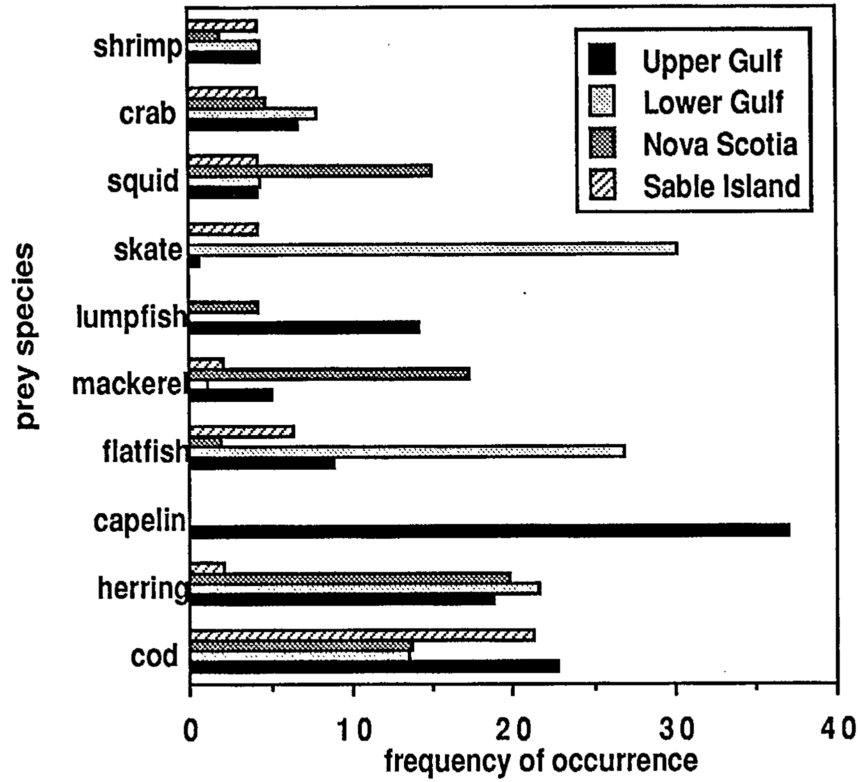

FIG. 2. Ten items occuring most frequently in the diet of grey seals in eastern Canada by geographical region.

Seasonal Variation

Sample sizes in the Upper and Lower Gulf of St. Lawrence regions were too small to permit statistical analysis of seasonal variation in diets. However, in the Upper Gulf of St. Lawrence, present data indicate that capelin occur most frequently in the diet early in the summer being replaced by cod later in August, with lumpfish as a consistent secondary prey. Based on limited number of food-containing stomachs, there appears to be a shift from groundfishes, such as flatfishes and skates, early in the spring to pelagic fish such as herring during the summer in the Lower Gulf region.

Based on 213 food-containing stomachs, there is clear evidence of seasonal changes in the species composition of the diet of grey seals collected in the Nova Scotia coast region (Table 3). None of the 17 seals killed during the breeding season had food or food remains in their stomach. However, during the dispersal/molt and feeding periods, the frequency of species-groups found in the diet differed significantly (χ^2 = 29.059, df = 4, $P<0.05$). This difference is largely caused by an increase in the frequency of cod and squid in the diet during the feeding period from July to December. Seasonal variation in the diet was not statistically significant at Sable Island (χ^2 = 9.711, df = 8, P = 0.286, Table 1.4), probably because only a few of the stomachs analyzed had any food remains. As expected, relatively little food was found in the stomachs of seals taken from the breeding season. Cod was important throughout the year with a highest occurrence in the dispersal/molt period. Sand lance tended to be important earlier in the year, but was replaced by haddock and hake in late summer.

TABLE 3. Number of occurrences and frequency of occurrence of different prey items found in grey seal stomachs in the Atlantic coast region by season.

	Breeding		Dispersal/molt		Feeding	
	no.	%	no.	%	no.	%
Fish	0		94	(82.5)	117	(70.1)
Lamprey	0	—	2	2.1	0	—
Hagfish	0	—	1	1.1	0	—
Gaspereau/shad	0	—	6	6.5	0	—
Herring	0	—	14	15.1	28	23.3
Smelt	0	—	0	—	2	1.7
Cusk	0	—	0	—	1	1.8
Cod	0	—	4	4.3	25	20.8
Haddock	0	—	0	—	3	2.5
Hake	0	—	4	4.3	3	2.5
Pollock	0	—	0	—	1	0.8
Sand lance	0	—	2	2.1	1	0.8
Mackerel	0	—	20	21.5	17	14.2
Wolffish	0	—	1	1.1	3	2.5
Prickleback	0	—	1	1.1	0	—
Lumpfish	0	—	6	6.5	3	2.5
Flatfish	0	—	1	1.1	3	2.5
Unid. fish	0	—	32	34.4	27	22.5
Invertebrates	0		10	(8.8)	46	(27.5)
Polychaeta	0	—	0	—	3	2.5
Shrimp	0	—	2	2.2	2	1.7
Crab	0	—	4	4.3	6	5.0
Clam	0	—	0	—	1	0.8
Urchin	0	—	0	—	1	0.8
Gastropoda	0	—	0	—	5	4.2
Squid	0	—	4	4.3	28	23.3
Seaweed, algae	0	—	10	10.8	4	3.3
Species-groups						
Groundfish	0	—	18	17.3	43	26.4
Pelagic	0	—	34	32.7	45	27.6
Other finfish	0	—	10	9.6	2	1.2
Invertebrate	0	—	10	9.6	46	28.2
Unidentified fish	0	—	32	30.8	27	16.6
no. stomachs:	17		312		277	
empty stomachs:	17		219		157	
food-containing:	0		93		120	

Discussion

Available data on the species composition of grey seal diets suffer in several respects. First, although frequency of occurrence has been used routinely to estimate diet composition in pinnipeds (Sergeant 1973; Mansfield and Beck 1977), it can only give us a rough indication of how these mammals satisfy their energy requirements. Second, analyzing geographic and seasonal variation in the diet is confounded by the lack of an appropriate sampling design which takes into account changes in the relative abundance of prey over time. As a result, it is difficult to determine to what extent the geographic and seasonal variation observed in this study reflects real differences in the diet of grey seals or is an artifact of the spotty nature of available data.

TABLE 4. Number of occurences and frequency of occurence of different prey items found in grey seal stomachs in the Sable Island region by season.

	Breeding		Dispersal/molt		Feeding	
	no.	%	no.	%	no.	%
Fish	5	(55.5)	20	(74.1)	23	(76.7)
Skate	1	16.7	1	5.0	0	—
Skate eggs	0	—	1	5.0	3	14.3
Herring	0	—	0	—	1	4.8
Cod	1	16.7	5	25.0	4	19.0
Haddock	0	—	2	10.0	3	14.3
Hake	0	—	3	15.0	6	28.6
Sand lance	1	16.7	3	15.0	2	9.5
Mackerel	1	16.7	0	—	0	—
Saury	0	—	0	—	2	9.5
Flatfish	0	—	2	10.0	1	4.8
Unid. fish	1	16.7	3	15.0	1	4.8
Invertebrates	4	(44.4)	7	(25.9)	6	(20.0)
Polychaeta	0	—	2	10.0	0	—
Shrimp	1	16.7	1	5.0	0	—
Crab	0	—	1	5.0	1	4.8
Clam	1	16.7	0	—	1	4.8
Gastropods	2	33.3	2	10.0	3	14.3
Squid	0	—	1	5.0	1	4.8
Seaweed, algae	0	—	0	—	1	4.8
Species-groups						
Groundfish	2	22.2	15	57.7	16	61.5
Pelagic	1	11.1	0	—	3	11.5
Other finfish	1	11.1	1	3.8	0	—
Invertebrate	4	44.4	7	26.9	6	23.1
Unidentified fish	1	11.1	3	11.5	1	3.8
no. stomachs:	57		95		95	
empty stomachs:	51		75		74	
food-containing:	6		20		21	

Diet Composition: Geographic Variation

Few studies of grey seals diets have been carried out in western Atlantic waters. Fisher and Mackenzie (1955) examined stomach contents of 44 grey seals (27 empty) from the Miramichi River estuary and from the east coast of Nova Scotia. Although a small number of seals were examined, seasonal and local variation in food habits was evident. Mansfield and Beck (1977) reviewed grey seal diets and concluded that herring (15.9 % of all items, which is equivalent to a frequency of occurence of 23.2 %), cod (11.6 % ≈ 16.9 %), flounder (9.9 % ≈ 14.5 %), skates (9.6 % ≈ 14.0 %), squid (5.6 % ≈ 8.2 %) and mackerel (5.0 ≈ 7.2 %) occurred most frequently. Their analysis suggested that grey seals rely primarily on skates and flounders for their year-round food, but take herring, cod, squid and mackerel as they become locally abundant seasonnally, perhaps as a result of migration onto banks or inshore. A high proportion of the seals in Mansfield and Beck's (1977) study were taken from the lower Gulf of St. Lawrence, coastal Nova Scotia and Sable Island. The large numbers of grey seals in the upper Gulf of St. Lawrence were underrepresented in their collection. The present study added 745 stomachs to their 37 from that region. These new data suggest that capelin and lumpfish are more frequently eaten than previously believed. The addition of summer samples taken in the upper Gulf of St. Lawrence coupled with new data throughout the range of the grey seal in eastern Canada modifies somewhat Mansfield and Beck's (1977) conclusions. Groundfishes such as skates, flatfishes, as well as lumpfish, are still occasionally taken, but the new results illustrate the importance of migratory species in the diet including capelin, taken when these are available in the Upper Gulf of St. Lawrence.

In the northwest Atlantic grey seals consume a mixed diet composed of fish and cephalopods, and some Crustacea. The number of species consumed by grey seals is considerable — 40 items were identified, of which 8 occured in between 5.0 % and 19.0 % of food-containing stomachs (Table 1). Five species of fish (cod, herring, capelin, flatfish and mackerel) contributed to over 55.0 % of the identifiable occurrences. Grey seal feeding has been more intensively studied in the northeast Atlantic (Rae 1968, 1973; SMRU 1984, 1985) and around Iceland (Hauksson 1984). A large proportion of the diet consists of demersal fish species in the order of 99.3 and 84.1 % in the United Kingdom (SMRU 1985) and Iceland (Hauksson 1984), respectively,. with pelagic fish accounting for only 0.6 and 5.7 %, respectively. The values from SMRU (1985) should be slightly lower because they did not include food items other than fish. The Canadian data indicated a higher proportion of pelagic species (27.7 % of food-containing stomachs) and a lower proportion of demersal species (47.1 %) than do the data for grey seals taken in European waters. These broad scale differences in the diet of grey undoubtedly reflect differences in the marine communities in these areas.

Seasonal Variation

To minimize the effect of geography, we analyzed seasonal variation of the diet within a geographical area. Because of small sample sizes and unequal number of stomachs collected between seasons, only two regions were examined statistically. Significant seasonal differences were found only from the coastal Nova Scotia area. During the breeding season feeding is greatly reduced (Boness and James 1979) and the stored energy reserves of both females and males are depleted. This depletion continues through the moult in late May (Mansfield and Beck 1977). With the inshore and on bank migration of fish of high energy density in late May and early June, seals appear to change from feeding on groundfish of relatively low energy to sand lance, herring and silver hake. This shift may be necessary to enable grey seals to replenish their energy reserves. With the off bank migrations of these energy-rich species in October, grey seals return to lower energy prey, such as cod and flafishes (B. Beck and W. T. Stobo, Marine Fish Division, Fisheries and Oceans Dept., Dartmouth, Nova Scotia, pers. commun.).

These seasonal shifts from low-energy to high-energy fish species not only result in energy grains for seals, but may also help explain variation in the level of infection of *P. decipiens* in seals. Sealworm infestation levels vary considerably with host length, season, year and geographical location (McClelland et al. 1983a, 1983b). By feeding on fishes such as herring, capelin and sand lance, which are not a part of *P. decipiens* life cycle, seals reduce the chance of being infected with immature stages of the parasite. During the summer seals feed intensively on herring and capelin, species which are not infected with *P. decipiens*. Thus the age composition and fecundity of *P. decipiens* in grey seals may change seasonally in response to seasonal variation in seal diets (see Stobo et al. 1990a).

Grey seal feeding has been poorly studied in the northwest Atlantic and the new information in this paper illustrates the need of long term diet studies. Also the use of qualitative data limits the conclusion that can be drawn with respect to fisheries-seal interactions. Benoit and Bowen (1990) present quantitative data on the summer diet of grey seals from the Upper Gulf of St. Lawrence. Future studies of geographic and seasonal variation in the diet of grey seals will benifit from more systematic sampling at selected locations throughout the year.

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Summer Diet of Grey Seals (*Halichoerus grypus*) at Anticosti Island, Gulf of St. Lawrence, Canada

D. Benoit and W. D. Bowen[1]

Biology Department, Dalhousie University, Halifax, N.S., Canada B3H 4J1

BENOIT, D., AND W. D. BOWEN. 1990. Summer diet of grey seals (*Halichoerus grypus*) at Anticosti Island, Gulf of St. Lawrence, Canada, P. 227-242. *In* W. D. Bowen [ed.] Population biology of sealworm (*Pseudoterranova decipiens*) in relation to its intermediate and seal hosts. Can. Bull. Fish. Aquat. Sci. 222.

During the summers of 1982, 1983, 1986 and 1987, 295 food-containing stomachs were collected from Anticosti Island in the Gulf of St. Lawrence to determine the diet of grey seals. There was significant inter-annual variation in the species composition of the summer diet. There was an inverse relationship between the occurrence of capelin (*Mallotus villosus*) and Atlantic herring (*Clupea harengus harengus*) in the diet. Lumpfish (*Cyclopterus lumpus*) was frequently found in 1982 through 1986 but was not recorded in 1987. In 1986 and 1987 fish eaten by grey seals ranged from 6.7 cm to 79.7 cm, with a mean length of about 18 cm. Approximately 88 % of prey were <30 cm in length. The mean length of prey (about 25-30 cm) eaten by grey seals was similar for cod, American plaice, herring, lumpfish and Atlantic mackerel (*Scomber scombrus*) despite differences in the size range of these species. Although it occurred less frequently than capelin, cod accounted for 41.5 % of the weight of food eaten, while capelin accounted for only 6.6 %. Between them, lumpfish and ocean pout (*Macrozoarces americanus*) accounted for 30.7 % of the weight of fish eaten. During the summer, grey seals on Anticosti Island fed mainly on young, schooling or aggregated fish species.

Au cours des étés de 1982, 1983, 1986 et 1987, 295 estomacs de phoques gris contenant de la nourriture ont été prélevés dans l'île d'Anticosti dans le golfe du Saint-Laurent afin de déterminer le régime alimentaire du phoque. On a observé d'importantes variations interannuelles dans la composition des espèces du régime alimentaire estival. On a noté un rapport inverse entre la présence de capelans (*Mallotus villosus*) et de harengs (*Clupea harengus harengus*) dans le régime. La présence de lompes (*Cyclopterus lumpus*) a été relevée fréquemment de 1982 à 1986, mais non en 1987. En 1986 et en 1987, les poissons mangés par les phoques gris variaient en taille de 6.7 cm à 79.7 cm, la longueur moyenne s'élevant à environ 18 cm. Environ 88 % des proies avaient moins de 30 cm de longueur. La longueur moyenne des proies (environ 25-30 cm) mangées par les phoques gris était semblable pour la morue, la plie d'Amérique, le hareng, la lompe et le maquereau (*Scomber scombrus*) malgré les différences dans la gamme de taille de ces espèces. Bien qu'elle apparaît moins souvent que le capelan, la morue constitue 41.5 % du poids des aliments mangés, le capelan blanc ne représentant que 6.6 %. Entre les deux, la lompe et la loquette d'Amérique (*Macrozoarces americanus*) représentaient 30.7 % du poids de poissons consommés. En été, les phoques gris de l'île d'Anticosti se nourrissent surtout de jeunes poissons d'espèces en banc ou agrégées.

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[1] Present address: Department of Fisheries and Oceans, Marine Fish Division, Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, N.S., Canada B2Y 4A2.
Reprint requests to W.D.B.

Introduction

A knowledge of the diet of grey seals (*Halichoerus grypus*) is critical to understand the dynamics of the sealworm parasite (*Pseudoterranova decipiens*) and competitive interactions between seals and man for commercially important fish species. The sealworm is one of the most important nematode parasites in the North Atlantic. Its larvae are found in the flesh of many species of commercially important fish, making the fillets unsightly and unappealling to consumers. Grey seals complete the life cycle of this parasite by feeding on fish that have been infected with sealworm larvae (McClelland et al. 1983a).

Although some quantitative studies of grey seal diets have been conducted in the United Kingdom (Rae 1968, 1973; SMRU 1984, 1985, Hammond and Prime 1990) and in Icelandic waters (Hauksson 1984), our knowledge of the feeding habits of the grey seal in the northwest Atlantic is based for the most part on qualitative analyses of stomach contents (Fisher and Mackenzie 1955; Mansfield 1965; Mansfield and Beck 1977; Benoit and Bowen 1990). These, along with additional feeding data from unpublished sources and from personal collections of animals from the St. Lawrence estuary, suggest that grey seals feed mainly on species such as capelin (*Mallotus villosus*), Atlantic cod (*Gadus mohua*) and Atlantic herring (*Clupea harengus harengus*). However, the size of prey eaten by seals and the contribution of different prey species to the total energy demand of the population at any one time are unknown. Since the abundance of *P. decipiens* in fish is size and species-specific (McClelland et al. 1983a), estimating the size of the prey consumed also provides information on parasite transmission from fish to seals.

In eastern Canada, grey seals give birth and mate from late December to February mainly on Sable Island and on the ice floes in the southern Gulf of St. Lawrence (Mansfield and Beck 1977). After the breeding season, the population disperses to both inshore and offshore feeding areas primarily on the Scotian Shelf, in the Gulf of St. Lawrence, and off southern Newfoundland (Stobo et al. 1990). A substantial number of seals of all ages congregate around Anticosti Island during the summer feeding period (D. Benoit, pers. observ.)

To date quantitative estimates of food consumption by eastern Canadian grey seals have been based on the frequency of occurrence of food items in seal stomachs. Here we report the food contents of 744 grey seal stomachs collected during summer months on Anticosti Island in the Gulf of St. Lawrence. The primary objectives of this study were to obtain quantitative information on the number and weight of different prey species consumed by grey seals and to determine the relative importance of different prey in meeting the energy requirements of grey seals in this primary summer feeding area.

Methods

The stomachs from 744 grey seals were collected by several researchers (Table 1) from Anticosti Island in the Gulf of St. Lawrence (Fig. 1). In the field, the stomach was ligated at the esophageal and pyrolic ends, then removed and preserved in formalin for approximately five months prior to analysis. An idendification number was given to each stomach, and the date and location of collection and sex were recorded. The following standard morphometric data were also obtained for 275 males and 407 females: standard length, axillary girth, xiphisternal blubber depth, front and hind limb length (American Society of Mammalogists 1967). In addition, the core mass (i.e. carcass with pelt and blubber removed) of 38 seals was taken in the summer of 1987. The age of all seals was determined by counting growth layers in the cementum of longitudinal sections of canine teeth (D. E. Sergeant and W. Hoek, Fisheries and Oceans, Canada).

TABLE 1. Sources of grey seal stomach contents collected from Anticosti Island, Gulf of St. Lawrence, Quebec between 1982 and 1987.

Date of collection	No. of stomachs with food	empty	total	Data type[a]	Collector[b]
July 11-Aug. 20, 1982	75	91	166	QL	1
July 14-Aug. 16, 1983	23	37	60	QL	2
June 14-Aug. 17, 1986	13	10	23	QL	3
July 04-Aug. 20, 1986	87	120	207	QL; QN	1
July 23-Aug. 20, 1987	97	191	288	QL; QN	4

[a] QL = Qualitative data; QN = Quantitative data

[b] (1) D. E. Sergeant (Fisheries and Oceans); (2) D. J. Murie (University of Victoria); (3) D. Benoit (Dalhousie University); (4) T. G. Smith (Fisheries and Oceans).

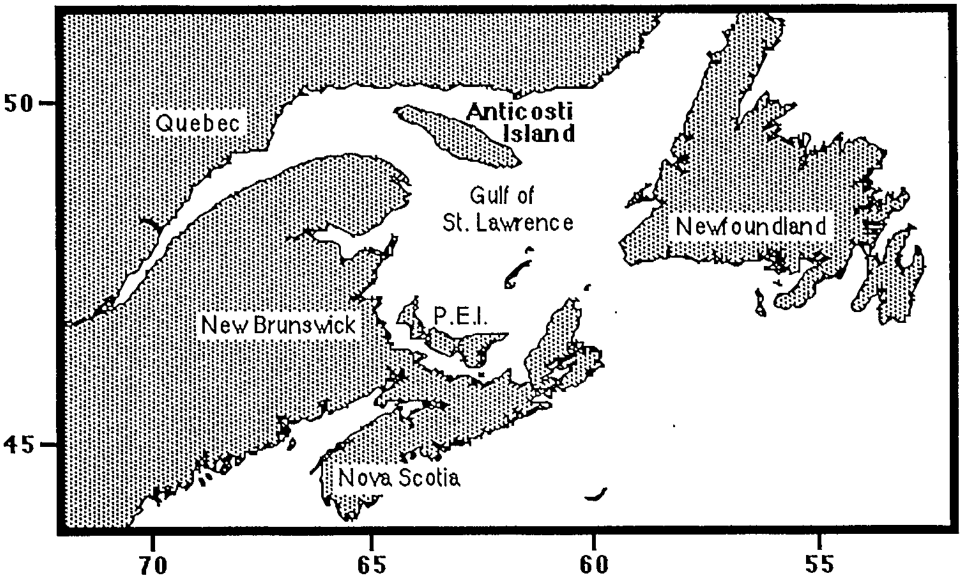


FIG. 1. Location of Anticosti Island, Gulf of St. Lawrence.

In the laboratory, stomachs were opened longitudinally along the greater curvature. Contents were manually sorted into the following categories: fish, invertebrate, seaweed, other contents and substrate. A stomach was operationally defined as food-containing when any remnants of food, including otoliths, invertebrate parts or other bony material, were recovered.

All undigested prey were identified from visual keys (Liem and Scott 1966) and measured (fish: standard length; Crustacea: carapace width). Hard parts and otoliths from stomach contents were recovered to reconstruct the species and size compostion of food eaten using the otoltih recovery technique developed by Murie and Lavigne (1985). Recovered material was preserved in 70 % ethanol. Otoliths were identified using Härkönen's (1986) key and reference material collected in eastern Canada (J. Hunt, St. Andrews Biological Station, St. Andrews, New Brunswick, pers. commun.). To test the accuracy of the otolith-recovery apparatus, 3 blind tests were conducted using simulated stomach contents each composed of approximately 2 kg of mascerated herring flesh to which 6, 12 and 47 herring otoliths were added respectively. In all 3 tests, 100 % of these otoliths were recovered.

TABLE 2. Fish weight (FW; g) - fish length (FL; cm) relationships and relationships between fish size {FW or FL} and otolith dimension {otolith length (OL; mm) or otolith width (OW; mm)} for fish species found in grey seal stomachs in eastern Canada. Fish species are listed in alphabetical order, and the scientific and common names are according to Leim and Scott (1966). Where regressions for western Atlantic fish species were not available, the eastern Atlantic regressions were used (Härkönen 1986).

Species (common name)	Fish weight/ fish length relationship	Otolith size/fish size regression	refs.[a]
Anarhichas lupus (Atlantic wolffish)		$FL = -24.227 + 21.651\ (OL)$ $FW = 1.000\ (OL)^{5\,595}$	2
Clupea harengus harengus (Atlantic herring)		$FL = -8.749 + 18.439\ (OW)$ $FW = 4.910\ (OW)^{2\,45}$	2
Cyclopterus lumpus (Lumpfish)	$FW = -1.305 + 32.71\ (FL)$	$FL = 20.8 + 6.000\ (OL)$	1,2
Gadus morhua (Atlantic cod)	$FW = 0.0084\ (FL)^{3\,021}$	$FL = EXP\ \{1.8337 + 1.3536\ (OL)\}$	3,4
Hippoglossoides platessoides (American plaice)	$FW = 0.0042\ (FL)^{3\,197}$	$FL = 56.481\ (OL)^{1\,2425}$	3,5
Macrozoarces americanus (Ocean pout)	ratio: 106.68 cm/5455 g		6
Mallotus villosus (Capelin)	$FW = EXP\ \{(\ln FL)\ (3.807\text{-}7.512)\}$	$FL = 1.483 + 4.558\ (OL)$	7.2
Melanogrammus aeglefinus (Haddock)	$FW = 0.0077\ (FL)^{3\,073}$	$FL = EXP\ \{2.0479 + 1.0087\ (OL)\}$	3,4
Merluccius bilinearis (Silver hake)	$FW = 0.014\ (FL)^{2\,92}$	$FL = 20.288\ (OL)^{1\,0239}$	3,4
Myoxocephalus scorpius (Shorthorn sculpin)		$FL = -0.995 + 3.484\ (OL)$ $FW = 0.2261\ (OL)^{3\,496}$	2
Pollachius virens (Pollock)	$FW = 0.015\ (FL)^{2\,93}$	$FL = 25.817\ (OL)^{1\,651}$	3,4
Reinhardtius hippoglossoides (Greenland halibut)		$FL = 3.9454\ (OL)^{1\,142}$ $FW = 0.2748\ (OL)^{3\,717}$	2
Salmo salar (Atlantic salmon)		$FL = -4.51 + 8.84\ (OL)$ $FW = 16.78\ (OL)^{2\,45}$	2
Scomber scombrus (Atlantic mackerel)		$FL = -2.041 + 8.759\ (OL)$ $FW = 1.094\ (OL)^{4\,039}$	2
Tautogolabrus adspersus (Cunner)	ratio: 43.18 cm/1480 g		6

[a] (1) Direct from study; (2) Härkönen (1986); (3) J. Hunt (pers. commun.) Fisheries and Oceans, Canada; (4) H. Stone (pers. commun.) Fisheries and Oceans, Canada; (5) Beacham (1982); (6) Liem and Scott (1966); and (7) J. Carscadden (pers. commun.) Fisheries and Oceans, Canada.

As otolith growth is proportional to fish growth, the size of prey consumed could be reconstructed using otolith size-body size regressions available in the fisheries literature for most species of interest in this study (Table 2). A minimum estimate of the number of individuals recently ingested by a seal was determined by dividing the total number of otoliths recovered by two.

Quantitative estimates of the number and size (i.e., length and weight) of prey consumed by grey seals were determined for the 1986 and 1987 collections. Only the frequency of occurrence of food items in grey seal stomachs collected in 1982, 1983 and between 10 June and 14 August 1986 was available. Therefore, the frequency of occurence of prey found in the 1986 and 1987 collections is also presented so that inter-annual variation in the composition of grey seal diets could be examined.

Because the number of food-containing stomachs was relatively small, prey species were classified into the following "species-groups" (NAFO 1985): groundfish, pelagic fish, other finfish, unidentified fish, and invertebrate. To examine the summer diets of grey seals for evidence of inter-annual variation, we statistically compared the frequency distributions of species-groups observed in stomachs using a χ^2 test (SYSTAT statistical package, Wilkinson 1986).

Results

Of the 744 grey seals stomachs examined, only 295 (39.7 %) contained food or food remains. The number of food-containing stomachs was significantly higher in males (46.2 % of 275) than females (38.6 % of 407; $\chi^2 = 4.898$, df = 1, $P = 0.027$; Fig. 2). To examine the effect of body size on the proportion of food-containing stomachs, the sample was divided into 4 length classes (<130; 130-169; 170-209; ≥ 210

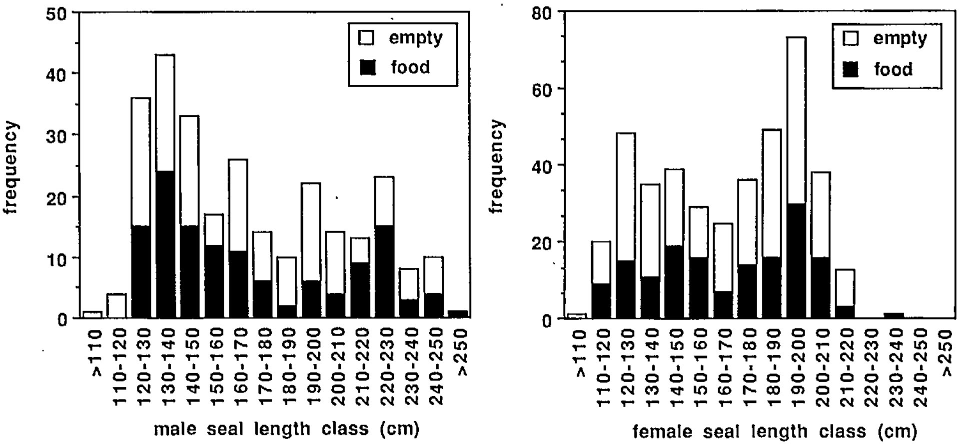


FIG. 2. Frequency distribution of empty and food-containing stomachs in relation to the body length of male and female grey seals.

cm). Male and female grey seals <130 cm in length are usually <1-yr-old, whereas seals >210 cm have reached sexual maturity. Immature seals, between 130 cm and 210 cm in length, were divided into two equal length classes. A three-way analysis of the effect of sex and body length on the frequency of food-containing stomachs indicated that mature males had a greater proportion of food-containing stomachs than mature females ($\chi^2 = 14.26$, df = 6, $P = 0.027$, Table 3).

TABLE 3. Grey seals classified according to sex, standard body length and presence or absence of food in the stomach.

		Length classes (cm)				
		<130	130-169	170-209	≥210	total
Females	empty	45	75	120	10	250
	with food	24	53	76	4	157
	total	69	128	196	14	407
Males	empty	26	57	42	23	148
	with food	15	62	18	32	127
	total	41	119	60	55	275

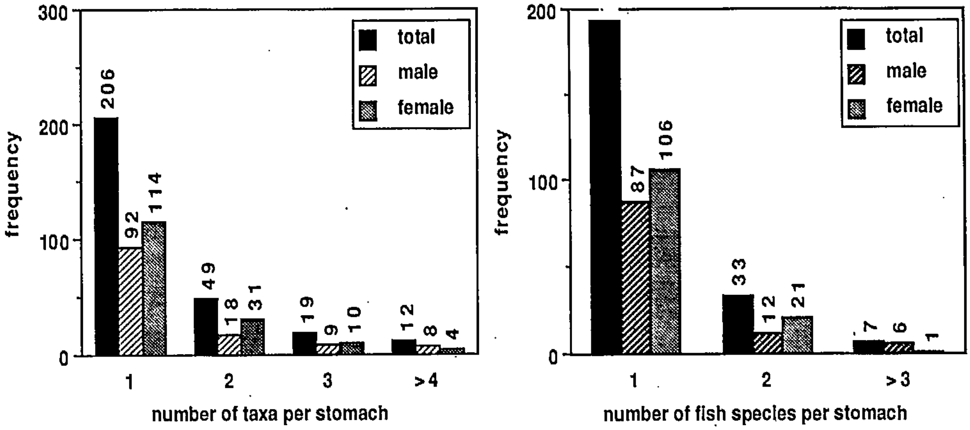


FIG. 3. Frequency distribution of the number of prey taxa (i.e., fish and invertebrate genera and/or species) and the number of fish species per grey seal stomach.

Frequency distributions of the total number of prey taxa (i.e., fish and invertebrate genera and/or species) and the number of fish species per stomach are shown in Fig. 3. Fully 72.0 % of seal stomachs sampled contained only one prey taxon. In stomachs where only fish was ingested, 93.7 % of these comprised only one fish species. There was no significant difference (χ^2 = 3.650, df = 3, P = 0.302) in the total number of prey taxa per stomach between males and females, however, females tended to have a greater number of stomachs with only a single fish species than males (χ^2 = 5.681, df = 2, P = 0.058).

The composition of the summer diet of grey seals at Anticosti Island during the period 1982 to 1987 is summarized in Table 4. A minimum of 26 prey items was found in the diet. The frequency of occurrence of species-groups was significantly different (χ^2

TABLE 4. Number of occurrences and frequency of occurence of different prey items found in grey seal stomachs in summers of different years at Anticosti Island.

	1982		1983		1986		1987	
	no.	%	no.	%	no.	%	no.	%
Fish	80	(81.6)	38	(80.9)	172	(94.5)	108	(79.4)
Cod	3	4.0	12	52.2	28	28.0	28	28.9
Herring	3	4.0	7	30.4	2	2.0	42	42.3
Capelin	31	41.3	2	8.7	81	81.0	1	1.0
Flatfishes	2	2.7	2	8.7	12	12.0	10	10.3
Mackerel	0	—	0	—	7	7.0	8	8.2
Lumpfish	11	14.7	6	26.1	27	27.0	0	—
Skate spp.	0	—	0	—	0	—	1	1.0
Skate eggs	0	—	1	4.3	0	—	0	—
Hake	0	—	0	—	2	2.0	0	—
Haddock	0	—	1	4.3	1	1.0	1	1.0
Ocean pout	3	4.0	0	—	5	5.0	3	3.1
Gaspereau/shad	0	—	1	4.3	0	—	0	—
Salmon	0	—	0	—	1	1.0	0	—
Wolffish	0	—	0	—	1	1.0	0	—
Sculpin	2	2.7	0	—	0	—	1	1.0
Pollock	0	—	1	4.3	2	2.0	0	—
Tomcod	0	—	2	8.7	0	—	0	—
Cunner	0	—	0	—	1	1.0	0	—
Unidentified fish	25	33.3	3	13.0	2	2.3	13	13.4
Invertebrates	18	(18.4)	9	(19.1)	4	(2.2)	24	(17.6)
Squid	13	17.3	0	—	0	—	0	—
Crab spp.	3	4.0	5	21.7	2	2.0	10	10.3
Shrimp spp.	2	2.7	2	8.7	2	2.0	8	8.2
Gastropoda	0	—	0	—	0	—	12	12.4
Euphausiacea	0	—	2	8.7	0	—	0	—
Lobster	0	—	0	—	0	—	1	1.0
Sponge	0	—	0	—	0	—	1	1.0
Seaweed, algae	0	—	0	—	6	6.0	4	4.1
Species-groups								
Groundfish	21	21.4	24	52.2	79	44.9	43	32.6
Pelagic	3	3.1	7	15.2	9	5.1	50	37.9
Other finfish	31	31.6	3	6.5	82	46.6	2	1.5
Invertebrate	18	18.4	9	19.6	4	2.3	24	18.2
Unidentified fish	25	25.5	3	6.5	2	1.1	13	9.9
no. stomachs:	166		60		230		288	
empty stomachs:	91		37		120		191	
food-containing:	75		23		87		97	

= 208.433, df = 12, $P < 0.001$) between the years with individual prey species exhibiting considerable variation. In 1982, capelin, lumpfish (*Cyclopterus lumpus*) and squid were frequent items with cod and herring occurring in only a few stomachs. In 1983, cod, herring, lumpfish and crabs were frequently observed, but capelin was a supplementary prey. In 1986 capelin was again the most frequent, with cod and lumpfish of secondary importance. As in 1982, herring occurred in low amounts. Cod and herrring were most frequently recorded in 1987, however, no lumpfish and only one occurrence of capelin were observed. Considering all years together, the most frequent species were capelin, cod, herring, lumpfish and flatfishes (Pleuronectidae), which accounted for 72.5 % of all occurrences. In general, groundfish (55.9 % of occurrences) and other finfish (40.0 %) appeared more frequently in grey seal stomachs than pelagic fishes (23.4 %) and invertebrates (21.3 %).

In the summers of 1986 and 1987, 15 different fish species occurred in 184 food-containing stomachs, representing a total of 1791 individuals and 233 kg. The number and relative weight of prey eaten are given in Table 5. Capelin, cod and herring were the most frequent species representing 38.6 %, 29.3 and 23.9 % of the items identified, respectively. Similarly, they comprised the largest number of individuals consumed at 66.5, 15.6 and 6.8 %, respectively. However, in terms of the percentage by weight consumed, cod was most important (41.5 %), followed by ocean pout (*Macrozoarces americanus*; 16.4 %) and lumpfish (14.3 %). Capelin and herring accounted for only 6.6 and 3.7 %, respectively, of the weight of food eaten. Five fish species accounted for 84.1 % of the biomass eaten.

Invertebrate prey occurred frequently but in small quantities in the summer diet, and thus were not used to derive quantitative estimates of food eaten. It is lilely that some of the invertebrates were from the digestive tracts of fish eaten by seals.

TABLE 5. Fish species recovered in stomach contents of grey seals collected at Anticosti Island during the summers of 1986 and 1987.

	Frequency of occurrence		Number of individuals		Weight (kg)	
		%		%		%
Capelin	71	38.6	1191	66.5	15.5	6.6
Cod	54	29.3	279	15.6	96.9	41.5
Herring	44	23.9	121	6.8	8.7	3.7
Lumpfish	25	13.6	41	2.3	33.4	14.3
Ocean pout	8	4.3	14	0.8	38.2	16.4
Plaice	20	10.9	80	4.5	12.3	5.3
Mackerel	15	8.2	30	1.7	10.6	4.5
Haddock	2	1.1	17	0.9	6.8	2.9
Salmon	1	0.5	6	0.3	6.3	2.7
Gr. Halibut	2	1.1	2	0.1	1.7	0.7
Hake	2	1.1	3	0.2	1.1	0.5
Pollock	2	1.1	2	0.1	<0.1	<0.1
Cunner	1	0.5	1	<0.1	0.9	0.4
Wolffish	1	0.5	3	0.2	0.5	0.2
Sculpin	1	0.5	1	<0.1	0.3	0.1

The frequency distribution of prey lengths, all 15 fish species combined (n = 1791), is given in Fig. 4. The estimated size of prey consumed ranged from 6.7 to 79.7 cm, with a mean of approximately 18.0 cm; 1267 (71 %) of the estimated prey lengths were less than 20 cm, and 1574 (88 %) were less than 30 cm. The length frequency distributions of cod, plaice (*Hippoglossoides platessoides*), capelin, herring, lumpfish and mackerel (*Scomber scombrus*) are given in Fig. 5. As no significant difference was found between the size of skull-recovered and loose capelin otoliths, these were pooled. With

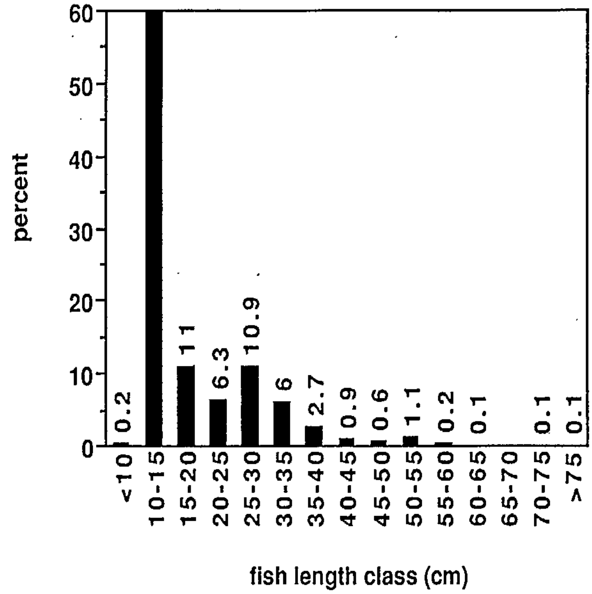


FIG. 4. Length-frequency distribution of fishes, all 15 species combined (listed in Table 5) consumed by grey seals.

the exception of lumpfish, capelin was the only ingested species with a high (47 %) proportion of skull-recovered otoliths. No loose lumpfish otoliths were retrieved likely because of their small size, averaging 1.5 mm. The percentage of skull-recovered otoliths of cod and plaice was 1 and 0 %, respectively. Most of the cod, plaice, herring and lumpfish eaten were 20-30 cm in length. Capelin, a smaller species, and the larger mackerel had mean ingested lengths of 13.9 and 32.6 cm, respectively. For all other species, the number of otolith-reconstructed and/or actual fish measurements were too low to present the length distributions graphically (Table 6).

TABLE 6. Mean length (cm) and range of fish species recovered in stomach contents of grey seals collected at Anticosti Island during the summers of 1986 and 1987. Based on otolith length-body length regressions and actual fish measurements.

Species	Mean	Range	Estimated length (*n*)	Actual length (*n*)
Capelin	13.9	8.3-17.4	884	7
Cod	28.2	6.7-79.7	264	5
Herring	24.9	20.0-37.3	15	96
Lumpfish	24.9	15.0-29.2	9	17
Ocean pout	53.3	45.7-61.0	9	3
Plaice	24.3	11.1-46.8	77	0
Mackerel	32.6	25.0-47.9	6	18
Haddock	32.4	14.8-57.2	2	0
Salmon	43.0	35.7-52.1	5	0
Gr. Halibut	46.1	43.0-49.1	2	0
Hake	30.3	21.1-42.3	2	0
Pollock	10.9	8.1-13.8	2	0
Cunner	25.4		0	1
Wolffish	29.6	22.9-35.6	3	0
Sculpin	24.6		0	1

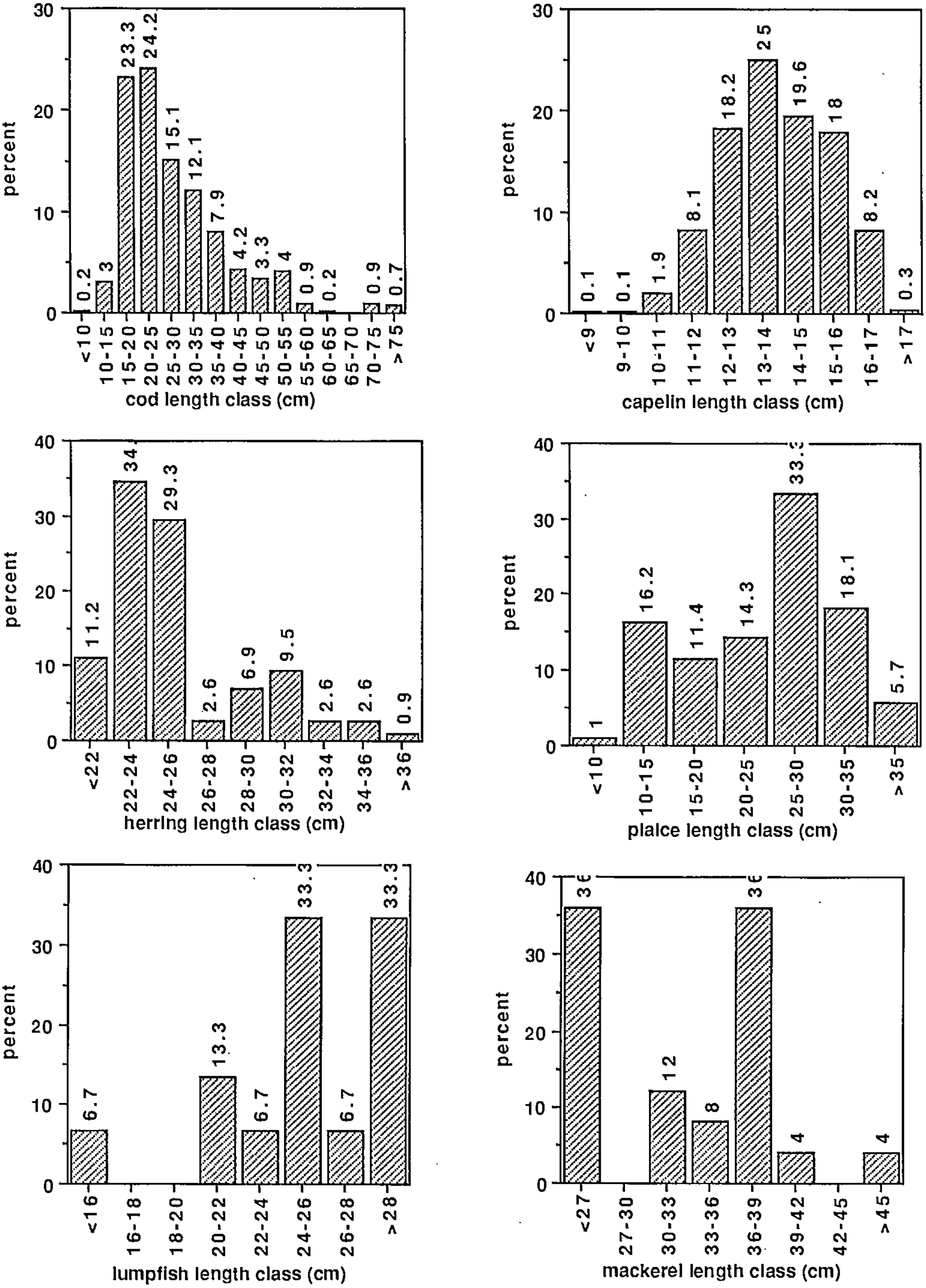
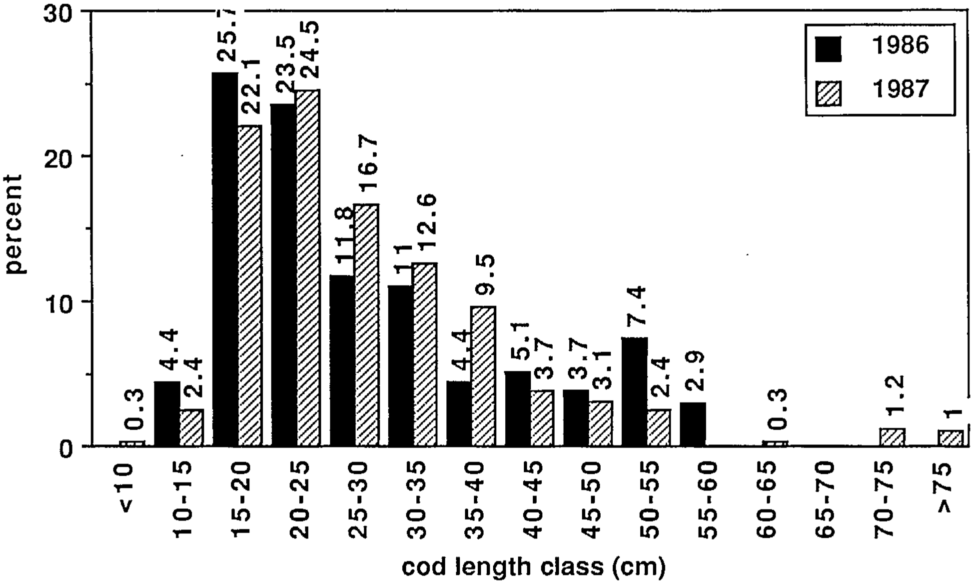


FIG. 5. Length-frequency distribution of cod, plaice, herring and capelin consumed by grey seals.

Only cod and plaice were eaten frequently by grey seals in both 1986 and 1987. The size distributions of cod eaten were not significantly different (χ^2 = 12.492, df = 9, *P* = 0.187) between years, with a mean length of 28.4 cm (*n* = 68) and 28.1 cm (*n* = 112) in 1986 and 1987, respectively (Fig. 6). Similarly, there was no significant difference (χ^2 = 10.166, df = 5, *P* = 0.071) in the size distributions of plaice eaten in 1986 (*x* = 27.6 cm; *n* = 17) and 1987 (*x* = 22.8 cm, *n* = 36).

In the summer of 1987, the core mass of 38 seals was taken in addition to the standard morphometrics. The regression between standard body length and core mass, sexes



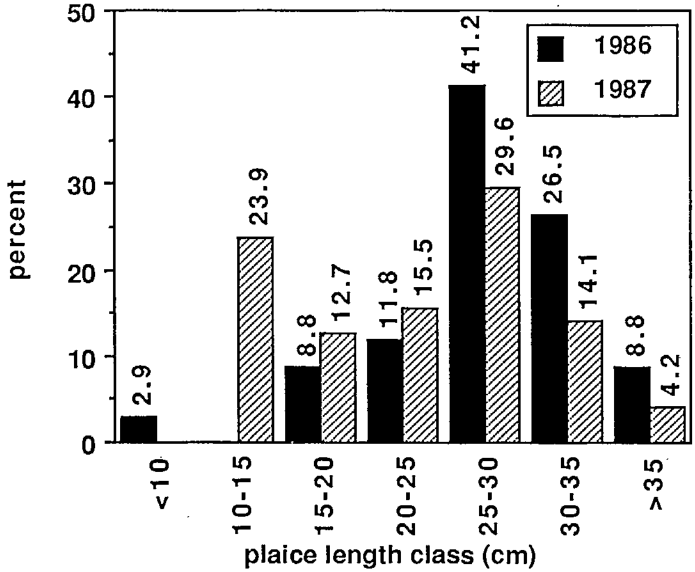


FIG. 6. Length-frequency distribution of cod and plaice consumed by grey seals in 1986 and 1987.

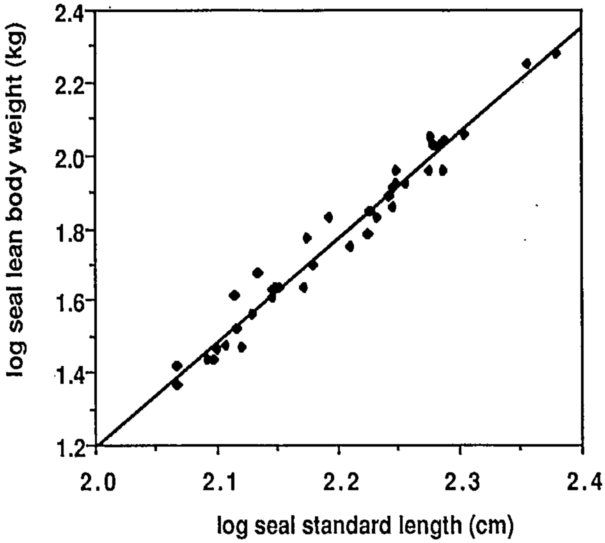


FIG. 7. Regression of standard body length on core mass ($y = -4.5923 + 2.8926\ x$, $r^2 = 0.98$, $n = 38$).

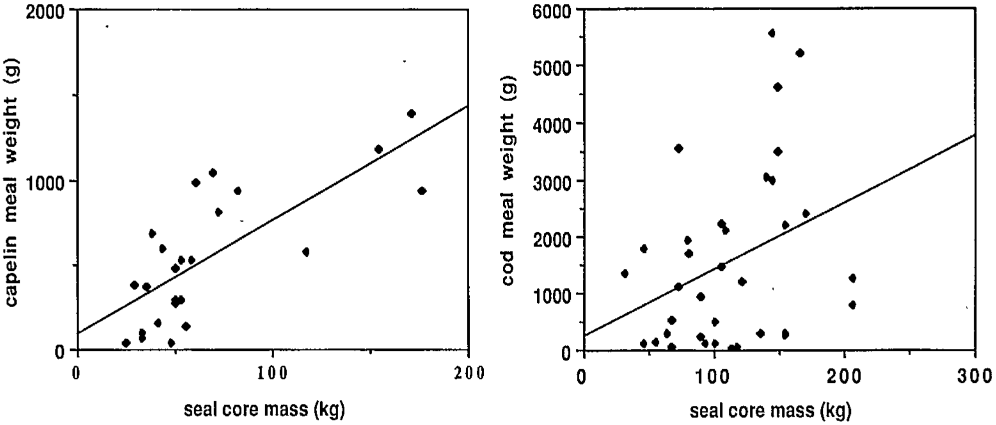


FIG. 8. Correlation between standard body length and the mass of capelin ($r^2 = 0.56$) and cod ($r^2 = 0.12$) observed in individual seal stomachs.

combined, is given in Fig. 7. Core mass of the remaining seals for both 1986 and 1987 was calculated using the regression equation. These estimates were used to determine the ratio of meal size to seal core mass for two prey species, cod and capelin. The estimated mass of cod eaten per meal was not significantly correlated with core mass ($r^2 = 0.12$), however, the weight of capelin eaten was ($r^2 = 0.56$; Fig. 8).

Average meal weight as a percentage of seal core mass was 1.5 % (*SE* = 0.2, n = 35) and 0.8 % (*SE* = 0.1, n = 24) for cod and capelin, respectively. Combined meal mass was 1.2 % (*SE* = 0.2, n = 59) ranging from 0.02 % to 4.9 %.

Discussion

A minimum of 24 species of fish and 12 invertebrate species have been identified from grey seal stomachs in eastern Canada (Benoit and Bowen 1990). Of this total, 26 prey items occurred in seal stomachs collected at Anticosti Island during summer months from 1982 to 1987 (Table 4). The predominance of fish in the diet is consistent with previous studies on grey seals both in eastern Canada (Mansfield and Beck 1977) and in the northeastern Atlantic (Hauksson 1984; Rae 1968, 1973; SMRU 1985, Hammond and Prime 1990). Although invertebrates were frequently recorded, they did not appear to comprise much of the diet.

At Anticosti Island, grey seals usually (72.0 % of stomachs) fed on only a single prey species at one time (Fig. 3). In Iceland, however, Hauksson (1984) reported that grey seals fed on a more diverse array of species at any one time, with only 23.5 % of stomachs having but one prey type. Since Hauksson's figures are based on an annual compilation over a period of 4 yr, it is possible that grey seals may feed mainly on single prey at certain times of the year and change to multiple prey meals at other times. George-Nascimento et al. (1985) also found that 80 % of South American sea lions (*Otaria flavescens*) had more than one prey taxon per stomach.

Like grey seals in this study, northern fur seals (*Callorhinus ursinus*) stomachs generally contained a single prey species (Kajimura 1984). Kajimura argued that this may reflect the availability and abundance of fish or invertebrate species more than if reflects the selection or preference of one particular species over another. This was also the conclusion of Antonelis et al. (1984) for California sea lions (*Zalophus californius*).

The Anticosti data suggests that male grey seals had a greater proportion of food-containing stomachs and a higher proportion of multiple prey per stomach than females. The larger proportion of food-containing stomachs in males may simply reflect their larger body size. This is consistent with our data in that it was among mature animals that the difference between sexes was significant. Their larger size and hence greater food requirements, may also explain why males tended to have a higher proportion of multiple prey types in their stomachs. However, until more is known about the foraging behaviour of grey seals, the significance of these findings will remain unclear.

There was significant inter-annual variation in the frequency of occurrence of different species-groups in the summer diet during the period 1982-1987 (Table 4). Although uncommon in 1982, cod became a frequent item in the diet between 1983 and 1987. This variation does not seem to reflect changes in the abundance of cod near Anticosti Island over this period, based on estimates of population trends in fisheries assessments (Fréchet 1988). It is also possible that many of the unidentified fish in the 1982 sample were cod and that the 1982 value is an artifact.

A striking feature of the data in Table 4 is the inverse relationship between the frequency of capelin and herring in the diet over the period. Unfortunately, population estimates for these species are not available for the waters surrounding Anticosti Island. However, in the waters south of Anticosti, known as the 4T stock, the abundance of herring age 2 and older has increased since 1982 (Chadwick and Cairns 1988). It seems likely, therefore, that the observed variation in the frequency of herring is related to the availability rather than simply abundance. The inverse relationship between these two species may reflect competitive interactions which affect their distribution relative to the waters hunted by seals.

Although we cannot be certain, the absence of lumpfish in the 1987 sample likely reflects the seasonal availability of this species to grey seals in the waters surrounding Anticosti Island. Lumpfish move into shallower waters to spawn in early summer, returning to deeper waters in late summer (Collins 1976). The 1987 sample was taken later than those in the other years (Table 1) at a time when lumpfish had returned to deeper waters and thus were unavailable.

Studies on South American seal lions (George-Nascimento et al. 1985) and harbour seals, *Phoca vitulina,* (Härkönen's 1987) also suggest that these species were not selecting prey simply based on their relative abundance. Clearly, a variety of factors can affect prey availability. Moyle and Cech (1982 cited in Antonelis et al. 1984) stated that seasonal migration, diel vertical migration, variability in schooling behaviour, or physiological changes associated with spawning could all be important factors affecting prey selection in seals.

The use of otoliths to reconstruct the size of prey consumed provides a means of calculating the actual biomass and hence energy ingested. This is particularly valuable since the relative importance of prey, as determined by its frequency of occurrence or numerical abundance, can often be misleading (Frost and Lowry 1980). This is clearly illustrated in the case of capelin (Table 5). Based on both its frequency of occurrence (38.6 %) and the number of individuals eaten (66.5 %), capelin appears to be the most important prey at this time of the year. However, on a weight basis capelin accounts for only 6.6 % of the food eaten. By contrast, cod, lumpfish, and ocean pout, ranked in second, fourth and fifth place based on occurence and number of individuals recorded, accounted for over 70 % of the estimated biomass consumed.

Although otoliths can be valuable in reconstructing the mass of food eaten by seals, the method is subject to various sources of bias. These have recently been discussed by Jobling and Breiby (1986). Perhaps the largest source of error arises from differences in the proportion of ingested otoliths recovered due to differences in the rate of digestion of the otoliths of different species once exposed to gastric acids. This will clearly depend on the size and morphology of the otolith, as well as on the anatomy of the head which can affect the length of time an otolith is exposed to gastric acids. The use of otoliths to reconstruct prey and meal size requires that seals eat the heads of all fish consumed. Although this will generally be the case, there is some evidence that the heads of larger fish may not always be eaten, thus biasing estimates of the average size of prey taken.

Although experimental data are needed to determine the extent of these various sources of error, the effect of otolith digestion on estimates of prey size within a species can be examined by comparing head-recovered otoliths with those found free in the same stomach. In the case of capelin, such a comparison revealed no significant difference indicating that reconstructed lengths are unlikely to be biased.

An unexpected finding of our study was that the estimated mean length of prey eaten by grey seals was largely independent of the species consumed. With the exception of capelin (x = 13.9 cm, n = 1010), whose maximum length is about 20 cm, the mean length of cod, herring, and plaice was 28.4 cm (n = 430), 24.9 cm (n = 116), and 24.3 cm (n = 105), respectively. Based on a rather small number of samples, it appears that the lumpfish eaten by seals are similar in size (x = 24.9 cm, n = 15) to these other species. Although the estimated mean length of mackerel taken by seals is somewhat larger (x = 32.6 cm, n =25), the sample size is again rather small. This remarkable similarity in the mean length of prey eaten suggests that grey seals feed primarily on aggregated or schooling species, such as herring and mackerel, or on species which exhibit a high degree of aggregation at this stage in their life history.

The size of prey eaten by seals has important implications for understanding the impact of fish predation on the transmission of the sealworm parasite and on commercial fisheries. Our Anticosti data indicate that most of the cod, herring, plaice and capelin eaten by grey seals are pre-recruits (i.e., fish which are generally too small to be retained in the gear normally used to harvest these species). According to Fréchet (1987), most commercial catches of cod in the northern Gulf of St. Lawrence are >40 cm or age 3. By contrast, 88 % of the cod consumed by grey seals were <40 cm in length. Similarly, about 76 % of the plaice eaten by grey seals are <30 cm or about age 4, whereas, over 95 % of the plaice in the 1986 and 1987 commercial catches were >30 cm (Tallman and Sinclair 1988). The 1986 commercial fishery for herring in the waters surrounding Anticosti took few fish <28 cm in length (Trudeau and McQuinn 1986), however, 78 % of the herring eaten by grey seals were <28 cm. The only data on the age (i.e., size) composition of the inshore fishery for capelin comes from Newfoundland. In 1986 and 1987, >90 % of the capelin landed were between 3 and 4 yr old (Carscadden et al. 1988). Assuming that age composition of the Gulf fishery is similar, then most of the 1 and 2 yr old capelin eaten by grey seals would not have been retained in commercial gear. In general, these data suggest that during the summer near Anticosti Island grey seals and fisheries interact indirectly rather than through direct competition for the same fish.

The size of prey eaten by grey seals will also directly affect the transmission rate of the sealworm parasite from intermediate fish hosts to the defenitive host. McClelland et al. (1983a) and McClelland et al. (1985) found that the mean abundance of sealworm larvae in cod and American plaice in the Gulf of St. Lawrence and elsewhere increases significantly with increasing fish length. Thus the size and species composition of grey seal diet will strongly influence the number of larvae ingested by seals and ultimately the egg production of sealworm.

Grey seals appear not to select prey size according to their own size. The lack of a significant correlation between seal standard length and mean length of cod eaten agrees with data on South American sea lions George-Nascimento et al. 1985).

We found a significant correlation between the mass of capelin eaten during a "meal" and seal core mass, but no relationship in the case of cod. However, in most of the stomachs that contained mainly cod, the contents consisted of hard parts only, and therefore, some of the cod otoliths could have been digested or have past through the gut prior to the time of death. By contrast, in most of the stomachs containing capelin, digestion had just begun. Thus based on the better quality capelin data, it appears that meal size does increase with seal size. George-Nascimento et al. (1985) also found this in South American seal lions.

The average mass of capelin and cod ingested per meal was estimated to be 0.8 % and 1.5 % of the core mass of grey seals, respectively. Frost and Lowry (1980) found that the mean quantity of fishes consumed by ribbon seals (*Phoca fasciata*) was 0.7 % of body mass. If we assume that the daily consumption of an average eastern Canadian grey seal is the same as that in the United Kingdom, 5530 kcals (SMRU 1985), then to satisfy its daily energy demands, a seal would need to consume 5.6 kg of cod or 3.1 kg of capelin, given that the caloric density of cod and capelin are 0.98 kcal/g and 1.80 kcal/g, respectively (summer estimates from southeast Labrador; Birkhead and Nettleship 1987). Thus differences in the observed meal size of cod and capelin are consistent with the difference in caloric density of these species, suggesting that grey seals may count calories consumed and not just biomass.

Care must by taken not to interpret our meal size estimated as estimates of daily food intake. In order to estimate daily food intake, it is necessary to know how many meals are taken each day. At present, this is unknown. Further, the rapid digestion of food by pinnipeds will tend to introduce a downwards bias in reconstructed estimates of meal size. From their study with captive seals, Murie and Lavigne (1986) estimated that digestion of approximately 18 % of ingested otoliths occurred in the stomach contents of a seal within 6 h of feeding, increasing to around 43 % after 9 h. Therefore, if a seal fed in the morning and is shot that afternoon, fewer otoliths will be found, and daily energy intake would be underestimated. Meal size estimates in ribbon seals were also lower than the average daily intake of captive animals (Frost and Lowry 1980).

Our results indicate that grey seals found on Anticosti Island in the summer feed on young, schooling or atleast aggregated fish species. Young cod, the single most important food (41.5 % of the biomass consumed), along with lumpfish, ocean pout and capelin accounted for 78.8 % of the food eaten on a wet weight basis. Flexibility in their feeding behaviour may be a major factor contributing to the success of grey seals in eastern Canadian waters.

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The Diet of British Grey Seals, *Halichoerus grypus*

P. S. Hammond and J. H. Prime

Natural Environment Research Council, Sea Mammal Research Unit
c/o British Antarctic Survey, High Cross, Madingley Road,
Cambridge CB3 0ET, U. K.

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The diet of British grey seals was investigated by analyses of otoliths from faecal samples collected at haulout sites. Over 1 400 samples from the Hebrides, Orkney, Isle of May, Farne Islands and Donna Nook, Lincolnshire contained over 60 000 sandeel (Ammodytidae) otoliths and over 6 000 otoliths from other species. Measurements of partially digested otoliths were converted to undigested otolith size using species-specific digestion coeficients calculated from data from feeding experiments on captive seals. Fish weight was predicted from undigested otolith size and relative consumption was obtained by summing all predicted weights for each sample. A small number of prey species formed the core of the diet of British grey seals. In all areas (except Lincolnshire) sandeels and large gadoids always predominanted (78-97 % of the diet by weight). The dominant gadoid was Atlantic cod (*Gadus morhua*) in all areas except the Hebrides, where a high percentage of ling (*Molva molva*) was found. Whiting (*Merlangius merlangus*) was also a consistent contributor. Flatfish (Pleuronectidae) contributed significantly to the diet in the Hebrides, Orkney and especially Lincolnshire but not at the Isle of May nor the Farne Islands. No evidence of predation on salmon was found.

Les auteurs ont étudié le régime alimentaire de phoques gris des îles britanniques en analysant les otolithes dans des échantillons de faecès prélevés dans des aires de repos. Plus de 1 400 échantillons ont été prélevés dans les Hébrides, les Orcades, l'îles de May, les îles Farne et à Donna Nook (Lincolnshire). Ces échantillons contenaient plus de 60 000 otolithes de lançon (Ammodytidae) et plus de 6 000 otolithes d'autres espèces. Les dimensions des otolithes partiellement digérées ont été converties en tailles avant digestion à l'aide de coefficients de digestion spécifiques déterminés à partir d'essais d'alimentation des phoques gardés en captivité. Le poids des poissons a été estimés à partir de la taille des otolithes avant digestion et la consommation relative a été calculée par sommation de tous les poids estimés dans chaque échantillon. Le régime alimentaire de phoques gris des îles britanniques était consitué d'un petit nombre d'espèces proies. À l'exception du Lincolnshire, le régime de toutes les zones était surtout constitué de lançons et de gros gadoïdes (78-97 % de la diète en poids). La morue de l'Atlantique (*Gadus morhua*) était le gadoïde dominant les régimes dans toutes les zones à l'exception des Hébrides où l'on a noté un pourcentage élevé de julienne (*Molva molva*). Le merlan (*Merlangius merlangus*) était aussi trouvé en quantité appréciable. Les poissons plats (Pleuronectidae) constituaient une partie appréciable du régime dans les Hébrides, les Orcades et, plus particulièrement au Lincolnshire, mais non à l'île de May ou aux îles Farne. Les auteurs n'ont décelé aucun indice de consommation de saumon.

Introduction

The grey seal, *Halichoerus grypus*, is found in temperate and sub-arctic waters of the North Atlantic. The estimated 92 000 animals around Great Britain (N.E.R.C. 1987) are thought to be at least half of the world population. The major breeding sites in Britain are on islands off Scotland and northeast England: the Hebrides, North Rona, Orkney, Shetland, the Isle of May and the Farne Islands. Smaller breeding colonies also occur on the Scottish mainland, in southwest Britain and in East Anglia. These areas also serve as haulout sites during the rest of the year.

The diet of grey seals has previously been investigated by examining the stomach contents of animals found dead, killed incidental to fishing operations or killed deliberately (Rae 1960, 1968, 1973; S.M.R.U. 1984; Hauksson 1985). However, there are several problems associated with such analyses of stomach samples:

> Seals usually have to be either killed or obtained from other sources such as a fishery. This can be expensive and disturbing in the first case or can lead to a biassed sample in the second. Recent attemps at stomach lavaging to collect stomach contents show promise, however (Antonelis et al. 1987).
>
> Seal stomachs are often empty. Rae (1968) found that 45 % of grey seal stomachs and 57 % of common seal (*Phoca vitulina*) stomachs were empty when sampled, rendering this an inefficient method of collecting data.
>
> Prey tissue is digested and hard parts are retained at different rates in seal stomachs (e.g. Miller 1978). As a result, contribution to the diet of prey items which remain longer in the stomach will be overestimated.

An alternative method of investigating seal diet is to use the hard parts of prey remains found in faeces (Prime and Hammond 1987). In particular, fish otoliths (sagittae) can be identified to species and measured to provide a means of estimating the size of ingested fish (e.g. Everitt et al. 1981; Bailey and Ainley 1982; Brown and Mate 1983; Prime and Hammond 1987; Harvey 1988). These studies do not suffer from the same problems associated with analyses of stomach contents. Faecal samples are easy to collect and can be obtained with the minimum of disturbance to the seals. In addition, estimates of the relative contribution to the diet will not be biassed by species-specific differences in the length of time that ingested prey take to pass through a seal's gut. The analysis of otoliths found in faeces has its own set of problems, however:

> Prey species without otoliths or whose otoliths are very small or are not ingested, will not be represented.
>
> Otoliths are partially digested as they pass through the gut (Prime and Hammond 1987) and some of the more fragile ones may be completely digested (da Silva and Neilson 1985; Murie and Lavigne 1985; Murie 1987; Dellinger and Trillmich 1988).

In reviews of the use of faecal analysis to investigate diet, Jobling and Breiby (1986) and Jobling (1987) concluded that because of these problems, the results of analyses of faecal material might not be reliable in quantitative estimation of prey consumption.

Partial digestion of otoliths can be accounted for by applying species-specific digestion coefficients estimated from feeding experiments on captive animals (Prime and Hammond 1987). Complete digestion of otoliths cannot be accounted for, but Harvey (1988) has shown that the low recovery rates of otoliths obtained from certain species of fish may be an artefact of experimental design. The ingestion of large fish whose heads have been discarded (e.g. Rae 1968) also cannot be accounted for, nor can the remains of other prey without measureable otoliths, such as cartilaginous fish. Crustacean and cephalopod remains can also be found in faeces but their contribution to the diet is difficult to quantity. The important question is whether or not these prey items comprise a significant proportion of the diet. Prime and Hammond (1987, in press) have addressed this by comparing digestive efficiency estimated from faecal material with independent estimates. This comparison suggests that no major component of the diet is unrepresented by otoliths in faecal samples.

Materials and Methods

Grey seal faeces were collected from various haulout sites in the Hebrides, Orkney, the Isle of May, the Farne Islands, and Donna Nook in the county of Lincolnshire. Table

1 gives a summary of the number of samples collected in each month in each year in each area. Faecal material produced by different animals was collected in separate polythene bags and deep frozen until processed.

TABLE 1. Number of faecal samples collected and number of otoliths identified in each area by year and month.

Area	Year	Month	Number of faecal samples	Number of sandeel otoliths	Number of other otoliths
Hebrides	1985	January	26	618	98
		June	25	723	145
		August	15	448	256
		November	37	408	135
Hebrides		Total	103	2 197	634
Orkney	1985	February	165	17 789	696
		June	69	7 120	64
		August	47	3 692	120
		November	115	4 779	508
Orkney		Total	396	33 380	1 388
Isle of May	1983	November	8	510	215
	1984	November	9	3	58
	1985	February	20	3	49
		November	23	1 492	47
		December	17	907	51
	1986	November	28	848	55
	1987	November	20	94	60
		December	20	2 381	157
Isle of May	Total	Total	145	6 238	692
Farne Is	1983	March	8	1	32
	1984	April	62	1 858	467
		November	26	559	119
		December	16	1 056	35
	1985	May	17	325	26
		November	51	1 321	89
	1986	November	40	3 221	85
	1987	April	2	14	14
		October	20	944	20
		November	20	1 156	43
	1988	March	14	62	115
Farne Is	Total	Total	276	10 517	1 045
Donna Nook	1985	January	56	2 231	643
		February	21	470	144
		March	51	635	282
		April	10	20	54
		May	83	162	164
		June	40	761	79
		July	48	1 270	338
		August	42	1 074	363
		September	34	1 220	146
		October	19	428	52
		November	40	150	236
		December	37	8	88
Donna Nook		Total	481	8 429	2 589

Processing of the faecal samples, measurement and identification of otoliths, feeding experiments to estimate digestion coefficients, and calculation of the contribution of various species to the diet have been described in detail by Prime and Hammond (1987). The following is a summary of these methods:

Each sample was washed with running water through a nest of sieves of decreasing size, from 4.00 mm to 0.25 mm, to extract the hard parts of food remains from the faeces. A nylon brush was used to assist in breaking down the material. Hard parts that remained in the sieves were collected and stored in 70 % alcohol. The most frequent remains extracted were fish otoliths, vertebrae and eye lenses.

All otoliths were identified to species where possible. This was not possible for sandeels (Ammodytidae) which were simply classified as such. Table 1 summarises the number of otoliths identified from the faecal material in each area, year and month. An otolith reference collection of more than 100 fish species and an identification guide (Harkonen 1986) aided this process. The thickness, width and length of each otolith was measured with digital calipers to the nearest 0.01 mm. Otoliths were occasionally found broken so that length and sometimes width could not be measured. When large numbers of sandeel otoliths were retrieved from a sample, a random subsample was measured and the results extrapolated to the entire sample. The extreme concavity of one of the faces of Dover sole (*Solea solea*) otoliths prevented accurate measurement of thickness with the available equipment.

To relate the size of a partially digested otolith to the size of the fish represented by that otolith, feeding experiments were carried out with captive grey seals (Prime and Hammond 1987). Fish of known species and size were fed to adult grey seals of both sexes and the faecal material they produced was collected. Digestion coefficients for each species were calculated as the ratio of mean undigested otolith thickness (from subsamples of fish in the same size range as those fed to the seals) to mean digested otolith thickness. These are given in Table 2 for the major fish species found in the diet of British grey seals. Table 2 also gives the Latin names of all major fish species found in the diet of British grey seals.

TABLE 2. Digestion coefficients for prey species in the diet of grey seals. Coefficients were estimated from data collected in feeding experiments on captive grey seals.

Common name	Scientific name	Digestion coefficient
Sandeels	Ammodytidae	1.36
Cod	*Gadus morhus*	1.65
Whiting	*Merlangius merlangus*	1.65
Haddock	*Melanogrammus aeglefinus*	1.54
Saithe	*Pollachius virens*	1.55
Ling	*Molva molva*	1.57
Pout whiting	*Trisopterus luscus*	1.114
Poor cod	*Trisopterus minutus*	1.114
Norway pout	*Trisopterus esmarkii*	1.114
Plaice	*Pleuronectes platessa*	1.83
Lemon sole	*Microstomus kitt*	1.89
Dover sole	*Solea solea*	1.25[a]
Flounder	*Platychthys flesus*	1.89
Dab	*Limanda limanda*	2.03
Megrim	*Lepidorhombus whiffiagonis*	*1.89*
Dragonet	*Callionymus lyra*	1.57
Bullrout	*Myoxocephalus scorpius*	1.57

[a] Digestion coefficient for Dover sole calculated using otolith width.

Undigested otolith thickness was related to fish weight by sampling as wide a range of fish species and sizes as were available. The cube root of fish weight was regressed on otolith thickness to provide a predictive relationship for each species. These relationships are given in Table 3. For Dover sole, otolith width gave a much better relationship than otolith thickness, reflecting the difficulty in measuring thickness accurately in this species. For a few species of minor importance there were insufficient data to fit a regression line to the data and a mean weight was calculated.

TABLE 3. Relationships between undigested otolith thickness and fish weight for prey species in the diet of British grey seals, estimated from sample data. The equations are regressions of the cube-root of fish weight in grams (y) on undigested otolith thickness in millimetres (x), except for Dover sole where the independent variable is undigested otolith width in millimetres (z). For those species where there were insufficient data to fit a regression, a mean weight in grams (w) of available fish was used.

Common name	Otolith thickness-fish weight relationship	Correlation coefficient
Sandeels	$y = 5.817x - 0.938$	0.99
Cod	$y = 6.064x - 3.403$	0.90
Whiting	$y = 3.434x - 0.012$	0.56
Haddock	$y = 3.199x - 1.001$	0.71
Saithe	$y = 5.288x - 1.742$	0.91
Ling	$y = 20.29x - 12.13$	0.81
Pout whiting	$y = 2.647x - 2.342$	0.85
Poor cod	same as pout whiting	
Norway pout	$y = 1.843x + 0.015$	0.93
Plaice	$y = 6.839x - 1.469$	0.91
Lemon sole	$y = 6.453x + 2.349$	0.46
Dover sole	$y = 2.017z - 0.645$	0.99
Flounder	$y = 6.059x - 1.010$	0.59
Dab	$y = 12.13x - 5.454$	0.93
Megrim	$y = 5.946x + 1.010$	0.55
Dragonet	$w = 60$	
Bullrout	$y = 6.050x - 0.292$	0.99

In calculating contributions to the diet of grey seals it was assumed that the samples were representative of the diet in each month. Relative consumption by weight of each fish species was calculated for each month by summing the weights estimated from the thickness of each otolith.

Results

Monach Isles

Table 4 shows the estimated percentage contribution, by weight, of the most important prey species to the diet of grey seals at the Monach Isles. Outer Hebrides, in 1985. The annual average shows the diet to be dominated by sandeels (21.9 %) and ling (22.8 %). Other gadoids (cod, whiting, haddock, *Trisopterus* spp. and saithe in descending order of importance) made up a further 35.1 %. Flatfish (plaice and megrim) contributed another 14.9 %.

The percentage of sandeels declined slightly but steadily through the year. Ling were more prevalent in the diet in the first half of the year; saithe and flatfish were more so in the second half. There was no obvious pattern of change in the contribution of cod through the year. Whiting contributed to the diet mostly in the winter; haddock predominantly in the summer.

TABLE 4. Estimated percentage by weight of the most important prey species in the diet of grey seals in the Monach Isles, Outer Hebrides,. in 1985.

Species	January	June	August	November	Mean
Sandeels	25.4	23.0	21.8	17.2	21.9
Cod	7.7	17.8	9.9	12.9	12.1
Whiting	8.0	2.8	5.4	21.3	9.4
Haddock	4.1	9.4	9.4	3.7	6.7
Saithe			5.4	4.8	2.6
Ling	37.0	34.1	8.6	11.6	22.8
Trisopterus	5.6	1.2	10.0	0.4	4.3
Plaice	6.0	1.3	17.0	3.0	6.8
Megrim	4.4	4.4	7.2	16.3	8.1
Total	98.2	94.0	94.7	91.2	94.7

Orkney

Table 5 shows the estimated percentage contribution, by weight, of the most important prey species to the diet of grey seals in Orkney in 1985. Sandeels dominated the diet in all the samples, averaging 55.9 % for the year as a whole. Gadoids (mainly cod and ling) contributed 26.1 % and flatfish (mainly plaice) a further 14.2 %.

TABLE 5. Estimated percentage by weight of the most important prey species in the diet of grey seals in Orkney in 1985.

Species	February	June	August	November	Mean
Sandeels	55.3	79.2	54.0	35.0	55.9
Cod	7.6	13.1	5.2	11.7	9.4
Whiting	0.8	0.6	1.3	7.5	2.6
Haddock	2.9	2.9	6.1	2.0	3.5
Saithe	6.7	0.3	1.2	1.1	2.3
Ling	7.3		16.0	9.9	8.3
Plaice	10.6	2.0	7.7	4.3	6.2
Lemon sole	3.7	0.8	1.8	5.8	3.0
Dab		0.2	5.9		1.5
Other flatfish	2.7	0.5		10.8	3.5
Bullrout	0.4			3.7	1.0
Sea scorpion	0.4			3.5	1.0
Total	98.4	99.6	99.2	95.3	98.2

The percentage of sandeels was highest in June and lowest in November, with intermediate values in February and August. The pattern was the reverse for both gadoids and flatfish as a whole, although not necessarily for the individual species.

Isle of May

Table 6 shows the estimated percentage contribution, by weight, of the most important prey species to the diet of grey seals at the Isle of May in November and December from 1983 to 1987 and in February 1985.

TABLE 6. Estimated percentage by weight of the most important prey species in the diet of grey seals at the Isle of May in the pupping season, 1983-87, and in February 1985.

	1983	1984	1985	1986	1987		1985
Species	Nov.	Nov.	Nov./Dec.	Nov.	Nov./Dec.	Mean	Feb.
Sandeels	11.0	0.6	38.6	40.1	21.0	22.3	0.6
Cod	63.5	51.4	35.5	43.1	55.3	49.8	22.3
Whiting	9.4	5.3	2.8	0.9	12.9	6.3	14.4
Haddock	5.3	9.6	5.6	1.0	1.3	4.6	6.0
Saithe	3.3		5.3	5.7	0.2	2.9	
Ling				1.0	0.4	0.3	30.7
Plaice	2.6	1.5	5.4	1.6	4.8	3.2	7.2
Lemon sole		16.5				3.3	4.8
Dab		11.7			2.9	2.6	
Bullrout							6.8
Total	95.1	96.6	93.2	93.4	97.4	95.2	92.8

In November and December, the pupping season, two species (cod and sandeels) dominated the diet. On average, they accounted for over 70 % of the diet at this time of the year. Other gadoids made up a further 14.1 % and flatfish another 9.1 % of the diet by weight. The percentage of sandeels in the diet ranged from 0.6 % to 40.1 %., from year to year. There was less variation in the contribution of cod (range 35.5 % to 63.5 %). Whiting, haddock and plaice were regular components of the diet but other less important species occured more sporadically.

In the single sample from February 1985, the composition of the diet was different. Cod accounted for only 22.3 % of the diet and sandeels were almost absent. Ling contributed over 30 % and whiting, haddock, plaice, lemon sole and bullrout all contributed more to the diet than in the pupping season. The percentage of sandeels was at the lower end of the range found during the pupping season and that of cod was below this level. These low percentages in combination suggest that the spring diet may be different from the diet in the pupping season.

Farne Islands

PUPPING SEASON

Table 7 shows the estimated percentage contribution, by weight, of the most important prey species to the diet of grey seals at the Farne Islands during the pupping season,

TABLE 7. Estimated percentage by weight of the most important prey species in the diet of grey seals at the Farne Islands in the pupping season, 1984-87.

	1984	1985	1986	1987	
Species	Nov./Dec.	Nov.	Nov.	Oct./Nov.	Mean
Sandeels	48.5	52.0	60.7	55.1	54.1
Cod	35.7	26.9	37.1	20.0	29.9
Whiting	10.4	17.4	1.6	5.8	8.8
Haddock	0.6	0.7	0.2	1.1	0.7
Saithe	4.1				1.0
Ling				10.4	2.6
Flatfish	0.3	2.1		6.9	2.3
Total	99.6	99.5	100.0	99.3	99.4

1984-87. Two species (sandeels and cod) dominated the diet in every year. On average, sandeels made up 54.1 % and cod 29.9 % of the diet. Whiting averaged 8.8 %. Other gadoids and flatfish made only small and irregular contributions. There was relatively little variability in the percentages of sandeels and cod in the diet amongst years.

SPRING

Table 8 shows the estimated percentage contribution, by weight, of the most important prey species to the diet of grey seals at the Farne Islands in spring, 1983-88. Three species (cod, whiting and sandeels) dominated the diet contributing, on average, 34.1, 23.0 and 20.1 %, respectively. Other gadoids and flatfish made up most of the rest of the diet. All species showed considerable variability among years in their contributions. There was, however, a clear pattern in this variability. The two samples from March, in 1983 and 1988, showed a very low percentage of sandeels (< 10 %) and a high percentage of gadoids (> 80 %). The two April samples, in 1984 and 1987, showed a higher percentage of sandeels (15-25 %), a lower percentge of gadoids (60-65 %), and a significant percentage of flounder (10-20 %). Contributions to the May 1985 sample were approximately 50 % each from sandeels and gadoids. Despite the small sample sizes in some of these months and the different years, this pattern suggests a progressive change in diet composition fom March to May.

TABLE 8. Estimated percentage by weight of the most important prey species in the diet of grey seals at the Farne Islands in spring, 1983-88.

Species	1983 Mar.	1984 Apr.	1985 May	1987 Apr.	1988 Mar.	Mean
Sandeels	9.1	23.3	50.4	15.7	2.1	20.1
Cod	12.6	33.6	27.1	32.2	64.8	34.1
Whiting	64.2	6.2	5.1	24.1	14.6	23.0
Haddock	3.7	2.7	12.6		1.1	4.0
Saithe		13.2				2.6
Flounder		11.8		19.8		6.3
Other flatifsh	2.4	4.6	1.6		4.3	2.6
Trisopterus	8.0	4.3	1.6	7.6	3.4	5.0
Total	100.0	99.7	98.4	100.0	90.3	97.7

Donna Nook

Table 9 shows the monthly variation in the estimated percentage contribution, by weight, of the most important prey species to the diet of grey seals at Donna Nook in 1985. For the whole year, three species made up 56.2 % of the diet — sandeels, cod and Dover sole. A further 21.6 % was comprised of three other species of flatfish and 14.9 % of the diet was made up of three other species of roundfish.

Sandeels made up a significant percentage of the diet by weight in all but four months: April, May, November and December. Cod made up at least 10 % in all months except July and August. The contribution of Dover sole ranged from less than 2 % from August to October, to 64.5 % in May.

The progressive changes through the year in these major contributions to the diet show a clear pattern. At the beginning of the year the diet was composed largely of sandeels, cod and other roundfish. As the year progressed into spring, flatfish became more important, especially Dover sole in May. Through the summer and into autumn,

TABLE 9. Estimated percentage by weight of the most important prey species in the diet of grey seals at Donna Nook, Lincolnshire in 1985.

Species	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Mean
Sandeels	28.9	31.5	21.4	2.6	1.8	48.3	34.2	45.8	63.5	34.4	4.3	0.6	26.4
Cod	24.3	26.1	13.1	14.8	12.3	24.6	0.9	3.5	10.6	50.0	11.5	19.3	17.6
Whiting	7.1	15.0	9.9	4.2	2.2	2.3	10.5	1.8	3.7	0.6	7.9	9.6	6.2
Dover sole	10.4	3.7	22.5	12.2	64.5	8.0	8.9	1.7	1.2		8.7	4.1	12.2
Dab	4.4		5.4	6.4	1.9	9.0	11.1	12.2	2.1	0.3	6.3	36.5	8.0
Flounder	1.2	1.3	9.5		7.3		13.1	18.5	0.5		12.3	26.5	7.5
Plaice	4.8	2.7	4.6	37.9		4.3	12.9		0.1		3.0	2.7	6.1
Dragonet	4.5	4.8	4.4	2.9	2.9	0.5	5.8	8.4	10.0		9.2		4.5
Bullrout	1.2	1.9	1.8	2.9	0.3			0.5	1.2	9.2	31.5		4.2
Total	86.8	87.6	93.2	83.9	93.2	97.0	97.4	92.4	92.8	94.5	94.7	99.3	92.7

sandeels dominated the diet. By October, cod had returned as an important prey item and at the end of the year, the pupping season, the diet consisted largely of roundfish and flatfish other than the three major species. Prime and Hammond (1989) describe a more detailed analysis of the data from Donna Nook.

Discussion

A small number of prey species form the core of the diet of grey seals in British waters. In all areas, sandeels and large gadoids accounted for 78-97 % of the diet by weight, except at Donna Nook where they made up only 50 %. At the major grey seal concentrations, a lower percentage of sandeels was always compensated for by a higher percentage of gadoids, and vice versa. The dominant gadoid in all areas was cod, except in the Hebrides where a high percentage of ling was found. Whiting was also a consistent contributor. Flatfish were the major component of the diet at Donna Nook. They also made up significant percentages in the Hebrides and Orkney but contributed less than 10 % to the diet at the Isle of May and the Farne Islands.

The only other major studies of grey seal diet in British waters were by Rae (1968, 1973) who compared proportions of stomachs containing the remains of various prey items. The most commonly found prey were gadoids (mainly cod, whiting and saithe) and salmonids. Flatfish and sandeels were not commonly found. The results of Rae's studies and those presented here are radically different in two respects. Firstly, Rae found a high proportion of stomachs to contain salmon remains, but no salmon otoliths have been found in the faecal material collected for our study. Secondly, sandeels were virtually absent in Rae's sample but formed 20-56 % of the diet by weight in our study. These differences are most likely a result of the different methologies used and the samples available.

Ninety-five percent of Rae's 1967-71 samples were from seals entangled in salmon nets or shot by fishermen, and 80 % of them came from the east coast of Scotland between the Firth of Tay and Moray Firth. Rae's sample was not, therefore, representative of grey seals in British waters as a whole and it is not surprising that salmon featured prominently in the diet. It is more surprising that our faecal analysis revealed an absence of salmon. The faecal samples were collected from the areas of highest grey seal concentration in an attempt to provide a representative sample of the seals around the British coast. There are two obvious explanations for the lack of salmon otoliths in our samples. Firstly, the seals which were consuming salmon were not sampled. This is quite plausible, because if seals limit their salmon predation to the vicinity of fishing nets, relatively few seals can be involved. Secondly, salmon could have been consumed but not their otoliths, or the otoliths were completely digested. However, no other hard remains from salmon were identified either. If salmon did form part of the diet which contributed to the faecal samples, it must have been very small.

The absence of sandeels in Rae's samples must be a result of either a lack of sandeels in the diet of these particular animals or a failure of stomach analysis to reveal the presence of sandeels. Most likely it is a combination of the two. Our data indicate that the large majority of the sandeel otoliths found in the faecal samples were consumed directly by the seals themselves. Typically, when large numbers of sandeel otoliths were found in a sample, several hundred being quite common, the number of other otoliths present was very small, usually zero. Conversely, there were usually only a few sandeel otoliths present when several prey species were found in a sample. Our interpretation is that only a very small proportion of the sandeel otoliths found came from the stomachs of other fish.

The data collected in our study should prove valuable as input to models describing the transmission of sealworm (*Pseudoterranova decipiens*) from fish to grey seals in British waters. Otolith thickness can readily be converted to fish length to provide length frequency distributions of prey consumed by seals (e.g. Prime and Hammond 1989). Young (1972) sampled over 5 000 cod from waters around Britain. He found different levels of infection in different areas and an increase in the numbers of sealworm larvae per fish with fish size. Combination of data such as these with the data on size specific consumption by grey seals from our study should allow estimates of the transmission rate of the parasite from fish to seal to be calculated.

To assess the impact of seal consumption on commercial fish stocks and their fisheries, a great deal of information is required (e.g. Harwood and Croxall, 1988). Relative consumption of fish by grey seals can be translated into estimates of actual consumption by converting weights to energy values and scaling the sum to equal the estimated energy requirement for the seals (S.M.R.U. 1984; Prime and Hammond 1987). Estimates of seal population size in different areas are also required. However, such estimates provide little insight into the extent of competition between seals and fisheries in the absence of additional data on the local distribution and movements of the fish prey and on the distribution of grey seal feeding effort. Prime and Hammond (1989) have attempted to synthesise the available information on local fish distribution and movements in the southwestern North Sea in order to interpret the results of the faecal analyses at Donna Nook summarised above. Telemetry studies to monitor the behavior of seals at sea are starting to yield some information on grey seal feeding behavior (McConnell 1986; S.M.R.U. unpublished data). As more data accumulate, quantitative assessments of the extent of competition between seals and fisheries should become possible.

Acknowledgements

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Group Report 4: Models

**S. des Clers and R. Mohn (*Rapporteurs*), D. Bowen,
P. Fanning, T. Landry, R. Misra, R. Myers, I. Ni, J. Smith,
and K. Zwanenburg**

Introduction

Modelling is taken in the broad sense of a synthesis of existing data and conceptualization. It covers statistical analyses to estimate parameter values, the identification of specific needs for further field or experimental data collection, as well as development of simulation models. In this context, the models developed by the Group are mathematical analogs of the system. Each model consists of a set of numerous non-independent and complex hypotheses written together to address as a set of questions. As such, the model becomes an hypothesis in itself. Model validation is achieved by comparing the modelled quantities with existing data. The fewer the data, the more speculative the model and the more helpful the use of existing theoretical frameworks. Once tested, a model provides an image of what might be happening in the real system, but this image remains an approximation, and depends on the current knowledge of the system, as well as on the objectives that were set *a priori.*

In the short-term, modelling helps to identify the key sealworm (*Pseudoterranova decipiens*) hosts and abiotic constraints on the parasite population and to identify the principal constituents of the system. Modelling also contributes towards the identification of spatial and temporal scales at which the system operates. A model reflects the dynamics of interacting parasite and host populations and the time trends of these dynamics. The simulation model may describe both annual and seasonal variations in infection levels on a regional basis. In the long-term, the model may provide a basis for testing management interventions, and should help in quantifying such measures.

Workshop Contributions

During both sessions of the workshop, the members of the Modelling Group took part in the discussions of as many other Groups as possible. Information relevant to the parasite's population biology was presented and assessed. Differences in the dynamics of sealworm infections in the eastern and western Atlantic were revealed. The least known parts of the life-cycle were identified. Based on these discussions, it was possible to assume reasonable values for most of the characteristic time scales, and roughly to define the spatial dimension of an infection.

At the end of the second workshop, after a year's modelling work, some important short-term objectives had been addressed, and two complementary approaches were proposed (Mohn 1990; des Clers 1990). However, modelling is very much a team effort with field and laboratory scientists, and a satisfactory description of the parasite population dynamics will not be possible before all key hosts and of stages the parasite are identified. Mohn's description of the parasite population dynamics, expressed as a simple delay between the egg and the larva in the fish stages, reflects the current lack of biological knowledge. On the other hand, des Clers' more detailed description of possible interactions at the egg and larval stages cannot be substantiated by existing data.

Analysis is still required to determine the extent to which smaller geographic areas may be aggregated into regional units, given the spacial ranges of the parasite and its different hosts. It is not yet clear whether the different areas should be discriminated on the basis of seal, fish or invertebrate populations and/or abiotic characteristics. At the moment, it is proposed that Atlantic Canada be divided into three areas: Southern Newfoundland (NAFO Division 3Ps), Gulf of St. Lawrence (4T, 4R, 4S), and the Scotian Shelf (4VsW). For Norway, U.K. and Iceland, the geographic units seem to be much smaller (e.g. Halten-Froan, the Moray Firth, Breidafjordur, respectively).

The temporal scales at which the sealworm system operates are not completely identified, but are known to vary from weeks in the seal stomach to years in fish. As the parasite spends a large part of its life-cycle in the fish, where it can remain infective for several years, the time needed for the system to respond will depend largely on life-span of fish. For commercial species such as cod (*Gadus morhua*) or American plaice (long rough dab, *Hippoglossoides platessoides*), the life-span depends largely on the age of the fish when it enters the fishery and on the fishing pressure. This could explain some regional differences in infection levels. The cold-water, slow-growing cod stocks (entering the fishery at 4 or 5 years of age; Canada, Norway, Iceland) are more infected than the faster growing cod from U.K. warmer waters (entering the fishery at the age of 1 and 2). Nevertheless, the average time spent by sealworm in the free-living stage and in invertebrate hosts is not yet known. These "internal clocks" must be set right before the past or future long-term behaviours of the system can be modelled accurately.

Models Developed by the Workshop

A biological model of an infection was identified during the workshop general discussions and two complementary approaches were developed (see Mohn 1990; des Clers 1990) which led to two different models. A gradual convergence was already suspected during the first part of the workshop. However, it was decided to keep the development of the models separate, to produce a more diverse contribution to the modelling of the sealworm population dynamics.

Mohn's (1990) framework is original, and combines the observed quantities into a synthetic structure, with conceptual foundations derived from Braitenberg (1986) and common population dynamics practices. The model attempts to integrate the major observations of the parasite's life history and hosts for the Sable Island area. The purpose was twofold: (i) to assess internal consistency of the various observations within the model framework, and (ii) to provide an environment to test the dynamics and sensitivity of the modelled system. The exercise showed that there was sufficient agreement in the observations to allow the construction of the model, but that there appear to be discrepancies in the seal infestation rate and in the stability of the modelled sealworm population. The poor stability is attributed to a lack of density-dependent controls acting on the modelled sealworms. Density-dependent controls for sealworms were not included because sufficient biological observations to construct them does not exist. The sensitivity analysis addresses errors or uncertainties in parameter estimation and the efficiencies of interventions. The results show that the model is very sensitive to the seal to fish transmission rate, a parameter which is not directely estimable. The sensitivity of interventions compares a cull regime and two hypothetical drug regimes.

The approach of the Clers for the parasite life-cycle part of the model is derived directly from a framework proposed more than 10 years ago (Anderson and May 1978; May and Anderson 1978). This framework has been used extensively since, notably to study the dynamics of helminth parasite populations with complex indirect life-cycles, parasites of man or other mammals (see, for example, Anderson 1982; Anderson and May 1985; Dobson and Keymer 1985; Grenfell et al. 1987). The parasite's population dynamics are described by four coupled equations, one for each subpopulation: the adult parasites in seals, the free-living stages, the larvae in invertebrate hosts and the larvae in fish. The model is only for the parasite population, and all host population sizes are fixed arbitrarily. In time, parasites transit through the successive stages and hosts.

With fixed numbers of hosts, the dynamics of the parasite population are regulated by the life-span of the longest lived stage: the larvae in fish. At equilibrium the predicted worm burden in fish is determined by the number of hosts involved in parasite transmission. Two different versions of the life-cycle model are presented (des Clers 1990), with the intrinsic control of parasite numbers either in fish, or in seals. Parameter values are chosen to describe a typical infection in a Scottish cod fishery. Both versions of the model are shown to describe existing infections equally well. The ability of an infection to spread is given by R_0, the basic reproductive rate for the parasite population in absence of density-dependent control. R_0 is common to the two versions of the model, and is shown to increase more rapidly with the number of fish than with the number of seals involved in transmission. At equilibrium, the number of parasites in fish is also a function of the number of hosts transmitting the parasite. However, the host in which intrinsic regulation occurs is more important, and acts as a limiting factor.

At the first workshop, des Clers proposed that the "Parasite model" be supplemented by a "Host populations model", to describe the dynamics of fish and seal populations in a predator-prey system. This part of the framework would be adapted from May et al. (1979) and Beddington and May (1980). At present, des Clers (1990) argues that the major intrinsic regulation of parasite numbers must be identified, and that the number of different hosts transmitting parasites must be known, before the effect of changes in host numbers can be modelled.

Statistical modelling of sealworm in cod was also presented at the Workshop (Myers and Brattey 1990). Their work showed that it was best to represent the distribution of sealworm with a Poisson lognormal distribution if the fish were disagregated by length. If, however, the fish were described on an age basis a negative binomial distribution provides a better description of infestation.

Future Research — Directions and Recommendations

Field and Experimental Data

Abiotic effects on the parasite have not been addressed by the workshop; they will need future analysis. The most appropriate sampling design to determined trends in sealworm abundance in fish and seal hosts over the large spatial scales involved in the sealworm system also will require more work. Data are most urgently needed to describe *P. decipiens* life-cycle between the adult worms producing eggs and the larvae in the fillets of the fish. It was suggested that the larval worms might suspend development during periods of seal fasting. Without data on the worms actual fecundity, it will be difficult to describe the dynamics of the parasite population accurately.

A catalogue of important parameters is presented in Table 1. It includes the parameters (e.g. parasite or host life-spans) and forcing functions (e.g. time series of sea temperature, fish mortality) that are needed in the development of a general model for a regional infection. An assessment of the current availability of the information is also provided. The code *F*, "Obtainable from further research" corresponds to recommended directions for further data collections, and the code *U*, "Unlikely to be obtainable.." identifies data which are known to be difficult to obtain, therefore pointing towards a possible unrealistic detail in the model description.

In general, the model development has been impeded by the lack of time series with which to estimate parameters concerning the spread of an infection. This is an area where research and ongoing monitoring are essential to further model development.

Model Development

The problem of the complexity of sealworm dynamics might be approached using a variety of models. For the best predictability a sparsely parameterized model is best. On the other hand, a less predictive but more descriptive model requires many parameters. The models developed at the workshop are descriptive rather than predictive.

TABLE 1. Model parameters.

Stage of life cycle	Parameter	Data status[a]
Egg & crustacean hosts	Delay from egg to fish	F
	Survival egg to crustacean	U
	Crustacean mortality	F
	Larval mortality in crustacean	U
	Crustacean density	O
Fish hosts	Susceptibility to infection (/habitat)	QN → F[b]
	Fish biomass/numbers	QN → F[b]
	Time trends in fish abundance	QN → F[b]
	Fish mortality	QN → F[b]
	Fish mortality by parasite	QL
	Parasite mortality	QN → F[b]
	Proportion of infective larvae	QL → F[b]
	Fish to fish transmission	QL → F[b]
Seals	Transmisson rate from fish to seal	QN, F
	Seal numbers	QN
	Seal seasonal behaviour	QN → F
	Seal mortality	QN
	Larval mortality in seal	QN, O
	Adult mortality in seal	QN, O
	Maturation time (& poss. arrested devt.)	QN
	Egg production	QN
	Density-dependency in egg production	F
	Prob. distribution indiv. larval worm burdens	QN
	Prob. distribution indiv. adult worm burdens	QN
	Adult worm sex ratio	QN
	Diet composition by weight/number, per fish sp., season	QL → F[c]
Abiotic	Bottom temperature, seasonal, and regional data	QN

[a] QN = quantitative estimate, QL = quanlitative estimate, O = obtainable from existing data, F = obtainable from further research, U = unlikely to be obtainable in the foreseeable future.

[b] QN for commercially important fish species, U for many non-commercial ones.

[c] Availability of data varies by geographic area and season.

The process of model development should be integrated within a general research program. Both the modelling and experimental aspects benefit from close liaison in their development.

A comprehensive model would include explicitly all known components, parasite sub-populations and hosts, that can be described in detail (for example, see des Clers 1990). Some more precise guidelines are proposed in the following:

1) The model might comprise three sub-models: (i) a parasite population dynamics model, (ii) a seal population dynamics model, and (iii) a fish population dynamics model.
2) The parasite population will be intrinsically controlled by some density-dependent mechanism.
3) The dynamics of the parasite population in the seal are on a shorter time scale than in fish and may require a daily time step.
4) A time delay might have to be incorporated, to describe the maturation process in the seal stomach. Alternatively, a separate model could be developed to describe the dynamics of larval and adult populations in seals, especially on a seasonal basis.
5) The accumulation of parasites in the fish with time will have to be incorporated in the model, to quantify the part of the worm population that is removed by the fishery, and the part that is available to seals.

6) The mortality and life-span as free-living stage or in the invertebrate hosts may be better described as a function of temperature.

Further analysis is recommended for the distribution of worm numbers in individual fish (see Myers and Brattey 1990), especially with regards to the underlying processes (host susceptibility, host response, host and parasite natural mortality and parasite-induced host mortality). Some larvae may loose their infectivity after a certain period of time, some may end up in fish too large to be eaten by a seal. The determinants and dynamics of these processes should be investigated further. The negative binomial distributions of larvae in fish and in seals used by des Clers are purely descriptive. They are not substantiated by a quantification of the infection process. A truly probabilistic model for the accumulation of larvae in the various hosts would further the understanding of the spreading of an infection. Of course, it is impossible to specify which models will be most effective and novel attempts are encouraged.

Model Validation

Model validation may be accomplished by comparing data from different areas as well as by comparing predictions for a given area. The descriptive capabilities of the model should be robust enough to be valid without requiring changes in their structure for each region. A first step in such a validation would be to apply the same basic model to a number of areas and examine the sensitivities of parameters.

Validation of the models as predictive tools to assess management interventions is a different matter. The models should be tested for their capacity to describe the historic evolution of an infection. Time series of the necessary data do not exist at the moment. In this context, validation could be accomplished by small-scale (tractable) experiments. This might be done by either introducing an infection into an area which had previously been clean or by modifying the structure or size of one or more host populations in a sufficiently closed region.

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A Synthesis to Explore Internal Consistency and Sensitivity of Sealworm Dynamics.

R. K. Mohn

Department of Fisheries and Oceans, Biological Sciences Branch,
P.O. Box 550, Halifax, N.S., Canada B3J 2S7

MOHN, R. K. 1990. A synthesis to explore internal consistency and sensitivity of sealworm dynamics, p. 261-272. In W. D. Bowen [ed.] Population biology of sealworm (*Pseudoterranova decipiens*) in relation to its intermediate and seal hosts. Can. Bull. Fish. Aquat. Sci. 222.

A model of sealworm dynamics is constructed which integrates the major observations of the parasite's life history and hosts for the Sable Island area. The purpose is twofold: (i) to assess internal consistency of the various observations within the model framework and (ii) to provide an environment to test the dynamics and sensitivity of the modelled system. The exercise showed that there was sufficient agreement in the observations to allow the construction of the model but that there appears to be discrepancies in the seal infestation rate and in the stability of the modelled sealworm population. The poor stability is the result a lack of density dependant controls acting on the sealworms. The sensitivity analysis addresses errors or uncertainties in parameter estimation and the efficiencies of interventions. The results show that the model is very sensitive to the seal to fish transmission rate, a parameter which is not directly estimable. The sensitivity of interventions compares a cull regime and two hypothetical drug regimes.

Un modèle de la dynamique du ver du phoque intégrant les principales observations sur le cycle biologique et les hôtes du parasite dans la région de l'île de Sable a été construit. La modélisation vise (i) à évaluer la cohérence interne des différentes observations dans le cadre du modèle et (ii) à fournir un milieu pour tester la dynamique et la sensibilité du système modélisé. Il a ainsi été montré que les observations étaient assez cohérentes pour construire le modèle, mais que des écarts semblaient exister dans le taux d'infestation des phoques et la stabilité de la population de vers du phoque modélisée. La faible stabilité résulte de l'absence de contrôles de densité sur les vers du phoque. L'analyse de sensibilité porte sur les erreurs ou les incertitudes dans l'estimation des paramètres et l'efficacité des interventions. Les résultats révèlent que le modèle est très sensible au taux de transmission du parasite, lequel ne peut être estimé directement. Les interventions comprennent l'abattage sélectif et l'administration hypothétique de vermicides.

Introduction

The purpose of this study is to combine the wide range of biological information concerning sealworm dynamics into a cohesive unit. The word "synthesis" in the title is used in place of the more traditional words "model" or "simulation" to emphasize the drawing together of observations and assumptions on various levels of organization. Braitenberg (1986) introduced the concept of synthesis in modelling psychological phenomena, a situation in which there was many parameters and insufficient data for classical analysis. A situation which is quite similar to sealworm dynamics. An important distinction between this synthesis and traditional population modeling is that we do not try to reproduce a time series. The requisite time series for the respective hosts and burdens do no exist. Thus, an alternative approach is required. The purpose of our synthesis is to reveal areas of internal inconsistency in our understanding of data. Also, a sensitivity analysis is carried out for the purpose of identifying critical parameters and to aid in the comparison of management strategies. The sensitivity analysis is not intended to be exhaustive, but rather to demonstrate the scope of sensitivity analysis applied to the simulation.

An animal which inhabits distinct environments at various life stages is said to exhibit a complex life cycle (Wilbur 1967). *Pseudoterrenova decipiens* would typically have three distinct environments (hosts) in addition to a period in the open environment. Such a high degree of complexity is reflected in the complexity of the resultant simulation. The sealworm's hosts are invertebrate, fish and mammalian. Observations have been made on the incidence of sealworm in various fishes (McClelland 1985, 1987) and in seal stomachs and fæces (Stobo et al. 1990). The dynamics of the seal populations, and specifically for the Sable Island area, have been reported in Mansfield and Beck (1976) and Zwanenburg and Bowen (1990). For many aspects of the sealworm's life, direct biological information is not available and assumptions or inferences must suffice; for example, the feeding preference of a 2-yr-old seal when offered equal opportunities to feed on pelagic or demersal fish.

The synthesis follows sealworm larvae in fish and the subsequent maturation in seal stomachs. No attempt is made to incorporate a description of the phases from eggs to fish except as a time delay. A single seal stock, based on the Sable Island grey seal herd, is the sole mammalian host for the parasites. Five fish groups are in the current synthesis; these are large and small cod, flatfish, pelagics and small demersals. The resolution of the temporal scale is quarter of a year and simulations are typically for 10 yr.

Any attempt to describe such a complex situation has a number of consequences. First, there is no unique or even "best" model. One of the definitions of complexity is that many models are possible of a single real (complex) system (Rosen 1985). Another consequence is that this paper cannot stand alone. The work attempts to synthesize the observations of many authors. Because the synthesis is broad in scope the coverage of the biological bases is not presented in depth and the interested reader is referred to other manuscripts (many of which were presented at the sealworm workshops and are published in this volume).

Methods

Computer models are used to synthesize the sealworm dynamics. Simulations were written in two languages (APL and FORTRAN) for two computers using different operating systems in an attempt to minimize the possibility of errors in software. Each version has its advantages. The FORTRAN version, developed for a Macintosh environment, executes more quickly and incorporates graphics. The APL version, developed in an MS-DOS environment, is more easily developed and more versatile, especially for sensitivity analysis.

The model contains a series of modules and interfaces amongst them. Figure 1 presents a schematic of the sealworm system and Fig. 2 is a schematic of our synthesis. The modules are (i) seal population dynamics, (ii) sealworm production in seals, and (iii) seal worm dynamics in fish. Each of these will be presented in turn and then the interconnections described. The concepts of parameter and state variable will be introduced as they are fundamental to sensitivity analysis. Parameters are defined as those quantities which typify a specific modelled entity, for example the natural mortality of seals. State variables indicate the status of aspects of the model, for example the number of pups born in a given year. Appendix A is a list of the parameters and state variables, their definitions, dimensions, and reference values. The variables and parameters are listed alphabetically by their mnemonics which are included below in parentheses. Mnemonics beginning with S, F, or W refer to seals, fish, or worms, respec-

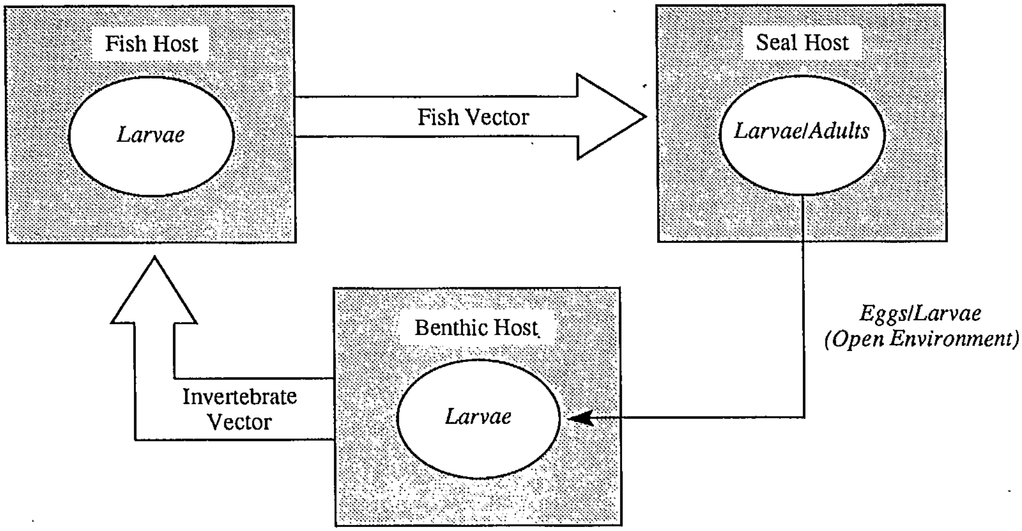

FIG. 1. Schematic of sealworm system showing the three distinct hosts. The broad arrows denote that many species are involved in the vector.

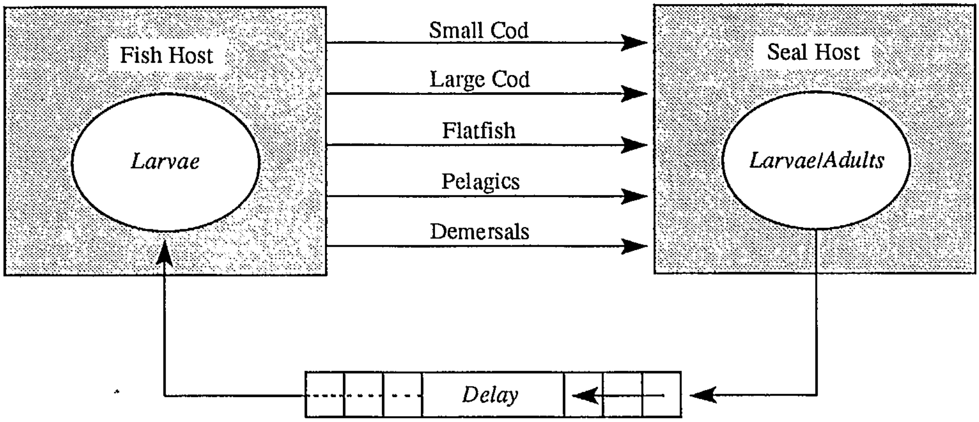

FIG. 2. Schematic of the sealworm system model. The benthic hosts and invertabrate vector have been greatly simplified from Fig. 1 and the fish vector has five distinct elements.

tively. Those ending in Q refer to quarterly or seasonal parameters and those ending in AA refer to values that vary with age.

The seal dynamic module is age structured and operates similarly to a Leslie matrix (Leslie 1945). There are six age classes, 0 through 4 and 5+. Natural mortality at age (SMAA) and maturity ogive (SRAA) are taken from Zwanenburg and Bowen (1990) and a 50:50 sex ratio is assumed. A logistic production model is assumed for seals with a seal carrying capacity (SCC). At the first of each year a biomass is estimated from the product of numbers at age and seal weight at age (SWAA) and is compared to the carrying capacity. If a cull is desired the cull mortality is also a function of age (SFAA). The number of pups is calculated from the maturity ogive, number of females and a density dependant term (the biomass in relation to the carrying capacity). Survivorship is updated on a quarterly basis. Natural mortality and cull, if any, take place simultaneously after whelping.

In order to keep the model simple, fish stocks are not expressed dynamically. Instead, a predetermined pattern is supplied for each species-size class on an annual basis. The model currently requires that patterns be specified for each of the five fish classes. If a simulation were run for longer than a specified pattern, that pattern is repeated as often as required. A matrix (FFI) is also specified which describes the transmission and retention of larval sealworms from macro-invertebrates to fish and from fish to fish. A positive number (or zero) is used to show the transmission from a potential source to a given fish class. The sources are the fish themselves and an influx from the macro-invertebrates. The influx is modelled as a time delay which corresponds to the time spent from eggs until ingestion by a fish host. For each class of fish there is a negative number which is a turnover rate. The turnover includes the death of fish, the death of larvae in the fish and the influx of fish. Algebraically, the new worm burden for the classes of fish is found by the matrix multiplication of the FFI matrix and a vector composed of the influx from the delay and the old values of the fish worm burdens (WBF_t).

$$WBF_{t+1} = FFI \times (\text{Influx}, WBF_t) \tag{1}$$

The seals are assumed to have a daily ration of 5 % of body weight, or approximately a factor of 4.6 times the body weight per quarter annum. A matrix is defined which contains food item preferences (SFI) for each seal age class, for each fish category and by quarter annum. The proportion of each of the fish classes in the total ration (TR) is the product of the food item preferences and the fish class abundances.

$$TR_a = \sum_i SFI_{a,i} \times FV_i \tag{2}$$

where a denotes age and i is an index of fish classes. After the composition of the total ration has been determined it is scaled to the appropriate daily ration. The susceptibility of seals to infestation and worm natural mortality in the seal gut are also specified as functions of seal age (WDS). In each quarter, the preferences are multiplied by the fish abundances. The product is then scaled to the total ration for each seal age class and the associated worm burdens of the diet are found. Food is assumed to be sufficiently abundant that reduced rations do not occur.

The number of mature worms is the product of worms in seal stomachs times a quarterly maturation fraction (WFM). Egg production is the product of all the mature worms in all seal stomaches. The transmission from eggs to fish, via invertebrate hosts, (TRANS-EF) is modelled as a single factor which accounts for the overall loss. The value for the transmission loss, or even its order of magnitude, is unknown. However, its magnitude may be inferred by comparing the modelled egg production to the subsequent fish worm burdens. The egg production is a large number and the loss in the is a small one. The product is chosen so that the subsequent infestation of fish is at a reasonable level. In our results the egg production is expressed in terms of subsequent infestation rate in fish in units of larvae per Kilogram, that is it has already been multiplied by the transmission loss factor. Also, there is a delay between egg production and expression in fish of up to 2 yr. An additional factor in the determination of sealworm production is a exchange term between Sable Island and Gulf of St. Lawrence seals (SEXQ). The mixing is a function of season and sealworm production is reduced by the influx of relatively cleaner seals from the Gulf later in the year.

The state variables and the worm delay require a set of initial values to start the simulation. They are also given in Appendix A.

The program currently saves 10 of the state variables for either plotting or sensitivity analysis. They are:

1 seal biomass,
2 seal cull,
3 seal recruitment,
4 seal numbers,
5 worm egg production,
6 worms in benthic stage,
7 average worm burden in fish,
8 worms in seals,
9 cull effort and
10 worm burden in large cod.

Sensitivity analysis is a measure of the influence of the parameters on state variables. Sensitivities are estimated by running a base run, saving the results, changing a parameter, rerunning and then comparing the resultant state variable. For convenience the sensitivities are relative values, which are the differences between the rerun and the base run divided by the base run value and expressed as percentages. We will use sensitivity analysis in two different ways. First, to investigate the sensitivity of our results to uncertainty in the parameters used. One would pose a question such as "How important is an uncertainty of 10 % in the seal natural mortality to the final results?". Such information could be used to guide future research by focussing on more important parameters. Secondly, sensitivity is used to compare the efficiency of interventions.

Parameter Estimation

The parameters (see Appendix A) expressing seal natural mortality and reproduction are taken from Zwanenburg and Bowen (1990). In order to reproduce the 13 % annual rate of increase the seal carrying capacity had to be set to a large (many times the current biomass) value, 100 kt. This carrying capacity results in an average rate of increase of 12.6 % for the first 5 yr of a base run. The starting numbers of seals are derived from a 1987 pup production of 7 500 animals (Stobo and Zwanenburg 1990). If pups represent 20 % of the herd, this would imply 37 500 animals which have been distributed over the 5 non-pup age classes. The seal weights at age are from Mansfield and Beck (1976). The partial recruitment for a cull is such that 2/3 of the effort is applied to pups and 1/3 to the remaining age classes. Seal food preferences allow the specification by seal age and season for each fish class. In the absence of empirical information the base run sets these preference the same for all ages and seasons. Fish abundances are difficult to ascertain for the Sable Island area. Mills and Fournier (1979) estimated a 3 to 1 ratio for demersal to pelagic biomass. Sinclair et al. (1984) review research survey biomass estimates for the Scotian Shelf which allows one to draw inferences about the relative abundance of cod, flatfish and other demersals. Based on these references, the assumed distribution is 9, 9, 18, 25, 39 %, respectively, for small cod, large cod, flatfish, pelagics, and small demersals. It is seen that cod are equally partitioned into large and small as these measure are relative to a seal's diet. Flatfish biomass is set equal to cod biomass and the pelagics are 1/3 of the demersal biomass. Sinclair et al. (1984) used a smaller proportion of cod to demersal biomass for the entire Scotian Shelf, but their fig. 2.b shows relatively higher concentrations of cod in the Sable Island area.

The proportions of the fish classes in seal's diets are also difficult to ascertain. Occurence data for Sable Island seals (Benoit and Bowen 1990) show approximately equal occurrences of cod and flatfish. The cod occurence level is roughly twice the pelagic level and about half of the remaining finfish level. This incidence of pelagics is much larger than one would expect from European data (Group Report 2, Table 1). Also, the European results show that sand lance can form the dominant proportion of a seals diet, a species for which we have no biomass information. Dietary contributions were set at 19 and 2 % for small and large cod, and 24, 13, and 41 % for flatfish, pelagics, and other demersals. With the fish abundances and dietary components set, the food preferences can be found algebraically. The resulting preferences are a 40:5:25:10:20 relationship for small cod, large cod, flatfish, pelagics, and other demersals.

The worm burdens in fish are modelled from the influx from invertebrates and an assumed trophic hierarchy among fish. Group Report No. 1 shows a high variance of worm burdens for the fish within any one of our classes, or indeed for a single species. The following were chosen as reasonable averages (in terms of #/kg round): 5 for small cod, 15 — large cod, 15 — flatfish, 1 — pelagics 20 for other demersals. If one assumes an influx of worms which would cause a fish burden of 10/kg then the fish interaction matrix may be determined to yield the above levels. The first column of the matrix is the transmission from invertebrates and all fish classes except large cod. However, only large cod are modelled to feed upon the other classes.

The initial worm burdens in fish are set at the 10/kg level that was used to determine the fish susceptibility. The delay representing the benthic period was intitialized at the 10/kg level for the first year and 11/kg for the second. Recall that the benthic densities are expressed in terms of subsequent fish infection levels. The susceptibility of seals to worms in their diet and the rate of clearance were initially set at 0.5 and 1, respectively, as suggested by empirical work of McClelland (1980). These values would mean that half the ingested larvae became implanted and that all worms were cleared in a 3-mo period. These values were found to be inconsistent with the other model parameters and in order to have a working model the susceptibility had to be reduced to 15 %. The analogous parameter relating transmission from eggs to fish was set at 10^{-6}, a value determined by varying over a range until fish and seal burdens were close to reported levels.

Results

Results of the modelling exercise are expressed in terms of a base run using the parameters shown in Appendix A and sensitivities relative to the base run. Figures 3, 4, and 5 contain the state variables from the 10-yr base run. The initial seal biomass of 3.8 kt eats approximately 18 t of fish in the first quarter. The initial worm burdens in fish (5, 15, 15, 1, 20) suggest that a 2-yr-old seal which eats 383 kg would also ingest approximately 5 100 worm larvae in the first quarter. The number of worms expected in a 2-yr-old seal would be about a tenth of the number ingested. When compared to the reported susceptibility of 0.5, it is obvious that the time scale of this model

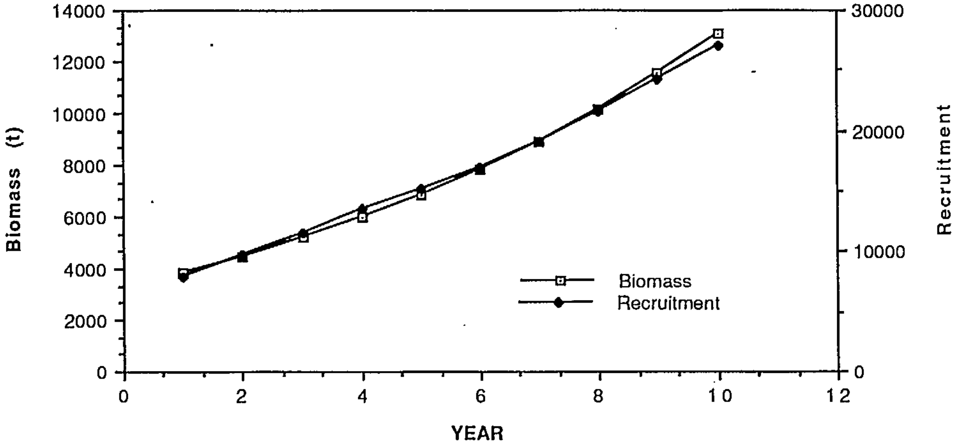

FIG. 3. Seal biomass (T) and recruitement (#) series for the 10-yr base run.

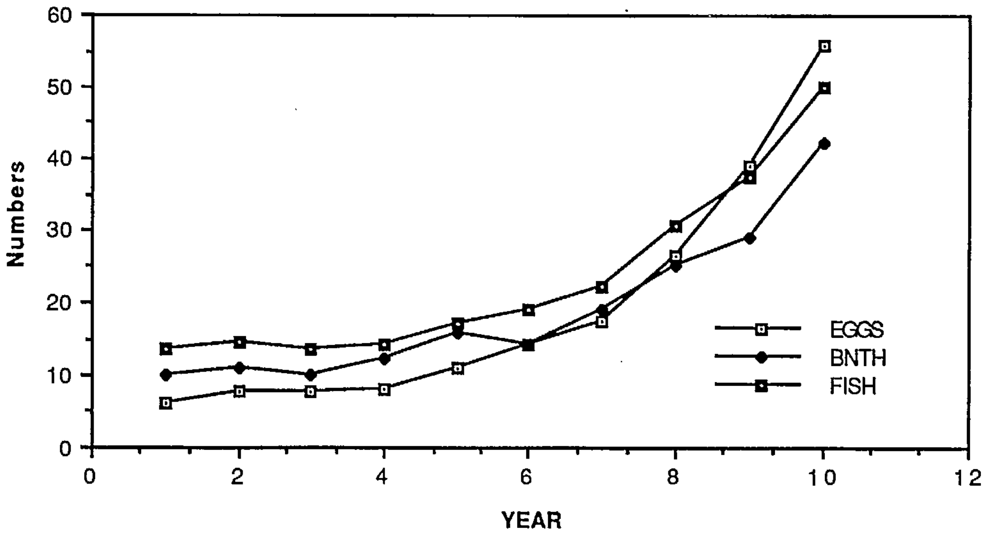

FIG. 4. Worm egg production (EGGS), benthic density (BNTH) and average fish burden (FISH) for the 10-yr base run. The units of all three curves are numbers of sealworms per kg-round of fish. (See text for details.)

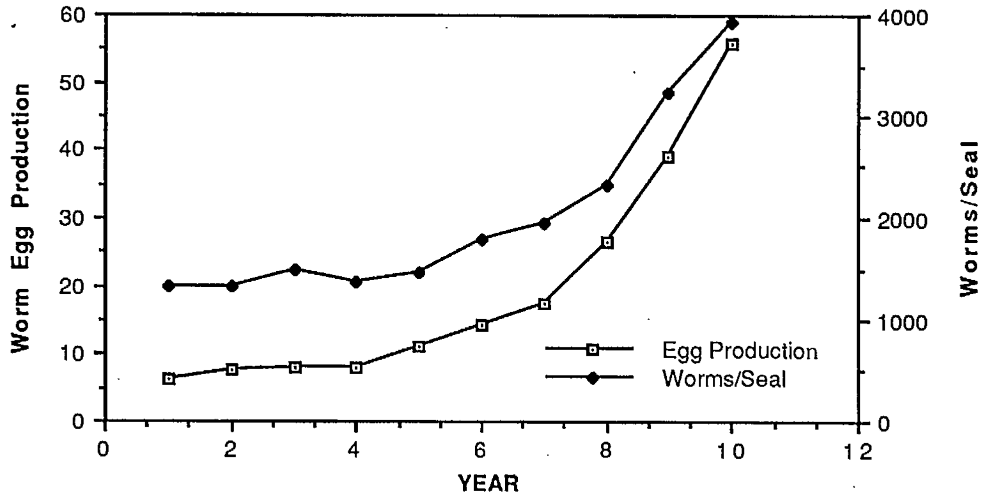

FIG. 5. Worm burden per seal and egg production. The worm burden includes mature and immature animals and is averaged over all seal ages.

is to coarse too describe dynamics in the seal gut or that perhaps 0.5 is too high for seals in the natural environment.

Figure 3 contains state variables related to seal dynamics over the 10-yr base run. The number of seals (not shown) increased at an annual rate of 11 % of the 10-yr base run. The rate of recruitment is seen to increase slightly less rapidly than seal biomass. This is because of the influence of a density dependent term in the seal reproduction.

Figure 4 displays worm related state variables which are seen to increase rapidly over the 10-yr base run. The egg production increases the fastest. The average worm burden in fish increases the slowest but still approximately triples. Over the same period the number of eggs produced increases more than fourfold while the burden per kilogram of large cod increases from 14 to 21.

Egg production and average worm burden in seals are shown in Fig. 5. Egg production increases by approximately fourfold while the worms per seal triples. In the absence of density dependence on seal worms (at any phase of its complex life cycle) or a curb on seal numbers the system soon reaches levels much higher than currently seen. The positive feedback nature of the parasites reproduction is not controlled by any negative feedbacks. The only negative feedback in the model is the weak influence of the seal carrying capacity.

Two groups of sensitivity analysis have been carried out with the model, the more classic use, sensitivity to descriptive parameters and sensitivity to a management regime or intervention. The state variables investigated are seal biomass, pup production, worm egg production, worms in the benthos, fish and seals and finally the worm burden of large cod. The sensitivities are assessed over the ten year base run and expressed as percentages (Fig. 6 and 7).

The sensitivity of the parameter describing natural mortality in seals to a 10 % increase is seen to have a modest effect on seal biomass and pup production after a decade (Fig. 6) The increased natural mortality has the greatest effect on sealworm egg production, about 13 %. Worm burdens in fish are only modestly affected. The parameter describing transmission from eggs to fish (Bars marked Egg to Fish Trans) is seen to be much more critical than seal natural mortality to the level of worm burdens. A 10 % increase in the transmission results in a greater than 40 % increase in sealworm egg production. As expected, changing this transmission rate has no effect on the two state variables related to seals. Unfortunately, this more important parameter is virtually unknown and unknowable except inferentially. Finally, the parameter describing large cod susceptibility to sealworm larvae has only a small effect on the worm abundance

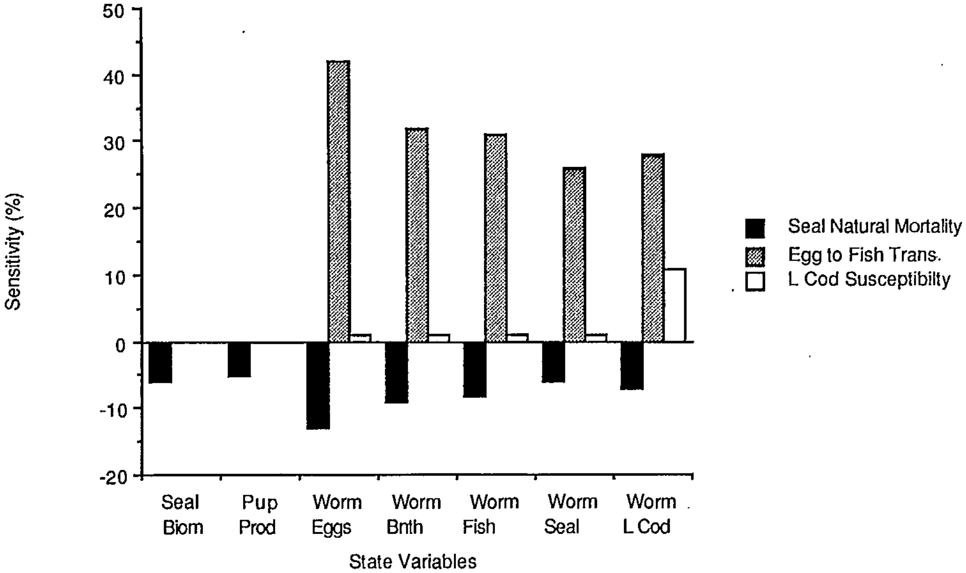

FIG. 6. Sensitivity of seal biomass, pup production, egg production, worms in benthos, worm burden of fish, worm burden of seals and worm burden of large cod (the figures columns from left to right) to 10 % increase in seal natural mortality, egg to fish transmission rate and large cod susceptibility.

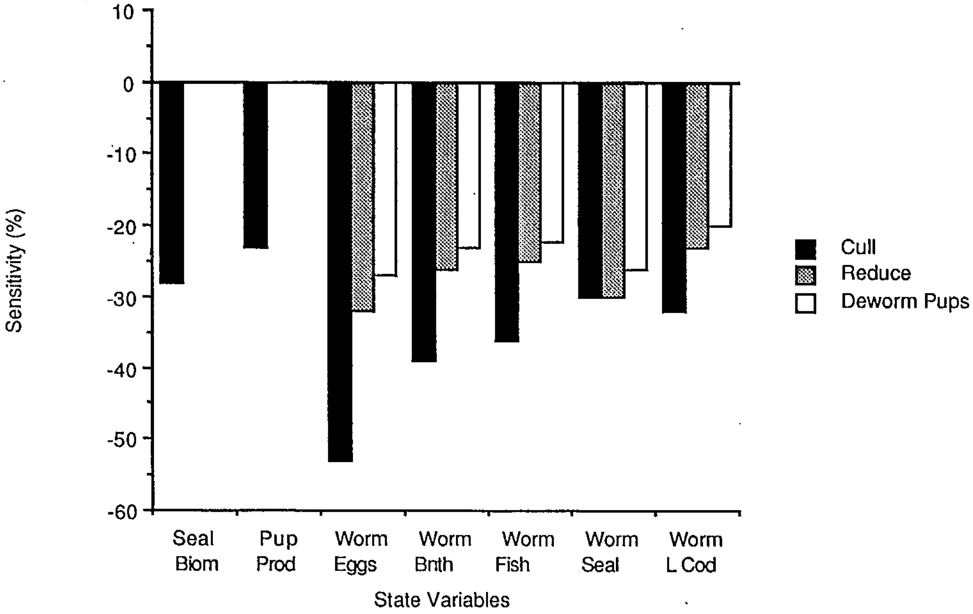

FIG. 7. Sensitivity of seal biomass, pup production, egg production, worms in benthos, worm burden of fish, worm burden of seals and worm burden of large cod (the figures columns from left to right) to interventions. The first intervention is a cull primarily of pups, the second is the administration of a drug which reduces worm infection rate by 10 % (Colomn labeled "Reduce") and the third is the administration of a drug which deworms pups for a year (Column labeled "Deworm Pups").

anywhere in the simulation, except in large cod. This reflects the "dead end" nature of large cod from an epidemiological point of view.

The intervention via a cull having an instantaneous mortality rate of 0.2 on pups and 0.02 on older animals for 10 yr yields the sensitivities in the colomn marked Cull in Fig. 7. The seal biomass is seen to drop 28 %, the sealworm egg production by 53 % and the average burden in fish falls 36 %. The large cod respond more slowly than fish on average with a decrease of 31 %. A fictitious drug which reduces the susceptibility to infection of seals by 10 % is displayed in the bars marked Reduce. Such an intervention reduces the worm burden by about 30 % in the modelled system. This agent is applied throughout the 10-yr simulation. A second intervention of a drug which deworms pups for 1 yr is shown in the bars marked Deworm Pups. This intervention is slightly less effective than the other and both have less effect than the cull. As expected, the sensitivities of such interventions are zero on the first two state variables which are related only to seal population dynamics.

Two other sensitivity results are of interest. If the initial starting numbers of seals are halved, after 10 yr, the resultant sealworm egg production is reduced 90 % and the large cod worm burden goes from 50 to 7 worms/kg. This shows the non-linear nature of the positive feedbacks in the model. Also, the parameter SEXQ (Seal EXchange Quarterly) in the base run assumes about a 50 % exchange during the 3rd quarter and 20 % in the 4th. The models response to eliminating all exchange is a 43 % increase in worm egg production and a 31 % increase in the large cod worm burden.

Discussion

The model allows investigators latitude in describing sealworm dynamics, significantly more latitude than data can support. Diverse observations are synthesized into a single simulation and more detail would be required if "realistic" fish population dynamics or if a closer description of sealworms in their mammalian hosts were desired. The goal was to provide a vehicle for others and for this reason the model has much more detail than would normally be warranted, especially for predictive purposes. The extra detail does not degrade the model's performance but it may lead to false interpretation based on the inappropriate inference that a model which includes more detail is superior to a simple description. Indeed, simpler models often have more predictive power than complex ones.

The "black box" nature of our understanding of the dynamics of the sealworm life cycle from egg to subsequent expression in fish is an obvious shortcoming. It would be difficult to design a research program that would aid in quantifiably elucidating this parameter. The egg to fish transmission was determined in the model by varying it and the functionally related seal susceptibility parameter until there was general agreement in the observed quantities. Although indirectly determined, the resulting value allows the model to run and sensitivities to be determined. In a preliminary, and unreported, attempt at fitting the model to the data the egg to fish transmission was fixed at less than half the current value and the fish to seal transmission was compensated upward. None of the six sensitivities differed by more than 2 % from those shown in Fig. 6 and 7. This observation allows us to attach some confidence to the sensitivities, even though the exact parameter values are difficult to estimate.

Survivorship and host infection are undoubtedly affected by environmental factors, e.g. advection or temperature. The model was designed with the ability to manipulate temperature, but, because of a lack of appropriate information or hypotheses the base run and subsequent analysis did not use this attribute.

The information upon which the model and the base run were developed does not seem consistent. Two major areas of inconsistency were encountered. The first is the disagreement between reported seal susceptibility to worm infestation and the lower values which were required by the model. With regards to the modelled system, one fault is that the time scale is too coarse for the dynamics of sealworms in seals. Also, infestation rates in seals in the wild may be lower than those measured in captivity and there is still a great deal of idealization in the seal ration portion of the model.

The second area of inconsistency is the tendency for the modelled sealworm abundances to "explode". Current levels of infestation and their rate of increase are not compatible. If the current level is fit the growth of infestation is unreasonably high. On the other hand if the growth rate is reduced, then the infestation level is not consistent with current observations The tendency to explode is the result of a lack of negative feedback controls in the modelled system. The positive feedback of the worms, more worms yields more eggs, more eggs yields more worms, etc. must be constrained inside an envelope of negative feedback, usually expressed in density dependent terms. Theoretical and real examples of positive feedbacks constrained by negatives are Lotka-Volterra equations and the spruce budworm epidemics (Caughley and Lawton 1981). The only density dependence we have assumed is a carrying capacity for seals. The carrying capacity is set much higher than the current seal biomass as a high level is required to reproduce the currently observed high rate of increase in the Sable Island herd. As a result sealworm abundances in our model have nothing to constrain them. Negative feedbacks on sealworms may take place in seal stomachs, increased mortality of fish hosts or some other density dependent process. In the absence of empirical bases, it was considered inadvisable to speculate on such mechanisms and they are not included in the model. Our results suggest more density dependent processes should exist than we have incorporated in the synthesis. Their nature cannot be inferred from this study and empirical bases have not been reported, but the seal's gut is probable site.

Another observation that would appear to need reconciliation is the ratio of larval to adult worms in the seal stomachs. We did not attempt to model sealworm dynamics in the seal's stomach but this discrepancy came to notice when data were being prepared. The larval/adult ratio was used on a seasonal basis to estimate egg production. McClelland (1980) suggests that larvae and adults have equal residence times, about 3 wk each. However, the larvae are much more prevalent (Stobo et al. 1990). This suggests a high larval mortality that has not been reported or that some other unknown factors are operating.

The basis system schematic, Fig. 1, is quite similar to that of des Clers (1990) but the resultant model differs considerably. This is a consequence of the complex nature of the underlying system which means many descriptions are possible. The multitude of possible models will be diminished as more data becomes available to judge their appropriateness. Future work should include more modelling as well as empirical studies. An obvious area would be sealworm dynamics in the seal's gut. Some data exist and the results would aid other modelling initiatives. This study is a early attempt and it is hoped that it will aid future theoretical and empirical studies; it is not meant, not able, nor should it be used, to evaluate management options.

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APPENDIX A. Principle parameters, state variables and initial values used in the base run.

Mnemonic	Value(s)	Dimension	Comment
CEF	-	t^{-1}	Fishing mortality on seals — Cull
DFILTER	0 0 0 0 0 0 0 0 1	—	Coefficients determining delay duration
FFI_1	7-3 0 0 0 0	—	Fish predation matrix for small cod
FFI_2	.0 .5-.2 .5 .3	—	Fish predation matrix for large cod
FFI_3	2 0 0-.3 0 0	—	Fish predation matrix for flatfish
FFI_4	.1 0 0 0-.3 0	—	Fish predation matrix for pelagics
FFI_5	3 0 0 0 0-.3	—	Fish predation matrix for demersals
FIQ	1.2 .7 .9 1.2	—	Quarterly ration profile
FQ	.7 .3 0 0	—	Quarterly cull effort distribution
SCC	100000	mt	Seal carrying capacity
SEXQ	1 1 .75 .9	—	Seal exchange between Gulf and Scotian Shelf
SFAA	1 .1 .1 .1 .1 .1	—	Seal cull partial recruitment
SFI	.4 .05 .25 .1 .2	—	Seal-Fish dietary preferences (by age and Quarter)
SIN	7.5 6 5.5 5 4.5 9	#'000	Initial seal numbers at age
SRAA	0 0 0.08 .35 .45	—	Seal maturity ogive (50:50 sex ratio)
SWAA	50 50 70 90 100 150	kg	Seal weight at age
WBFIN	5 15 15 1 20	#/kg	Initial fish worm burden (round)
WBSIN	500 720 840 940 1080 2000	#/seal	Initial seal worm burdens
WDELIN	10	*	Initial value in worm delay
WDS	.15 1	t^{-1}	Worm uptake and loss in seal, all ages.
WFM	.15 .25 .5 .2	—	Worm fraction mature by quarter
TRANS-EF	1.E-6	—	Worm transmission factor — eggs to fish

* Units are described in text.

— Dimensionless quantity.

Modelling the Life Cycle of the Sealworm (*Pseudoterranova decipiens*) in Scottish Waters

Sophie des Clers

Renewable Resources Assessment Group
and Parasite Ecology Research Group
Imperial College, 8 Prince's Gardens, London SW7 1NA, U. K.

DES CLERS, S. 1990. Modelling the life cycle of the sealworm (*Pseudoterranova decipiens*) in Scottish waters, p. 273–288. *In* W. D. Bowen [ed.] Population biology of sealworm (*Pseudoterranova decipiens*) in relation to its intermediate and seal hosts. Can. Bull. Fish. Aquat. Sci. 222.

A model of a sealworm (*Pseudoterranova decipiens*, Anisakidae, Nematoda) population describes the dynamics of four parasite sub-populations: one free-living and three parasitic stages. Three successive hosts are taken to be necessary for the parasite to complete its life cycle, a benthic invertebrate, Atlantic cod (*Gadus morhua*) and the grey seal (*Halichoerus grypus*). It is assumed that parasite numbers are intrinsically regulated. Two versions of the model describe two possible modes of density-dependent regulation: parasite-induced fish mortality, and reduced parasite fecundity in seals. Both versions predict infection levels in seals and cod in Scottish waters. The parasite population's reproductive rate increases faster with the number of fish than with the number of seals. However, at equilibrium, the overall number of parasites increases more acutely with the numbers of the host in which intrinsic regulation occurs. As parasites accumulate along the food chains, they are most numerous in individual seals. Hence intrinsic regulation will be more efficient at this level.

Un modèle d'une population de ver du phoque (*Pseudoterranova decipiens*, Anisakidae, Nématodes) décrit la dynamique de quatre sous-populations de parasites, un stade libre et trois stades parasitiques. Il semble que trois hôtes successifs soient nécessaires au parasite pour achever son cycle biologique, un invertébré benthique, la morue franche (*Gadus morhua*) et le phoque gris (*Halichoerus grypus*). On pense que l'effectif des parasites est soumis à une régulation intrinsèques. Deux versions du modèle décrivent deux modes possibles de régulation en fonction de la densité: mortalité du poisson induite par les parasites, et réduction de la fécondité des parasites chez les phoques. Les deux versions prédisent les taux d'infestation des phoques et des morues dans les eaux d'Écosse. Le taux de reproduction de la population de parasites augmente plus vite en fonction du nombre de poissons qu'en fonction du nombre de phoques. Cependant, à l'équilibre, le nombre global de parasites croît plus nettement en fonction de l'effectif de l'hôte chez lequel se produit la régulation intrinsèque. Les parasites s'accumulant le long de la chaîne trophique, leur effectif est maximal chez les phoques pris individuellement. La régulation intrinsèque sera donc plus efficace à ce niveau.

Introduction

The sealworm (*Pseudoterranova decipiens*) has a complex life cycle and has to go through several hosts to develop and grow before being able to reproduce in seals. A model parasite population is designed to provide a better understanding of sealworm population dynamics and ultimately, to analyse the relation between numbers of parasites and numbers of hosts. The biological details of the model correspond to the current understanding as reflected in the working group reports of this volume. However, in this first attempt, host numbers are fixed and it is only the transition between parasite sub-populations which is studied. The model describes an equilibrium level of parasitism for an arbitrarily set number of hosts.

Life Cycle and Parameter Values

Only three hosts are assumed to be instrumental in parasite transmission in Scottish waters (Fig. 1); a benthic crustacean, Atlantic cod (*Gadus morhua*), and grey seals (*Halichoerus grypus*). The parasite is transmitted through predation, which is taken to modify only the numbers of parasites in each host or stage. All host numbers are kept constant, with a dead host, infected or not, replaced by an uninfected one. The transition rates for the parasite through the stages of its life cycle are functions of individual rates of transmission, numbers of predators and numbers of parasites in all prey.

Host numbers in the model are fixed arbitrarily at 100 seals, 100 000 (10^5) fish and 100 000 000 (10^8) crustaceans. In seals, the larvae mature to adult male and female worms with a sex-ratio around 1 (Stobo et al. 1990). Fertilised eggs (7 000 per female per day, during 3 wk, McClelland 1980) develop and are passed with the faeces to seawater where they sink. In crustaceans, the larvae are assumed to live for 3 months, as long as their hosts. Parasite numbers do not increase in hosts through reproduction, and sub-population sizes (in a host or free-living) at any time, are given by the number of larvae transmitted from the previous sub-population, less the number that dies or is lost due to host mortality. A further proportion of the survivors may not develop to become infective, or reach maturity. In fish, larvae have a low death rate, assumed negligible because of the short average life span (around 18 months) of cod in U. K. fisheries. Most parameter values that determine parasite transition between sub-populations can be obtained from experimental (e. g. life span of free-living larva) and field data (e. g. egg production per female, life span of cod). Values for these parameters

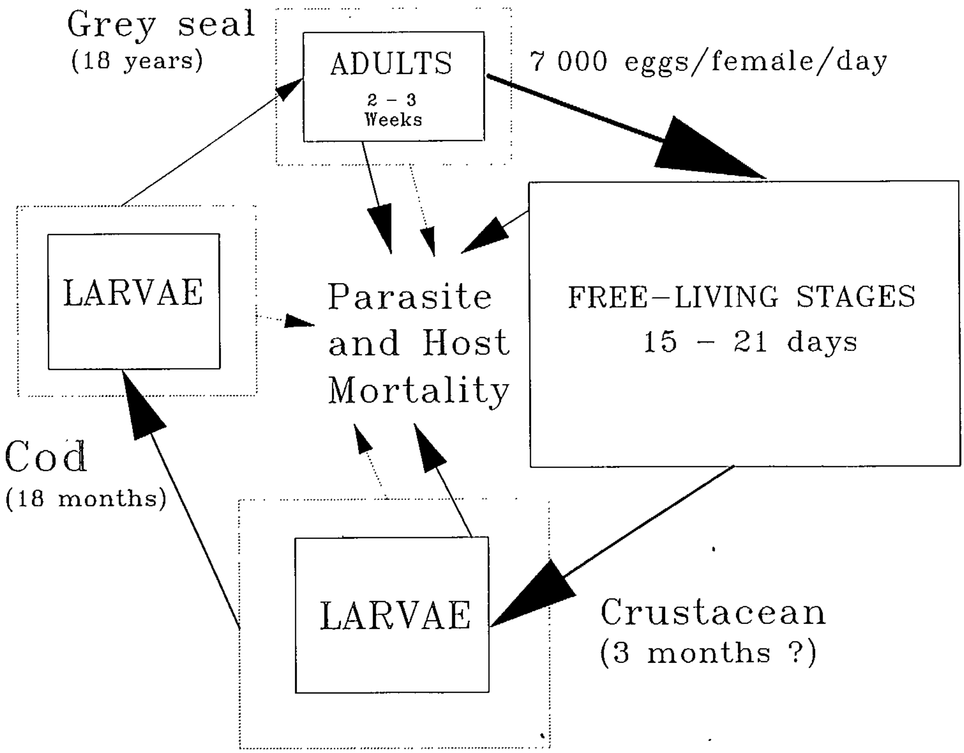

FIG. 1. Flowchart of the sealworm (*Pseudoterranova decipiens*) model with an indication of assumed average life-spans of the parasite at each stage of its life cycle.

are given in Table 1. Existing data on parasite numbers in grey seals and cod in Scottish waters unfortunately do not relate to hosts at the same time and place (Table 2).

TABLE 1. Parameter values. (All rates are per capita for parasite and host, and per day.)

S	number of hosts	100 seals
prs	% larvae-> adults	60 %
pms	adult parasite mortality in seals	1/(21 d)
sm	seal mortality	1/(18 yr)
F	number of hosts	10^5 fish
prf	% infective larvae	60 %
fm_0	natural cod mortality	1/(5 yr)
fhm	fish harvesting mortality	1/(18 mo)
pmf	parasite mortality in fish	0
C	number of hosts	10^8 crust.
prc	% infective larvae	10 %
cm	crustacean mortality	1 (3 mo)
pmc	larva mortality in crust.	0
$0.5Ep_0$	Egg production Sex ratio	3 500 /worm/d 1
pre	% eggs hatching to L2	1 %
em	Egg mortality	1/(3 wk)

Negative binomial distribution of parasites per host

Adults in the seal: $ks = 0.3$ (version S)
Larvae in the fish: $kf = 0.28 \times Pf/F$ (average worm burden, version F)
NOTE: The egg production parameter, $0.5Ep_0$ is, with a patency pms of 21 days and a sex ratio of 1, equivalent to $3500 \times 2 \times 21 = 147\,000$ eggs by one female)

TABLE 2. Infection levels reported in cod and grey seals from Scottish waters.

Average adult worm burdens per grey seal

Location	Sample size	Average	Range	Reference
Orkney Is.	8	179	(0-543)	Young and Lowe (1969)
Farne Is.	10	167	(28-380)	Prime (1973)
Scottish waters	9	58	(0-350)	Wootten (1973)

Average larval burden in 2-yr-old cod

Location	Av.	Prev.	Reference
Clyde	0.77	20.5 %	Wootten and Waddell (1977)
Moray Firth	0.34	14.7 %	"

TABLE 3. Parameter values estimated through the model.

Exponential density-dependent effects

In seals	$ds = 4.5\ 10^{-3}$	(version S)
In fish	$df = 2.23\ 10^{-1}$	(version F)

Daily rates of transmission (both versions)

From egg to crustacean	tec	$4.76\ 10^{-9}$ /egg/crust
From crustacean to fish	tcf	$1.85\ 10^{-8}$ /crust/fish
From fish to seal	tfs	$5.48\ 10^{-5}$ /fish/seal

It is assumed that the dynamics of sealworm infections are primarily regulated intrinsically, rather than directly by the number of hosts. This typically provides increased parasite population stability and adaptation to survive at low endemic levels, as has been illustrated using simple mathematical models (Anderson 1976). However, there is no evidence to date, of the nature and extent of an intrinsic density-dependent regulation for *P. decipiens*. A further assumption is needed to define a mechanism by which the model parasite population remains stable.

In analogy with helminth infections in man (Bradley 1972; Croll et al. 1982), cattle (Smith 1984), fish (Brassard et al. 1982) or laboratory models (Dobson and Keymer 1985), two mechanisms are considered separately, in two versions of the model. In version *F*, parasites increase the mortality of the host in which they spend most of their life cycle, and overall parasite numbers are regulated through the death of highly infected fish. In version *S*, individual worm fecundity is decreased in seals with high adult worm burdens.

Mathematical Models

A theoretical statistical distribution of the number of worms per host, and a relation for the effect of crowding on parasites are necessary to describe an intrinsic control of parasite numbers.

Statistical Distribution of Parasites per Host

In both fish and seals, the distribution of parasites is assumed to be negative binomial. This theoretical description accounts for large individual differences in worm burdens per host. In fish, most larvae are in just a few hosts, while the majority of fish remain uninfected (see Young 1972; Palsson 1979; McClelland et al. 1983, 1985). Even at relatively high infection levels for Scottish waters, with 27 % of the cod infected, only 2 % fish harboured more than 20 larvae (Young 1972). Consequently, although an increased mortality of the few fish carrying very large worm burdens can efficiently regulate overall parasite numbers, it can safely be taken to have a negligible impact on fish numbers when compared to other causes of mortality. Values for the negative binomial parameter *kf*, an inverse measure of the degree of aggregation, between 0.01 and 0.6 with average worm burdens between 0.05 and 2 (Fig. 2) describe typical infections of Scottish cod stocks (des Clers and Wootten 1989).

There is too little comparable data for parasites in seals to obtain a frequency distribution of individual worm burdens (Young and Lowe 1969; Prime 1973; Wootten unpubl., 1973). For average adult worm burdens of 75, 100 and 150, the value of the negative binomial parameter *ks* is chosen to be 0.3 to obtain a shape of simulated distributions which complies with infections described in other seal colonies (Fig. 3, Group Report 2 and Stobo et al. 1990).

Density-Dependent Control

In version *S* of the model, worm fecundity decreases exponentially with increasing numbers of adult worms (cf. *Ascaris* infections in man, Croll et al. 1982). The effective number of eggs produced is then a function of the aggregation of parasites in a small number of seals (as described by the average worm burden and the negative binomial parameter *ks*), and of the severity of the exponential effect (parameter *ds*). The resulting expression for the net rate of egg-production is derived in the Appendix. The larger *ds*, the more pronounced the reduction in fecundity. At a given level of heterogeneity (say $ks = 0.3$), an increase in average worm burden will increase the number of highly infected hosts (right-most class Fig. 3). This will result in increased density-dependent control, with a lower egg production per worm (Fig. 4). In absence of density-dependence

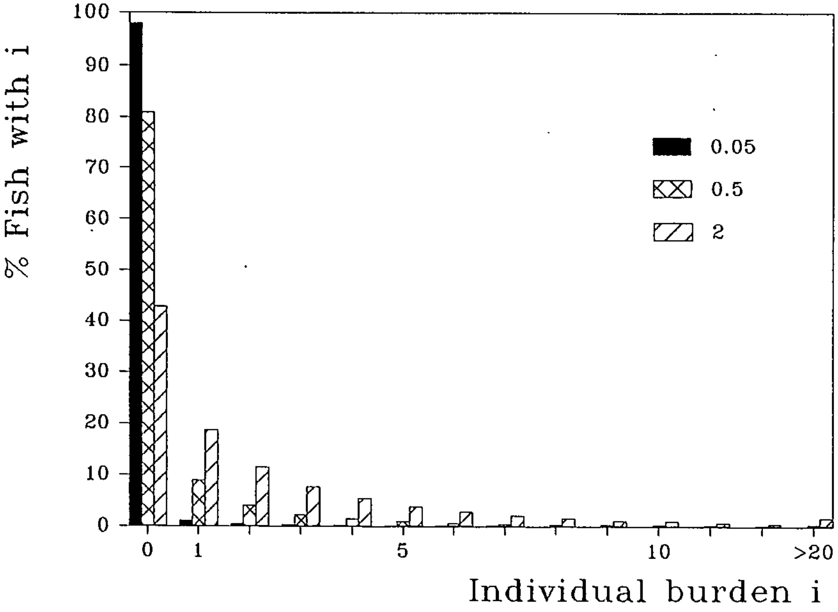

FIG. 2. Theoretical distribution of worm numbers in individual fish, given by three negative binomial distributions with kf = 0.014, 0.14 and 0.56 and average burdens of 0.05, 0.5 and 2 worms per fish.

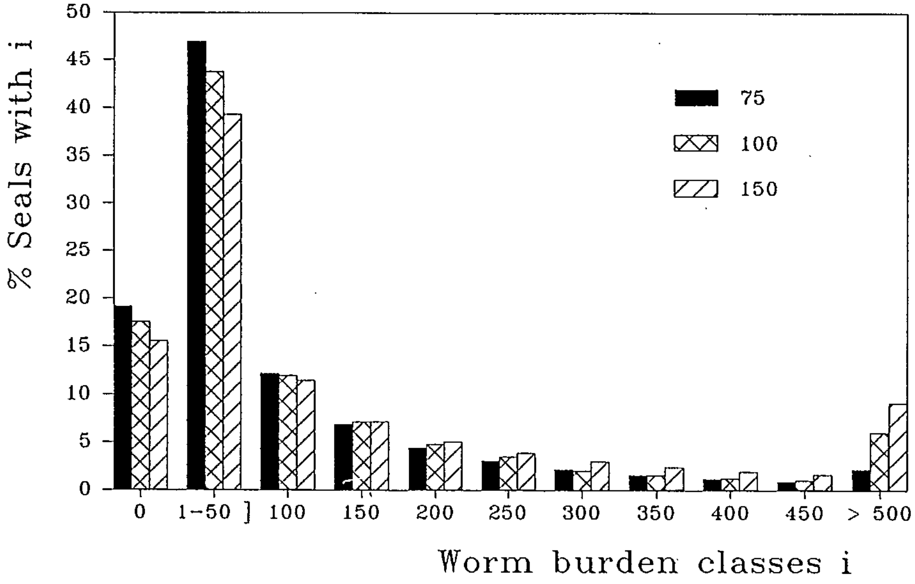

FIG. 3. Theoretical distribution of adult worm burdens in seals given by three negative binomial distributions, with ks = 0.3 and averages of 75, 100 and 150 adult worms per seal.

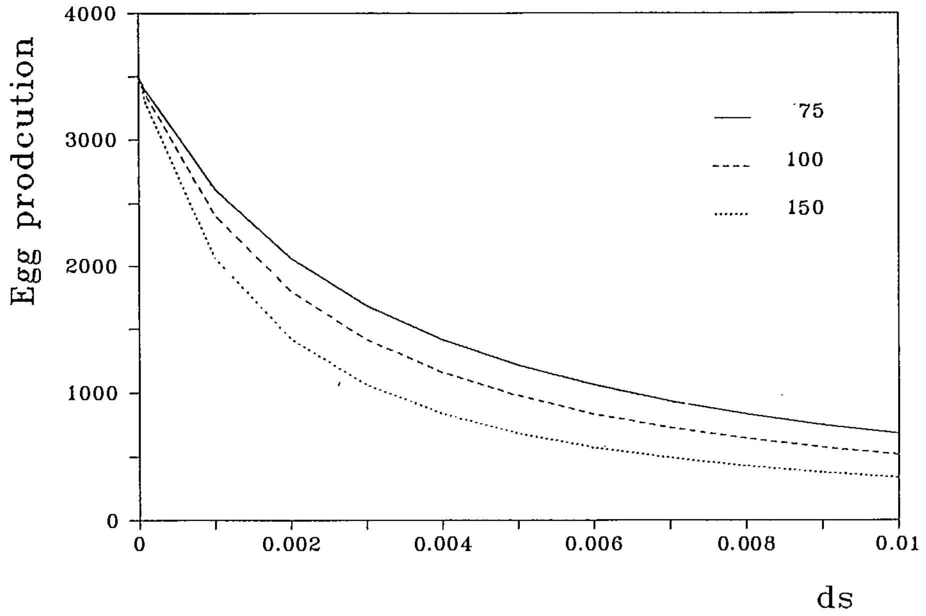

FIG. 4. Egg production (per worm per day) as a function of the density-dependent effect parameter *ps*, for increasing negative binomial densities of 75, 100 and 150 adult worms per seal and *ks* = 0.3.

(*ds* = 0), the egg production per worm (male and female, with a sex-ratio of 1) per day (for 21 d, Table 1) is 3 500.

In version *F* of the model, the density-dependent effect in fish is also chosen to be exponential. Large numbers of worms in the white muscles of a fish may reduce its ability to escape predators. However, the effect would be two edged. It could increase parasite losses through increased host mortality, but it would also increase parasite numbers by making fish easier for grey seals to catch. The latter would destabilise the system by ever increasing transition (May and Anderson 1978). If the two aspects of the density-dependent effect are to be modelled, increased losses have to outweigh increased gains for the model to be stable. The existence and magnitude of the effect require experimental investigation.

Until the two aspects can be quantified, only the stabilising effect of a net loss of parasites is incorporated in the model. Parasites losses depend on *kf*, the degree of parasite aggregation in individual fish. In Scottish waters, the number of heavily infected fish increases with increasing overall levels of infection. A maximum likelihood estimation of *kf* (see Elliott 1977) is obtained from the detailed data of Wootten and Waddell (1977). Worm accumulation in fish results in a decrease in aggregation, with more fish being infected with more worms, and *kf* increases with the average number of worms per fish *Af* (Fig. 5). For infections with less than two worms per cod, the relation is approximately linear and *kf* is 0.28 times *Af*. Thus in version *F*, the degree of parasite aggregation *kf* is linked to *Af**, the predicted equilibrium worm burden per fish. The resulting expression for the net loss of parasites through added fish mortality is derived in the Appendix. In a way similar to a control in seals, the effect increases with the average burden (*Af*) and the severity of the control, *df* (Fig. 6). In absence of density-dependent mortality, the per capita mortality rate for cod is 0.55 10^{-3} per day, which is equivalent to a life span of 5 years. In the commercial fishery, the life span is reduced

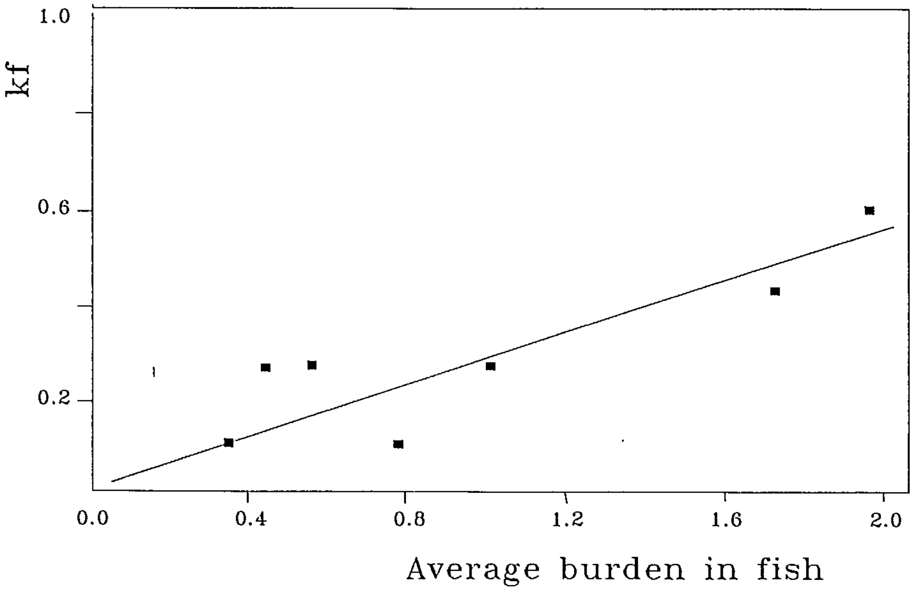

FIG. 5. Parasite aggregation *kf* for different average levels of infection (*Af*, in worms per fish) in Scottish cod. (■ : estimated from Wootten and Waddel 1977, (———) best fit with *kf* = 0.28 × *Af*.)

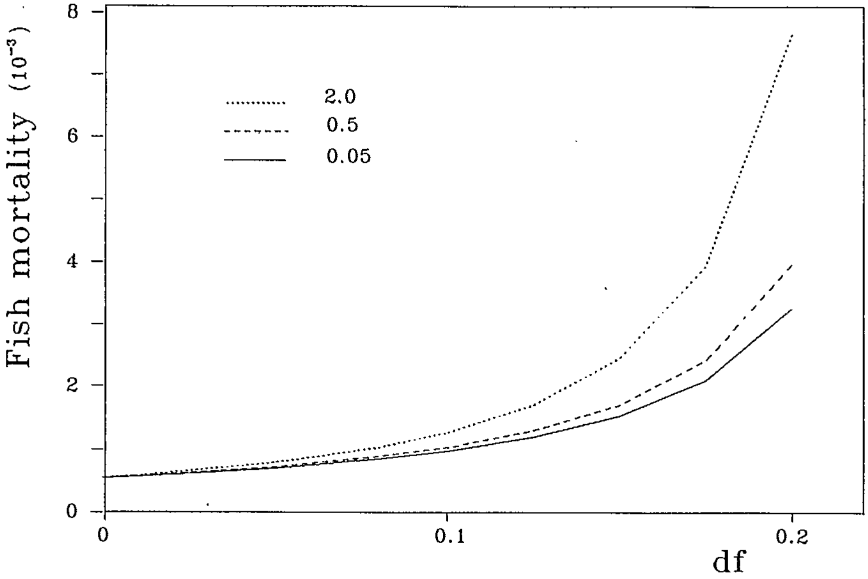

FIG. 6. Increase in fish mortality (per fish per day) with the density-dependent effect *df*, for a theoretical negative binomial distribution of 0.05, 0.5 and 2 worms per fish on average (*Af*) and *kf* a linear function of the average.

to 18 months, i.e. a mortality rate of $1.85\ 10^{-3}$ per fish per day. With a fixed number of fish in the model, a dead fish in instantaneously replaced by an uninfected one. Hence fish mortality only affects parasite numbers, and the higher the mortality, the fewer parasites remain for the infection to spread.

Life Cycle Model

The mathematical model for the parasite life cycle has been developed in the framework of Anderson and May (1978), and May and Anderson (1978). Four equations describe the variations in time of each of the four parasite sub-populations — adults in seals (*Ps*), larvae in fish (*Pf*), in crustaceans (*Pc*) and eggs/free-living stages (*E*):

Adult parasites in seals:
$dPs/dt = \mathrm{TRANS}fs.Pf - \mathrm{LOSS}s.Ps$
Larvae in fish:
$dPf/dt = \mathrm{TRANS}cf.Pc - \mathrm{LOSS}f.Pf$
Larvae in crustaceans:
$dPc/dt = \mathrm{TRANS}ec.E - \mathrm{LOSS}c.Pc$
Eggs & Free living stages:
$dE/dt = \mathrm{TRANS}se.Ps - \mathrm{LOSS}e.E$

Changes in parasite numbers with time are given by the difference between transition (TRANS) from the previous host and losses (LOSS) in the present host. The detailed equations are given in the Appendix. The time trajectory for each parasite sub-population is described by an ordinary differential equation. The model is studied at equilibrium, with all time derivatives equal to zero. The solutions of the equations correspond to average sizes of the four parasite sub-populations over the years, once an initial infection has become established. The density-dependent control introduces a non-linear relation between equilibrium sizes of the two parasite sub-populations involved (see Appendix).

Each version of the model has 21 parameters, 16 of which can be measured in the field, or in the laboratory, and 1 (*kf* or *ks*) can be estimated from data on individual worm burdens (Table 1). The remaining 4 parameters (severity of the intrinsic control *df* or *ds*, and the 3 transmission rates) cannot directly be estimated from data. Their values depend also on the other parameter values, for example on the numbers of hosts taken into account. In theory, observations in the field on infections in fish and their invertebrate prey could allow a test for density-dependent control of parasites in fish. Similarly, observations on the per female egg-production rates, at different levels of infection in seal should allow a test for control of parasite fecundity. In practice, there is no data to date, which describe concurrent infections in successive hosts, and current knowledge on the population biology of *P. decipiens* makes both versions of the model equally plausible.

The transmission rates are taken to be the same in both versions of the model (Table 3), and their values are chosen to predict around 1 parasite per fish, between 50 and 200 adult parasites in seals, and less than 1 infected crustacean in a hundred. The parameters values are then kept the same, to examine the influence of the numbers of hosts on the overall level of infection.

Basic Reproductive Rate

The ability of an infection to spread can be described by the number of matured female offspring produced per one female parasite before the population becomes regulated intrinsically. This is given by R_0, the basic reproductive rate, which is, in absence of density-dependent control, the ratio of the product of all transition terms over the product of all loss terms:

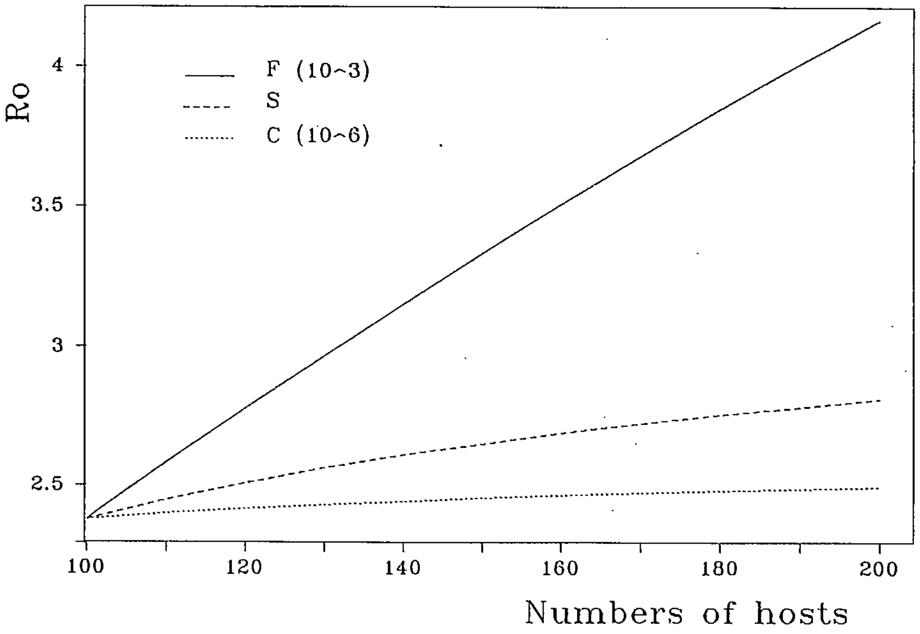

FIG. 7. Theoretical increases in R_0 with independently increased numbers of hosts, F = fish, S = seals and C = crustaceans.

$$R_0 = \frac{TRANSse.TRANSec.TRANScf.TRANSfs}{LOSSe.LOSSc.LOSSf.LOSSs}$$

There is no data on the spreading of new sealworm infections that could provide estimates for R_0. By analogy with other helminth infections, it is assumed that a typical value for Scottish infections could lie between 2 and 3 (cf. human helminths, Anderson and May 1982). This would correspond to low levels of infection over the years, and to an actual reproductive rate around 1, once the parasite population is controlled intrinsically at equilibrium.

A detailed expression for R_0 (Appendix) illustrates how it reflects the present understanding of the parasitic life cycle inbedded in the model structure. The sensitivity of R_0 to the three host numbers is the same for both versions of the model, as no assumption is made on the governing instrinsic control mechanism. All other parameter values being fixed, an increase in the number of fish has a greater influence on R_0, i. e. on the ability of an infection to spread, than an increase in the number of final or crustacean hosts (Fig. 7). This is explained by the unique role of fish in the life cycle, with low losses through parasite and host mortalities. The more fish, the larger the reservoir of parasites, and the higher the potential ability of an infection to spread.

Model predictions

Equilibrium solutions for individual sealworm burden in fish exist for both versions of the model. They are obtained by substituting equilibrium solutions for the other three equations into the equation for parasites in fish *dPf/dt*, and then solving the resulting equation (see Appendix).

The density-dependent parameter values were adjusted so that parasite numbers in fish are approximately 0.9 larva per cod, in 100 000 susceptible fish. This corresponds, in both versions of the model, to an equilibrium burden around 65 adult *P. decipiens* per seal, and complies with existing observations (Table 2).

Stability of the Equilibrium Solutions

The two versions illustrate how parasite numbers may be regulated through reduced transition (model *S*) or increased loss (model *F*). Equilibrium solutions are obtained when rates of transition and loss are equal (Fig. 8 a, b). These equilibrium points are stable

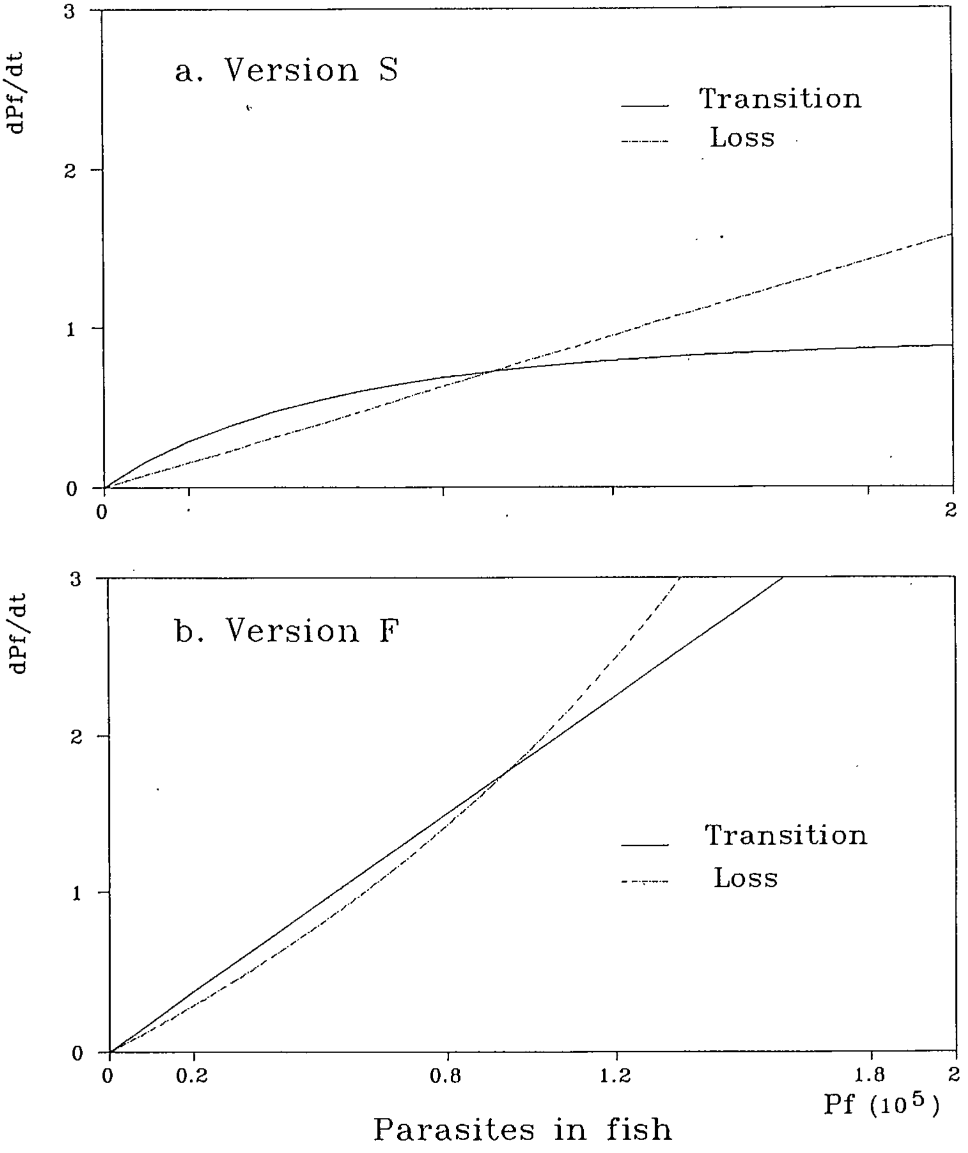

FIG. 8. Rates of parasite transition and loss in fish (worms per day) given by the equation *dPf/dt*, as a function of the number of parasites in fish *Pf*, with two equilibrium solutions at 0, and $Pf^*/F = 0.9$ sealworm per fish, for both versions of the model.

if losses are outweighed for infection levels smaller than equilibrium but take over for infections larger than equilibrium. In both versions, conventional stability analysis (cf. May 1973) shows that the zero solution (i.e. no infection) is not stable, and that t;he non zero solution is locally stable. This illustrates the role of density-dependent control in the model which, for a given set of life history parameters, maintains the system around a given level of infection, and explains long-term persistence of an endemic infection.

Equilibrium Infection Levels in Fish and Host Numbers

The equilibrium number of parasites in fish in the two versions of the model react differently to increased numbers of fish and seals (Fig. 9 a, b). In both versions, parasite

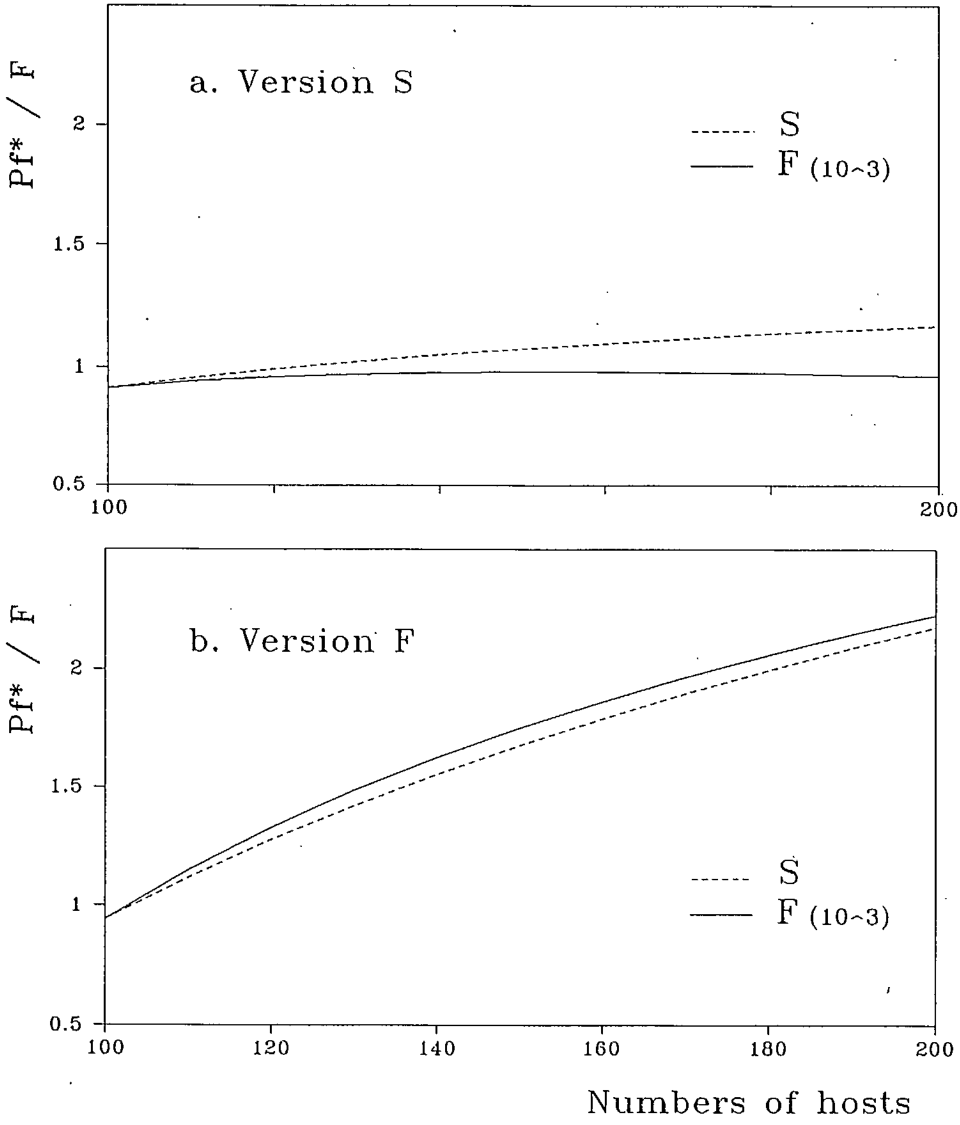

FIG. 9. Predicted equilibrium sealworm burdens in fish (*Pf*/F* worms per fish) as a function of independent increases in the numbers of seals (*S*) of fish (*F*).

numbers in fish increase more acutely with the number of hosts in which the density-dependent control operates (seals for model *S*, fish for model *F*). This stresses the importance of identifying the control mechanism at the parasite level. Overall sensitivity, however, is higher for version *F* of the model, in which parasite numbers increase more with fish and seals numbers than in version *S*. This reflects the role played by fish, which harbour more parasites for a longer time period than any other host. This role was also illustrated by R_0, the parasite basic reproductive rate. An additional explanation lies in the difference between the two modes of intrinsic control. At relatively low infection levels, few fish have more than one worm, and parasite induced fish mortality is in any case much smaller than fishing mortality. In seals, parasites accumulate and crowding is the rule. An intrinsic control operates more efficiently in seals than in fish.

Discussion

It is possible to describe *P. decipiens* infections observed in Scottish waters with a mathematical model of the parasite life cycle. Two versions of the model describe how the dynamics of parasite transition from free-living stages through into crustaceans, fish and back to seals can be regulated in two different ways. In the final host, an intrinsic decrease of the parasite fecundity has a clear stabilising effect, with parasites in fish increasing only slowly with the number of seals. In fish, sealworms are not obviously pathogenic, and intrinsic regulation at this level is not as efficient with parasite numbers at equilibrium increasing more acutely with the numbers of fish and seals. It is not possible at present to tell which one of these mechanisms is most important, and it is also possible that both mechanisms control a sealworm population, at different times or places. Experimental evidence is needed to understand further the relation between infection levels in the fishery and number of fish or seals.

So far, emphasis has been placed on modelling changes in parasite rather than host numbers. The parasites are transmitted through constant numbers of hosts so that infection levels could reach an equilibrium value in each host. Therefore, the model is not appropriate to describe an infection linked to rapidly increasing number of seals. Rather it is proposed to illustrate the importance of two major features of helminths with complex life cycles. Firstly, the parasite population is very likely to be intrinsically regulated, and the mechanism needs to be identified to understand fully the indirect link between numbers of parasites and numbers of hosts. Secondly, it is crucial to identify the numbers of fish and seals effectively interacting in transmitting parasites. In the model, 100 seals are preying upon 100 000 fish. These numbers were chosen arbitrarily, and this choice largely determines the values of the rates of transmission between hosts. It could be, for example, that sealworms are mostly transmitted seasonally, between seals and very localised highly infected fish stocks. In such a situation seals would interact with relatively far fewer fish and, in the absence of a commercial fishery, seals might even control fish numbers.

Knowledge of the parasite control mechanism and the numbers of interacting hosts is definitely needed before it is possible to assess the influence of changing seal and fish abundances on the level of parasitism in a fishery.

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Appendix

Exponential Density-Dependent Effect When the Individual Parasite Burden is Negative Binomial (May 1977).

The generating function for the negative binomial probabilities gives:

$$\sum_i i \bullet P(X = i) \bullet z^i = m \bullet z \bullet (1 + m \bullet (1 - z)/k)^{-(k+1)}$$

with i, discrete value taken by the random variable X; $P(X = i)$ the probability attached to the variate; m, the average and k the aggregation parameter of the negative binomial distribution of X.

Net Egg-Production (cf. Smith et al. 1987)

The sex ratio in the adult parasite population is 1:1, so the fecundity per worm is half that per female worm. In one seal, the net daily egg production $Ep(i, t)$, decreases exponentially with i, the number of adult worms in the host at time t:

$$Ep(i, t) = 0.5\ Ep_0 \bullet i \bullet \exp^{-(ds \bullet i \bullet t)}$$

Ep_0 is the average per capita egg-production per female worm, in absence of density-dependency. ds is the degree of severity of the density dependent control.
For S seals, the net egg output rate is $DDe \bullet Ps$, with Ps the size of the adult worm population in the seals. This rate of egg production is obtained by summing the exponential effect over the frequency distribution of individual burdens in seals. The distribution is assumed to be negative binomial, and is described by the average burden (Ps over S), and the parameter ks. The density of probabilities defined above gives:

$$DDe \bullet Ps = S \bullet 0.5\ Ep_0 \bullet \text{pre} \bullet zs \bullet (Ps/S) \bullet \{1 + (Ps/ks \bullet S) \bullet (1 - zs)\}^{-(ks+1)}$$

with $zs = \exp^{-ds \bullet t}$
In the absence of dendity-dependent control at this level (model F) $ds = 0$ so $zs = 1$.
The per worm egg-production is : $0.5\ Ep_0 \bullet EPs$

Net Loss of Parasites from Fish Mortality

The per capita rate of worm mortality due to fish mortality, fm, increases exponentially with the individual burden i:

$$fm(i, t) = fm_0 \bullet \exp^{(df \bullet i \bullet t)}$$

with fm_0 the per capita natural fish mortality rate in absence of density-dependent added mortality, and df the degree of severity of the effect.
Pf is the number of parasites in the fish, and F is the number of fish. The distribution of individual worm burdens in the fish is negative binomial with parameters Pf over F, the average burden, and kf. The exponential effect is weighed by the frequency of each worm burden and summed, to produce the net rate of parasite loss due to the fish mortality:

$$DDf \bullet Pf = F \bullet fm_0 \bullet zf \bullet (Pf/F) \bullet \{1 + (Pf/kf \bullet F) \bullet (1 - zf)\}^{-(kf+1)}$$

with $zf = \exp^{df \bullet t}$
In the absence of dendity-dependent control at this level, $df = 0$ so that $zf = 1$. The loss of worms through natural fish mortality becomes: $fm_0 \bullet Pf$

Core Model for *P. decipiens* Life Cycle

The mathematical model consists of one ordinary differential equation describing the time variations of parasite numbers in each four sub-populations. Each transition term (TRANS) is the product of the per capita transmission rate between hosts (*tec*, *tcf* and *tfs*, from egg to crustacean, crustacean to fish and fish to seal, respectively), the number of predators (*C*, *F* and *S*) and the proportion of parasites remaining infective (*prc*, *prf* and *prs* in crustaceans, fish and seals, respectively).

Adult parasites in seals:
$dPs/dt = (tfs \bullet S \bullet prs) \bullet Pf - (sm + pms) \bullet Ps$
Larvae in fish:
$dPf/dt = (tcf \bullet F \bullet prf) \bullet Pc - (DDf + fhm + pmf + tfs \bullet S) \bullet Pf$
Larvae in crustaceans:
$dPc/dt = (tec \bullet C \bullet prc) \bullet E - (cm + pmc + tcf \bullet F) \bullet Pc$
Egg & Free living stages:
$dE/dt = DDe \bullet Ps - (em + tec \bullet C) \bullet E$

The parasite population is controlled intrinsically either in fish (model *F*) or in seals (model *S*), and only one of the density-dependent term (*DD*) is operating. The names of the parameters are given in Tables 1 and 3.
The detailed expression for R_0 is:

$$R_0 = \frac{(0.5\ Ep_0 \bullet pre)(tec \bullet C \bullet prc)(tcf \bullet F \bullet prf)(tfs \bullet S \bullet prs)}{(em + tec \bullet C)(cm + pmc + tcf \bullet F)(fm_0 + fhm + pmf + tfs \bullet S)(pms + sm)}$$

Equilibrium Burdens

The system is assumed to be at equilibrium, with the time derivatives all equal to zero. The equations for parasites in fish, with all other sub-populations replaced by their sizes at equilibrium (denoted by *), illustrate the difference between the two versions of the model:

	Model *S*		Model *F*
Pf^*	$\frac{(tcf \bullet F \bullet prf)}{(fm_0 + fhm + pmf + tfs \bullet S)} \bullet Pc^*$		Non-Linear in Pc^*
Ps^*		$\frac{tfs \bullet S \bullet prs}{(sm + pms)} \bullet Pf^*$	
E^*	Non linear in Ps^*		$\frac{(0.5\ Ep_0 \bullet pre)}{(em + tec \bullet C)} \bullet Ps^*$
Pc^*		$\frac{(tec \bullet C \bullet prc)}{(cm + pmc + tcf \bullet F)} \bullet E^*$	

Parasites in fish at equilibrium, with the details of the rates of transition and loss for the two versions of the model:

Model S

$dPf/dt = 0 =$ Transition — Losses

$$= 1/2Ep_0 \bullet pre \bullet zs \bullet \{1 + (tfs \bullet S \bullet prs \bullet zs \bullet Pf/((sm + pms) \bullet S \bullet ks))\}^{-1/(ks+1)}$$

$$\frac{(tec \bullet C \bullet prc)\,(tcf \bullet F \bullet prf)\,(tfs \bullet S \bullet prs)}{(em + tec \bullet C)\,(cm + pmc + tcf \bullet F)\,(sm + pms)} \bullet Pf - (fm_o + fhm + pmf + tfs \bullet S) \bullet Pf$$

with $zs = \exp^{-ds \bullet t}$

Model F

$dPf/dt = 0 =$ Transition — Losses

$$\frac{(0.5\, Ep_0 \bullet pre)\,(tec \bullet C \bullet prc)\,(tcf \bullet F \bullet prf)\,(tfs \bullet S \bullet prs)}{(em + tec \bullet C)\,(cm + pmc + tcf \bullet F)\,(sm + pms)} \bullet Pf$$

$$- \{fm_0 \bullet zf \bullet (1 + (Pf(1 - zf)/F \bullet kf))^{-(kf+1)} + hmf + pmf + tfs \bullet S\} \bullet Pf$$

with $zf = \exp^{df \bullet t}$

Non-zero equilibrium burden in fish:

Model S

$$Pf^* = \left[\frac{\{(em + tec \bullet C)\,(cm + pmc + tcf \bullet F)\,(fm_0 + hmf + pmf + tfs \bullet S)\,(sm + pms)\}}{(zs \bullet 1/2\, Ep_0 \bullet pre)\,(tec \bullet C \bullet pre)\,(tcf \bullet F \bullet prf)\,(tfs \bullet S \bullet prs)}^{-1/(ks+1)} - 1\right] \bullet \frac{tfs \bullet prs \bullet (1 - \exp^{-ds})}{(sm + pms) \bullet ks}$$

Model F (with $kf = 0.28\, Pf/F$)

$$Pf^* = \frac{-\left|\mathrm{Log}\left\{\frac{(1/2\, Ep_0 \bullet pre)\,(tec \bullet C \bullet prc)\,(tcf \bullet F \bullet prf)\,(tfs \bullet S \bullet prs)}{(em + tec \bullet C)\,(cm + pmc + tcf \bullet F)\,(sm + pms)} - hmf - pmf - tfs \bullet S\right\} / fm_0 \bullet \exp df) + 1\right|}{\{\mathrm{Log}\,(1 + ((1 - \exp^{df})/0.28))\}} / 0.28$$

Statistical Models of Age-Specific and Length-Specific Aggregation of *Pseudoterranova decipiens* (Nematoda: Ascaridoidea) in Atlantic Cod, *Gadus morhua*

Ransom A. Myers and John Brattey

Department of Fisheries and Oceans, Science Branch,
P.O. Box 5667, St. John's, Nfld., Canada A1C 5X1

MYERS, R. A., AND J. BRATTEY. 1990. Statistical models of age-specific and length-specific aggregation of *Pseudoterranova decipiens* (Nematoda: Ascaridoidea) in Atlantic cod, *Gadus morhua*, p. 289–301. *In* W. D. Bowen [ed.] Population biology of sealworm (*Pseudoterranova decipiens*) in relation to its intermediate and seal hosts. Can. Bull. Fish. Aquat. Sci. 222.

Maximum-likelihood methods were used to estimate host age-and length-specific abundances and dispersion patterns of larval sealworm, *Pseudoterranova decipiens*, in stocks of Atlantic cod, *Gadus morhua*, off eastern Canada. Within any region studied, the length-specific data was well described by a simple three-parameter model in which the nematode counts followed a Poisson lognormal distribution and mean abundance increased as an exponential function of length. The aggregation was constant for all length-classes within a region. However, the age specific data was better described by a negative binomial distribution in which the level of aggregation decreased with age. These differences are probably caused by combining several age-classes with different mean levels of infection into one length-class.

Les auteurs ont fait appel à des méthodes par maximum de vraisemblance pour estimer les allures d'abondance et de dispersion des larves du ver du phoque (*Pseudoterranova decipiens*) en fonction de l'âge et de la longueur de leurs hôtes, des morues de l'Atlantique (*Gadus morhua*) des stocks des côtes de l'est du Canada. Au sein de toute région étudiée, les données relatives à l'âge étaient bien décrites par un modèle simple à trois paramètres où la valeur dénombrée des nématodes se présentait sous forme d'une distribution logarithmique normale de Poisson et où l'abondance moyenne augmentait en fonction exponentielle de la longueur. Le groupement était constant pour toutes les classes de longueurs au sein d'une même région. Les données relatives à l'âge étaient cependant mieux décrites par une distribution binomiale négative dont le degré de regroupement diminait en fonction de l'âge. Ces différences s'expliquent probablement par le regroupment, en une seule classe de longueurs, de diverses classes d'âge à niveaux d'infestation moyens différents.

Introduction

The purpose of this paper is to model changes in the abundance and dispersion pattern of larval sealworm, *Pseudoterranova decipiens* (formerly *Porrocaecum* or *Phocanema*), in Atlantic cod, *Gadus morhua*, as a function of host age and length. Models of the dispersion pattern of parasites within their host population are of central importance to the study of the parasite population dynamics particularly with respect to density-dependent regulation of host and parasite abundance (May 1977; Anderson 1978, 1982; Anderson and May 1978; May and Anderson 1978). Knowledge of the frequency distribution of sealworm in different cod stocks may also have practical significance because it may not be economical for the fishing industry to catch and process fish with more than a certain number of worms per fillet. Information about how aggregation of *P. decipiens* changes as a function of fish length and mean parasite burden could also be used as a basis for economic decisions on what proportion of infected fish should be discarded or candled during processing.

Aggregation of parasites within the host population can arise via several mechanisms (Anderson and Gordon 1982), i.e. through heterogeneity in host feeding behaviour and susceptibility to infection, and through clustering of parasite infective stages within host food items. Anderson and Gordon (1982) reviewed most sources of variability in mean parasite burden, and suggested using changes in the variance-to-mean ratio to investigate age-specific changes in the distribution of parasites among hosts. Plotting the variance-to-mean ratio is a useful exploratory tool, but it is difficult to use in formal hypothesis testing. The variance-to-mean ratio may not detect changes in skewness of parasite burden. Also, the bias in the sample variance-to-mean ratio as an estimator of the true ratio is inversely related to the number of observations (Reed 1983); this bias can be large for skewed distributions and particularly for the oldest host age-or length-classes which often have the smallest sample sizes.

Here we develop a model which describes simultaneously changes in mean abundance and degree of aggregation of sealworm over a wide range of host age- or length-classes. In this way a simple model (i.e., defined by few parameters) can provide a comprehensive description of the parasite distribution within a host population. It provides a standard against which to compare the results of more complex models, such as those developed by Anderson (1978, 1982), Anderson and May (1978), and May and Anderson (1978).

Data Sources

The data used in this study consist of counts of larval *P. decipiens* obtained from cod collected off Newfoundland and Labrador during 1985-87 (Brattey et al. 1990), and from a survey of *P. decipiens* in cod from the Gulf of St. Lawrence conducted during 1980-81 (Fig. 2, 3, and 4 in McClelland et al. 1983). These surveys covered four of the major cod stocks and stock complexes found off eastern Canada. Details of the methods used to detect the parasites and the location of the sampling areas are given by Brattey et al. (1990) and McClelland et al. (1983); only a brief outline is given here. In the Brattey et al. (1990) study only the musculature (fillet and nape) was examined by candling and slicing, whereas in the McClelland et al. (1983) study viscera and musculature were examined by systematic destruction of the flesh. The efficiency of these methods at detecting larval *P. decipiens* is similar (Brattey et al. 1990).

Lengths of cod were recorded during both surveys. McClelland et al. (1983) grouped cod from the Gulf of St. Lawrence into ten 5 cm length-classes ($\leq$30 cm, 30-35 cm, ..., 65-70 cm, $\geq$70 cm), whereas Brattey et al. (1990) categorized cod sampled from 21 areas off Newfoundland into 10 cm length classes (30-39 cm, 40-49 cm, ..., 60-69 cm). Cod greater than 70 cm in length were not used in our analyses because their ages varied much more than those of smaller cod. In addition, age data were available for a subset of the cod sampled from 21 areas around Newfoundland and Labrador; counts of *P. decipiens* in cod from five adjacent areas off southern Newfoundland (numbered 17-21 in Brattey et al. 1990) were used herein to investigate age-related changes in the dispersion pattern of *P. decipiens*.

Parameter Estimation

Fitting Age- and Length-Classes Individually

The observed numbers of parasites in each age- or length-category were initially fitted to four discrete distributions: Neyman Type A, Pólya-Aeppli, negative binomial, and Poisson lognormal. These distributions differ in their degree of relative skewness, the Neyman Type A being the least skewed and the Poisson lognormal being the most skewed. The Maximum Likelihood Package (Ross 1980) was used for this initial fitting.

The negative binomial and the Poisson lognormal gave better fits to the data and these distributions are used exclusively throughout the remainder of this paper. If the variation in parasite burden follows a negative binomial distribution then the probability of x parasites occurring in a fish is

$$\frac{\Gamma(k+x)}{x!\Gamma(k)} \left(\frac{\mu}{\mu+k}\right)^{x} \left(\frac{k}{\mu+k}\right)^{k}$$

where the two parameters of the distribution are the mean μ and the parameter k; $\Gamma(\ )$ is the gamma function. The negative binomial distribution can be derived by a number of processes (Johnson and Kotz 1969), e.g. by random sampling from a heterogenous population consisting of a mixture of Poisson distributions with means obeying a Gamma distribution with shape parameter k.

The Poisson Lognormal distribution, which is relatively more skewed than the negative binomial, can be generated by sampling a heterogeneous population that consists of a mixture of Poisson distribution whose means follow a lognormal distribution. The probability a host is infected by x parasites is

$$\frac{1}{x!\sigma(2\pi\ )^{1/2}} \int_{0}^{\propto} z^{x-1} e^{-(\frac{1}{2\sigma^2}(\log z - m)^2) - z} dz$$

where m and σ are, respectively, the mean and standard deviation of the underlying normal distribution. Equation 2 is the Poisson lognormal distribution and has a mean of $\exp(m + \sigma^2/2)$.

Fitting Age-and Length-Classes Simultaneously

Here the aggregation parameters k and σ were considered to be a function of the location parameter, while the location parameter was a function of the age or length. Hence, the aggregation parameter was modeled via the location parameter, or directly as a function of the age or length. Although discrete distributions are used for the nonsystematic variation in regression models, they are usually restricted to Poisson, binomial, or negative binomial (with fixed k) models (Lawless 1989 or the GLIM computer package; Baker and Nelder 1985). A variety of empirical functions for the location and aggregation parameters were considered: polynomial, exponential, logarithmic, or power functions.

The method of maximum likelihood was used for all estimation and a quasi-Newton optimization algorithm was used to maximize the likelihood equations. First and second partial derivatives were calculated numerically. Estimates of the standard errors and correlations among the parameter estimates were computed from the inverse of the observed information matrix. The goodness of fit of the model to the data was determined by the likelihood ratio statistic, G^2 (sometimes called the residual chi-square). The G^2 statistic is calculated from

$$G^2 = 2\sum_{i} f_i \ln\left(\frac{f_i}{F_i}\right)$$

where f_i represents the number of fish with i parasites, F_i represents the expected frequency, and the summation is over all cells. The likelihood ratio statistic is asymptotically distributed as chi-square, where the degree of freedom equals the number of observed cells minus the number of parameters fitted minus one. A likelihood ratio test was used to determine if an extra parameter should be included in a model.

If random sampling had been used to collect the fish specimens then the likelihood ratio statistic, G^2, could have been used as a goodness-of-fit test; however, it is important to check if the data are amenable to such a test because they are cluster samples (Fienberg 1979), i.e. more than one fish was taken from each trawl sample. In the companion paper to this one, Brattey et al. (1990) determined that cluster sampling is a minor problem in this data set, i.e. cluster sampling had the effect of decreasing the effective sample size by a median of only 17 %. Although comparing the goodness-of-fit value of G^2 when the two models are not nested is purely informal (i.e., no significance level can be given), it does provide an index of relative fit if both models have the same number of parameters and are fitted to identical data. The adequacy of the model was also checked by comparing each of the predicted and observed frequency distributions at age (or length). This procedure is similar to the plotting of residuals in regression analysis.

Results

Models for Individual Age and Individual Length-Classes

In nearly all cases the Poisson lognormal or the negative binomial distribution fitted the data for individual age- or length-classes better (lower G^2) than the Neyman Type A or Pólya-Aeppli distributions; therefore only the results for the two distributions giving the better fits are presented (Table 1). The results of the fit of the model to individual length-classes for the Southern Gulf of St. Lawrence cod is typical of the length-specific data (Table 1). The Poisson lognormal tended to be superior for the length-class data; in contrast, the negative binomial distribution tended to be superior for the age-class data from cod collected off southern Newfoundland. The parameter estimates in Table 1 also indicate that m and μ increase as functions of length or age of cod, whereas k and σ remain relatively constant. One difficulty in determining the fits of age- and length-class individually is that sample sizes, particularly for the largest (oldest) hosts, are often not large enough to discriminate among alternative distributions.

Models for all Length-Classes Simultaneously

When all length classes of cod from the Southern Gulf of St. Lawrence were considered simultaneously, the Poisson lognormal model generally provided a superior fit to the data compared to the negative binomial (Table 2). The fits to individual length classes described above showed that μ increased and σ tended to remain constant with cod length and the following three parameter model provided a superior fit to nearly all the data when all length classes were considered simultaneously; the parasite burden is distributed as a Poisson lognormal in which the parameter σ is constant, and the parameter, m, is a linear function of length, with the intercept (± SE) estimated as $-3.44(0.16)$ and the slope as $0.06(0.003)$ (Fig. 1). The parameter σ was estimated as $1.40(0.03)$.

Although the Poisson-lognormal model adequately described the frequency distribution of *P. decipiens* in a wide range of length-classes of cod from the southern Gulf of St. Lawrence, it is of interest to compare this result with the fit of the more com-

TABLE 1. Maximum-likelihood estimates of the Neyman Type A, Pólya-Aeppli, negative binomial and Poisson lognormal models fitted to data on the distribution of *Pseudoterranova decipiens* in individual length or age classes of Atlantic cod, *Gadus morhua*. If the sample variance was less than the mean the Lognormal model was not fit (indicated by '*'). Relative goodness-of-fit to the model is judged by the likelihood ratio statistic G^2. Data for southern Gulf of St. Lawrence cod from McClelland et al. 1983; data for southern Newfoundland cod from Brattey et al. (1990).

Category			Neyman Type A	Pólya-Aeppli	Negative binomial parameters			Poisson lognormal parameters		
Length class (cm)	(yr)	df	G^2	G^2	μ	k	G^2	m	σ	G^2
Gulf of St. Lawrence										
≤30	—	1	0.0	0.0	0.22	−1.76	0.0	*	*	*
31-35	—	5	10.0	6.2	0.53	0.40	4.9	−1.5	1.34	6.4
36-40	—	9	56.7	32.9	0.72	0.36	19.7	−1.3	1.43	11.5
41-45	—	9	81.0	41.7	1.2	0.48	22.2	−0.67	1.33	14.5
46-50	—	10	160.4	76.0	1.3	0.39	35.0	−0.71	1.44	14.7
51-55	—	10	193.6	77.7	1.80	0.44	26.0	−0.36	1.43	7.8
56-60	—	11	244.4	189.4	3.12	0.42	76.6	0.09	1.47	16.0
61-65	—	12	299.1	205.0	4.29	0.39	83.1	0.17	1.38	95.0
66-70	—	12	238.3	179.1	6.40	0.49	68.7	0.66	1.32	102.4
Southern Newfoundland										
—	3	1	1.3	1.6	0.16	0.24	1.9	−2.81	1.42	2.5
—	4	1	0.2	0.2	0.12	0.74	0.3	−2.55	0.91	0.4
—	5	2	1.3	0.1	0.26	0.09	0.1	−3.85	2.45	0.8
—	6	2	5.1	4.9	0.23	0.04	5.4	−4.87	2.64	6.6
—	7	4	22.8	6.8	1.08	0.11	1.9	−2.50	2.45	1.3
—	8	4	29.0	13.4	1.59	0.18	5.9	−1.53	2.10	2.0
—	9	3	33.4	18.4	2.51	0.11	12.1	−1.80	2.31	10.6
—	10	3	24.1	9.8	4.28	0.31	4.1	0.01	1.94	2.5
—	11	6	26.8	15.9	5.99	0.28	8.5	0.15	1.97	5.6
—	12	8	53.7	10.7	9.80	0.13	4.7	−1.50	2.62	18.1
—	13	6	28.6	5.9	75.86	0.10	5.0	−6.22	3.42	26.8
—	14	8	22.0	14.4	50.31	0.20	8.6	0.26	2.40	10.9
—	15	8	19.2	9.8	61.68	0.59	7.6	3.32	1.66	10.4
—	16	7	20.0	15.5	28.76	0.90	12.8	2.94	1.38	18.2

TABLE 2. The observed numbers of larval *P. decipiens* in various length classes of Atlantic cod from the southern Gulf of St. Lawrence (data from McClelland et al. 1983) and the numbers predicted by the Poisson lognormal (PLN) and negative binomial (NB) models. Each model was fitted to the data from all length classes simultaneously using three parameters (see text for details).

Length class (cm)		Number of parasites per fish														
		0	1	2	3	4	5	6	7	8	9	10	11-20	21-50	51-100	≥100
≤30	observed	70	18	1	0											
	predicted (PLN)	67.4	14.1	4.1	3.4											
	predicted (NB)	74.2	11.0	2.7	1.1											
31-35	observed	141	35	9	6	3	2	2	0							
	predicted (PLN)	140.0	35.1	11.5	4.8	2.4	1.3	0.8	2.0							
	predicted (NB)	148.9	30.9	10.8	4.3	1.8	0.8	0.3	0.3							
36-40	observed	252	77	22	11	4	2	4	2	4	0	0	2			
	predicted (PLN)	247.5	73.9	27.2	12.3	6.5	3.8	2.4	1.6	1.1	0.8	0.6	2.4			
	predicted (NB)	254.1	65.9	28.8	14.3	7.5	4.1	2.3	1.3	0.7	0.4	0.2	0.3			
41-45	observed	271	117	39	29	14	9	5	3	5	0	5	5			
	predicted (PLN)	296.7	104.3	42.9	21.0	11.6	7.1	4.6	3.1	2.2	1.6	1.2	5.7			
	predicted (NB)	296.6	89.2	45.2	26.0	15.8	10.0	6.4	4.2	2.8	1.8	1.2	2.6			
46-50	observed	377	142	70	26	22	8	14	6	6	5	0	7	4		
	predicted (PLN)	362.2	148.5	67.7	35.6	20.9	13.2	8.9	6.2	4.5	3.4	2.6	9.6	3.6		
	predicted (NB)	358.6	119.0	66.5	42.1	28.3	19.7	14.0	10.1	7.3	5.4	4.0	11.3	0.8		
51-55	observed	338	154	71	41	29	23	8	8	8	5	8	14	6		
	predicted (PLN)	329.3	156.1	78.5	44.2	27.3	18.0	12.5	9.0	6.7	5.1	4.0	15.7	6.6		
	predicted (NB)	329.7	116.9	69.7	47.2	33.9	25.1	19.1	14.7	11.4	9.0	7.1	25.5	3.7		
56-60	observed	225	121	65	58	31	14	20	14	6	6	4	19	10	6	
	predicted (PLN)	237.5	129.0	71.1	42.8	27.7	19.0	13.6	10.1	7.7	6.0	4.8	19.9	8.1	1.6	
	predicted (NB)	246.6	91.4	57.1	40.4	30.4	23.6	18.7	15.1	12.3	10.1	8.3	35.9	9.1	0.1	
61-65	observed	160	77	55	32	28	28	15	15	11	6	5	18	6	5	3
	predicted (PLN)	143.7	88.7	53.4	34.2	23.2	16.5	12.2	9.3	7.3	5.8	4.7	19.3	8.9	1.6	0.4
	predicted (NB)	171.0	65.4	42.2	30.8	23.9	19.2	15.7	13.0	11.0	9.3	7.9	39.1	15.0	0.5	0.5
66-70	observed	81	54	35	39	28	18	18	11	11	7	5	28	11	4	4
	predicted (PLN)	87.3	60.8	39.4	27.0	19.2	14.2	10.8	8.5	6.8	5.5	4.5	20.0	10.3	2.1	0.6
	predicted (NB)	117.4	46.0	30.3	22.7	18.0	14.7	12.3	10.5	9.0	7.8	6.8	37.3	19.8	1.4	0.0

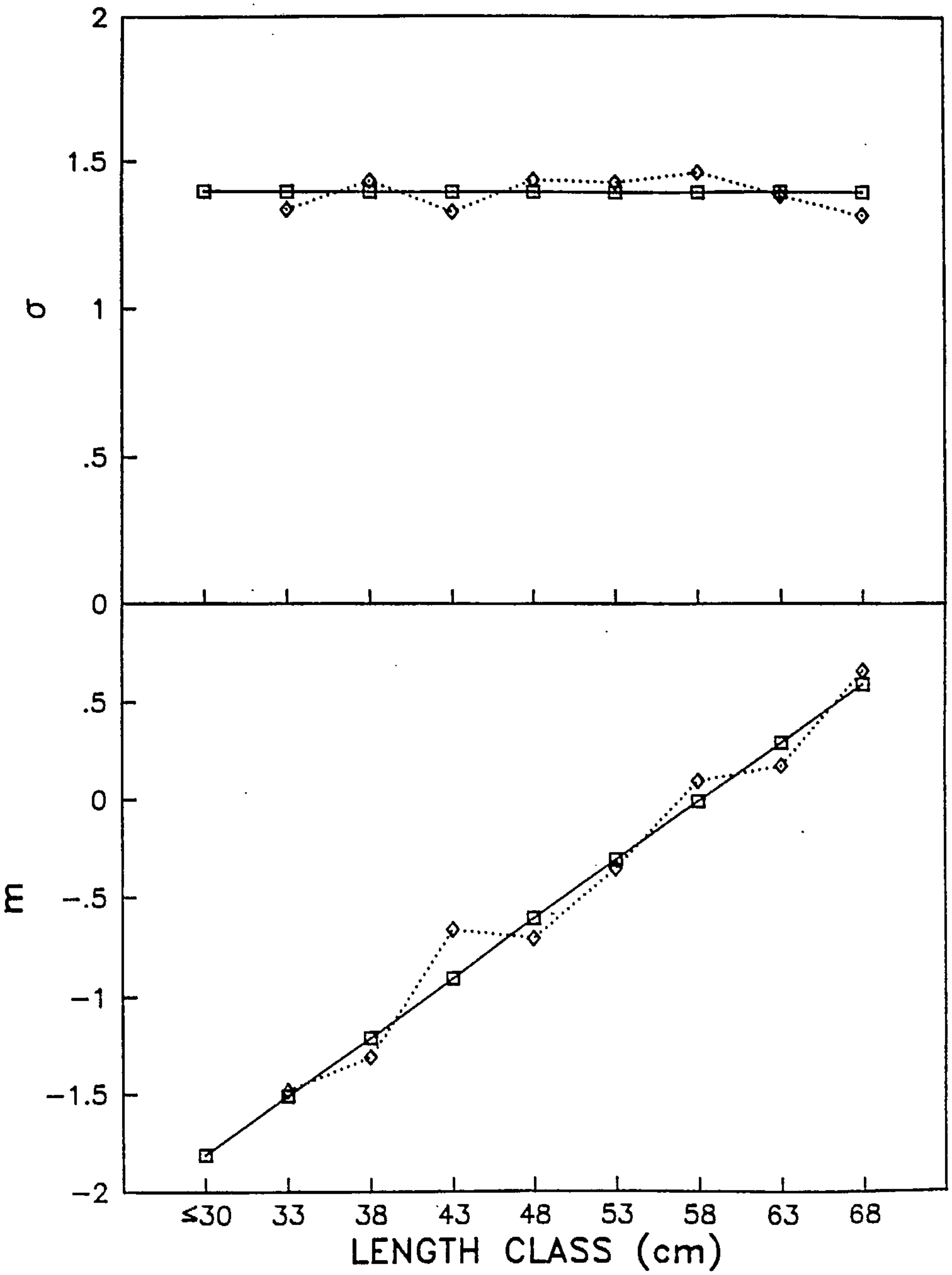

FIG. 1. Parameters of the Poisson lognormal model fitted to the distribution of *P. decipiens* in cod from the southern Gulf of St. Lawrence (data from McClelland et al. 1983). The model was fit to each 5 cm length group of cod individually (◇ · · · ◇) and simultaneously (□ — □).

monly used negative binomial model to the same data (Table 2). The best model based on the negative binomial distribution also produced a constant level of aggregation, i.e. k was constant; the mean in this model was a power function of length, i.e. $\mu = \alpha l^{\beta}$, where l is the median length of the length class. However, the fit was much worse; the likelihood ratio statistic for the negative binomial model was 377.8 compared with 296 for the Poisson-lognormal model (both had 94 degrees of freedom). Comparison of the two fits indicates that the negative binomial model systematically understimates the numbers of fish with large parasite burdens; similarly, the Neyman Type A and Pólya-Âeppli distributions.

The Poisson lognormal model was superior to the negative binomial model for the cod-*P. decipiens* data from the Gulf of St. Lawrence when all length classes were considered simultaneously; however, the Poisson lognormal model did not provide a superior fit for the two largest length-classes of cod when distributions were fit to the length specific data individually (Table 1). This indicates that a model restricted to any two-parameter family of frequency distributions may not be adequate to describe these data. One interpretation of the shift from a Poisson lognormal to a negative binomial distribution among the largest length-classes is that the degree of heterogeneity is decreasing.

The dispersion pattern of *P. decipiens* in individual length classes of cod from each of 21 regions around Newfoundland and Labrador sampled by Brattey et al. (this volume) is similar to that observed for cod from the Gulf of St. Lawrence; with only 1 exception, the fit of the Poisson Lognormal with constant σ was superior to a negative binomial with constant k, or any other negative binomial model (Fig. 2). For the Poisson lognor-

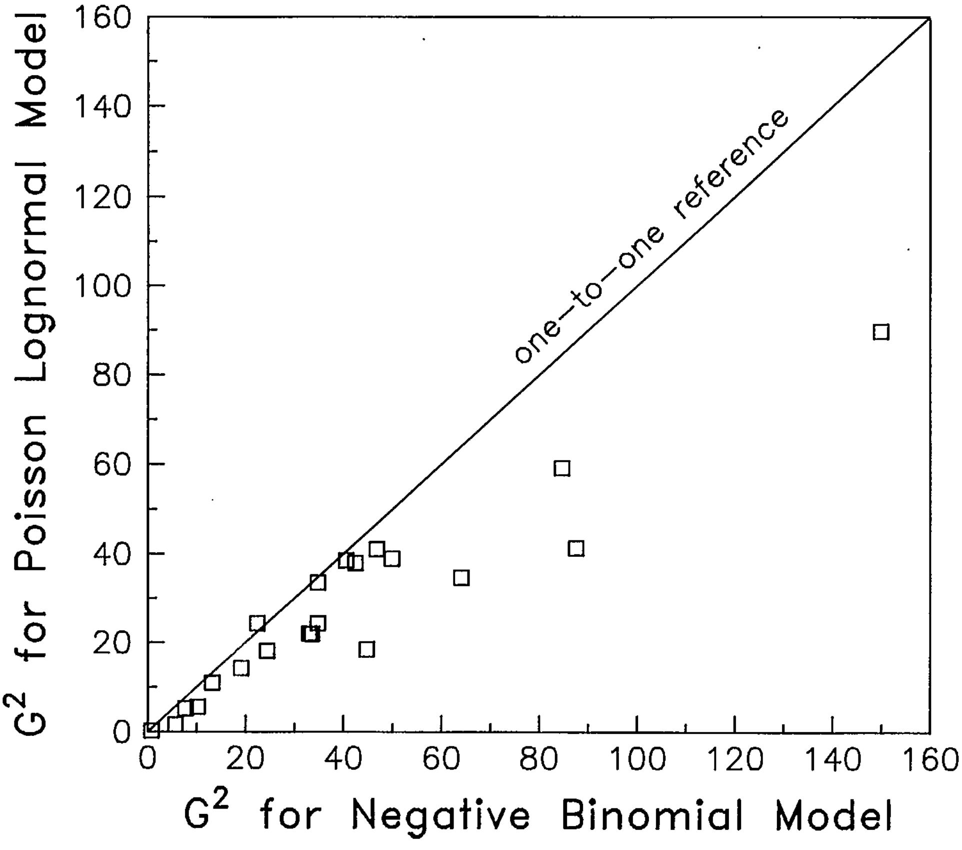

FIG. 2. Comparison of the fit of the Poisson lognormal model with a constant σ versus the fit of the negative binomial model with a constant k to data on the distribution of *P. decipiens* in cod from 21 regions off Newfoundland and Labrador (data from Brattey et al. 1990). The points indicate the values of the G^2 statistic and smaller G^2's indicate a better fit.

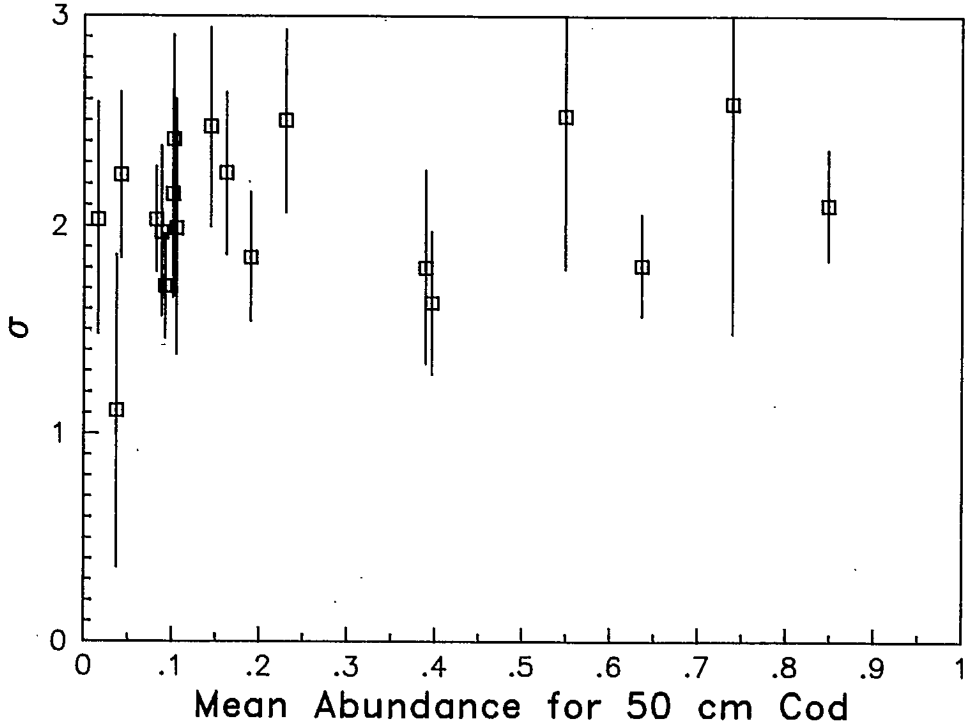

FIG. 3. Comparison of the σ parameter of the Poisson lognormal distribution, with 95% confidence intervals, and the estimated mean abundance of *P. decipiens* in a cod of 50 cm for 19 of 21 regions sampled off Newfoundland and Labrador by Brattey et al. (1990). Two regions are not shown because of small sample size.

mal model the parameter *m* was first estimated under the assumption it was constant, and then under the assumption it was a linear function of length. Using a likelihood ratio test in nested models, we determined that *m* increasing linearly was a better model ($P < 0.05$) than a constant *m* model in 16 of the 21 cases. In no case was the fit significantly improved by allowing σ to be a linear function of length or *m*. The parameter σ was similar for almost all the 21 regions around Newfoundland and Labrador independent of the mean worm abundance (Fig. 3).

Models for All Age-Classes Simultaneously

In the survey of *P. decipiens* in cod from Newfoundland and Labrador, ages were determined for 541 cod collected from five adjacent areas off the south coast of Newfoundland; data from these fish were used to fit age-specific models.

The Poisson lognormal model did not prove superior for the age-specific data when all age classes were considered simultaneously. The best fit was a negative binomial model in which the mean increased as a power function of age, and the negative binomial parameter *k* increased proportional to the predicted mean (Fig. 4). The G^2 of this model was 115.8, while the best 3 parameter Poisson lognormal model had a G^2 of 124.8. That is, although the degree of aggregation of parasites within cod is constant for the length specific model, the degree of aggregation appears to decrease, i.e. *k* increases, with age. The individual estimates of the negative binomial parameters for the older age-classes are based upon small sample sizes, and are thus more variable (Fig. 4).

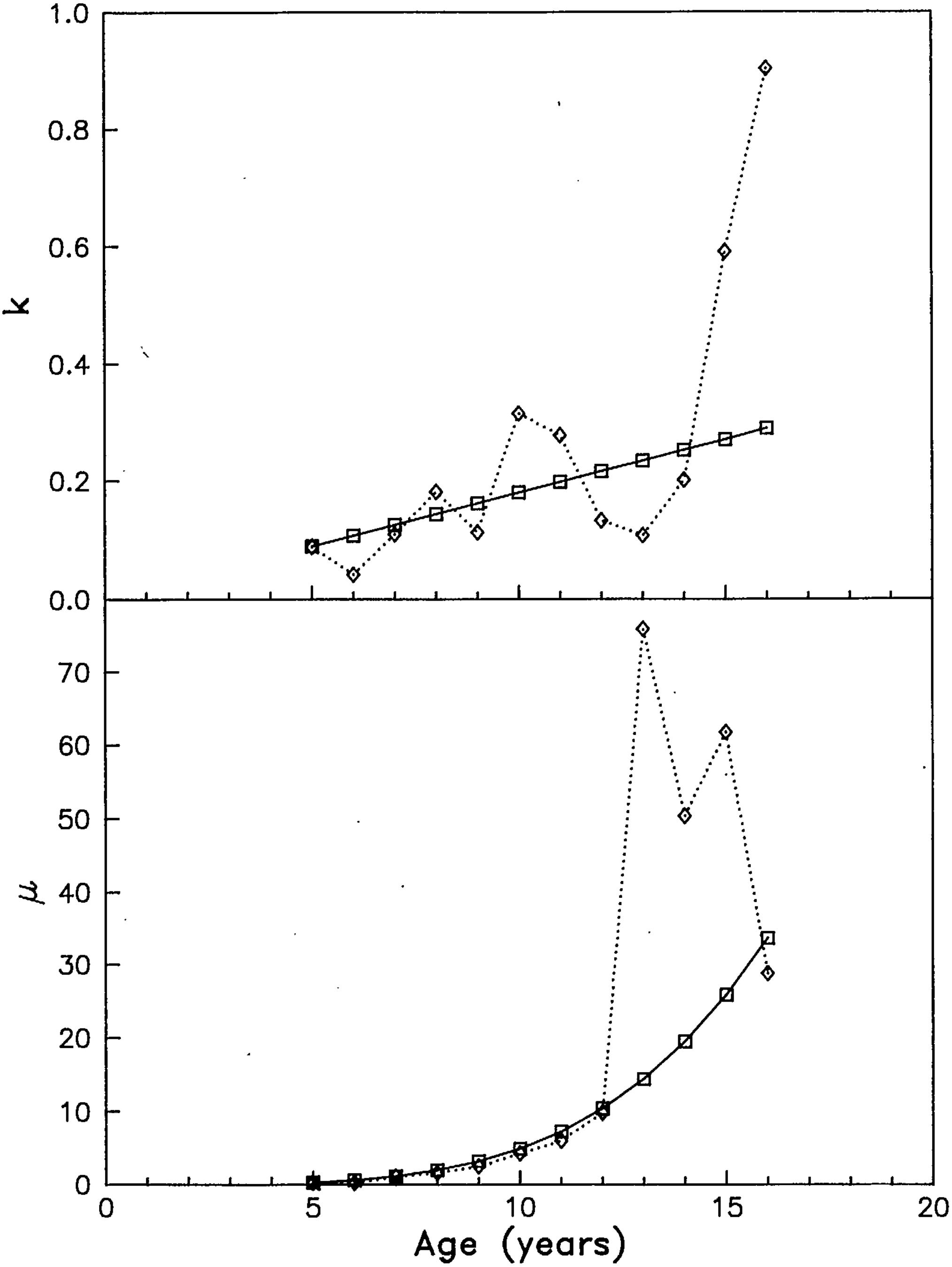

FIG. 4. The parameters of the negative binomial model fitted to data on the distribution of *P. decipiens* in various age-classes of cod from five adjacent areas off southern Newfoundland (areas numbered 17–21 in Brattey et al. 1990). The model was fitted to each age-group of cod individually (◇ · · · ◇) and simultaneously (□ — □).

The maximum likelihood procedure accounts for this difference in sample size, whereas an unweighted ordinary least squares fit may give misleading results.

Since either age or length are often used to investigate changes in parasite burden within host populations it is interesting to compare model fits for the length-specific data from southern Newfoundland to models fits for the age-specific data from the same sample of cod. In this case the negative binomial model did not provide a superior fit to the length-specific data. The G^2 for the negative binomial fit in which the mean increased as a power function of length was 189.6 for a constant k model, and 325.3 if k increased proportional to the predicted mean with zero intercept. A Poisson lognormal model in which the parameter m increased as a linear function of the length and σ was constant had a $G^2 = 117.3$ (all of the above models were fit with 3 parameters, and had 87 degrees of freedom).

Discussion

Our results show that the distribution of *P. decipiens* in length-classes of cod from 4 stock complexes follows a common pattern, i.e. a Poisson lognormal distribution in which the parameter σ is constant. However, when the data for southern Newfoundland were analysed by age the best model was a negative binomial distribution in which the parameter k increases proportional to age. These results are not contradictory; the constant degree of aggregation with length is probably an artifact of combining cod of different ages, and thus infection rates. That is, the greater skewness in the length specific data, which results in a better fit of the Poisson lognormal, may be a result of combining data from several age-classes each of which separately fits the less skewed negative binomial distribution. Also, if dispersion patterns of *P. decipiens* among cod stocks were to be compared, any differences could be a result of stock-specific differences in length at age rather than differences in aggregation at age. This result emphasizes the importance of using age rather than length when investigating changes in the dispersion patterns of parasites among hosts; the use of length-classes increases heterogeneity.

However, modeling changes in the frequency distribution of parasites with host length can still provide useful empirical descriptions of the data. Our results show that for several geographic regions changes in the distribution of *P. decipiens* with cod length follow a Poisson lognormal distribution in which the parameter σ is constant. This allows data from different regions to be compared using a common model. Brattey et al. (1990) used this finding to compare data on sealworm abundance in cod from 21 regions off Newfoundland and Labrador. This approach has the significant advantage that all data from several regions can be compared using a regression approach, instead of using only one length-class as is commonly done.

The models presented here provide simple descriptions of the abundance and distributions of parasites within populations of marine fish in that large complex data sets are described by relatively few parameters. These models allow ecological hypotheses to be formally tested, although these tests cannot rule out all alternatives. Without formal statistical tests of alternative hypotheses the interpretation of age-specific patterns of parasite infections is subjective. An alternative to fitting the data simultaneously is to estimate the parameters of a distribution such as the negative binomial separately for each age-category and then use ordinary least-squares regression to study the relationship among them. However, the regression model's residuals will be neither symmetrically distributed nor homoscedastic. Transforming the data and using weighted least squares will mitigate both these problems. If the form of the residual variation from the model is of primary interest it may be difficult to use such methods.

The negative binomial distribution has usually been used to describe the dispersion pattern of parasites among hosts (Anderson 1982). While the negative binomial distribution has considerable mathematical advantages, we have found that for *P. decipiens* the negative binomial is not the best model to describe the length-specific data. Also, models of parasite population dynamics often assume that the level of aggregation remains constant with host age (Anderson 1982; Dietz 1982), even though there are numerous examples of age-related changes in the dispersion pattern of parasites among hosts (Pennycuick 1971; Boxshall 1974; present study) and the concept of a spectrum of dispersion patterns has been described in detail elsewhere (Anderson and Gordon 1982).

The reasons for the decreasing aggregation of *P. decipiens* with cod age are difficult to determine because several biological mechanisms are influencing the shape of the distribution simultaneously and there are few data to assess the relative importance of each mechanism. However, one aspect of cod biology which will influence the dispersion pattern of *P. decipiens* is the change in the behaviour of cod with age. Juvenile cod are more geographically localized than mature fish (Templeman 1979), and there is also geographic heterogeneity with respect to parasite abundance (McClelland et al. 1983; Brattey et al. 1990). This would result in a more heterogeneous parasite burden, i.e. the negative binomial *k* would be smaller, among younger fish.

Parasite-induced host mortality, either directly or through increased susceptibility to predation, could also result in a reduction in the degree of aggregation of sealworm among older fish. However, only certain forms of parasite-induced host mortality would result in a decreased aggregation with age. For example, Dietz (1982) showed that if the variability in susceptibility was described by a gamma distribution and mortality increased proportional to parasite abundance in a host, then the negative binomial *k* would remain constant. Although there is abundant evidence of selective predation of parasitized individuals in other host-parasite systems (Holmes and Bethel 1972), there is little data to indicate the functional form of the relationship between predation rates and parasite burden, and no studies of parasite-induced mortality among hosts of *P. decipiens*. Therefore, although this mechanism may be a significant source of decreasing aggregation of *P. decipiens* with cod age, at present its importance cannot be evaluated.

Other possible explanations for this pattern of decreasing aggregation include an effective immune response that increases with parasite burden, and mortality of parasites within the host. If an immune response were responsible for this distribution it would have to be strong, and should be comparatively easy to detect. The flesh of some fish species, such as sculpins (*Myoxocephalus* spp.) often contains large numbers of dead melanized larvae of sealworm suggesting a strong host reaction; however, there appears to be little mortality of *P. decipiens* within cod because relatively few necrotic larvae are found in cod flesh (J. Brattey, personal observation).

In summary, we have identified empirically useful models for describing the distribution of *P. decipiens* in cod. Geographical heterogeneity in worm abundance combined with the age-related changes in cod migratory behaviour may be an important cause of the age specific changes in the dispersion pattern of the infection. However, the importance of other mechanisms, such as parasite-induced host mortality through selective predation, cannot be resolved without experimental studies.

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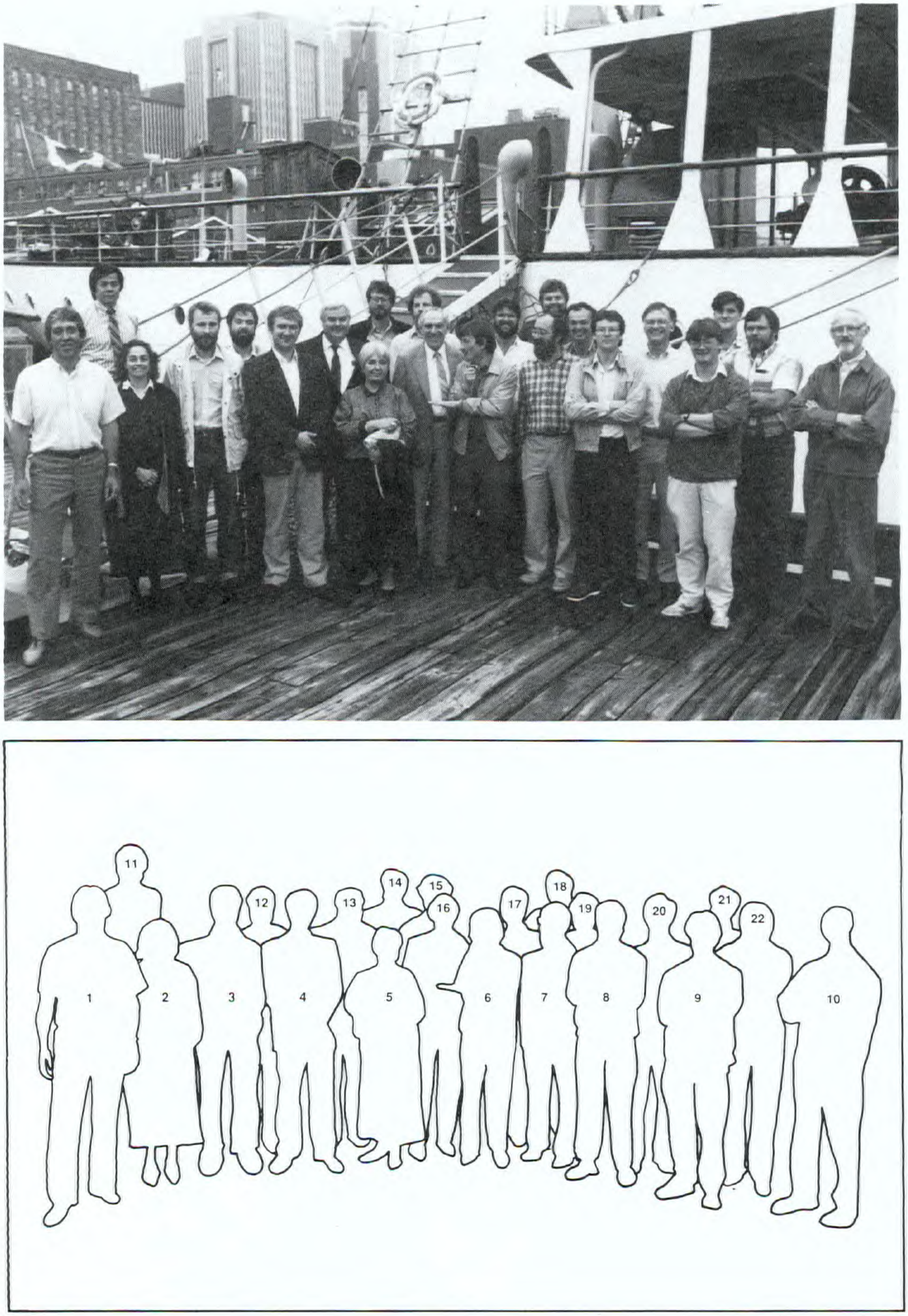
Appendix 1. List of Workshop Participants

		1987	1988
Beck, B.	Department of Fisheries and Oceans Marine Fish Division Bedford Institute of Oceanography Dartmouth, Nova Scotia, Canada B2Y 4A2	x	x
Benoit, D.	Department of Biology Dalhousie University Halifax, Nova Scotia, Canada B3H 4J1		x
Bishop, C.	Northwest Atlantic Fisheries Center Department of Fisheries and Oceans Science Branch St. John's, Newfoundland, Canada A1C 5X1	x	
Bjørge, A.	Ministry of Environment Box 8013, DEP Oslo, Norway	x	x
Bowen, W. D.	Department of Fisheries and Oceans Marine Fish Division Bedford Institute of Oceanography Dartmouth, Nova Scotia, Canada B2Y 4A2	x	x
Brattey, J.	Northwest Atlantic Fisheries Center Science Branch Department of Fisheries and Oceans St. John's, Newfoundland, Canada A1C 5X1	x	x
Burt, M. D. B.	Department of Biology University of New Brunswick Fredericton, New Brunswick, Canada E3B 6E1	x	x
des Clers, S.	Renewable Resources Assessment Group and Parasitology Group Imperial College London, England	x	x
Fanning, L. P.	Department of Fisheries and Oceans Marine Fish Division Bedford Institute of Oceanography Dartmouth, Nova Scotia, Canada B2Y 4A2	x	x
Hammill, M.	Department of Fisheries and Oceans Maurice Lamontagne Institute Mont-Joli, Quebec, Canada		x
Hare, G.	Department of Fisheries and Oceans Science Branch Moncton, New Brunswick, Canada E1C 9B6	x	
Hauksson, E.	Icelandic Fisheries Laboratories Reykjavik, Iceland	x	x
Jarecra, L.	Department of Biology University of New Brunswick Fredericton, New Brunswick, Canada E3B 6E1		x
Landry, T.	Department of Fisheries and Oceans Science Branch Moncton, New Brunswick, Canada E1C 9B6	x	x

		1987	1988
Mansfield, A. W.	Department of Fisheries and Oceans Arctic Biological Station Ste-Anne-de-Bellevue, Quebec, Canada H9X 3R4	x	x
Maguire, J.-J.	Department of Fisheries and Oceans Maurice Lamontagne Institute Mont-Joli, Quebec, Canada	x	
Margolis, L.	Department of Fisheries and Oceans Pacific Biological Station Nanaimo, British Columbia, Canada V9R 5K6		x
McClelland, G.	Department of Fisheries and Oceans Marine Fish Division Bedford Institute of Oceanography Dartmouth, Nova Scotia, Canada B2Y 4A2	x	x
McGladdery, S.	Department of Fisheries and Oceans Science Branch Moncton, New Brunswick, Canada E1C 9B6	x	
Misra, R. K.	Department of Fisheries and Oceans Marine Fish Division Bedford Institute of Oceanography Dartmouth, Nova Scotia, Canada B2Y 4A2	x	x
Mohn, R. K.	Department of Fisheries and Oceans Marine Fish Division Bedford Institute of Oceanography Dartmouth, Nova Scotia, Canada B2Y 4A2	x	x
Möller, H.	Institute fur Meereskunde University of Kiel Dusternbrooker Weg 20 D 2300 Kiel 1 West Germany	x	x
Myers, R. A.	Northwest Atlantic Fisheries Center Science Branch Department of Fisheries and Oceans St. John's, Newfoundland, Canada A1C 5X1	x	x
Ni, I-Hsun	Northwest Atlantic Fisheries Center Science Branch Department of Fisheries and Oceans St. John's, Newfoundland, Canada A1C 5X1		x
Palsson, J.	Marine Research Institute P.O. Box 390 Skulagata 4, 121 Reykjavik Iceland	x	x
Pippy, J.	Northwest Atlantic Fisheries Center Science Branch Department of Fisheries and Oceans St. John's, Newfoundland, Canada A1C 5X1	x	
Smith, J. W.	Department of Agriculture and Fisheries for Scotland Marine Laboratory Victoria Road, Aberdeen Scotland	x	x

		1987	1988
Stewart, J. E.	Department of Fisheries and Oceans Marine Fish Division Bedford Institute of Oceanography Dartmouth, Nova Scotia, Canada B2Y 4A2	x	x
Stobo, W. T.	Department of Fisheries and Oceans Marine Fish Division Bedford Institute of Oceanography Dartmouth, Nova Scotia, Canada B2Y 4A2	x	x
Thompson, D.	Natural Environment Research Council Sea Mammal Research Unit c/o British Antarctic Survey Madingley Road Cambridge, United Kingdom	x	x
Wootten, R.	Department of Agriculture and Fisheries for Scotland Marine Laboratory Victoria Road, Aberdeen Scotland	x	x
Zwanenburg, K. C. T.	Department of Fisheries and Oceans Marine Fish Division Bedford Institute of Oceanography Dartmouth, Nova Scotia, Canada B2Y 4A2	x	x



1, Don Bowen; 2, Sophie des Clers; 3, Jonbjorn Palsson; 4, Heino Moller; 5, Lene Jarecra; 6, John Smith; 7, Ransom Myers; 8, John Brattey; 9, Dave Thompson; 10, Arthur Mansfield; 11, I-Hsun Ni; 12, Erlinger Hauksson; 13, Michael Burt; 14, Kees Zwanenburg; 15, Bob Mohn; 16, Leo Margolis; 17, Paul Fanning; 18, Arne Bjørge; 19, Rod Wootten; 20, Wayne Stobo; 21, Tom Landry; 22, Gary McClelland.