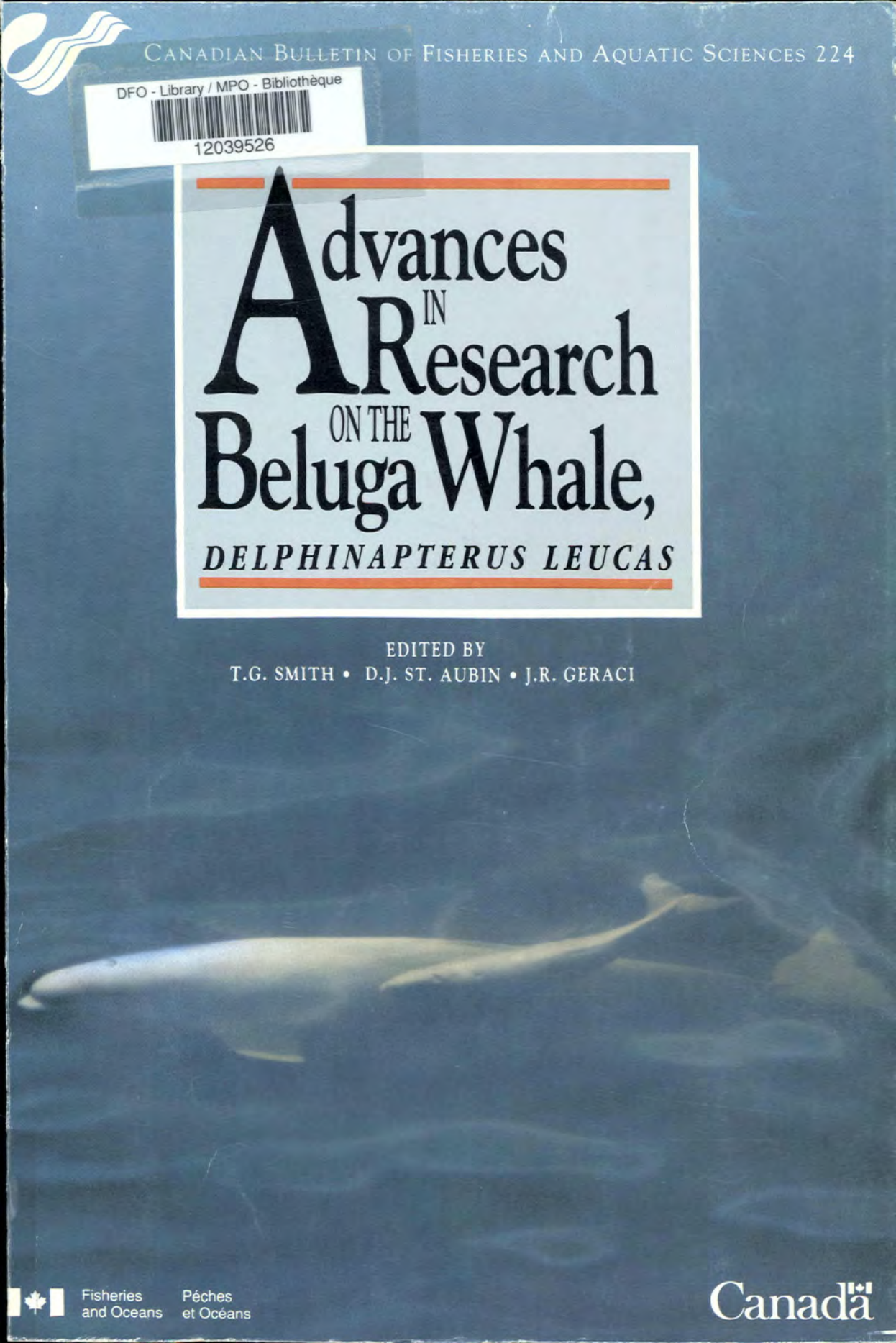
CANADIAN BULLETIN OF FISHERIES AND AQUATIC SCIENCES 224

Advances in Research on the Beluga Whale, *Delphinapterus leucas*

EDITED BY
T.G. SMITH • D.J. ST. AUBIN • J.R. GERACI



Fisheries and Oceans Pêches et Océans

Canada

Canadian Bulletin of Fisheries and Aquatic Sciences 224

Advances in Research on the Beluga Whale, *Delphinapterus leucas*

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DEPARTMENT OF FISHERIES AND OCEANS
Ottawa 1990

The *Canadian Bulletins of Fisheries and Aquatic Sciences* are designed to interpret current knowledge in scientific fields pertinent to Canadian fisheries and aquatic environments.

The *Canadian Journal of Fisheries and Aquatic Sciences* is published in annual volumes of monthly issues. *Canadian Special Publications of Fisheries and Aquatic Sciences* are issued periodically. These series are available from authorized bookstore agents and other bookstores, or you may send your prepaid order to the Canada Communication Group — Publishing, Supply and Services Canada, Ottawa, Ont. K1A 0S9. Make cheques or money order payable in Canadian funds to the Receiver General for Canada.

Communications Directorate

Acting Director General: John Camp
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Printed on
recycled paper

Available from authorized bookstore agents, other bookstores
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Canada Communication Group — Publishing
Supply and Services Canada, Ottawa, Ont. K1A 0S9.

Make cheques or money orders payable in Canadian funds
to the Receiver General for Canada.

A deposit copy of this publication is also available
for reference in public libraries across Canada.

Cat. No. Fs 94-224E
DFO/4426
ISBN 0-660-13817-4
ISSN 0706-6503

Cover photograph courtesy of Jack Orr

This publication has been peer reviewed.

Correct citation for this publication:

SMITH T. G., D. J. ST. AUBIN, AND J. R. GERACI [ed.]. 1990. Advances in research on the beluga whale, *Delphinapterus leucas*. Can. Bull. Fish. Aquat. Sci. 224: 206 p.

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Abstract

SMITH, T. G., D. J. ST. AUBIN, AND J. R. GERACI [ed.]. 1990. Advances in research on the beluga whale, *Delphinapterus leucas*. Can. Bull. Fish. Aquat. Sci. 224: 206 p.

This collection of 14 articles represents a cross-section of current research on beluga whales, *Delphinapterus leucas*, in North American waters.

The evolution and taxonomic status of belugas was examined using immunological characteristics of serum albumin and electrophoretic properties of enzymes, to establish the beluga's relationship to other small odontocetes. The findings confirm morphological studies linking the beluga and the narwhal as the sole members of the Monodontidae.

Aerial surveys of belugas in the eastern Canadian Arctic and Alaskan waters yielded population estimates for stocks identified by their summer distribution in these regions. However, stock discreteness has not been established conclusively; morphometric analysis of animals from Hudson Bay and the St. Lawrence River showed that even these isolated populations cannot be distinguished on the basis of length–weight and age–length relationships. As an aid to identifying and tracking the movements of individual whales, a number of marking and tagging techniques were evaluated in a study on captive animals. Observations on belugas occupying the Nastapoka River reaffirmed the strong fidelity that whales have for specific estuaries, despite disturbance and hunting pressure.

Belugas are highly social animals, and employ an elaborate vocal repertoire for communication. Comparison of their echolocating abilities with those of the bottlenose dolphin shows the beluga's sense to be specially adapted to deal with an ice-infested habitat. Incursion of ice-breaking ships into that environment was shown to affect herd behavior and vocalization.

Like other cetaceans, belugas rely on blubber for insulation, but an analysis of heat transfer through skin and blubber did not reveal any specific adaptations associated with their seasonal occupation of warm estuaries.

Three studies were undertaken on captive whales. Tetracycline effectively marked growing teeth, and provided some insight into the deposition of calcium in dentinal formations. Stimulation with adrenocorticotropic hormone (ACTH) elicited the characteristically strong aldosterone response seen in other marine mammals. A distinct humoral response to red blood cell antigen confirmed the value of this technique as a test of immune function.

Measurements of tissue levels of heavy metals and chlorinated hydrocarbon residues in belugas from various Arctic stocks and from the St. Lawrence River revealed regional differences, and provide important data for monitoring the accumulation of contaminants from the environment.

Résumé

SMITH, T. G., D. J. ST. AUBIN, AND J. R. GERACI [ed.]. 1990. Advances in research on the beluga whale, *Delphinapterus leucas*. Can. Bull. Fish. Aquat. Sci. 224: 206 p.

Cette série de quatorze articles donne un aperçu des recherches en cours sur le béluga, *Delphinapterus leucas*, des eaux de l'Amérique du Nord.

L'évolution et la taxonomie de bélugas ont été étudiées par examen des caractéristiques immunologiques de l'albumine sérique et des propriétés électrophorétiques de certains enzymes dans le but de déterminer leurs rapports avec d'autres petits odontocètes. Les résultats obtenus confirment ceux d'études morphologiques selon lesquelles le béluga et le narval sont les seuls membres des Monodontidés.

Des dénombrements aériens des bélugas dans l'est de l'Arctique canadien et les eaux de l'Alaska ont permis d'estimer les effectifs de stocks que l'on avait délimités dans ces régions à partir de leur répartition d'été. Le caractère discret des stocks n'a cependant pu être établi de façon concluante et des analyses morphométriques d'animaux provenant de la baie d'Hudson et du fleuve Saint-Laurent ont montré que même ces populations isolées ne pouvaient être différenciées à partir des relations longueur–poids et âge–longueur. Diverses techniques de marquage et d'étiquetage ont été évaluées dans le cadre d'une étude portant sur des animaux en captivité dans le but de trouver des moyens d'identifier et de suivre les déplacements de certains individus. Des observations des bélugas de la rivière Nastapoka ont permis de reconfirmer la forte tendance des baleines à occuper certains estuaires en dépit des perturbations et des pressions de chasse.

Les bélugas sont des animaux à comportement social important qui communiquent en utilisant un répertoire vocal élaboré. La comparaison de la capacité d'écholocation du béluga avec celle du dauphin à gros nez a montré que le béluga était particulièrement adapté aux habitats engorgés de glaces. Il a été montré que le passage de brise-glaces à cet endroit avait pour effet de modifier le comportement du groupe et la vocalisation.

Comme les autres cétacés, les bélugas possèdent une couche de graisse qui leur sert d'isolant, mais une étude du transfert de chaleur au niveau de la peau et de la graisse n'a pas permis de noter une adaptation particulière à la présence en estuaires à eau plus chaude.

Trois études ont été réalisées sur des baleines captives. La tétracycline a permis de marquer la croissance dentaire de sorte que certaines connaissances ont pu être acquises sur le dépôt de calcium dans les formations de dentine. La stimulation par l'hormone adrénocorticotrope (ACTH) a provoqué une forte réponse d'aldostérone caractéristique chez les autres mammifères marins. Une réponse humorale caractéristique à l'antigène des érythrocytes a confirmé la valeur de cette technique en tant que test de la fonction immunitaire.

La détermination des teneurs tissulaires en métaux lourds et hydrocarbures chlorés chez des bélugas de différents stocks de l'Arctique et du fleuve Saint-Laurent a montré l'existence d'écarts entre les régions et constitue un important moyen de contrôler l'accumulation des contaminants présents dans le milieu.

Research on Beluga Whales, *Delphinapterus leucas*: Introduction and Overview

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Introduction

Beluga whales have long been in the eye of the public and continue to be a subject of research. They among all cetaceans have the unusual habit of congregating close to shore on a predictable schedule, thereby making them accessible to people. Perhaps for this reason, belugas were one of the first cetaceans kept in captivity (Defran and Pryor 1980), and today are popularly displayed in aquaria throughout the world.

Their timed movements into estuaries also made the whales easy prey for shore-based fisheries, principally in Russia, Svalbard (Spitsbergen) and throughout the northern territories occupied by the Inuit people. Some of the catches were substantial and made available large numbers of specimens for studies into the biology of the species. Vladykov (1944) assembled one of the first treatises on belugas in the Gulf of St. Lawrence, and Kleinenberg et al. (1964) did the same for the population in Soviet waters. In the Canadian Arctic, Sergeant's (1973) data from commercial hunts in Hudson Bay and Brodie's (1971) from Inuit subsistence catches on Baffin Island helped to provide information needed to manage the harvests.

While hunting is still an important issue in some parts of the Arctic, other human activities, such as those associated with offshore oil development (Smith et al. 1979), and contaminants (Martineau et al. 1987) are demanding the attention of scientists and resource managers. This focus continues to gain strength.

Presently the literature on beluga comprises over 600 articles touching every aspect of beluga biology (Smith and Hammill 1990). This monograph offers 14 more, with no less diversity. Population assessment and management issues feature prominently, as expected from our continuing need to monitor stocks of whales. Also represented are studies on behavior, acoustics, molecular systematics, growth, metabolism and thermoregulation, endocrine function, tissue contaminant burdens, and the immune system - disparate topics that come together to shape our current understanding of the beluga whale.

Systematics and Evolution

The beluga is the only representative of the genus *Delphinapterus* and, along with the narwhal, *Monodon monoceros*, comprises the Family Monodontidae. Its relationship to other members of the Delphinidae, particularly the Irrawaddy dolphin, *Orcaella brevirostris*, has been the subject of debate (Kasuya 1973). Traditional taxonomic approaches, such as analysis of skull morphology, have supported the early (i.e. 6–23 Myr) divergence of belugas from delphinid odontocetes (Barnes et al. 1985). Currently, molecular techniques are being used to explore the systematics of numerous mammalian groups, including the Cetacea (Shimura and Numachi 1987). Two approaches are the immunologic characteristics of albumin and the electrophoretic properties of marker enzymes. In this volume, Donald Lint

and co-workers characterized samples from belugas and narwhals from various sites in the Canadian Arctic, and compared their results to those for Irrawaddy dolphins, killer whales, *Orcinus orca*, Pacific white-sided dolphins, *Lagenorhynchus obliquidens*, and Amazon River dolphins, *Inia geoffrensis*. The data support the taxonomic positions established through morphometric analysis, linking belugas and narwhals as the only two members of the Monodontidae and excluding the Irrawaddy dolphin from this grouping.

Population Status

A circumpolar species, belugas are found principally in waters off Canada, Alaska, Russia, Norway and Greenland. Within Canadian waters alone, there may be at least 7 separate beluga populations: Beaufort Sea; high Arctic; Cumberland Sound (Eastern Baffin Island); Ungava Bay; eastern Hudson Bay; western Hudson Bay; and St. Lawrence River. Within these areas, there may be sub-stocks which exploit the same estuaries each summer. Recent analysis of mitochondrial DNA has shown that the females from western Hudson Bay are genetically distinct from those in the Nastapoka estuary of eastern Hudson Bay (Helbig et al. 1990). Such genetic subdivision of stocks is known to occur in humpback whales; in which groups of females and calves occupy certain different summering areas and return to a common winter area where breeding and genetic mixing occur (Baker et al. 1990). The issue of stock discreteness is vital to those managing beluga whales as part of resource utilization.

An estimated 39 000 to 58 000 belugas live in Canadian waters; by far the largest aggregations still occur in western Hudson Bay, where at least 23 000 belugas are estimated to spend the summer. Pierre Richard and associates with the Canadian Department of Fisheries and Oceans studied the whales in Hudson Bay, to update the work Sergeant (1973) had done in the late 1960's, and examined again the important question of the unity of stocks within subregions of the Bay.

For the Alaskan population, Kathryn Frost and Lloyd Lowry's account of the distribution, abundance, and seasonal movements of belugas summarizes nearly 15 years of observations by the Alaska Department of Fish and Game. They identify three major areas occupied by belugas: Bristol Bay, the Norton Sound/Yukon River delta region, and the eastern Chukchi Sea. Populations in each of these areas are estimated to be in the range of 1 000–3 000 animals, and are thought to have been stable over the past 20–30 years.

Beyond the need for regular population censusing is a requirement to identify sub-groupings. In the past, we have relied on rather crude indices such as maximum body size (Sergeant and Brodie 1969). Here, Bill Doidge reexamines this approach and uses new data to dispute the claim that whales from the high Arctic, eastern Hudson Bay, and the St. Lawrence River can be distinguished on the basis of body size. New and more sensitive techniques are required. Genetic analysis promises to resolve some basic questions on stock identity. Telemetry has proved useful for short-term tracking of animals (Frost et al. 1985), but is limited because the signalling devices are too soon rejected. Joseph Geraci and Gary Smith examined some of the processes which lead to rejection of substances implanted in odontocete skin. The work shows that we are far from having achieved a method for long-term marking.

Behavioral Ecology

The estuarine habitat of belugas has kindled considerable speculation about the adaptive significance of this behavior (Sergeant 1973; Finley 1983). Whatever the motivation, the attraction is certainly strong. The work by Louise Caron and Tom Smith at the Nastapoka estuary in eastern Hudson Bay shows that individuals, identifiable by scars, return to the

estuary in successive years. Repeated disturbances from motor traffic and Inuit hunts may displace the animals for periods of hours or days, but then they return to the site. This remarkable tenacity, undeterred by hunting pressure, makes belugas vulnerable to human-induced changes to their habitat and to over-exploitation.

Belugas are disturbed by human activities even in the open ocean, as reported by Kerry Finley who observed the response of belugas and narwhals to ice breakers in the high Arctic. The whales, which presumably had not been exposed to motor traffic, reacted to the noise from ships even at remarkably long distances. Each species showed a characteristic response. Beluga herds dispersed and the animals scattered widely, whereas narwhals tended to huddle together and remain motionless. These differing responses seem to mimic the predator-avoidance strategies of each species. Yet the beluga seems capable of tempering this behavior in areas such as the St. Lawrence, Churchill and Mackenzie rivers, where they have presumably become habituated to heavy maritime traffic.

The vocal repertoire of belugas has earned them the epithet "canaries of the sea." Sjare and Smith (1986a) described their vocalizations, but could not relate the sounds to specific situations or activities (Sjare and Smith 1986b). Studies on captive subjects might hold the key to further understanding. Here, C. Wayne Turl of the United States Navy analyses the echolocation abilities of trained captive belugas compared to those of the Atlantic bottlenose dolphin, about which infinitely more is known. The more highly developed and refined capacities of the beluga are thought to relate to the complex ice-filled winter Arctic habitat and possibly to their use of shallow water areas in the summer.

Physiological Ecology

Belugas, as periodic inhabitants of estuaries, are clearly more tolerant of freshwater than are most other marine odontocetes. Little is known of the adaptations that allow for this behavior, but several studies have highlighted some important physiological transformations associated with incursion into warmer freshwater.

Studies on thyroid hormones in free-ranging belugas have shown a distinct annual cycle in activity, which appears to be centered around the time of estuarine occupation (St. Aubin and Geraci 1989a). Stimulation of hormone secretion at this time is thought to promote somatic growth, in part through mobilizing energy stores, principally blubber. Reduction of the blubber layer can occur in the warm water of the estuaries without risking excessive loss of body heat. Doidge measured the insulating blubber shell and rate of heat conductance in belugas from the Nastapoka River, and used the data to estimate thermostatic energy requirements. He found that belugas in fact appear to be overinsulated in estuaries, and hence could readily yield some of this reserve to satisfy the needs of growing tissue.

Estuarine occupation promotes at least one other biological process in belugas: accelerated growth of epidermis, or molting (St. Aubin et al. 1990). Passive elevation of skin temperature in these warmer waters appears to stimulate cellular processes, and the reduction in thermal gradient between the whales and their environment allows for greater blood flow to the skin, particularly if the animals are overinsulated. Increased circulation delivers growth-enhancing thyroid hormones which are present at elevated concentrations during this phase of the belugas' annual cycle. All these factors combine to stimulate epidermal proliferation, causing molt-like shedding which so far appears to be unique to belugas.

Determining Age

The exact age of animals has been used traditionally as a key piece of information to describe physiological growth rates and vital parameters of populations. Using tetracycline to mark the dentinal layers, Paul Brodie and associates were able to measure growth rate in the teeth of belugas held captive for up to 10 weeks, and thereby to confirm the view that one

year's growth is represented by the deposition of two growth-layer-groups within a tooth. The study also provided some new insights on the dynamics of tooth growth in the species.

Immunology and Health Evaluation

Virtually all of the information on the health of free-ranging belugas comes from studies on stranded carcasses along the St. Lawrence (Martineau et al. 1988). There is concern that impaired immune function underlies some of the observed conditions. Yet we know little about the functioning of the immune system in cetaceans. Tests developed for laboratory species have only recently been applied, and the results, though promising, are preliminary. David St. Aubin, Joseph Geraci and Patricia Shewen report on a pilot study testing the ability of captive belugas to mount an antibody response to sheep erythrocytes, a widely used T-cell antigen. The approach was successful and lays the groundwork for further studies using such techniques.

Other constituents in blood can be used to assess the health of an animal. Normal ranges for blood constituents have been established for captive (Cornell et al. 1988) and free-ranging belugas (St. Aubin and Geraci 1989b). Using blood, it has also been possible to track the course of acclimation to captivity, a process that includes elements of the stress response. The endocrine component of this response was examined in some detail by St. Aubin and Geraci, who used adrenocorticotropic hormone (ACTH) to stimulate the secretion of hormones from the adrenal cortex of captive belugas. Like the bottlenose dolphin (Thomson and Geraci 1986), belugas show only a modest cortisol response, in contrast to the pronounced release of aldosterone. The apparent advantage of this adaptation is to secure electrolyte balance during stress by retaining sodium at a time when the whales are in a low-sodium environment.

Toxicology

Tissue burdens of contaminants such as chlorinated hydrocarbons and heavy metals signal the extent to which by-products of human activity have entered the marine environment. The presence of xenobiotics has been documented widely in marine mammals (Aguilar 1983; Martineau et al. 1987; Muir et al. 1988; Addison 1989) with some attempt to link pathological conditions to the presence of contaminants (Helle et al. 1976; Reijnders 1986; Martineau et al. 1988). Addison (1989) has pointed out the weakness of such associations, resulting either from lack of proper control or baseline data, or from inconsistent methods of analysis. Standardizing methodology will improve our ability to make comparisons between different populations. Toxicological laboratories headed by Derek Muir and Rudolph Wagemann of the Canadian Department of Fisheries and Oceans have done so for chlorinated hydrocarbons and heavy metals, respectively. Clear differences are apparent between the level of hydrocarbons in Arctic belugas and those from the St. Lawrence River, and for heavy metals among some subpopulations in the Arctic as well. Future studies may be able to incorporate these findings as part of epidemiological studies linking contaminant levels with functional disturbances.

Direction of Future Research

The works of Vladykov (1944) and Kleinenberg et al. (1964) established the biological character of the beluga whale, using as a theme anatomy, feeding habits, age, growth, reproduction, and other elements of natural history that were relevant to the management issues of the day. Research for management purposes is still the dominant need, but, as evidenced by the topics covered in this monograph, current approaches are more varied and include new technology. Data on whale abundance and distribution, long viewed as the cornerstone of management research, become more valuable when infused with an under-

standing of behavior and physiology. Factors contributing to morbidity and mortality must be identified to enable us to recognize pathological conditions that might be linked to human activities and contaminants. The modern-day manager needs to draw on the full spectrum of information about what influences the life and death of whales. Future studies should probe deeply into any discipline that promises to nourish that body of knowledge.

Acknowledgments

Gary Sleno and George Horonowitsch (Dept. of Fisheries and Oceans) helped ready the papers for publication, verifying literature cited and scrutinzing page proofs; G. Sleno also prepared some of the figures. Dr. Michael Hammill (DFO) was involved in the initial planning of the monograph, and was a convenor of a workshop that led to its production. We thank Nikki Garwood and Dr. Claude Desjardins (DFO) (for Muir et al.) for translating the abstracts, Dale-Marie Smith and Elizabeth Crossey (Univ. of Guelph), and Dora Goddard (DFO) for secretarial assistance and Lenore Latta (Guelph) for copy editing. The Department of Fisheries and Oceans (Quebec Region) funded the project, as part of the Programme d'Action du St. Laurent (PASL) of the Government of Canada.

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Evolution and Systematics of the Beluga Whale, *Delphinapterus leucas*, and Other Odontocetes: A Molecular Approach

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LINT, D.W., J.W. CLAYTON, W.R. LILLIE, AND L. POSTMA. 1990. Evolution and systematics of the beluga whale, *Delphinapterus leucas*, and other odontocetes: a molecular approach, p. 7–22. *In* T.G. Smith, D.J. St. Aubin, and J.R. Geraci [ed.] Advances in research on the beluga whale, *Delphinapterus leucas*. Can. Bull. Fish. Aquat. Sci. 224.

The evolution and systematics of the beluga whale (*Delphinapterus leucas*) and 11 other odontocetes were investigated using immunological and enzyme electrophoresis procedures. Rabbit antibodies were prepared to serum albumins from *Delphinapterus leucas*, *Monodon monoceros*, *Orcinus orca*, *Lagenorhynchus obliquidens*, *Orcaella brevirostris*, and *Inia geoffrensis*. Reaction of these antibodies with odontocete albumin antigens, by the micro-complement fixation procedure, indicated a very close relationship between *Delphinapterus* and *Monodon* (family Monodontidae), and another close relationship among *Orcinus*, *Lagenorhynchus obliquidens*, and *Orcaella* (family Delphinidae). *Inia*, although closer to the Monodontidae than to the Delphinidae, was clearly not associated with either group.

Electrophoretic mobilities of enzymes were compared from all the species used for the immunological comparisons, except *Inia*, plus *Physeter macrocephalus*, *Mesoplodon bidens*, *Phocoena phocoena*, *Phocoenoides dalli*, *Pseudorca crassidens*, *Globicephala melas*, and *Lagenorhynchus albirostris*. The electrophoretic data were strongly correlated with the immunological data (r^2 = 0.83) and confirmed the branching pattern among the species revealed by the immunological data as well as the extremely close relationship between *Delphinapterus* and *Monodon*. Like the immunological data, the electrophoretic data associated *Orcaella* with a group that includes all the representatives of the family Delphinidae that were examined, and not with *Delphinapterus* or *Monodon*. The data were discussed in terms of a phylogeny for the odontocetes and a time scale of odontocete evolution.

Des recherches sur l'évolution et la systématique chez le marsouin blanc (*Delphinapterus leucas*) et 11 autres odontocétés furent faites utilisant des procédés immunologiques et d'électrophorèses enzymatiques. Des anticorps de lapins ont été préparés aux albumines de sérum de *Delphinapterus leucas*, *Monodon monoceros*, *Orcinus orca*, *Lagenorhynchus obliquidens*, *Orcaella brevirostris* et *Inia geoffrensis*. La réaction de ces anticorps avec les antigènes albuminés d'odontocete, par la méthode de fixation micro-complément, témoignèrent d'une parenté, très étroite entre *Delphinapterus* et *Monodon* (de la famille Monodontidae), et d'une autre proche parenté entre *Orcinus*, *Lagenorhynchus*, et *Orcaella* (famille

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Delphinidae). *Inia*, quoique plus rapprochée du Monodontidae que du Delphinidae n'était clairement associée ni à un groupe ni à l'autre.

Les mobilités électrophorétiques des enzimes furent comparées chez toutes les espèces utilisées pour les comparaisons immunologiques, excepté *Inia*, en plus de *Physeter macrocephalus, Mesoplodon bidens, Phocoena phocoena, Phocoenoides dalli, Pseudorca crassidens, Globicephala melas* et *Lagenorhynchus albirostris*. Les données électrophorétiques furent correlées très étroitement avec les données immunologiques ($r^2 = 0.83$) et confirment la tendance de ramification parmi les espèces révélées par les données immunologiques en plus de la relation très étroite entre *Delphinapterus* et *Monodon*. Tout comme les données immunologiques, les données électrophorétiques associèrent *Orcaella* avec un groupe qui comprend tous les représentants de la famille Delphinidae qui ont été examinés, et non avec *Delphinapterus* ou *Monodon*. La discussion sur les données a été faite en rapport avec une phylogénie pour les odontocétés et un barème d'évolution d'odontocété.

Introduction

The living members of the Order Cetacea are divided into two suborders: Mysticeti (baleen whales) and Odontoceti (toothed whales). In the suborder Odontoceti, some six (Gaskin 1982) to nine (Rice 1984) living families are recognized. Reviews by Kleinenberg et al. (1964) and Stewart and Stewart (1989) (*Delphinapterus*), and Reeves and Tracey (1980) (*Monodon*) accept the classical taxonomy in which the beluga, *Delphinapterus leucas*, and the narwhal, *Monodon monoceros*, comprise the two species of the family Monodontidae. These reviews attribute the first description of beluga to Pallas (1776) as *Delphinus leucas* from animals examined at the mouth of the River Ob on the Arctic Ocean coastline of what is now the USSR. Apparently the name *Delphinus* had already been used by Linnaeus (1758) to describe another group of small odontocetes (Barnes 1976). It seems to be unclear whether Pallas (1776) actually considered the beluga to have affinities to the other *Delphinus* species (Kleinenberg et al. 1964). The current name *Delphinapterus leucas* was evidently first put forward by Lacépède (1804) (Kleinenberg et al. 1964; Stewart and Stewart 1989). There is a long history of debate as to the family or subfamily status of the species, and although the assignment of *Delphinapterus* and *Monodon* to the family Monodontidae has had many supporters including Simpson (1945), there have also been many other differing opinions.

A complex alternative taxonomy has been advocated by Kasuya (1973). Briefly, Kasuya proposed, on the basis of ear bone morphology, that the Irrawaddy River dolphin, *Orcaella brevirostris*, merits a position of affinity with *Delphinapterus* such that the two species would constitute a grouping to the exclusion of *Monodon* which would form a monospecific sister group. This taxonomy has received qualified endorsement from Barnes (1976), Gaskin (1982), and Barnes et al. (1985) who simply expand Monodontidae to include *Orcaella*.

Our approach consists of the use of the quantitative immunological method, microcomplement fixation (MC'F), based on serum albumin, to examine the taxonomy and phylogenetic relationships of the beluga (Champion et al. 1974; Wilson et al. 1977; Maxson and Maxson 1986). We have used the immunological comparison of odontocete serum albumins not only because it has been successful in investigations of many other taxa and there is therefore a considerable body of comparative data available (Maxson and Maxson 1986) but also because unpublished data (Vincent Sarich, pers. comm.) indicated that this method would be appropriate. We have supplemented the information available from serum albumin immunology with a comparison of electrophoretic mobilities of a number of enzymes among accessible odontocete species (Sarich 1977; O'Brien et al. 1985).

The primary questions addressed in this paper are whether *Delphinapterus* is so closely related to *Monodon* that together they constitute a separate family Monodontidae within the suborder Odontoceti, or whether there is justification to associate *Orcaella* with either

Delphinapterus in particular or more generally with Monodontidae. We will also discuss odontocete phylogeny and evolution as revealed by the serum albumin immunological and enzyme electrophoretic data.

Materials and Methods

Odontocete Specimens

The odontocete species included in this study are presented in Table 1. *Delphinapterus* and *Monodon* tissue and blood samples were obtained by Canada Department of Fisheries and Oceans staff, from animals killed by native hunters in the Canadian Arctic.

TABLE 1. Odontocetes represented in this study: Famillies, species abbreviations, systematic and vernacular names, and waters where sampled.

Physeteridae
Pm – *Physeter macrocephalus* (Linnaeus, 1758; Husson and Holthius, 1974*)
– Sperm whale (Northwest Atlantic)

Ziphiidae
Mb – *Mesoplodon bidens* (Sowerby, 1804)
– Sowerby's beaked whale (Northwest Atlantic)

Platanistidae
Inia – *Inia geoffrensis* (deBlainville, 1817)
– Amazon river dolphin (Amazon River)

Monodontidae
Mm – *Monodon monoceros* (Linnaeus, 1758)
– Narwhal (Arctic)
Dl – *Delphinapterus leucas* (Lacépède, 1804)
– Beluga (white) whale (Arctic)

Phocoenidae
Pp – *Phocoena phocoena* (Linnaeus, 1758)
– Harbour porpoise (Northwest Atlantic)
Pd – *Phocoenoides dalli* (True, 1885)
– Dall's porpoise (Northeast Pacific)

Delphinidae
Gm – *Globicephala melas* (Traill, 1809; Rice, 1990*)
– Longfinned pilot whale (Northwest Atlantic)
Oo – *Orcinus orca* (Linnaeus, 1758)
– Killer whale (Northeast Pacific)
Pc – *Pseudorca crassidens* (Owen, 1846)
– False killer whale (Northeast Pacific)
La – *Lagenorhynchus albirostris* (Gray, 1846)
– Whitebeaked dolphin (Northwest Atlantic)
Lo – *Lagenorhynchus obliquidens* (Gill, 1865)
– Pacific whitesided dolphin (Northeast Pacific)
Ob – *Orcaella brevirostris* (Gray, 1866)
– Irrawaddy river dolphin (Southeast Indian)

* See References.

Blood samples from *Orcinus* (Hyack) and *Lagenorhynchus obliquidens* (White Wings) were obtained from the Vancouver Public Aquarium. *Inia* serum, originally collected by the late Robin Best of Instituto Nacional de Pesquisas da Amazonia, Manaus, Brazil, was provided by Joseph Geraci, University of Guelph. Other samples came from animals stranded or accidently entrapped in fishing gear.

Immunological Procedures

Serum albumin was recovered from isoTris (Champion et al. 1974) rinsings of *Orcaella* liver and kidney tissue. *Monodon* liver and kidney were also treated in this way to augment albumin derived from whole blood. Treatment of blood-rich isoTris tissue rinsing solution with Rivanol (2-ethoxy-6, 9-diaminoacridine lactate) precipitated albumin as a Rivanol–albumin complex (Baker et al. 1981). Albumin was released from this complex by dialysis against 0.5 M Tris-HCl (Baker et al. 1981). The resulting albumin solution was desalted and concentrated to 1 mL in an Amicon 10 mL ultrafiltration stirred-cell. For the other species, a column of Cibacron-Blue bound to Affigel agarose beads was used to separate albumin from other major plasma proteins and hemoglobin in plasma, serum, and whole blood. The albumin-rich fractions from the column were desalted, and concentrated as described above for the tissue-derived protein. Both types of preparation were then subjected to polyacrylamide–gel electrophoresis (Maxson 1973, and Linda Maxson, pers. comm.). Albumin-containing bands, located by staining with 8-anilino-1-naphthalene sulphonate, were cut out and albumin was extracted into isoTris. All procedures were conducted at 0–4°C and all tissues, preparations, and solutions were stored at -20°C or colder.

Antibodies were prepared in rabbits, starting with four rabbits per antigen, according to established methods for a 13 wk immunization schedule (Maxson et al. 1979). For *Delphinapterus* only, an additional set of rabbits was immunized over a 30 wk period according to the protocol of Prager and Wilson (1971). The sera from individual rabbits were titred by the MC^{1}F procedure and for each antigen species the corresponding antisera were combined in inverse proportion to titre (Champion et al. 1974). Inter-species comparisons were made with the pooled sera except for the anti-*Monodon* sera, for which the titres were very low and the serum from only one rabbit was satisfactory. Immunological distances (ID) were calculated from homologous and heterologous slopes derived from several microcomplement fixation curves for each determination (Champion et al. 1974; Lint 1987).

Enzyme Electrophoresis Procedures

Isozymes were resolved by the semi-micro starch–gel electrophoresis method of Tsuyuki et al. (1966) as described by Clayton and Tretiak (1972) and detected with enzyme-specific staining procedures as described in Table 2. Most species were represented by few individuals and the genetic heterozygosity was very low. In these circumstances genetic similarities (S) were determined for each species pair by simply counting, on a locus-by-locus basis, the number of loci with identical electrophoretic mobility and then dividing by the number of loci resolved in common in both species (Cronin and Sarich 1976). Electrophoretic distance (D) (Sarich 1977) was calculated as:

$$D = -\ln S$$

TABLE 2. Enzyme electrophoresis and staining conditions.

Enzyme[a] abbreviation, E. C. No., and Name	Preferred tissue[b]	Electro.[c,d,e] buffer	Stain buffer and components[d]	Concentration[e,f]
G6PD, 1.1.1.49 glucose-6-phosphate dehydrogenase	l	AC, pH 6.1 with: NADP, 0.1	Tris; 0.1 M, pH 8.0 glucose-6-phosphate (Na_2 salt)	1.6
			$MgCl_2 \cdot 6H_2O$	0.4
			NBT	0.4
			PMS	0.09
GDH, 1.1.1.47 glucose dehydrogenase	l	AC, pH, pH 6.1	Tricine; 0.15 M, pH 8.0 glucose	200
			sodium pyruvate	8.0
			NAD	0.7
			NBT	0.4
			PMS	0.03
GLUD, 1.4.1.3 glutamate dehydrogenase	l	TEB, pH 8.0 with: sucrose, 40; NAD, 0.1	Tris; 0.1 M, pH 8.0 sodium glutamate	10
			sodium pyruvate	1
			NAD	1.2
			NBT	0.2
			PMS	0.03
GOT, 2.6.1.1 glutamic-oxaloacetic transaminase (aspartate aminotransferase)	m	AC, pH 9.0	Tris; 0.1 M, pH 8.0 L-aspartic acid	1.5
			2-oxoglutaric acid	0.8
			pyridoxal-5-phosphate	0.01
			Fast Blue BB	0.6
GPD, 1.1.1.8 glycerol-3-phosphate dehydrogenase	m	AC, pH 8.0	Tricine; 0.15 M, pH 8.0 DL-glycerol-3-phosphate (Na_2 salt)	20
			pyruvic acid	8
			NAD	0.4
			NBT	0.3
			PMS	0.02
GPI, 5.3.1.9 glucose phosphate isomerase	m	AC, pH 9.0	Tris; 0.1 M, pH 8.0 fructose-6-phosphate (Na_2 salt)	1.4
			glucose-6-phosphate dehydrogenase	1.8
			$MgCl_2 \cdot 6H_2O$	0.7
			NADP	0.2
			NBT	0.2
			PMS	0.02

TABLE 2. *(Continued.)*

Enzyme[a] abbreviation, E: C. No., and Name	Preferred tissue[b]	Electro.[c,d,e] buffer	Stain buffer and components[d]	Concentration[e,f]
IDH, 1.1.1.42 isocitrate dehydrogenase	l	AC, pH 6.1 with: NADP, 0.1; Nonidet P 40[g], 0.1	Bicine; 0.15 M, pH 8.5	
			DL-isocitric acid (Na_2 salt)	1.3
			$MgCl_2 \cdot 6H_2O$	0.4
			NADP	0.3
			NBT	0.2
			PMS	0.03
LDH, 1.1.1.27 lactate dehydrogenase	m	AC, pH 6.1	diethanolamine; 0.15 M, pH 9.0	
			lactic acid (pH 7.0, NaOH)	11
			NAD	0.7
			NBT	0.4
			PMS	0.02
MDH, 1.1.1.37 malate dehydrogenase	m	AC, pH 6.1	diethanolamine; 0.15 M, pH 9.0	
			malic acid (pH 7.0, NaOH)	16
			NAD	0.7
			NBT	0.4
			PMS	0.02
ME, 1.1.1.40 malic enzyme (malate dehydrogenase, oxaloacetate-decarboxylating)	m	AC, pH 6.1	Tricine; 0.15 M, pH 8.0	
			malic acid	16
			$MgCl_2 \cdot 6H_2O$	0.2
			NADP	0.3
			NBT	0.4
			PMS	0.02
MPI, 5.3.1.8 mannosephosphate isomerase	m	AC, pH 8.0	Tricine; 0.15 M, pH 8.0	
			D-mannose-6-phosphate (Ba salt)	1
			glucosephosphate isomerase	2
			glucose-6-phosphate dehydrogenase	2
			$MgCl_2 \cdot 6H_2O$	0.2
			NADP	0.2
			NBT	0.2
			PMS	0.05
PGD, 1.1.1.43 phosphogluconate dehydrogenase	l	AC, pH 8.0 with: NADP, 0.1; Nonidet P 40[g], 0.1	Tris; 0.1 M, pH 8.0	
			6-phosphogluconic acid (Na_3 salt)	2
			$MgCl_2 \cdot 6H_2O$	1
			NADP	0.5
			NBT	0.5
			PMS	0.05

TABLE 2. *(Continued.)*

Enzyme[a] abbreviation, E. C. No., and Name	Preferred tissue[b]	Electro.[c,d,e] buffer	Stain buffer and components[d]	Concentration[e,f]
PGM , 5.4.2.2 phosphoglucomutase	1	AC, pH 6.1	Tricine; 0.15 M, pH 8.0	
			glucose-1-phosphate (Na_2 salt)	4
			glucose-6-phosphate dehydrogenase	1.6
			$MgC1_2 \cdot 6H_20$	2
			NADP	0.4
			NBT	0.4
			PMS	0.03

[a] Enzyme nomenclature according to Shows et al. (1987) and McAlpine et al. (1988).

[b] Tissue abbreviations: m, muscle; 1, liver.

[c] Abbreviations and references for electrophoresis buffers:
AC, Amine-citrate buffers described by Clayton and Tretiak (1972);
for pH 9.0, 2-amino-2-methyl-1,3-propanediol was used,
for LDH the buffer concentration in the starch was doubled;
TEB, Tris-EDTA-borate described by Siciliano and Shaw (1976).

[d] Abbreviations for buffer and stain ingredients:
Bicine, N,N-bis-(2-hydroxyethyl)-glycine;
EDTA, ethylenediaminetetraacetic acid;
NAD, nicotinamide adenine dinucleotide;
NADP, nicotinamide adenine dinucleotide phosphate;
NBT, Nitroblue tetrazolium;
Nonidet P 40, ethylphenylpolyethyleneglycol,
(nonionic detergent, Registered Trademark of Shell, also known as NP 40);
PMS, phenazine methosulphate;
Tricine, N-(tris-(hydroxymethyl)-methyll-glycine;
Tris, tris-(hydroxymethyl)aminomethane;

[e] All concentrations of chemicals in $mg \cdot mL^{-1}$, and concentrations of linking enzymes in $units \cdot mL^{-1}$.
All stains were incubated at 22°C except GDH which was incubated at 37°C.

[f] The stain recipes were adapted from the following sources:
GPD, (Clayton et al. 1973);
GPI, (Siciliano and Shaw 1976; Nielsen et al. 1989);
LDH and MDH, (Clayton and Gee 1969; Nielsen et al. 1989);
MPI, (Allendorf et al. 1977);
PGM, (Nielsen et al. 1989).
For other enzymes the present procedures represent extensive adaptations of published procedures to produce optimum results with cetacean enzymes. The methods of Harris and Hopkinson (1976) were used as a general guide.

[g] The inclusion of an unusual ingredient, the nonionic detergent Nonidet P 40, significantly enhanced the respective isozyme stains.

Distance Diagrams

Unrooted distance diagrams were constructed and the associated standard deviations determined from the molecular data (reciprocal ID's and electrophoretic *D*'s) by the Fitch and Margoliash (1967) method using the Runtime program by George Wilson in the PHYLIP version 3.2 package of computer programs (J. Felsenstein, University of Washington, 1989).

The program was run 13 times on each data set according to Felsenstein's recommendations, using a procedure to add species to the trees in different orders, in an attempt to discover the best trees. The standard deviation for phylogenetic trees is not the same as the usual one but instead reflects the agreement between the actual distance data, in this case ID and *D* values, with the distances measured between species along the branches in the distance diagrams. The Fitch–Margoliash programs in the PHYLIP package are incompatible with zero distances; therefore zero values were arbitrarily changed to 0.0001.

Results

Immunology

The reciprocal ID data (Table 3) clearly associate *Delphinapterus* and *Monodon* (average ID = 2.4) to the exclusion of any of the other species tested. These same data also clearly associate *Orcaella, Orcinus* and *Lagenorhynchus obliquidens*, (average ID = 5.9), in another separate group. *Inia* is not closely associated with either group, although it is certainly closer to *Delphinapterus–Monodon* (average ID = 10.7) than to the *Orcinus–Lagenorhynchus obliquidens–Orcaella* group (average ID = 21.7).

Where more than one ID determination was conducted, the entries in Table 3 are the average of all multiple determinations with their associated standard deviations. While the standard deviations of replicate determinations are mostly less than 10%, there is substantial disagreement among many of the reciprocal distances (Table 3). This lack of reciprocity is typical of these kinds of ID data sets and has been quantified as percentage deviation of the average ID value by Champion et al. (1974), and has been discussed extensively (Maxson and Wilson 1975; Beverley and Wilson 1982).

For the data in Table 3, the percentage deviation in reciprocal ID values ranged from 0.4 to 36% and the average (13.6%) is similar to other data sets (Beverley 1979; Maxson and Maxson 1979). Much of this lack of reciprocity centres on *Inia* where every ID measured with the anti-*Inia* serum was greater than the corresponding reciprocal ID (Table 3). The similarity

TABLE 3. Reciprocal immunological distances determined with antisera raised against odontocete serum albumin. Species abbreviations are given in Table 1. Entries in parentheses represent ID's obtained with a 30–wk anti-*Delphinapterus* serum. Entries with ± attached represent averages of two or more determinations; all other entries were determined from comparisons of homologous and heterologous slopes.

Antigens		Antisera					
		Dl	*Mm*	*Oo*	*Lo*	*Ob*	*Inia*
Dl			1.5±.4	9.5±1.2	11.2	13.1	12.4±.2
Mm	(1)	3.2±.2		9.2±1.6	9.8	12.8	13.5±.1
Oo	(8)	11.4±1.4	8.8±.6		5.4	4.7	23.0
Lo	(10)	11.7±1.4	11.1±.2	7.4		6.5	23.5
Ob	(13)	13.0±1.7	13.1±2.3	7.1	4.5		30.0
Inia	(12)	8.8±2.0	8.2±2.8	18.0	20.3	15.2	

of results with the 30-wk and 12-wk anti-*Delphinapterus* sera indicates that the 12-wk sera were, as expected, satisfactory for the present kind of investigation (Champion et al. 1974).

Isozyme Electrophoresis

Only one or a few individuals were available for analysis for all species except *Delphinapterus* and *Monodon*, thus the enzyme electrophoretic mobility entries (Table 4) represent the only, or the most common, allelic form observed at each locus. The 211 *Delphinapterus* tested were invariant except for 1 LDHa, 1 PGM, and 11 IDH heterozygotes. Rare alleles aside, *Monodon* and *Delphinapterus* enzymes differed in electrophoretic mobility (Table 4) only at the mannose phosphate isomerase locus (MPI) among the 15 loci resolvable in both species. Perhaps less expected was the identity of *Globicephala* and *Pseudorca* at 10 loci. *Inia* is not included in the electrophoretic data set (Table 4) because our only *Inia* material was serum from which we were able to display only lactate dehydrogenase (LDH) activity subsequent to electrophoresis.

In Fig. 1, average immunological distances (ID) were plotted against the corresponding electrophoretic distances (*D*) among the five species, *Delphinapterus, Monodon, Lagenorhynchus obliquidens, Orcinus,* and *Orcaella*, for which both types of data were available. The correlation was $r^2 = 0.83$, and the slope was 15.3.

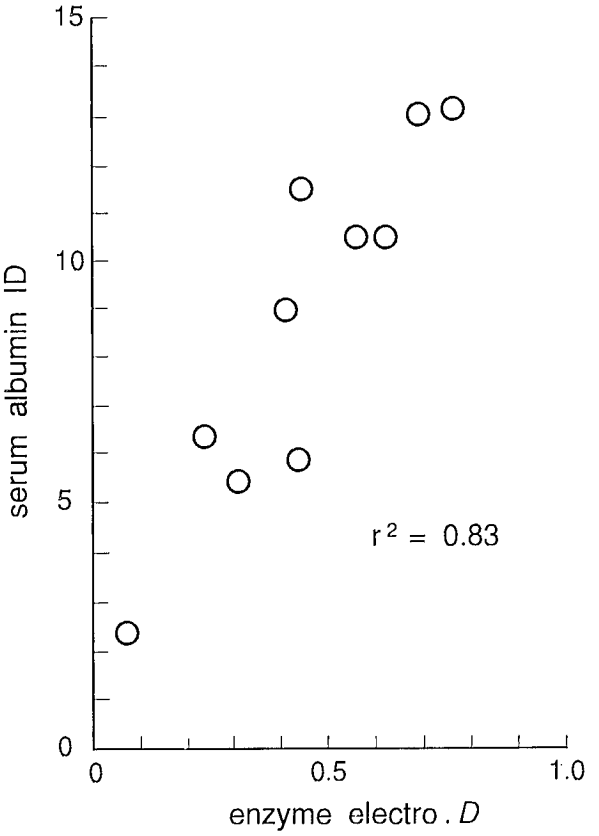

FIG. 1. Albumin immunological distance (ID) plotted against enzyme electrophoretic distance (*D*) for 10 pairs of odontocetes; $r^2 = 0.83$, slope = 15.3.

TABLE 4. Relative electrophoretic mobilities of odontocete enzymes, approximately in mm; nd, not determined. Species abbreviations as given in Table 1. Tissue abbreviations: m, muscle; l, liver; h, heart.

Species and (Tissue tested)	Enzyme abbreviation and enzyme commission number												
	G6PD 1.1.1.49	GDH 1.1.1.47	GLUD 1.4.1.3	GOT 2.6.1.1	GPD 1.1.1.8	GPI 5.3.1.9	IDH 1.1.1.42	LDH 1.1.1.27	MDH 1.1.1.37	ME 1.1.1.40	MPI 5.3.1.8	PGD 1.1.1.43	PGM 5.4.2.2
Pm (m)	+22	nd	+28	nd, nd	+24	+15	-14, +10	-6, nd	-20, +16	+16, +20	+38	+22	+2
Mb (l, m)	+22	+15	+28	-12, +19	nd	+15	-14, +14	-10, nd	-20, +16	+16, +20	+38	nd	+10
Mm (l, m)	+22	+15	+28	-12, +19	+20	+9	nd, +10	-10, +25	-20, +16	+12, +20	+40	nd	+2
Dl (l, m)	+22	+15	+28	-12, +19	+20	+9	-12, +10	-10, +25	-20, +16	nd, +20	+38	+20	+2
Pp (l, m)	+22	+15	+28	-12, +19	+20	+9	-12, +10	-10, +25	-20, +16	+16, +28	+32	+17	-5
Pd (l, m)	+22	nd	nd	-12, +19	nd	+9	-12, +10	-10, +25	-20, +16	nd, +20	+32	+28	-2
Gm (l, m)	+22	nd	nd	-9, +24	nd	+15	nd, +10	-10, +25	-20, +16	+16, +20	+40	+20	0
Oo (l, h)	+22	nd	nd	-9, +24	nd	+15	-15, +10	-10, +25	-20, +16	nd, +20	+40	+20	0
Pc (m)	nd	nd	nd	-9, +24	nd	+15	nd, nd	-10, +25	-20, +16	nd, +20	+40	nd	0
La (l, m)	+22	+15	+28	-9, +24	+20	+15	-14, +10	-10, +25	-20, +16	+16, +20	+32	+20	0
Lo (l, m)	+22	nd	nd	-9, +24	nd	+15	-14, +10	-10, +25	-20, +16	+16, +20	+38	+20	0
Ob (l, m)	+22	nd	+28	-9, +24	nd	+15	-13, +16	-10, +25	-20, +16	+16, +20	+26	+15	0

Distance Diagrams

The Fitch–Margoliash distance diagrams (Fig. 2a–d) are all drawn to a scale derived from the slope of Fig. 1 (15.3), thus the index bars in Fig. 2 show that 0.1 electrophoretic *D* units is the same linear distance as 1.53 serum albumin ID units. These diagrams (Fig. 2a–d) all clearly demonstrate the strong association of *Delphinapterus* and *Monodon*. It is also clear from each diagram that all the representatives of the family Delphinidae, including *Orcaella*, are closely associated. The standard deviations for these diagrams calculated with the PHYLIP program are shown here:

Figure	Data set	Percent SD	No. trees tested
2a	all ID	18.7	28
2b	all ID except *Inia*	17.1	15
2c	electro. *D*; 5 species as in 1b	11.0	15
2d	all electro *D*; 12 species	18.2	196

The relatively large percent standard deviations for diagrams derived from the reciprocal ID data (Fig. 2a and 2b) evidently reflect the deviations from perfect reciprocity in these data (Table 3), considering the number of species involved.

Discussion

All the distance diagrams (Fig. 2a–d) demonstrate a close relationship between *Delphinapterus* and *Monodon* to the exclusion of any other species, thereby supporting the classical taxonomic assignment of *Delphinapterus* and *Monodon* to a two species family Monodontidae. These diagrams show that *Orcaella* is definitely not a member of Monodontidae but is clearly associated with the family Delphinidae. Neither *Inia, Physeter,* nor *Mesoplodon* appear to represent distinct outgroups to the other odontocetes in this investigation. [A legitimate outgroup would display an essentially identical ID or *D* to all members of the study group; see for example the position of *Hyaena* relative to the *Felis* cats in Collier and O'Brien (1985).]

The addition or subtraction of taxa in the data set used to calculate these Fitch–Margoliash distance diagrams (Fig. 2a–d) may be expected to change the relationships among the taxa. However, the present diagrams show essentially the same branching pattern and similar distance relationships regardless of the number of species in the data set. Evidently this is another indication of the reliability of the data. These Fitch–Margoliash diagrams may not be as familiar as the U-shape phylogenetic trees derived from pair group data reduction methods [see for example Shimura and Numachi (1987)] but they are much more representative of the actual data because the branch lengths are not adjusted to an arbitrary baseline as in the usual pair group presentation.

A similar enzyme electrophoresis study of odontocete relationships (Shimura and Numachi 1987) included *Pseudorca crassidens, Lagenorhynchus obliquidens, Phocoena phocoena,* and *Phocoenoides dalli*, species also represented in the present work. Of the 19 loci examined by Shimura and Numachi, and the 18 loci tested in the present work, 13 were the same loci. Shimura and Numachi examined large numbers of individuals and expressed their results as Nei genetic distances (*D*). A plot of these Nei *D*'s against the present band counting

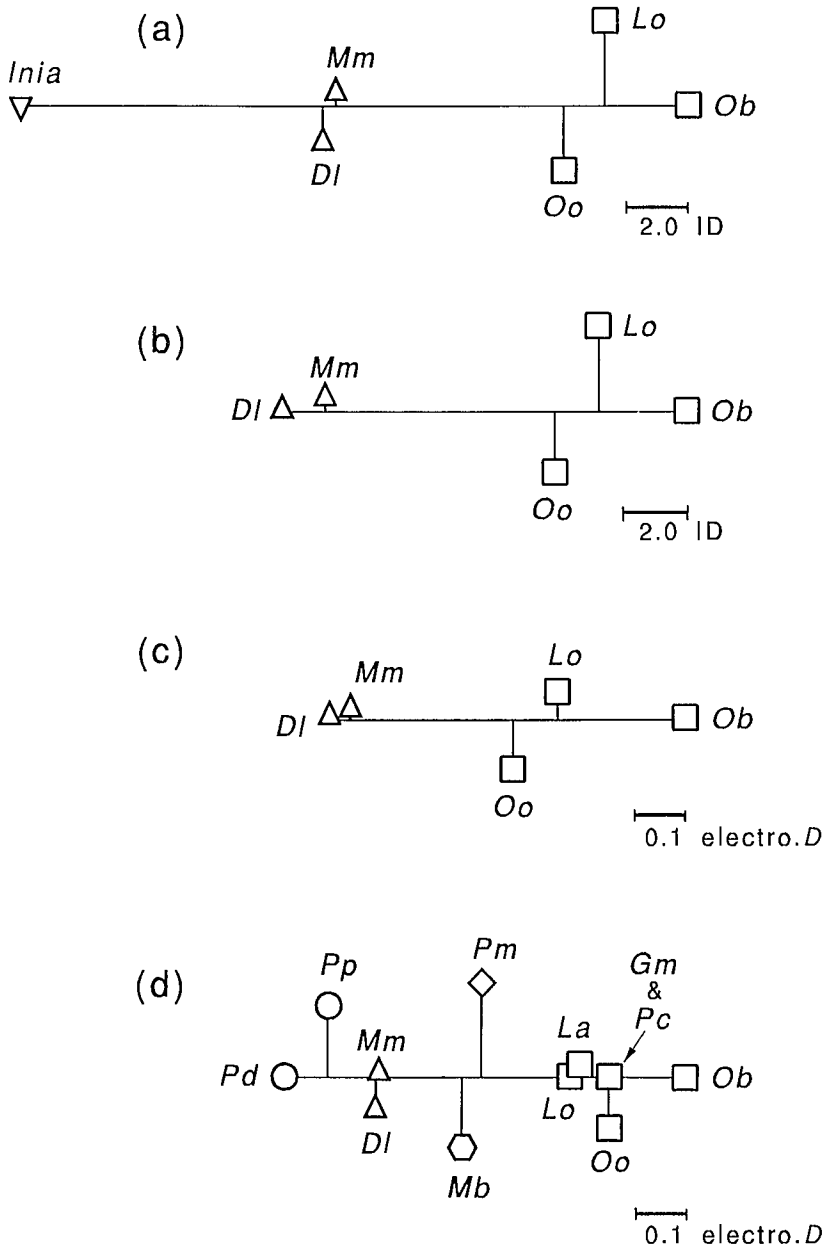

FIG. 2. Fitch–Margoliash distance diagrams derived from serum albumin immunological distances (ID) and enzyme electrophoretic distances (*D*); species abbreviations are given in Table 1. (a) all immunological distance data; (b) all immunological distance data except *Inia*; (c) electrophoretic distance data for the same species as in (b); (d) electrophoretic data for all species. Symbols for odontocete families:

Physeteridae ◇ ; Ziphiidae ⬡ ; Platanistidae ▽ ;

Monodontidae △ ; Phocoenidae ○; Delphinidae □ .

electrophoretic *D*'s for the interspecies distances common to the two data sets was highly correlated ($r^2 = 0.98$, slope = 1.50).

The similarity of these two independent data sets may be examined further by recalculation of the Shimura and Numachi data as a Fitch–Margoliash distance diagram. If the slope (1.50) of the Nei *D* against electrophoretic *D* plot is used to estimate distances in a Fitch–Margoliash diagram derived from the Shimura and Numachi data, the following comparison emerges:

	Phocoenidae to Z. node	Ziphiidae to P./D. node	Delphinidae to Z. node
Present results (Fig. 2d)	0.25	0.15	0.30
Shimura and Numachi (1987)	0.30	0.17	0.45

We interpret this remarkable similarity as further confirmation of the strength of the data and the correctness of our interpretation. A further indication of the robustness of this approach may be seen from the fact that in the present work Ziphiidae is represented by *Mesoplodon bidens* but by *Bairdius bairdii* in the Shimura and Numachi (1987) study. These observations also reaffirm one of the main points put forward by Sarich (1977): that it is as effective to investigate taxonomy by band counting using one individual per taxon as by analyzing large numbers of individuals to get to the Nei *D* kind of calculation.

Heyning (1989) has presented the results of a new cladistic, parsimony analysis of anatomical data together with a review of odontocete taxonomy based upon the organization of the families into a number of superfamilies. In the Heyning phylogeny, Phocoenidae and Delphinidae were sister groups at one extremity of a midline, while Ziphiidae and a somewhat distant Physeteridae were sister groups at the opposite extremity. The other families, Monodontidae (nearest to Phocoenidae), Iniidae, and Platanistidae, were distributed along the midline and connected to it by relatively short character state branches.

Heyning's phylogeny agreed with the classical superfamily taxonomy that associates the families Monodontidae, Phocoenidae, and Delphinidae in a superfamily Delphinoidea to the exclusion of all other families (Heyning 1989; Rice 1984). This is quite different from the present phylogenetic trees (Fig. 2a–d) and the results of Shimura and Numachi (1987), which were characterized by a marked separation of Delphinidae from Phocoenidae, and, in the present work only, also from Monodontidae. Although it is difficult to compare character state data to distance data, it is obvious that the Heyning (1989) topology and branch lengths are very different from the present phylogeny (Fig. 2d). The only similarity is an association between Monodontidae and Phocoenidae. It would seem that resolution of the discrepancies between the present phylogeny (Fig. 2a–d) and the Heyning (1989) phylogeny, together with the classical organization of the odontocetes into superfamilies, will require more data from additional character sets.

A time scale for odontocete evolution may be approached by consideration of the present results and the independent data set of Shimura and Numachi (1987). The slope (1.50) of a plot of the Shimura and Numachi Nei *D* against the present electrophoretic *D* may be used to convert the slope of the ID against electro *D* plot (Fig. 1, 15.3) to a slope of 10.2 for an equivalent plot of ID against Nei *D*. Comparison of this result with slopes ranging from 22 to 55 for plots of serum albumin ID against Nei *D* presented by Wyles and Gorman (1980) suggest that either the pesent ID's may be low or the electrophoretic *D*'s may be high relative to other data sets. Shimura and Numachi have already suggested that their electrophoretic Nei *D* values are not high in comparison with other data sets.

Thus it seems that the ID's may be low and may produce minimal estimates of divergence time if we use the widely accepted calibration that 1 ID unit = 0.6 million years (Myr) of

evolutionary divergence time (Wilson et al. 1977; Collier and O'Brien 1985). If this calibration is used the 2.0 ID index bars in Fig. 2a and 2b become equivalent to 1.2 Myr of divergence time and the divergence of Monodontidae from both Delphinidae and *Inia* may each be estimated at about 6 Myr. Similarly, the divergence of *Inia* and Delphinidae may be estimated at about 12 Myr.

It may also be possible to calibrate some kind of electrophoretic clock. Sarich (1977) has suggested that for slowly evolving loci, the type used in the present work and by Shimura and Numachi (1987), T(Myr) = 30 Nei *D*. If we again use the slope of 1.5 for the plot of Nei *D* against electrophoretic *D*, presumably T(Myr) = 45 electrophoretic *D* units and the 0.1 *D* index bar represents 4.5 Myr of evolutionary divergence time. On this basis, divergence times may be estimated from Fig. 2d as follows: Monodontidae–Delphinidae, 23 Myr; Monodontidae–Phocoenidae, 10 Myr; Monodontidae–*Mesoplodon,* 13 Myr; and Monodontidae–*Physeter*, 18 Myr.

If these estimates of divergence times are interpreted as being a minimum for the ID data and a maximum for the electrophoretic *D* data, then the divergence of Monodontidae and Delphinidae for example would date somewhere between 6 Myr and 23 Myr which is the Miocene. These estimates seem to be in reasonable agreement with the paleontological data which show that, although primitive forms of cetaceans (archaeocetes) are found in Eocene deposits (Barnes 1976; Whitmore and Sanders 1976), the major radiation of odontocetes is a Miocene event (5–25 Myr) (Barnes 1984; Barnes et al. 1985). This analysis would also suggest that intra-family odontocete divergences are more recent Pliocene events, a result in general agreement with the paleontological data (Barnes 1984).

This analysis of the immunological and electrophoretic results has shown that the whole set of immunological distances may be lower than those in other comparable data sets. There is also the possibility that one or another of the present species may have produced anomalous results. An example of a species that yielded anomalous ID's is the New-World monkey *Aotus* in which an ID of only 42 was observed between human and *Aotus* in contrast to ID's of 39, 35 and 36, respectively, between Old-World monkeys and human, chimpanzee, and gorilla, and ID's of 62–70 between human and three other New-World monkeys (Sarich and Wilson 1966). Is there some similar anomaly in our data that could reconcile the present results with the suggestion of Kasuya (1973) of a close relationship between *Orcaella* and *Delphinapterus*? We think not. The average ID (2.4) between *Delphinapterus* and *Monodon* is clearly distinct and much smaller than the ID's between these species and any other species in the present study (approximately 7–13, Table 3). This difference in ID is not likely due to experimental error; the standard deviations where they were measured (Table 3) ranged from 0.2 to 2.8. After the *Delphinapterus–Monodon* pair, the next most similar group of comparisons was found among the Delphinidae (including *Orcaella*) with an average ID of 5.9 (Table 3). We have also shown that the ID data are closely correlated to our enzyme electrophoretic data and that the two sets of data produce very similar phylogenetic trees (Fig. 2a–d). The enzyme electrophoretic data are also closely correlated with another independent enzyme electrophoretic data set (Shimura and Numachi 1987). All this evidence suggests that there is nothing exceptional about the *Orcaella* data and we conclude that the classical assignment of *Orcaella* to the family Delphinidae should be maintained. Rice (1984) has also favored this classical taxonomy in an interpretation of the morphological data in which he suggests that while *Orcaella* superficially resembles a small *Delphinapterus*, it is more like Delphinids in skull morphology and air-sinus system, and that the similarity of its tympano periotic to that of *Delphinapterus* may be plesiomorphic or convergent. We therefore conclude that the present data confirm the classical assignment of *Delphinapterus* and *Monodon* to a two species family Monodontidae and the association of *Orcaella* with the family Delphinidae.

Acknowledgments

We thank M. Bigg, L. Maxson, E. Mitchell, and V. Sarich for advice and J. Heyning for a copy of a recent paper. Canada Department of Fisheries and Oceans staff, including H. Cleator, B. Dunn, W. Doidge, L. Dueck, M. Kingsley, W. Macdonald, P. Richard, M. Roberge, T. Smith, R. Stewart, T. Strong, R. Walker, and P. Weaver, collected and transported *Delphinapterus* and *Monodon* tissue and blood samples from animals killed by native hunters in the Canadian Arctic. R. Baird, J. Bannister, P. Brodie, P. –Y. Daoust, D. Hembree, K. Langelier, J. Lien, A. Read, and P. Stacey provided samples from stranded animals or animals taken incidentally in fishing gear. T. Carmichael, M. Daniels, and D. Tretiak provided laboratory assistance. We thank S. Cosens, S. Innes, D. St. Aubin, and two anonymous reviewers for comments.

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The Distribution and Abundance of Belugas, *Delphinapterus leucas*, in Eastern Canadian Subarctic Waters: A Review and Update

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RICHARD, P. R., J. R. ORR, AND D. G. BARBER. 1990. The distribution and abundance of beluga, *Delphinapterus leucas*, in eastern Canadian waters: a review and update, p. 23–38. *In* T. G. Smith, D. J. St. Aubin, and J. R. Geraci [ed.] Advances in research on the beluga whale, *Delphinapterus leucas*. Can. Bull. Fish. Aquat. Sci. 224.

Aerial surveys document a continuous July distribution of belugas along the coast of Hudson Bay from Eskimo Point, N.W.T., to James Bay and the occurrence of a small July population in northern Hudson Bay, and confirm that few belugas occupy the southeast Baffin Island coast in August, outside of Cumberland Sound. The western Hudson Bay population is estimated to number in excess of 23 000 individuals and more than 1 300 belugas were seen along the southern Hudson Bay coast. Northern Hudson Bay has a population estimated at more than 700 animals, while fewer than 500 were found in southeast Baffin Island. We review arguments pertaining to stock discreteness of subarctic beluga populations. We conclude that evidence for geographic isolation between the eastern and western Hudson Bay populations is inconclusive and that the stock identity of northern Hudson Bay belugas is unknown. Southeast Baffin belugas could be a separate genetic stock, as evidenced by their morphometric differences from other subarctic populations, but further evidence is needed to discriminate the stocks within these populations.

Des inventaires aériens ont permis de décrire une distribution continue de bélugas en juillet le long des côtes de la baie d'Hudson entre Eskimo Point, T.N.O., et la baie James, ainsi que la présence d'une petite population dans le nord de la baie d'Hudson. Ils ont aussi permis de confirmer qu'en dehors de la baie de Cumberland, en août, peu de bélugas occupent les côtes du sud-est de la terre de Baffin. On estime que la population de l'ouest de la baie d'Hudson dépasse 23 000 individus et plus de 1 300 bélugas ont été observés tout au long des côtes du sud de la baie d'Hudson. Le nord de la baie d'Hudson a une population de plus de 700 individus, tandis que moins de 500 ont été trouvés dans le sud-est de la terre de Baffin. Nous examinons différents arguments sur la séparation des stocks de bélugas subarctiques et en venons à la conclusion qu'il n'y a pas de preuves concluantes pour croire à la séparation géographique des populations de l'est et de l'ouest de la baie d'Hudson et que l'on ne sait pas à quel stock appartient la population du nord de la baie d'Hudson. Les bélugas du sud-est de la terre de Baffin pourraient appartenir à un stock génétique distinct, comme le suggère des différences morphométriques avec les autres populations sub-arctiques, mais des preuves supplémentaires sont nécessaires avant de conclure sur l'identité de tous ces stocks.

Introduction

This paper pertains to Canadian beluga populations south of the Arctic circle and north of the Gulf of Saint-Lawrence. Summer concentrations of these belugas are commonly called western Hudson Bay population, eastern Hudson Bay population and Cumberland Sound or southeast Baffin Island population. The paper also reports on belugas near the Ontario coast of Hudson Bay and in the northern part of Hudson Bay.

Stock separation and numbers of subarctic beluga stocks are not well defined. We present results from extensive surveys and opportunistic sightings in Hudson Bay, southern Foxe Basin and south-east Baffin Island. We give population estimates for western Hudson Bay, northern Hudson Bay and southeast Baffin Island and report on numbers observed in southern Hudson Bay. Our distribution data combined with recently published results of surveys in eastern Hudson Strait and Ungava Bay (Smith and Hammill 1986) yield a new pattern of beluga summer distribution in Hudson Bay and open new questions about stock definition of subarctic beluga populations.

Methods

Aerial surveys covered coastal and near-offshore waters of four areas (Fig. 1): the southeast Baffin area which includes all coastal waters of Baffin Island between Exeter Sound, in Davis Strait, and Markham Bay, in Hudson Strait; the northern Hudson Bay area which covers waters between Rankin Inlet and Baffin Island up to 67°N latitude; the "southern Hudson Bay" area which covers waters from Cape Henrietta Maria at the mouth of James Bay to the Kaskattama River (57°N, 90°W) near the Ontario–Manitoba border; the "western Hudson Bay" area which covers waters from the Kaskattama River, in Manitoba, to Rankin Inlet, Northwest Territories (N.W.T.). Reconnaissance surveys were flown to locate beluga concentration areas. Census surveys centered on these areas of concentration and were designed to estimate population size. All census surveys were systematic strip transect surveys (Fig. 2–4). We used a systematic sampling design because it is more operationally convenient than random surveys and is also more efficient than random sampling as a means of mapping distribution (Caughley 1977). It is more precise to estimate population size when sample units are unequal in size (Cochran 1977) or when sample counts are serially correlated (Kingsley and Smith 1981), as was often the case in our surveys.

Systematic surveys were planned by delimiting a survey area, dividing it into parallel strips of desired width (e.g.: 1.6 km in visual surveys) and selecting the desired sampling fraction (e.g.: 10% or one transect flown for every 10 strips). The sampling fraction varied from survey to survey, depending on available funds, but generally we tried to obtain the highest sampling fraction affordable (25%) in known areas of beluga concentration. The first transect was chosen by randomly selecting a number from one to '*n*' (eg.: from one to ten) where '*n*' is the total number of strips divided by the sampling fraction and the following were chosen at equal distance from the first (e.g.: every 10 strips).

All reconnaissance surveys and several census surveys (Table 1) were done visually. The 1981 reconnaissance surveys were flown in a De Havilland Beaver with one observer in the right front seat and the other in the left rear. Navigation was done by dead-reckoning using land forms. All other visual surveys were flown in a De Havilland Twin Otter with observers seated directly behind wing struts, one on each side of the aircraft. Struts and windows were marked to delimit a survey strip of 800 m on each side of the aircraft. Flight position was determined by pilot and navigator with Omega Navigation and were regularly checked against landmarks. Air speed and altitude were maintained at 185 km • h^{-1} and 305 m during visual surveys, except in southeast Baffin surveys where we kept an altitude of 457 m. Cumulative counts were recorded every five min.

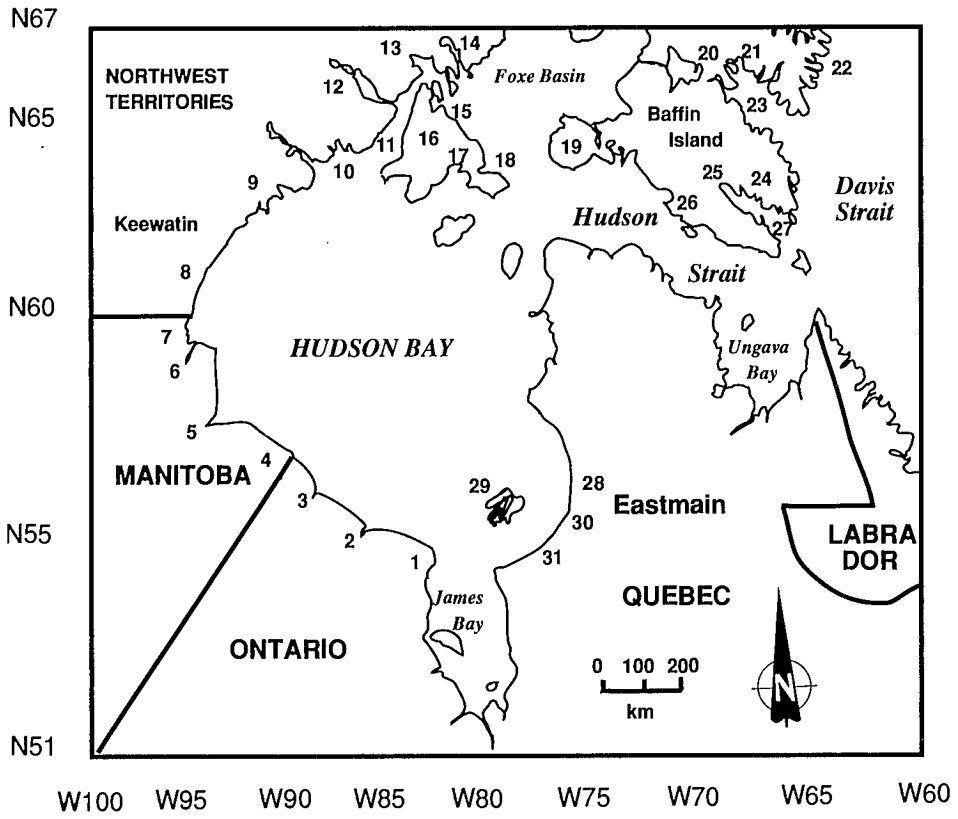

FIG. 1. Study area with placenames. (Note: placenames are numbered clockwise on the map.)

Belcher Islands	29	Kaskattama River	4
Cape Henrietta Maria	1	Little Whale River	30
Churchill (River & munic. of)	6	Lyon Inlet	14
Clearwater Fiord	20	Markham Bay	26
Coral Harbour (hamlet of)	17	Nastapoka River	28
Cumberland Sound	23	Nelson River	5
Daly Bay	10	Pangnirtung (hamlet of)	21
East Bay	18	Rankin Inlet (hamlet of)	9
Eskimo Point	8	Repulse Bay (& hamlet of)	13
Exeter Sound	22	Roes Welcome Sound	11
Foxe Peninsula	19	Seal River	7
Frobisher Bay	27	Severn River	3
Frozen Strait	15	Southampton Island	16
Great Whale River	31	Wager Bay	12
Hall Peninsula	24	Winisk River	2
Iqaluit (munic. of)	25		

TABLE 1. Procedures of subarctic beluga census surveys 1982-87.

Fig.	Survey date(s)	Survey design	Method of recording	Altitude	Transect spacing	Strip width	Transect orientation
2	July 14-15 1987	Systematic	Photographic 225×225 mm	914 m	5.5 km	1.34 km	90°-270°
2	July 17-18 1987	Systematic	Visual	305 m	15 km	2 × 0.8 km	40°-220°
2	July 19 1987	Systematic	Photographic 225×225 mm	1219 m	5.5 km	1.88 km	90°-270°
3	July 23 1982	Systematic	Visual	305 m	block1: 19 km block2: 11 km	2 × 0.8 km	block 1: 90°-270° block 2: 0°-180°
3	July 24-25, 1982	Random	Photographic 96x122 mm	914 m	random	0.45 km	90°-270°
3	July 26-27,1983	Systematic	Photographic 96x122 mm	914 m	9.4 km	0.45 km	90°-270°
3	July 27 &29,1984	Systematic	Photographic 225x225 mm	914 m	5.5 km	1.34 km	90°-270°
3	March18-21 1982	Systematic	Visual	305 m	block1: 7.5 km block2: 13 km block3: 19 km	2 × 0.8 km	block 1: 45°-225° block2: 0°-180° block3: 0°-180°
4	August 18-22, 1985	Systematic	Visual	457 m	9.5 km	2 × 0.8 km	90°-270°
4	August 16 &23,1986	Systematic	Visual	457 m	9.5 km	2 × 0.8 km	90°-270°

Photographic surveys were used to census areas of high concentration. The northern Hudson Bay photo-surveys are an exception in that they were designed to census narwhal concentrations but also provided us with beluga counts. We chose to conduct photo-surveys in concentration areas because they do not suffer from problems of reliability due to observer fatigue, boredom or bias such as are encountered in visual surveys. Beluga detectability changes with distance are much reduced by vertical photography. The 90° angle of the camera allows a more uniform water penetration accross the image plane compared with the oblique angles of view of visual observers. Glare and fog are also less of a problem at high angles. Variation in image coverage due to airplane roll can almost be eliminated by maintaining the camera level during operation, whereas there is no way of correcting strip width variation during visual surveys. Observer errors during film counts do exist but they can be corrected by recounts or multiple observers. Photo-surveys are particularly useful in estuaries and other areas where large groups or herds are encountered and visual observers have inadequate time for an accurate count.

Photographic census surveys (Table 1) were flown in a De Havilland Twin Otter with aerial cameras mounted in a port at the back of the aircraft. In 1982 and 1983 we used a Linhof Aeroteknica (format 953120 mm) with a 150 mm lens and Kodak Ektachrome transparency film. From 1984 to 1987, we used a Wild-Leitz RC8 (format 2253225 mm) with a 153 mm lens and Kodak aerocolor 2445 negative film. Cameras were triggered by an intervalometer at settings calculated to obtain a stream of adjoining frames. Flight position was determined by Inertial Navigation in 1984 and Omega Navigation in all other years. Land references were used to verify position and update navigation systems. Air speed and altitude were maintained at 185 km • h^{-1} and 914 m, except for the 19 July 1987 survey of western Hudson Bay which was flown at 1219 m.

The aerial film was scanned with a Nikon SMZ-1 dissecting scope on a Richards GFL-940-MC light table. We recorded belugas identified on each frame as well as any image which might be a whale. Frames with unidentified images were re-examined a second time for final classification.

Surveys were flown between July 1981 and August 1988 (Fig. 2–4). Southern and western Hudson Bay were first surveyed visually in July 1981 (Fig. 2). A second visual reconnaissance survey in August 1981 covered western and northern Hudson Bay (Fig. 2–3). From 1982 to 1984, three systematic census surveys (visual and photographic) were flown in July in northern Hudson Bay (Fig. 3). In the southeast Baffin area, both systematic and reconnaissance surveys (visual and photographic) were flown in August 1985 and 1986 (Fig. 4). In July

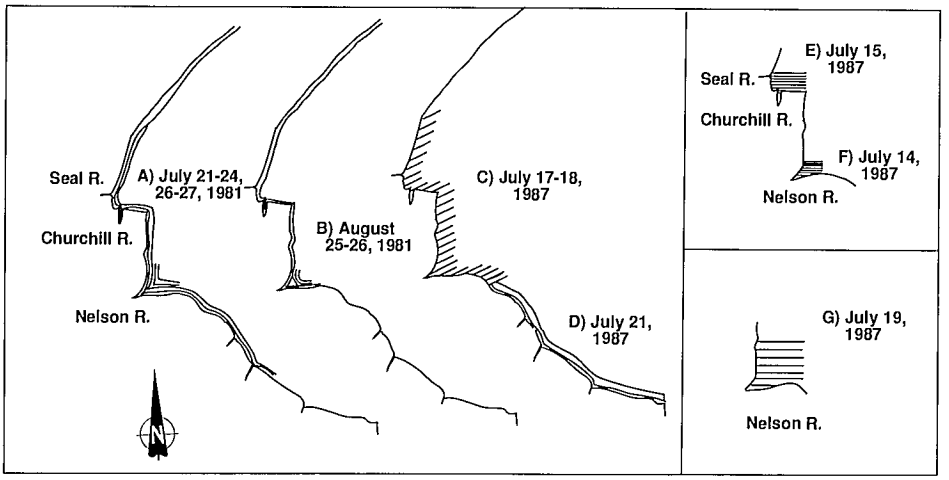

FIG. 2. Transect lines flown during July and August surveys of western and southern Hudson Bay.

1987, census surveys covered concentration areas of western Hudson Bay and a reconnaissance survey was flown in southern Hudson Bay (Fig. 2). Systematic and reconnaissance visual surveys in March 1983 and in August 1988 (Fig. 3) were also flown in northern Hudson Bay.

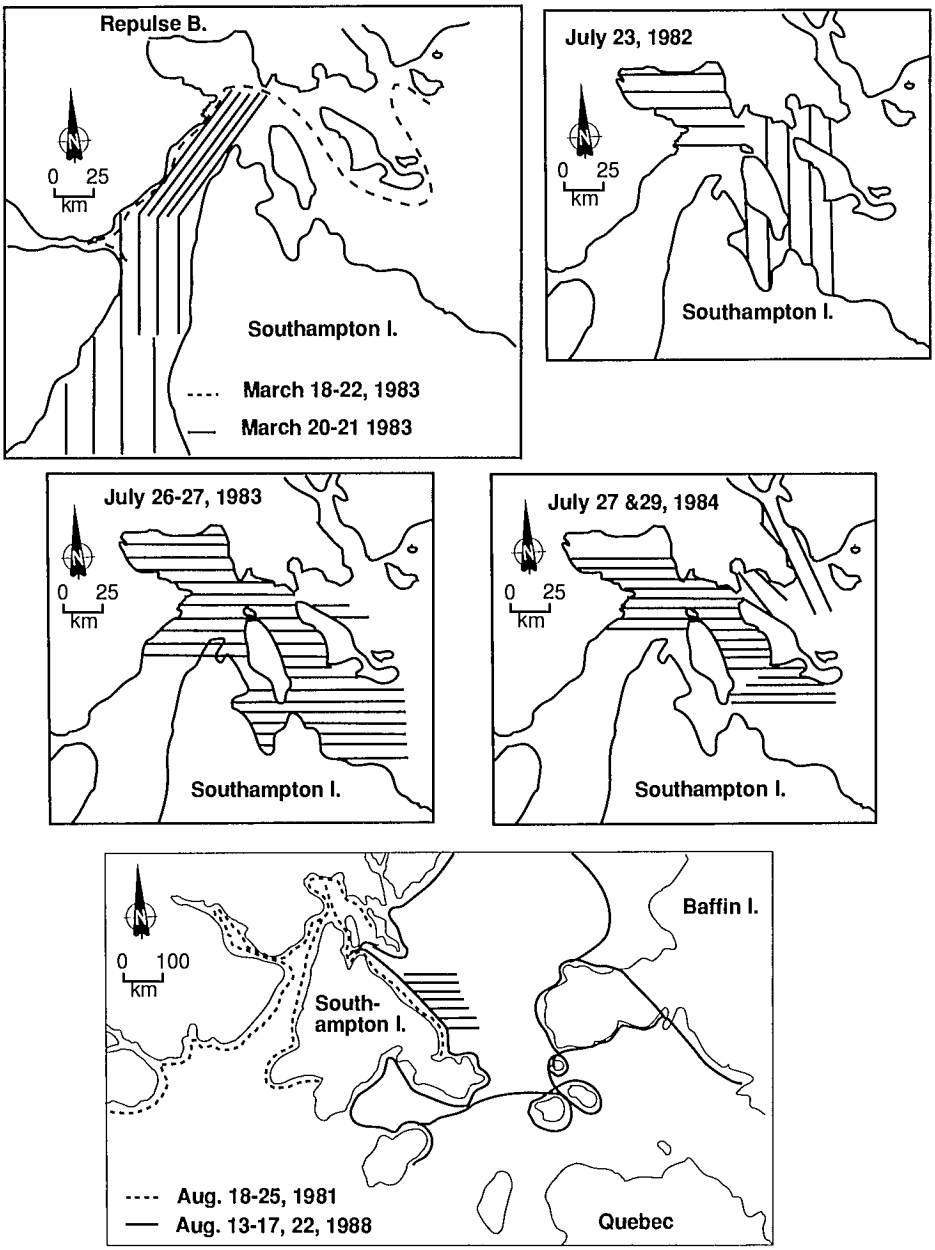

FIG. 3. Transect lines flown during March, July and August surveys of northern Hudson Bay.

Estimates of the total numbers were derived from each systematic census survey. The number of belugas and the surveyed area were totalled for each transect. In the case of photo-surveys, the area of each transect was the sum of frame areas. Land or fog encountered on the strip or photos were removed from the area total. Transect counts and areas were summed and the ratio of total count over total area gave a mean density. Estimates for each census area were obtained by multiplying the beluga density by the total census area. In cases where the census area was divided into strata, estimates from all strata were summed to obtain an estimate for the whole survey area.

We did not apply correction factors to the estimates to compensate for submerged animals missed during the flights. Water clarity varied greatly within and between surveys, from the silted waters of estuaries to the relatively clear offshore waters. Beluga diving behavior probably also varies from one area or time to the next but we had no way of measuring behavior during surveys. Correction factors are not yet available to compensate for these problems. Sergeant and Hoek (1988) used the overlap of adjacent photos to obtain a minimum correction for diving animals but our survey data is composed of non-overlapping visual intervals or photos. Consequently, in areas of high turbidity such as the head of the Nelson estuary, the results would tend in the direction of underestimation.

Methods described by Kingsley et al. (1985) were used to obtain estimates of variance for systematic surveys. Confidence limits were calculated as in Smith et al. (1985). Minimum and maximum population estimates for each survey were calculated by multiplying the upper and lower confidence limits by the total census area.

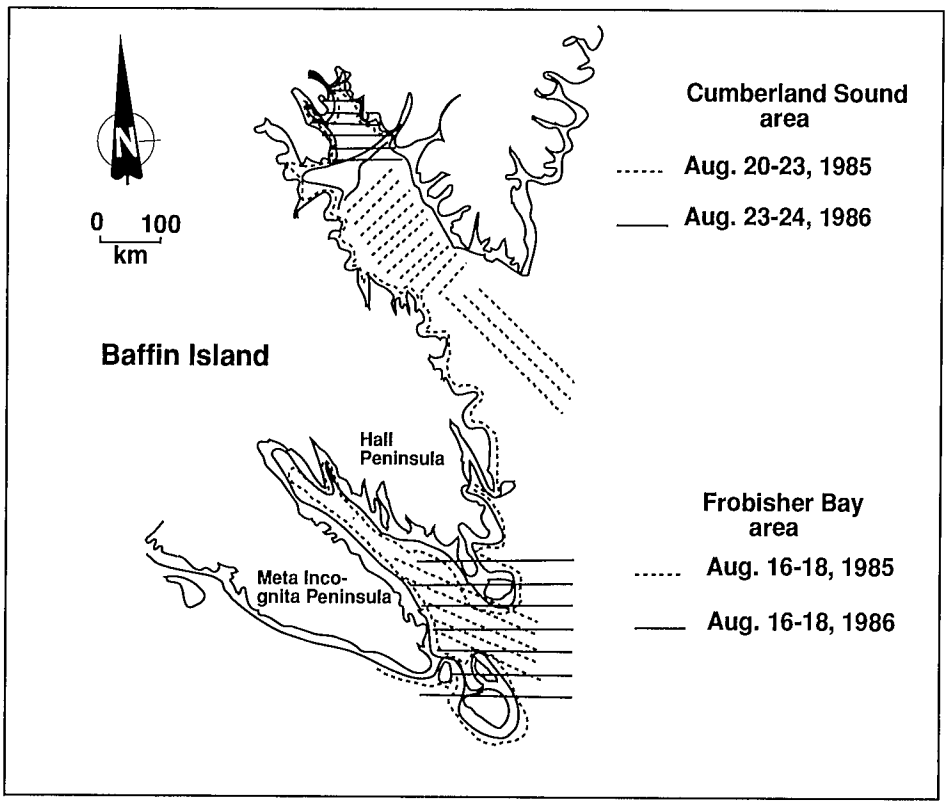

FIG. 4. Transect lines flown during August surveys of southeast Baffin Island.

In one case, on 15 July 1987, right after the systematic photo-survey of the Churchill–Seal River area, we obtained an additional photographic pass over a large concentration near the Seal River. The count from these photos (3 758) was added to the count (331) from the portions of the transects which did not overlap with that pass. That total rounded to the nearest hundred (4 100) was used in place of the lower confidence limit (1 200).

Results

During 1981 reconnaissance surveys along the coast of western Hudson Bay (Fig. 2a), we found belugas to be widely distributed near the coast of Manitoba as well as along the coast of Ontario and as far east of the Severn estuary as 86°409W where surveys ended. Mean densities at the heads of the Nelson, Seal, and Churchill estuaries were, respectively, 8, 5, and 8 belugas • km^{-2} during July surveys and 1, 4, and 5 belugas • km^{-2} during August surveys.

Only 62 belugas were seen north of the Manitoba border (60°N) during the July 1981 coastal reconnaissance surveys but, during similar surveys in August 1981, 329 belugas were found north of the border, including a small herd (128) at the mouth of the Thlewiaza River (60°309N). The northernmost sighting in July along the southern Keewatin coast was at latitude 60°409N while, in August, we sighted a beluga at latitude 62°209N.

In 1987, during visual and photo surveys of western Hudson Bay (Table 1, Fig. 2b–d), belugas were distributed throughout all survey transects from Eskimo Point to the Kaskattama River (Fig. 1). During the first photo survey of the Nelson estuary (Fig. 2c), we noted that survey lines did not cover the entire beluga concentration and we later repeated the survey over a broader area, farther north and more offshore from the estuary (Fig. 2d).

On this second photo survey of the Nelson concentration, belugas were again found throughout transects and as far offshore as survey lines reached, 110 km from any coast and 160 km from the mouth of the river. Beluga density was highest along the two transects closest to the mouth of the river (average 5 belugas • km^{-2}). Beluga density on the other five transects was lower but still substantial (average 1 beluga • km^{-2}).

The 14–15 July 1987 photo surveys (Fig. 2c) centered around the estuaries of the Nelson River and of the Churchill and Seal rivers, respectively. The total mean estimate for the two surveys combined is 12 500 (Table 2) but our coverage of the concentration in or near the Nelson estuary was incomplete. The second survey of the Nelson concentration (Fig. 2d) covered more offshore areas and yielded a mean estimate of 19 500 belugas (Table 2). When summed with the 15 July 1987 Churchill–Seal mean estimate of 5 600 (Fig. 2c, Table 2), this gives a total mean estimate of 25 100 for the western Hudson Bay population.

The fact that there were 4 d between the Churchill Seal and Nelson surveys raises the issue of possible movement of belugas between the two areas. A case in point is a 3 m radio-tagged male beluga released on 12 August 1988 in the Churchill river that was relocated in the Nelson estuary five days later (P. Weaver, Dep. Fisheries and Oceans, Winnipeg, Manitoba, personal communication). If movement of large numbers of belugas had occurred during the interval between the two July 1987 photo surveys, counts would be biased upwards or downwards depending on the direction of that movement. Nevertheless, the 17–18 July 1987 visual survey of approximately the same area (less the farthest offshore portion) gave very similar results, a total of 23 000 belugas (Table 2). As explained earlier, these results are uncorrected for submerged animals and therefore give negatively-biased estimates of the population size.

During 21 July 1987 reconnaissance surveys of the Ontario coast, which covered coastal waters from the Kaskattama River to Cape Henrietta Maria and back (Fig. 2b), we sighted an additional 1 299 belugas. The first transect 3 km inshore had most of the belugas, a total of 1 269 belugas, of which 232 belugas were concentrated at the estuary of the Severn River and 393 at the estuary of the Winisk River. Along the second transect flown parallel to the coast about 28 km offshore, we sighted a total of 30 belugas dispersed in small groups.

TABLE 2. Counts and estimates from systematic surveys performed in western and northern Hudson Bay (note: estimates over 100 rounded to nearest 100).

Survey	Census area (km^2)	Coverage	Total count	Estimate	95% confidence limits
Western Hudson Bay					
Nelson (14/07/1987)	3 015	24%	1 704	6 900	6 000-7 900
Churchill-Seal (15/07/1987)	3 035	24%	1 367	5 600	4 100-26 000
Total				12 500	10 100-33 900
Churchill-Seal (17/07/1987)	9 854	10%	1 184	11 300	3 300-38 700
Nelson (18/07/1987)	6 569	10%	1 209	11 700	7 700-17 800
Total				23 000	11 000-56 500
Nelson (19/07/1987)	15 022	10%	1 912	19 500	14 200-26 800
Northern Hudson Bay					
(23/07/82) Strat 1	2 769	11%	28	300	50-1 400
(23/07/82) Strat 2	5 396	7%	32	400	100-2 000
Total				700	200-3 300
(26-27/07/83)	8 103	10%	104	1 000	621-1 627
(27/07/84)	5 712	17%	109	700	400-1 100
(29/07/84)	2 069	11%	11	100	30-300
Total				800	400-1 400

In northern Hudson Bay (Fig. 3), the March survey of Roes Welcome Sound did not result in any sighting of belugas. Similarly, no beluga was seen during the reconnaissance flight of Frozen Strait and the mouth of Lyon Inlet. July 1982–1983 census surveys were limited to the area around Repulse Bay-Frozen Strait. Estimates of beluga population size from these surveys vary between 700 and 1 000 belugas (Table 2). In addition, we photographed a herd of 143 belugas on 27 July 1983 in the estuary of the Canyon River, Southampton Island, south of Frozen Strait.

In August 1981 and 1988, during reconnaissance surveys, belugas were dispersed in small groups all around Southampton Island, except for one large herd of 685 photographed at the head of East Bay on 17 August 1988. We also found 18 belugas in Foxe Basin, north of Foxe Peninsula.

In southeast Baffin Island, during August 1985 reconnaissance and census surveys, a total of 407 belugas were counted. The majority (398) were photographed in Clearwater Fiord, in or near the estuary of the Ranger River. Nine were sighted near the mouth of Frobisher Bay. There was no sighting along Hall Peninsula or along the Hudson Strait coast of Baffin Island.

During 1986 reconnaissance and census surveys, 442 belugas were photographed from the air near the mouth of Clearwater Fiord and, at the same time, 43 were counted by a ground crew from a cliff overlooking the estuary of the Ranger River in Clearwater Fiord. Two more belugas were sighted by aerial observers in Cumberland Sound, near Clearwater Fiord, and one near Frobisher Bay, off Hall Peninsula.

Again, no correction factors for submerged animals were applied to these counts but the 442 belugas photographed in 1986 were travelling in clear water, moving fast and making short, shallow dives and we feel certain that few if any were missed by the camera. The 43 whales counted from a cliff in Clearwater Fiord were in the silted waters of the Ranger estuary but they were relatively easy to count because the whales were well dispersed.

The difference in herd count between 1985 and 1986 is due to the fact that the 1985 count was obtained from photographs of the herd in the silted water of the Ranger River in Clearwater Fiord compared to the 1986 count in the clear water at the mouth of the fiord. Although a systematic survey design was used for these surveys, a population estimate cannot be derived from these data because of the extreme clumping of this relatively small population.

Discussion

In managing beluga populations, it is important to know the stock size and identity of animals taken at different hunting locations. The term "population" is used here in the sense of the total number of belugas occupying a defined area. The term "stock" can be defined as a management unit, a population in particular areas where harvesting occurs, or as an isolated population, one which increases solely by reproduction and not through emigration from other populations. In recent beluga literature, the term "stock" has meant the latter of these definitions. Summer concentrations in or near estuaries have been hypothesized to be discrete stocks. The problem for managers is that most hunting of subarctic belugas does not presently take place in estuaries and it is not clear if belugas landed by any particular community belong to one "stock" or several "stocks."

Subarctic belugas have been hypothesized to belong to four discrete "stocks": the western Hudson Bay "stock" (Sergeant 1973, 1981), the eastern Hudson Bay "stock" (Finley et al. 1982), the Ungava Bay "stock" (Finley et al. 1982) and the Cumberland Sound or southeast Baffin "stock" (Brodie et al. 1981; Richard and Orr 1986). The discussion that follows will review available information pertaining to the size and discreteness of these "stocks" and the possibility of mixing between "stocks."

Our results show that the western Hudson Bay beluga "stock" which summers along the Manitoba coast numbered about 23 000 animals in 1987. In addition, we observed at least 1 300 belugas along the Ontario coast. These numbers far exceed previous estimates of the

western Hudson Bay beluga "stock" obtained from 1965 surveys (Sergeant 1973, 1981). This difference can be explained in two ways. One is that the population has increased substantially in the 22 yr that separated the two surveys. The other is that survey coverage and methods of estimation were so different that they produced very different results. It is also possible that both factors have contributed to this difference.

Comparison of the 1965 (Sergeant 1973, 1981) and our 1987 surveys suggests that the early estimates may have been low for the Nelson estuary because of extrapolations from very low coverage of the upper Nelson estuary (2.4%) and no coverage of the offshore. In the 19 July 1987 survey of the Nelson estuary, beluga density was lower in the offshore portion than in the portion inshore corresponding to Sergeant's coverage of the estuary (approx. 1 beluga • km^{-2} offshore as compared to 5 belugas • km^{-2} inshore). Despite that, the offshore portion amounted to twice as many belugas because it was 10 times the area of the inshore estuarine portion. Sampling error is also a probable factor in the 1967 survey which was flown with no apparent sampling design. The same comments apply to the Churchill–Seal area where our systematic coverage was greater and farther offshore.

The hypothesis that the western Hudson Bay population has increased between 1965 and 1987 cannot be tested by comparing the two studies. Errors of estimation in the 1965 survey due to the lack of a sampling design and to low and incomplete coverage are just as likely to produce a large discrepancy with the 1987 results as a population increase would. A greater understanding of beluga distribution and movements and surveys with comparable coverage and methods would have been needed to document a change in the western Hudson Bay population's size.

Census surveys of northern Hudson Bay gave mean estimates of 700 and 1 000 belugas in July (Table 2). In addition, individuals or small pods have frequently been reported along the south coast of Southampton Island (Sutton and Hamilton 1932) and schools of 100 or more have also been observed in Wager Bay in summer (Degerbøl and Freuchen 1935; Anon. 1978). Our 1988–89 reconnaissance surveys found a group of over 600 belugas in East Bay in both July and August (Richard, unpubl. data). These surveys and opportunistic sightings suggest that a population of 1 000 or more summers in northern Hudson Bay every year.

In eastern Hudson Bay and James Bay, belugas were recently estimated to number about 1 400 and 1 200, respectively, while the Ungava Bay population was deemed too low to derive a population estimate (Smith and Hammill 1986).

The summer distribution of belugas in southeast Baffin Island is not limited to the concentration in Cumberland Sound. In the past, sightings in August in Frobisher Bay have varied from a few individuals to as many as 380 (MacLaren Marex Inc. 1978, 1979, 1980). Catches of belugas are frequently reported in summer at Iqaluit and Lake Harbour (D. Pike, DFO Iqaluit, personal communication). These observations motivated us to survey as large an area of southeast Baffin Island's coastal waters as possible.

Despite the wide coverage of our surveys, we found only small numbers of belugas other than the herd seen in both years at the head of Cumberland Sound. We therefore conclude that there were fewer than 500 belugas in the southeast Baffin summer population in 1985–86. Considering that the annual beluga catch in Pangnirtung and Iqaluit exceeds estimates of population replacement rate (Richard and Orr 1986), it is probable that the population has declined further since these surveys. This decline is consistent with an earlier decline over several generations described by Brodie (1971).

Four lines of reasoning have been used to suggest stock discreteness of subarctic beluga summer concentrations: morphometric differences (Sergeant and Brodie 1969; Finley et al. 1982), geographic isolation (Sergeant and Brodie 1975; Finley et al. 1982), site specificity in estuarine use (Finley et al. 1982; Smith and Hammill 1986) and depletion through long-term exploitation (Mitchell and Reeves 1981).

Sergeant and Brodie (1969) argued for stock isolation when they observed that western Hudson Bay belugas had a smaller adult size and girth at age than Cumberland Sound belugas.

Eastern Hudson Bay and Ungava Bay belugas, on the other hand, have the same size at age as do western Hudson Bay belugas and those captured in Hudson Strait in the fall (Finley et al. 1982). The Hudson Strait animals are thought to be migrants from western Hudson Bay. These assumptions have been questioned because sample sizes used for comparisons were small and subject to ageing errors, particularly for the Ungava Bay animals, and they were made without detailed statistical analysis (Perrin 1980; see also Doidge 1990).

The argument of geographic isolation was also used for delimiting stocks. In 1980, the International Whaling Commission distinguished year-round resident beluga populations and summering beluga populations which share common wintering grounds (Perrin 1980). The western Hudson Bay beluga population, then estimated at about 10 000 (Sergeant 1973), was thought to winter in the leads of Roes Welcome Sound and to be a resident population, geographically isolated year-round from other populations. The eastern Hudson Bay and Cumberland Sound populations, estimated respectively at "a few hundred" and 500 (Perrin 1980) were thought to share the same wintering area in Hudson Strait but to be separate in summer.

Surveys in March 1982 failed to find a large concentration in northern Hudson Bay, the hypothesized wintering area for the western Hudson Bay population (Sergeant 1973), while surveys of Hudson Strait resulted in a much larger estimate than the eastern Hudson Bay and Cumberland Sound populations combined (Finley et al. 1982). It was therefore concluded that the western Hudson Bay "stock" must also winter in Hudson Strait. It was still thought to be geographically separate from the other populations in summer (Finley et al. 1982).

Our own March surveys found no beluga in Roes Welcome Sound or Frozen Strait but local sources have reported to us occasional winter sightings at the floe edge of Daly Bay, in Lyon Inlet and off Cape Bylot (65°209N, 84°109 W), northern Southampton Island. Belugas have also been seen in James Bay during winter months (Jonkel 1969) and in Hudson Bay near the Belcher Islands (Breton et al. 1984). These reports are relatively small in numbers and do not suggest that a large population of belugas winters in either Hudson Bay or James Bay.

Various authors have speculated that summer concentrations constitute discrete stocks (Sergeant 1973; Brodie et al. 1981; Finley et al. 1982). Finley et al. (1982), referring to the western Hudson Bay, eastern Hudson Bay and Ungava Bay summer concentrations, concluded that "there is clearly no mixing among these three groups during the summer." Our survey results combined with those of Smith and Hammill (1986) contradict that assertion. Belugas were found throughout James Bay and were widespread between the eastern Hudson Bay coast of Northern Quebec and the Belcher Islands (Smith and Hammill 1986). Belugas are apparently regular summer occupants of southern Hudson Bay. Johnston (1961) mentions that "during summer months, the schools of beluga move randomly along the coastline, with large concentrations centered around the bigger river mouths." He reports sightings of 100 belugas at both the Severn and Winisk estuaries in July 1961. Belugas have been reported by local Indians before spring breakup at both the Severn and Winisk estuaries (Johnston 1961).

Sergeant (1968) also mentions beluga "herds extending at least to Winisk" in late July. Herds of 100–150 belugas have been seen near the mouth of the Winisk River on 1 July 1979 and 25 June 1982 (K. F. Abraham, Ontario Ministry of Natural Resources, Moosonee, Ontario, personal communication). When these results are combined with our own from the coasts of Manitoba and Ontario, it becomes clear that belugas have an essentially continuous distribution along the Hudson Bay and James Bay coasts of the three provinces in summer.

It is unclear what route is taken by belugas to reach the western Hudson Bay and Ontario summering areas. Although there are reports of spring sightings of belugas near the Keewatin coast (Sergeant 1973; Reeves and Mitchell 1989), belugas are rarely seen or hunted in spring and early summer despite frequent seal hunting trips at the floe edge. Most catches in Keewatin communities occur in August and few occur before the end of July (Gamble 1984, 1987a,b, 1988). If 23 000 belugas migrated in May and June near the Keewatin coast, that would not go unnoticed by residents who are always eager to hunt belugas. On the east side

of Hudson Bay, reports of a spring southward migration of belugas have been well documented (Finley et al. 1982; Breton et al. 1984).

In the fall, a return northward migration occurs along both the east and west coasts of Hudson Bay (Sergeant 1973; Finley et al. 1982). This northward migration is apparent from catch records and local informants (Breton et al. 1984; Gamble 1984, 1987a,b, 1988) and was demonstrated at least for the western Hudson Bay by recoveries at Whale Cove and Repulse Bay of belugas tagged at the Seal River (Sergeant 1973). Our 1981 surveys show a reduction in density on the Manitoba coast in August and an extension of the range of belugas northward along the Keewatin coast.

The stock identity of northern Hudson Bay belugas is unclear. Their distribution appears not to overlap with western Hudson Bay belugas until late summer. According to local hunters, belugas are seen near Repulse Bay and Frozen Strait as early as April or May (Repulse Bay and Coral Harbour Hunters and Trappers Association, personal communication), but none are seen along the Keewatin coast before late July or August (see above). Repulse Bay hunters also report that more belugas are seen in the fall than in summer, presumably as a result of the western Hudson Bay return migration through that area.

Some belugas winter along the Labrador coast (Boles 1980; McLaren and Davis 1982). They were once found in summer along the central and northern coasts of Labrador but it is unsure how many still remain (Boles 1980). Sightings of approximately 200 belugas were made during 8 and 10 June 1979 surveys but there is no information on numbers found later in the summer (Boles 1980). According to Degerbøl and Freuchen (1935), some Labrador belugas move into Ungava Bay and Hudson Strait in the spring.

The above observations show that mixing between neighboring populations is possible during a significant portion of the year. The exchange potential is greatest in winter when most subarctic belugas occupy a small geographical area from northern Hudson Bay to southeast Davis Strait and the Labrador Sea. More importantly, mating is thought to occur in April or May (Sergeant 1973; Brodie 1971) while many belugas are still in their wintering area, which means that genetic mixing through cross-breeding could also take place.

The argument that Canadian subarctic belugas may be site-specific in summer was first suggested by Brodie et al. (1981) although the concept of homing on estuaries was implicit in earlier works of Tomilin (1967) and Kleinenberg et al. (1969). Caron and Smith (1990) give evidence of philopatry (site fidelity) and site tenacity for individually recognizable belugas using the Nastapoka estuary in eastern Hudson Bay. They present data which suggests that there were four times more adult females than males in the Nastapoka estuary during their study and that neonates comprised 16–19% of the total number of individuals observed. This preponderance of calves and females indicates that other age and sex classes were underrepresented in the estuary.

Since 68-80% of animals censused were observed more than 10 km from the eastern Hudson Bay coast (Smith and Hammill 1986), a substantial portion of the eastern Hudson Bay population may not, at least in a given year, be as site tenacious as the river occupants. On the other hand, if females and calves are more numerous in estuaries and more site tenacious than males and juveniles, female-calf concentrations then form seasonally isolated stocks of their own. If so, the survival of such estuarine female stocks would be of specific concern because eradication of any such stock would mean reduction in the species' genetic diversity.

Another argument that has been used to infer stock discreteness is the long term decline in catches that some populations have experienced over years of commercial exploitation (Brodie 1971; Mitchell and Reeves 1981). This is considered the strongest line of evidence available for the Cumberland Sound population because it suggests that the effect of exploitation has not been moderated by recruitment from adjacent populations (Mitchell and Reeves 1981). It was also suggested that the historical decline of commercial catches in eastern Hudson Bay was an indication of over-exploitation of that "stock," and of an absence of recruitment from western Hudson Bay (Finley et al. 1982; Reeves and Mitchell 1987).

Unfortunately, there is no direct information on the pre-exploitation size of those populations to verify the validity of these conclusions.

The depletion of both the eastern Hudson Bay and Ungava Bay populations appears to have taken place in the 1800's and 1900's prior to that of Cumberland Sound (Finley et al. 1982). As late as the mid-1970's, there was still considerable hunting pressure on those two beluga populations (Finley et al. 1982). Belugas are now very scarce in Ungava Bay in summer (Smith and Hammill 1986). There is some evidence that the Labrador population also suffered a decline in numbers in the early 1900's (Brice-Bennett 1978; Boles 1980). If neighboring populations such as Cumberland Sound, Ungava Bay and Labrador normally exchanged animals, the reductions in numbers which they all suffered could have prevented the benefits of emigration from neighboring populations. Mitchell and Reeves (1981) suggested the possibility that the Cumberland Sound population could also be part of a much larger stock which is itself declining.

The only population which has apparently maintained large numbers during the same period is the western Hudson Bay population. However, information available on its historic size is not sufficiently precise to conclude on a trend in abundance (Perrin 1980; Richard and Orr 1986; see also above discussion on its population size).

The eastern Hudson Bay–James Bay population still numbers several thousand animals despite the heavy exploitation to which it has been subjected. It is possible that the large size of the western Hudson Bay population could have acted as a buffer against its own depletion and, through emigration of its animals, against a more drastic decline in the eastern Hudson Bay population size. Yet the disappearance of historical beluga concentrations at Great Whale and Little Whale rivers (Finley et al. 1982; Reeves and Mitchell 1987) suggests that immigration, if it occurred, was not sufficient to buffer those two concentrations. Their disappearance lends support to the hypothesis of philopatric estuarine stocks.

In this review, we present two recurring ideas. The first is that belugas are widespread in distribution throughout the year and opportunities for mixing between populations are frequent. The second is that belugas concentrate at estuaries in summer and these estuarine concentrations could be made largely of philopatric female-calf stocks. In other words, we might have wide-ranging males and juveniles but sedentary females and calves and the site-tenacity of the latter would make them more vulnerable to hunting at estuaries. If these estuarine stocks are distinct genetic stocks then there is indeed concern for their conservation where they are hunted directly at the estuary such as in the Nastapoka River. On the other hand, most catches of subarctic belugas today do not take place in estuaries but at locations along the coasts of Hudson Bay and Hudson Strait where the identity of landed belugas is much less clear.

This review shows that new approaches are needed to clarify the stock identity of subarctic belugas hunted by about 20 N.W.T. and Quebec communities. Future studies of these populations should concentrate on monitoring movements of individuals, using mark–recapture or telemetric tracking, and on genetic markers (Hellbig et al. 1989) that could elucidate the relationships between estuarine concentrations and catches at locations throughout the range of subarctic belugas.

Acknowledgments

We thank the many people who assisted in various aspects of the surveys. Thanks particularly to A. Blouw for his help in the design and operation of the photographic systems. M. Kingsley gave us valuable advice on population estimation methods. Thanks also to T. Smith, R. Reeves and two anonymous reviewers for their comments. Polar Continental Shelf Project and Bradley Air Services provided continued support during the program. Hunters and Trappers Associations from N.W.T. settlements on sub-arctic coasts were very helpful in sharing their knowledge about the seasonal distribution of belugas.

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Distribution, Abundance, and Movements of Beluga Whales, *Delphinapterus leucas*, in Coastal Waters of Western Alaska

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FROST, K. J., AND L. F. LOWRY. 1990. Distribution, abundance, and movements of beluga whales, *Delphinapterus leucas*, in coastal waters of western Alaska, p. 39–57. *In* T. G. Smith, D. J. St. Aubin, and J. R. Geraci [ed.] Advances in research on the beluga whale, *Delphinapterus leucas*. Can. Bull Fish. Aquat. Sci. 224.

A compilation of sightings indicates that belugas occur in coastal waters of western Alaska during the ice-free period, which ranges from year-round in parts of Bristol Bay to July–September in the northeastern Chukchi Sea. Their distribution and abundance appears to be influenced mostly by a combination of food availability and the presence of estuarine conditions which may be important for molting. Sea ice, killer whales, and human activity may also affect distribution in some areas. Major concentration areas, in which belugas can be considered as provisional management stocks, occur in Bristol Bay, the Norton Sound/Yukon River delta region, and the eastern Chukchi Sea (including Kotzebue Sound and the Kasegaluk Lagoon region). These hypothetical stocks are based on distribution and timing of sightings, and should be confirmed by tagging and genetics studies. Tentative estimates of stock sizes are as follows: Bristol Bay — 1 000 to 1 500; Norton Sound/Yukon Delta — 1 000 to 2 000; and eastern Chukchi Sea — 2 500 to 3 000. Limited data suggest that numbers have generally stayed stable over the past 20–30 yr, although substantial fluctuations in local distribution have occurred in the Kotzebue Sound region.

Une compilation basée sur l'observation visuelle dénote que les marsouins blancs se produisent dans les eaux côtières de l'Alaska de l'ouest durant la saison sans glace, qui s'étend sur toute l'année dans des parties de la baie de Bristol, et de juillet-septembre dans le nord-est de la mer de Chukchi. Leur répartition et abondance semblent être principalement influencées par une combinaison de la disponibilité de la nourriture et de la présence de conditions estuarines qui sont peut-être importantes pour la mue. La glace océanique, les orcs et l'activité humaine affectent peut-être aussi la distribution dans certaines zones. Des zones de concentration majeures dans lesquelles les marsouins blancs peuvent être considérés comme des stocks pour la gestion se produisent dans la baie de Bristol, la région de l'anse de Norton/rivière du Yukon, et de l'est de la mer Chukchi (incluant l'anse de Kotzebue et la région du lagun de Kasegaluk. Ces stocks hypothétiques sont calculés sur la distribution et la répartition saisonnière d'observations visuelles, et devraient être confirmés par l'étiquetage et des études génétiques. Des estimations préliminaires de grosseurs de stocks sont les suivants: baie de Bristol — 1 000 à 1 500; l'anse de Norton/delta du Yukon — 1 000 à 2 000; et l'est de la mer Chukchi — 2 500 à 3 000. Des données limitées suggèrent que les nombres sont demeurés généralement stables sur une période s'échelonnant sur les 20–30 dernières années, quoique de réelles fluctuations dans la distribution locale ont eu lieu dans la région du détroit de Kotzebue.

Introduction

Beluga whales (*Delphinapterus leucas*) are a common but relatively unstudied component of the Alaskan marine mammal fauna. The majority of beluga whales in Alaska occur in the Bering, Chukchi and Beaufort seas. Seasonal distribution and movements of this group of whales, which we will refer to as the Bering Sea population, are complex. Most winter sightings have been in pack ice of the central Bering Sea (Brueggeman and Grotefendt 1988; Ljungblad et al. 1986), which is thought to be the main wintering area for the population (Seaman and Burns 1981). Beluga distribution and movements are affected by ice (Fay 1974; Lowry et al. 1987a), and in some circumstances winter range may extend into the northern Bering and southern Chukchi seas.

As sea ice cover loosens in late March and April, major seasonal movements begin. Many whales migrate northward through leads and shear zones of the Bering, Chukchi and Beaufort seas (Fraker 1979). The belugas often travel in association with bowhead whales (*Balaena mysticetus*), and are observed and hunted during spring near settlements along the west coast of Alaska (Seaman and Burns 1981; Braham et al. 1984). The majority of this group probably summers in the eastern Beaufort Sea, Amundsen Gulf and the Mackenzie Delta (Fraker et al. 1978; Davis and Evans 1982). They migrate westward in August–October through offshore waters of the Alaskan Beaufort Sea (Burns and Seaman 1988; Ljungblad et al. 1987). Due to ice conditions and seasonal movement patterns, this group of belugas spends little time in coastal waters of western Alaska, though they frequent nearshore areas in the eastern Beaufort Sea and Amundsen Gulf.

This paper deals with the beluga whales that appear along the coast of western Alaska during the open water season. Although they probably share a common wintering area with whales from the eastern Beaufort Sea/Mackenzie stock, and may be part of the same population, it is likely that these groups should be considered as one or more separate stocks for management purposes. Our objectives in this paper are to compile and present all available data on distribution and abundance of belugas in coastal waters of western Alaska, identify concentration areas, suggest provisional management stocks based on movements and seasonal distribution patterns, and estimate abundance and, where possible, trends in abundance for each provisional stock.

Methods

Information on beluga distribution and abundance has been obtained from both opportunistic and systematic observations. Opportunistic sightings have come from a network of informants, including scientists, fishermen, hunters, and others who live and work along the coast of Alaska, We have received many unsolicited reports, and regularly query certain individuals to obtain their observations. Sources of these personal communications are listed in Frost et al. (1983a, 1983b) and Seaman et al. (1988).

Much information has come from aerial surveys of spawning herring (*Clupea harengus*) conducted by the Commercial Fisheries Division of the Alaska Department of Fish and Game from 1976 through 1988 (C. Whitmore, unpublished data), and aerial surveys of endangered whales conducted by the Naval Ocean Systems Center from 1979 through 1986 (Ljungblad et al. 1987). All beluga sightings were recorded during those surveys.

We conducted aerial surveys specifically to enumerate beluga whales at various times between 1978 and 1987. Surveys did not cover the entire habitat of belugas along the coast of western Alaska but were directed to specific areas at the times of year when belugas were expected to concentrate. Surveys were of two general types depending on the type of aircraft available and the anticipated distribution of whales. Search surveys were usually flown parallel to the coast at a distance of 0.5–3 km offshore and an altitude of 152–457 m. One or two observers, seated beside or behind the pilot in a fixed-wing aircraft or helicopter, looked

for and recorded all whales within view. Large concentrations were frequently circled and counted or photographed. Aerial photographs were 35 mm slides taken obliquely from the window of the aricraft. Slides were projected and all visible animals counted. Transect surveys covered areas where belugas were thought to occur, or where concentrations were located during search surveys. Transect surveys were flown at an altitude of 305 m at speeds of 180–275 km/h with 1 observer on each side of the aircraft counting all whales visible within a strip 0.9 km wide.

Sightings, whether opportunistic or made during surveys, may not detect all the animals present in a area. Beluga whales, especially young animals, are difficult to detect in muddy or rough water. Also, belugas often spend little time at the surface where they can be seen. Correction factors may be developed and applied to adjust for undercounting (Sergeant 1973; Davis and Evans 1982; Frost et al. 1985). Unless noted otherwise we have not applied any correction factors to the data, and have presented the numbers provided by the original observers.

Information on movements was obtained either directly from locations of radio-tagged animals, or inferred from the sequence of occurrences of groups of animals at adjacent localities.

Results and Discussion

Regional Distribution and Abundance

The southern limit of the normal distribution of belugas in western Alaska occurs in Bristol Bay at approximately 56° N latitude. We know of no sightings from the Aleutian Islands, Unimak Pass, or the Alaska Peninsula south of Port Moller (contrary to Gurevich 1980), and local residents say that belugas do not occur in this area.

Although few sightings have occurred in the period from November through March (Fig. 1), belugas have been reported from coastal waters of Bristol Bay northeast of Port Moller throughout the year. Autumn and winter sightings occur infrequently which suggests that belugas do not regularly occur in large numbers at predictable nearshore locations during those months. In most years pack ice extends into Bristol Bay, and belugas may spend much of their time offshore in or near the ice. Formation of shorefast ice in bays and river mouths excludes them from some nearshore areas of Bristol Bay during winter.

Belugas begin to appear regularly in northern Bristol Bay in early April (Fig. 2). They often swim up rivers to the edge of the ice as it begins to break up. Whales become increasingly common in May and June with frequent sightings through August (Fig. 2–4). Most sightings occur in Kvichak and Nushagak bays. Belugas have seldom been sighted in outer, northwestern Bristol Bay.

The first sightings of the year along the Yukon and Kuskokwim deltas and in Norton Sound usually occur in late April and early May (Fig. 2). Sighting effort in this area is limited and belugas may often go unnoticed, especially in the muddy waters that occur near river mouths at breakup. Most reports come from aerial surveys for herring, or from residents of coastal villages where belugas are occasionally hunted when they appear shortly after the shorefast ice moves away. Whales occur in this region during the summer and autumn, with most sightings near the mouths of the Yukon River and in Norton Sound (Fig. 2–4). According to local residents, belugas were common in the lower portion of the Kuskokwim River earlier in this century but stopped using the lower river in the 1940's. However, during April–August 1988, frequent sightings of a few to several hundred belugas were reported in Kuskokwim Bay and in the Kuskokwim River as much as 40 km upstream. Overall, the lack of sightings in northwestern Bristol Bay, Kuskokwim Bay, and along the Bering Sea coast south of the Yukon River suggests that there is little movement of belugas between Bristol Bay and the Norton Sound/Yukon Delta region.

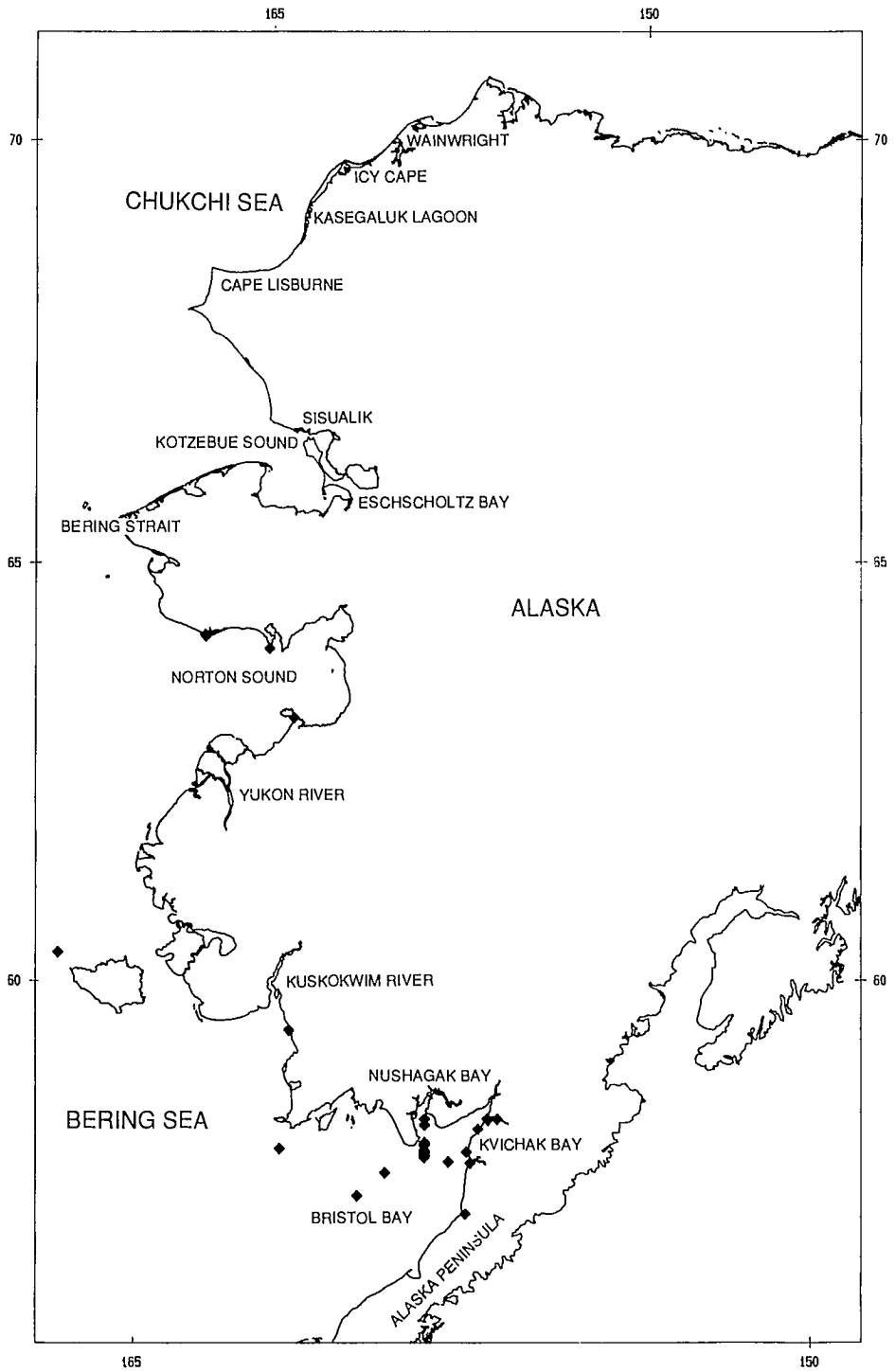

FIG. 1. Sightings of beluga whales in ice-free coastal waters of western Alaska during the months of November through March.

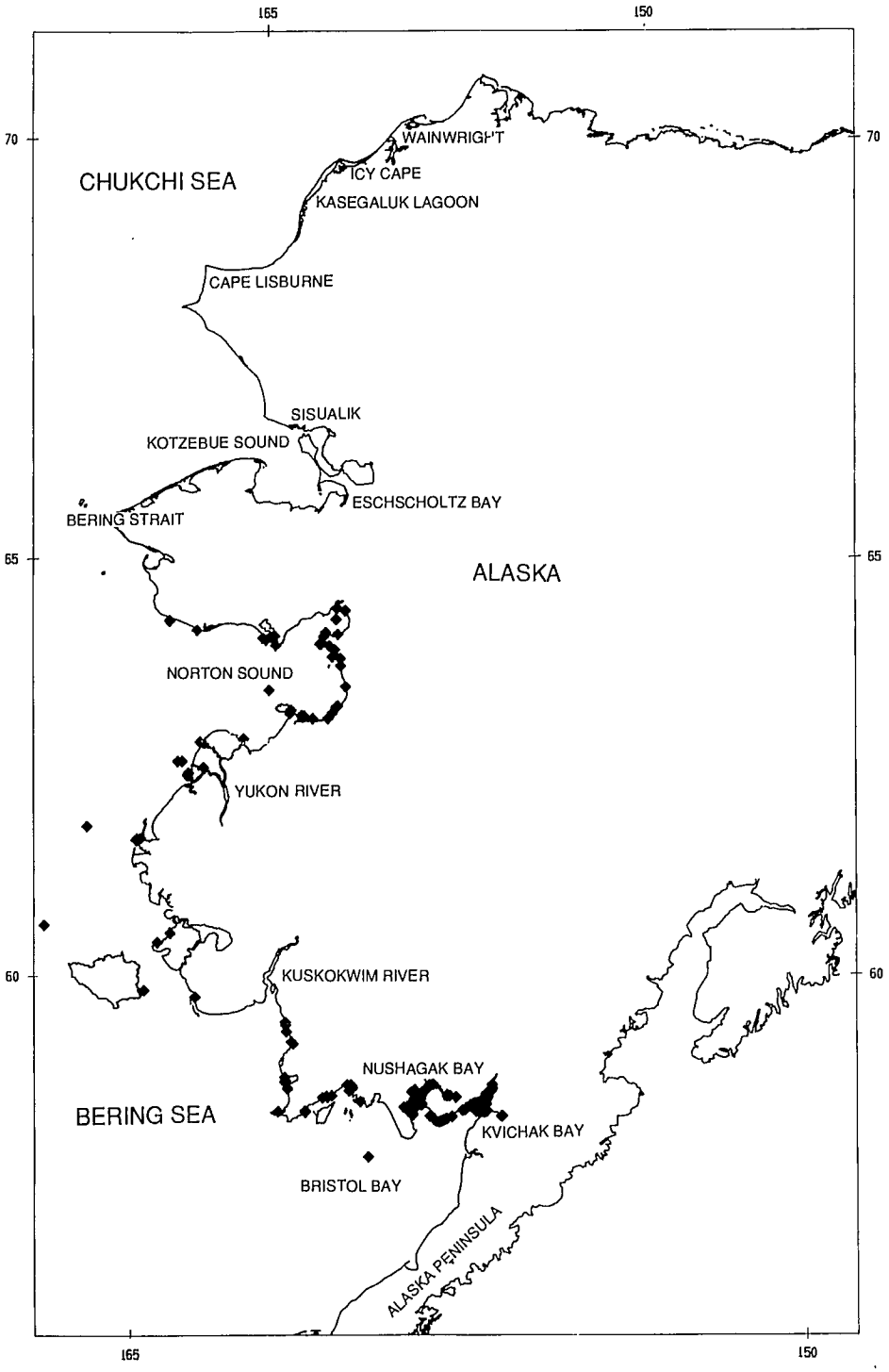

FIG. 2. Sightings of beluga whales in ice-free coastal waters of western Alaska during the months of April and May.

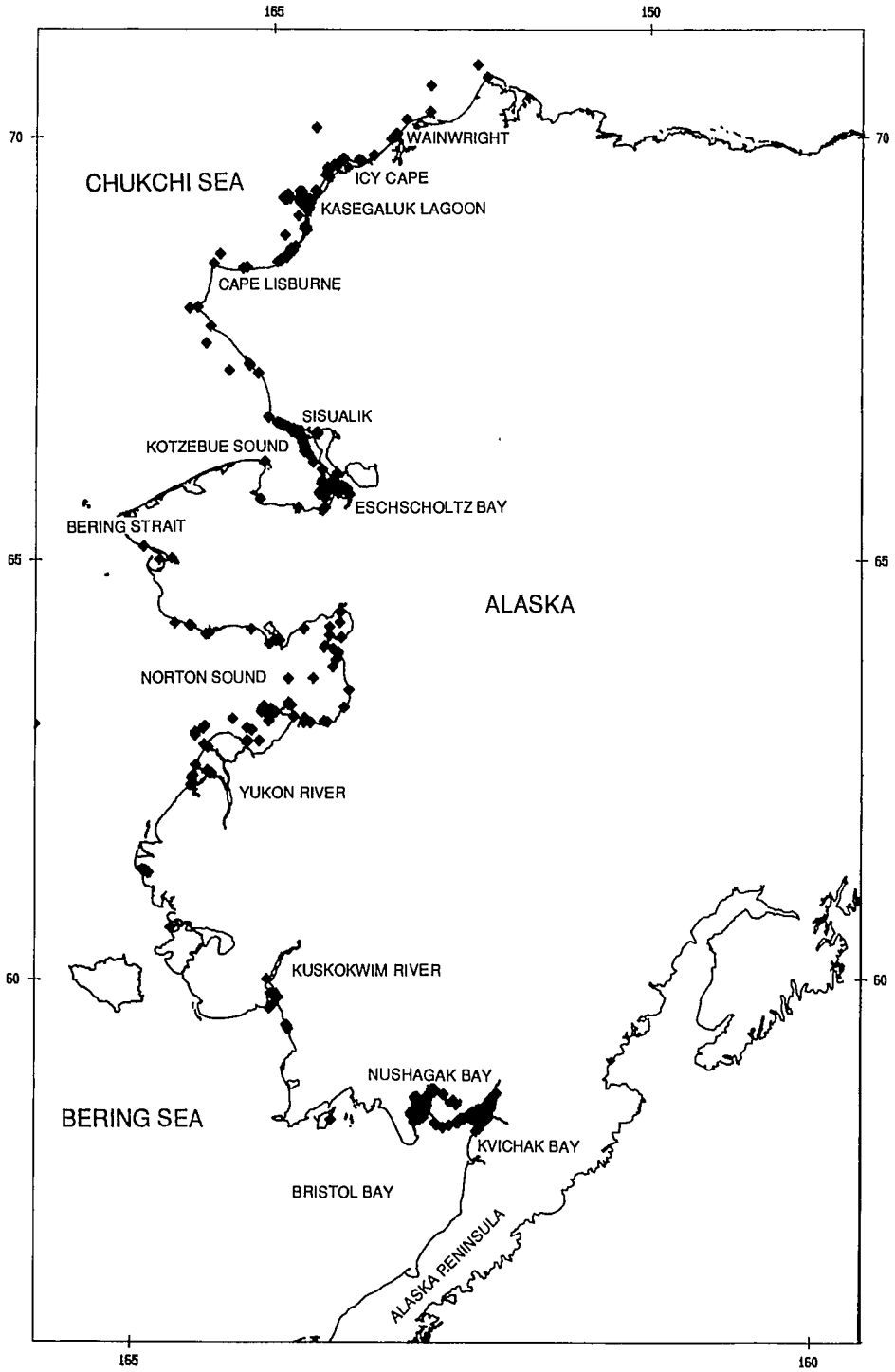

FIG. 3. Sightings of beluga whales in ice-free coastal waters of western Alaska during the months of June and July.

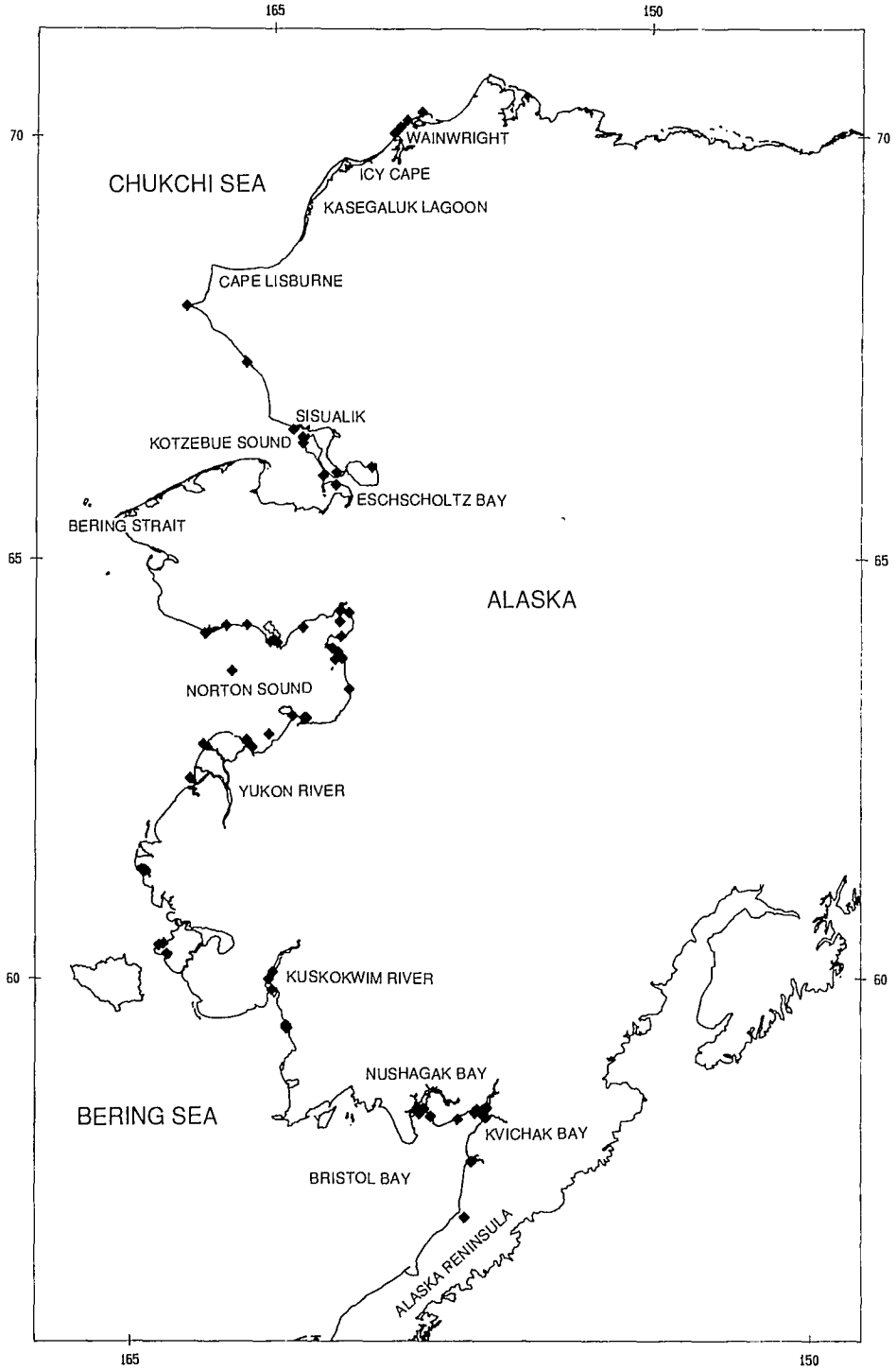

FIG. 4. Sightings of beluga whales in ice-free coastal waters of western Alaska during the months of August through October.

There have been very few recent reports of belugas in the Bering Strait region during the open water season. Whales begin appearing in Kotzebue Sound in early to mid-June, where they are commonly seen until early July (Fig. 3). Large groups are sometimes reported, especially near Sisualik (in the Inupiat language meaning the place of white whales) and Eschscholtz Bay. In late June and July whales are seen along the Chukchi Sea coast northwest of Kotzebue and east of Cape Lisburne. Large numbers of whales appear near the barrier islands and passes off Kasegaluk Lagoon, both south and east of Icy Cape, in July (Fig. 3). Belugas are occasionally reported further to the northeast, especially near Wainwright, in late July through early September (Fig. 4).

Based on the distribution and timing of sightings, four regions can be identified along the west coast of Alaska where substantial numbers of belugas occur each year during the open water season: Bristol Bay, Norton Sound/Yukon River delta, Kotzebue Sound, and the northeastern Chukchi Sea near Kasegaluk Lagoon. Specific aspects of the distribution, abundance, and movements of belugas in each of those areas are discussed in the following sections.

Bristol Bay

The group of belugas inhabiting Bristol Bay has received more attention by scientists than any other in Alaska. Whales come to this area to feed on rainbow smelt (*Osmerus mordax*) and salmon (*Oncorhynchus* spp.) that occur in the rivers and bays (Brooks 1955). The possibility that belugas could have been impacting the world's largest run of red salmon (*Oncorhynchus nerka*) led to a variety of detailed studies in Kvichak and Nushagak bays (Brooks 1954, 1955, 1956; Fish and Vania 1971).

We conducted studies of beluga whales in this area in May–June 1982 and April–August 1983. Observations and surveys were conducted from small boats and aircraft (Frost et al. 1984a), and VHF radiotags were applied to two whales (Frost et al. 1985). Additional surveys were flown in Nushagak Bay by Stewart et al. (1983). A plot of all sightings made during 1982–83 (Fig. 5) shows that some areas are more heavily used than others. In Nushagak Bay most sightings occurred in the area between the Snake and Igushik rivers and Clark's Point, and in the north part of the bay near the intersection of the Wood and Nushagak rivers. In Kvichak Bay most sightings occurred in the upper bay near Nakeen, and in Halfmoon Bay. Whales have been seen in the Kvichak, Naknek, Nushagak, Igushik, Snake and Wood rivers, sometimes as much as 50 km upstream. The two whales radiotagged in Kvichak Bay moved between areas within this bay, but did not move into Nushagak Bay during the 11- and 14-d tracking periods. However, seasonal shifts in abundance (Brooks 1955) and sightings of whales in the intermediate area (Fig. 5) suggest that movement of whales between the two bays, which are about 80 km apart, does occur.

Kvichak and Nushagak bays have a large range (7–8 m), strong currents, very muddy water, and extensive mud flats separated by narrow river channels. During low tides belugas are restricted to the river channels and deeper portions of the bay, while on high tides they may range over the mudflats as well. Whales radiotagged in Kvichak Bay in 1983 commonly made daily movements of 20–50 km, generally up and down the bay (Frost et al. 1985). Movements were both with and against the tide with no apparent pattern. However, visual observations of groups of whales made during the same period indicated that whales moved with the direction of the tide 77% of the time. All movements against the tide occurred within 2 h of a tidal change, and were usually (82%) against an ebb tide. Such a pattern would help keep the whales within the same general portion of the bay from day to day.

We conducted nine aerial surveys from 15 April through 14 August 1983 (Frost et al 1984b). Eight were search type surveys that covered all known concentration areas in Kvichak and Nushagak bays and the intermediate coastline. On 29 June we flew a strip transect survey over the concentration areas in addition to flying along the coast and up the

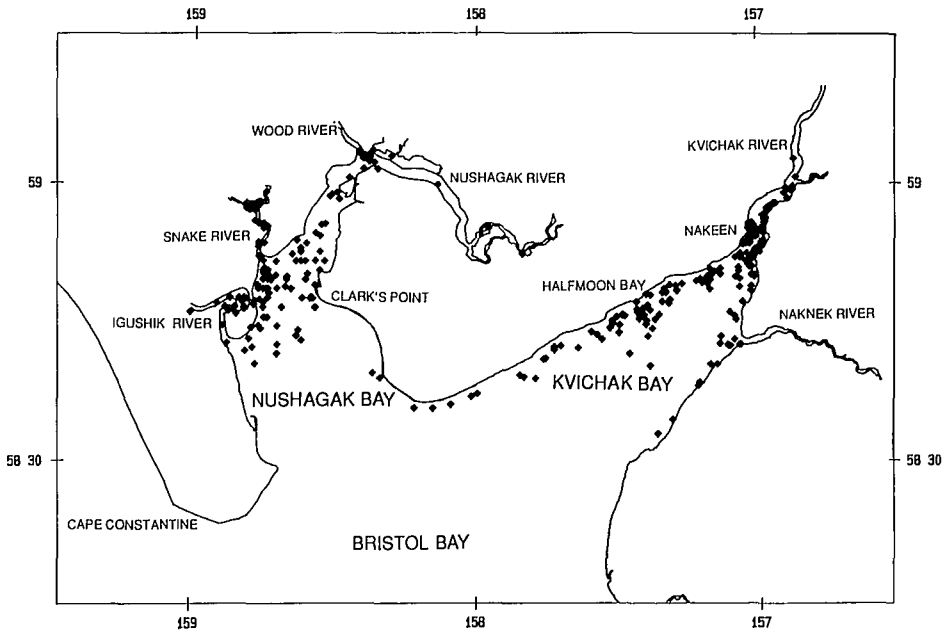

FIG. 5. Kvichak and Nushagak bays showing sightings of beluga whales made during 1982–83.

rivers. Transects were spaced so that the concentration areas were completely counted. The water was muddy and whales were visible only when breaking the surface, so we applied correction factors to account for animals that were diving as the plane passed over. The probability that a whale will be at the surface is equal to the mean length of a surfacing plus the length of time an area is within the field of view, divided by the mean length of a surfacing plus the mean length of a dive. The correction factor by which aerial survey counts can be multiplied to derive the actual abundance of whales is the reciprocal of this probability.

The correction factors that we used were based on surfacing and dive time data from radiotagged whales (Frost et al. 1985), and depended on the length of time a part of the transect was in view (which related to ground speed). Correction factors were 2.75 for a survey speed of 180 km/h and 3.7 for a survey speed of 275 km/h. Counts were further adjusted upward by 8% to account for dark-colored yearlings (Brodie 1971) which could not be seen in muddy water. The number of whales estimated to occur in the area varied from 258 on 13 May to 993 on 29 June (Table 1) which suggests that animals were moving in and out of the area and were absent during some search surveys. Nonetheless it is evident that several hundred belugas were in the area throughout the study period, with largest numbers in Kvichak Bay from mid-April through mid-June, and in Nushagak Bay during late June and July. Brooks (1955) estimated there were about 1 000 belugas in Kvichak and Nushagak bays in 1954, which is very close to our 1983 maximum estimate of 993 belugas. We have no reason to think that the number of belugas in Bristol Bay has changed in recent years. They are not hunted to a significant degree, and fisheries-related mortality is quite low (Frost et al. 1984b).

Neonates are not included in the counts shown in Table 1. However, it is clear that calves are born in this area, as we found 7 dead neonates and one abortus on the beach during our operations in Kvichak Bay in 1983 (Frost et al. 1984b).

There have been very few sightings of belugas in the northern part of Bristol Bay to the west of Nushagak Bay. This is an area of considerable human activity particularly during the spring and summer fishing seasons, and it is likely that we would receive reports if substantial

TABLE 1. Estimated numbers of beluga whales in Nushagak and Kvichak bays, April–August 1983. Neonates are not included.

Date	Nushagak Bay	Kvichak Bay	Total	Adjusted total[a]
15 April	218	474	692	747
2/5 May	41	584	625	675
17 May	85	274	359	388
31 May	27	212	239	258
14 June	49	259	308	333
24 June	182	55	237	286
29 June	347	572	919	993
14 July	496	181	677	731
14 August[b]	0	309	309	334

[a] Total estimate increased by 8% to account for dark-colored yearlings.
[b] Correction factor was not applied because whales were in very shallow water and the observer thought all whales were counted.

numbers of whales utilized the area. The absence of animals during April–June is confirmed by surveys for herring which annually cover the nearshore area from Cape Constantine to Kuskokwim Bay. Since 1967 only the following sightings were recorded: a single animal in June 1975, two in May 1978, and 1–11 in April–May 1988.

Norton Sound/Yukon Delta

There have been no systematic surveys of beluga whales in the Norton Sound and Yukon River delta areas, and available information on distribution and abundance is very limited. During aerial surveys conducted during or shortly after breakup, belugas are regularly seen in association with herring schools (Fig. 6). Whales occur in the Sound until freezeup in November. They occasionally move long distances up the Yukon River. In June 1982 we received reports of 4–5 belugas in the river above the settlement of Tanana, which is 1 200 km from the river mouth, and of a single large adult 130 km further upriver.

There may be considerable movement of whales in the Norton Sound area. Belugas appear to feed on herring and capelin (*Mallotus villosus*) in coastal waters of Norton Sound in May–June, move to the Yukon River mouth to feed on salmon during June–August, then return to coastal Norton Sound to feed on saffron cod (*Eleginus gracilis*) in September-November (Seaman et al. 1982, 1988). Such a pattern is also suggested by the timing of whale hunting at coastal villages in the Sound, which occurs mostly during June and September–October. However, some area residents think that the fall whales may not be part of the Norton Sound group, but are "northern" whales on their way south for the winter.

Kotzebue Sound

There are two important beluga whale hunting sites in Kotzebue Sound, Sisualik and Elephant Point, and most sightings of whales occur near these areas (Fig. 7). They are also seen occasionally in Hotham Inlet, Selawik Lake, and the Buckland River. Whales arrive as the ice cover is breaking up, appearing first in the northern portion of the Sound, then penetrating southeastward as ice conditions allow (Burns and Seaman 1988). Belugas arrive as early as the first week in June, are most common from mid- to late June, and are only occasionally seen in July and August (Table 2).

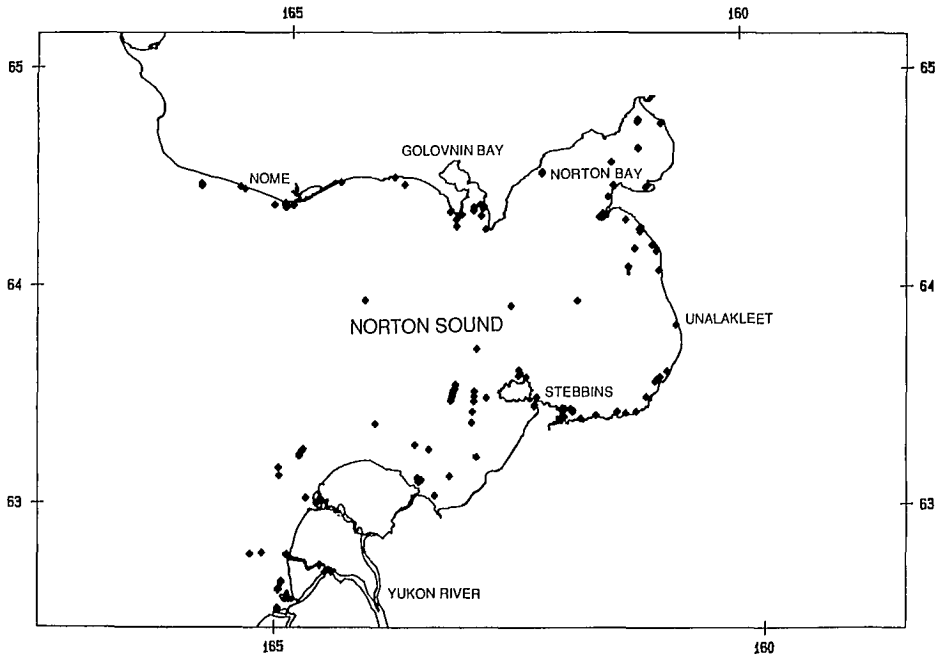

FIG. 6. The Norton Sound region showing beluga whale sightings made during surveys for herring, 1976–88.

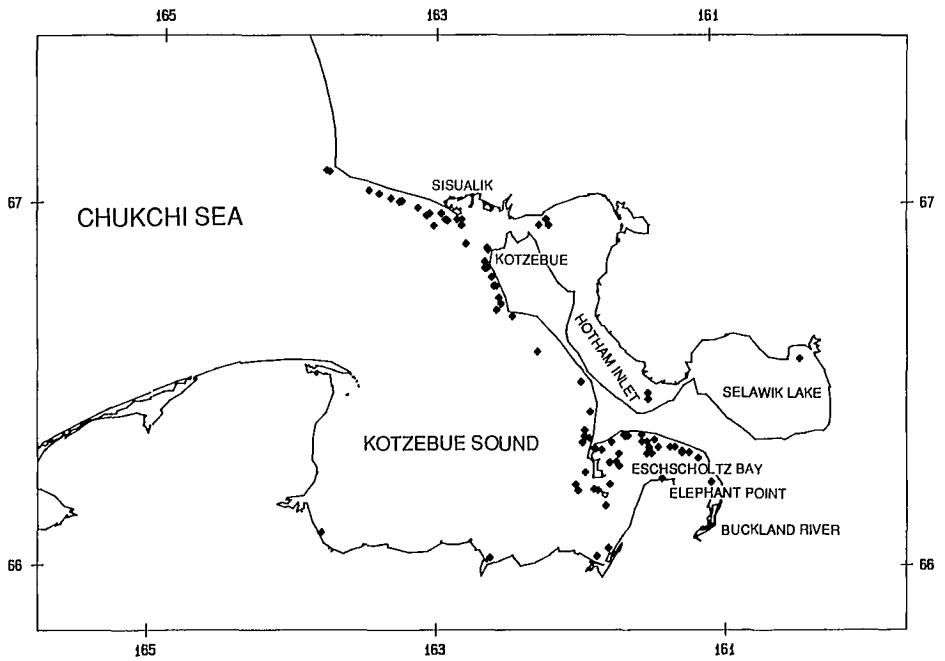

FIG. 7. The Kotzebue Sound region showing major hunting sites and the distribution of beluga sightings, 1970–86.

TABLE 2. Major sightings of beluga whales in the Kitzebue Sound region, 1960–88.

Date	Location	Number	Comments
July 60	N of Chamisso I.	900–1200	
June 73	Choris Peninsula	1000+	covered area 1x9 km
11 June 78	S of Chamisso I.	20–25	first report of the year
8–9 July 78	NW Eschscholtz Bay	900–1000	calves present, largest sighting
1–2 June 79	near Cape Blossom	30+	first report of the year
12 June 79	Eschscholtz Bay	300+	first report in Eschschlotz Bay
15–25 June 79	Sisualik area	many	groups of 10 to 75–100
19 June 79	NW of Chamisso I.	300–600	largest sighting
13 June 80	near Kotzebue	many	first report of the year
15 June 80	Eschscholtz Bay	many	first report in Eschscholtz Bay
23 June 80	Eschscholtz Bay	800+	largest sighting
13 June 81	S of Kotzebue 22 km	1000+	first report and largest sighting
15–16 June 81	Eschscholtz Bay	present	first report in Eschscholtz Bay
9–12 June 82	Sisualik area	many	moving SE into Kotzebue Sound
21 June 82	Eschscholtz Bay	100+	first report in Eschscholtz Bay
17 June 83	Eschscholtz Bay	50+	first hunt of year
18–19 June 83	Sisualik area	25+	
late June 86	Sisualik	20–30	seen on 2 d, then no more
June 86	S of Kotzebue	200	pilot report, only large sighting
July–Aug. 86	Eschscholtz Bay	a few	no June hunt, not enough whales
15–24 June 87	Sisualik area	present	hunted
20–26 June 87	N Eschscholtz Bay	20–50+	aerial survey, ice present in bay
8 Sept. 87	near Kotzebue	10+	about 1 mile off shore
June 88	near Sisualik	1 few	in ice 4–5 mi off shore
26–28 June 88	Eschscholtz Bay	75–200	aerial observation
August 88	W of Sisualik	5+	unusual, taken during salmon fishing

Some information on occurrence and abundance of belugas in Kotzebue Sound can be inferred from the magnitude of harvests at the major hunting sites, which have varied considerably (Table 3), in combination with observations of local hunters and a knowledge of local hunting patterns. In northeastern Kotzebue Sound, animals are harvested by hunting from boats, and with nets that have become more common since the early 1970's (Bob Uhl, pers. comm.). Whales taken near Sisualik are generally moving to other parts of the Sound, and harvests may be affected both by movement patterns and by overall numbers. In contrast, the hunting site at Elephant Point provides access to an area where large numbers of whales regularly congregate. Whales are taken in drive hunts that are an organized effort of the entire village of Buckland, as well as people from other settlements. Harvests were large and relatively consistent from 1977–83, averaging 74 whales per year. According to hunters the harvest was low in 1979 because of disturbance by boats in the constricted entrance to Eschscholtz Bay, and a lack of coordination among hunting groups. The number of whales sighted in 1979 was not particularly low. Hunters got together to regulate disturbance in the area and organize hunting activities, which resulted in greater success in 1980-83. However, beginning in 1984 and continuing through 1988, whales have been much less common in the

TABLE 3. Numbers of beluga whales taken by subsistence hunters in Kotzebue Sound, 1977–88.

Year	NE Kotzebue Sound–Sisualik	SE Kotzebue Sound-Elephant Point
1977	3	105
1978	5	90
1979	2	5
1980	13	101
1981	4	39
1982	25	129
1983	19	48
1984	31	0
1985	13	2
1986	6	3
1987	2	7
1988	±5	17

southeastern part of Kotzebue Sound (Table 2), and harvests at Elephant Point have been greatly reduced in spite of the usual amount of hunting effort.

In response to this apparent change in the occurrence of belugas in Kotzebue Sound, we conducted aerial surveys of the area in 1987. In order to address the possibility that shifts in distribution and habitat utilization might explain the lack of belugas in Eschscholtz Bay, surveys were designed to cover all of the Kotzebue Sound region. Nine surveys covering 4 130 km were flown along the coast and on north–south running transects between 13 June and 9 July. The only whales seen were in Eschscholtz Bay on 21, 22, and 26 June, with a maximum count of 51 animals on 22 June. Whales were in very turbid water and could only be seen while at the surface. If surface and dive patterns were similar to what we have recorded for whales in Bristol Bay (Frost et al. 1985) a correction factor of 3 could be applied to account for whales below the surface, resulting in an estimate of about 150 whales in the area in 1987. Hunters reported an increase in the number of whales in Eschscholtz Bay in 1988.

Food, primarily saffron cod, sculpins (family Cottidae), smelt, and herring, commonly occurred in the stomachs of whales taken at Elephant Point in 1978–80, and a beluga taken in the Buckland River had eaten at least 11 large arctic char, *Salvelinus malma* (Seaman et al. 1982). Local residents report that calving occurs throughout coastal waters of Kotzebue Sound, and both near-term and postparturient females are taken at Elephant Point (Burns and Seaman 1988).

Northeastern Chukchi Sea

The annual occurrence of belugas near Kasegaluk Lagoon was not well-known prior to the mid 1970's. Conversations with residents of Point Lay in 1978 indicated that large numbers of whales occurred in the area each year (Seaman et al. 1988), and studies of beluga whales were conducted in 1978, 1979, 1981, and 1987.

Search surveys of the nearshore area were conducted in 1978, 1979, and 1981. Although residents of Point Lay report that belugas sometimes occur in the deeper parts of Kasegaluk Lagoon (which is mostly less than 2 m deep), most of our sightings have been made outside the barrier islands, particularly near passes (Fig. 8). The first sightings of the year usually occur between 22 June and 5 July, and whales are usually seen in the area until mid-July (Frost et al. 1983b). In 1981 we conducted five surveys between 6 and 22 July. The number of

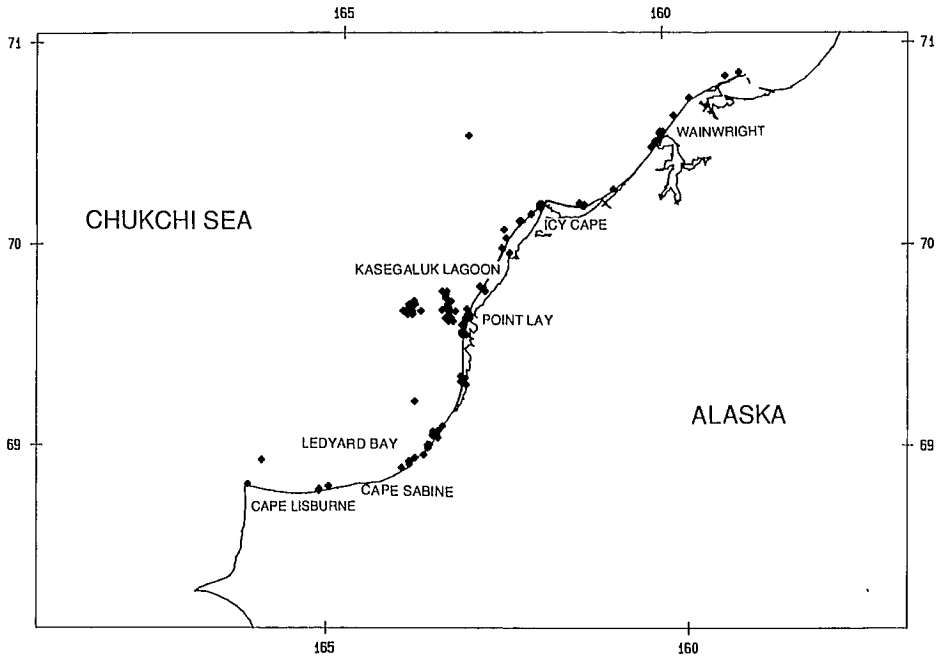

FIG. 8. The Kasegaluk Lagoon region showing sightings of beluga whales made during 1978–87.

whales seen was: 6 July — 15; 8 July — 460–670; 11 July — 40–51; 15 July — 75–100; 22 July — 0. Earliest sightings tend to occur at the southern end of the lagoon, and large groups are more commonly seen further north in July. Whales sometimes occur at several widely separated locations at the same time. Sequential sightings of large groups and observations of movements indicate that whales may move fairly rapidly while in the area (Seaman et al. 1988).

Abundance of whales was estimated from aerial photographs taken in 1979 (Seaman et al. 1988) The number of belugas counted from the slides was 1 104 on 13 July and 1 601 on 15 July. Survey personnel estimated that approximately 10% of the whales were outside of the concentrations and not included in photographs. Although whales were in relatively clear and shallow water, not all of them were close enough to the surface to be counted. Based on sequential photographs of the same groups of whales, it was estimated that in a single photograph, 20% were too deep to be visible. The following correction factors were therefore applied to the actual photographic counts: 10% for whales outside the concentration area; 20% for whales too deep to be visible; and 8% for dark-colored yearlings. This resulted in estimates of 1 575 on 13 July and 2 282 on 15 July. Braham (1984) reported observing 9.6% dark-colored calves along the northwest coast of Alaska in 1981. Using this instead of Brodie's (1971) estimate of 8.0% for dark-colored yearlings would result in a slightly higher estimate for the Chukchi Sea. It is the opinion of the authors that there is considerable confusion between young-of-the-year and yearling calves, and that both may be included in estimates of calves. It is likely that most small belugas that are called calves in April–June are in fact yearling calves, not neonates. Young-of-the-year are extremely difficult to see, particularly from the air or at any distance.

On 8 July 1987 we flew an aerial strip transect survey over a large concentration of whales offshore from Point Lay. The entire concentration area was covered with transects spaced 1.8 km apart, and 723 whales were counted. Double counting was not considered to be a problem since transects were very short. After completion of the strip transect survey we conducted

a search survey of the remainder of the area off Kasegaluk Lagoon and saw only 1 other beluga. The water in the concentration area was relatively clear but deep, and it was evident that not all whales in the area were counted because some were diving out of sight. Applying correction factors of 2 and 3 would result in estimates of approximately 1 400 and 2 100 whales, which are very similar to those obtained in July 1979.

Although there is usually little or no food in the stomachs of belugas taken by hunters at Point Lay, local residents say that whales feed in the area. Both local residents and researchers have observed calves being born, and neonates are frequently seen (Frost et al. 1983b).

There is some evidence to suggest that the belugas that occur near Kasegaluk Lagoon have come from Kotzebue Sound and are part of the same stock. Although there is a certain amount of overlap within a given year, belugas generally appear along the eastern Chukchi Sea coast in a sequence from south to north. In most of the nine years for which we have sighting information, whales are mostly gone from Kotzebue Sound by the time the first arrivals are seen near Point Lay. Sightings at intermediate locations indicate that whales move along the coast between the two areas. For example, in 1987, belugas were present in Kotzebue Sound from 14–26 June, at Cape Sabine from 27 June–13 July, and near Point Lay from 3–9 July.

While we think it is likely that Kotzebue Sound and Kasegaluk Lagoon whales belong to the same stock, it appears that they do not always travel as one large group, and that not all whales go to both areas each year. On 3 July 1982, an estimated 2 000–2 500 whales were seen off Cape Sabine, suggesting that the entire group was travelling together. In contrast, in early July 1978 approximately 1 000 whales were seen in Kotzebue Sound during the same week that 1 000+ whales were seen near Kasegaluk Lagoon. In late June 1987, a maximum of 51 whales was counted in Kotzebue Sound, while a few days later over 700 were seen off Kasegaluk Lagoon. We consider it unlikely that such a large group was present but not detected in Kotzebue Sound during over 4 000 km of surveys. Observations in eastern Hudson Bay suggest that large summering concentrations may consist of several smaller groups that arrive at different times and come and go independently (Smith and Hammill 1986). Observations of three belugas radiotagged in a high arctic summer concentration area in 1988 also indicated independent movements in and out of the area (Frost, Martin and Smith, unpubl. data). Groups of belugas moving from offshore areas to the Chukchi Sea coast may arrive at slightly different times, and late-arriving groups may first join the concentration off Kasegaluk Lagoon resulting in larger sightings later in July in the more northern area. Overall we think that the whales occurring along the eastern Chukchi Sea coast during June and July are interrelated, and should for now be considered a single stock for management purposes. However, further research is necessary to confirm this relationship.

Conclusion

Identity and Abundance of Management Stocks

The data we have presented, although not entirely systematic or comprehensive, indicate that beluga whales occur in coastal waters of western Alaska from Bristol Bay to the northern Chukchi Sea during the open water season. However, their distribution and abundance is far from uniform. Whales occur very rarely in some areas, occasionally in others, and regularly in large numbers at certain locations. A generally similar pattern probably occurs throughout the arctic and subarctic regions inhabited by belugas, but the pattern may be obscured by the tendency of investigators to focus their efforts on known concentration areas.

In coastal waters of western Alaska, summering belugas occur primarily in four concentration areas: Bristol Bay, Norton Sound/Yukon Delta, Kotzebue sound, and Kasegaluk Lagoon. Based on distributional information, we think that the groups in Bristol Bay and Norton Sound/Yukon Delta should be considered as separate management stocks, while those in Kotzebue Sound and Kaselaguk Lagoon should be considered a single stock. Behavioral

observations support distributional information and suggest that the same whales return to the same concentration area each year. Within an area, belugas use the same rivers, channels, or passes with similar timing from one year to the next, and react to human activities in a similar manner. For example, belugas in Kotzebue Sound are extremely shy of boats, while those in Bristol Bay regularly co-occur with an intensive fishery. However, further research, particularly tagging and DNA studies, is necessary to confirm hypothetical stock identity.

Seaman et al. (1988) made initial estimates of the abundance of whales in each of these provisional management stocks, based on data collected through 1983, as follows: Bristol Bay—1 000–1 500; Norton Sound/Yukon Delta—1 000–2 000; and eastern Chukchi Sea—2 500–3 000. Our recent information does not suggest any changes to these estimates. There is good reason to think that the Bristol Bay stock is stable at or near its historical size. Little is known about the Norton Sound–Yukon Delta stock, since no comprehensive surveys for belugas have been conducted there. Our counts in June–July 1987 and other information indicate that the number of belugas utilizing Kotzebue Sound has decreased since 1984, but that large numbers of whales still occur each year at Kasegaluk Lagoon.

Factors Affecting Distribution and Abundance

Along the west coast of Alaska belugas move into coastal waters as soon as ice conditions permit. In areas south of Bering Strait, belugas remain resident throughout the open water season, and by late summer they are hundreds of km south of the pack ice. However, in the Chukchi Sea, pack ice may remain close by while whales are present in Kotzebue Sound and near Kasegaluk Lagoon. We have no direct observations of belugas in the Chukchi Sea pack ice during June and July, but movements between the coast and the pack ice have been inferred from fluctuations in nearshore abundance at Kasegaluk Lagoon (Seaman et al. 1988). Local residents think that belugas move back and forth between the coast and the pack ice especially when it is near the shore. Belugas seen along the Chukchi Sea coast in July may move to the pack ice in August-September, and join the large group of whales that is moving westward across the Beaufort Sea from the Mackenzie Delta area (Burns and Seaman 1988). Therefore, it appears that while belugas are a pagophilic (ice-loving) species, their attraction to ice is weakest during summer months and is overcome to varying degrees by other factors. These other factors seem to operate most strongly in the Bering Sea. The reasons for pagophily by belugas, particularly in northern regions during summer, are unknown. It is possible that belugas feed under the ice on species such as arctic cod (*Boreogadus saida*) which are also pagophilic during most of the year.

Previous investigators have suggested that the main reason that belugas inhabit coastal areas during summer months is because they are warmer and provide a thermal advantage to all age classes (Fraker et al. 1978) and particularly to neonates (e.g. Sergeant and Brodie 1969; Fraker et al. 1979). While Fraker et al. (1978) consider that the thermal advantage is the most reasonable explanation, they also note that other characteristics of the Mackenzie concentration areas include low salinity and shallow water depth. The relationship to water temperature, if it exists, is complex and quite variable. Small calves, presumed to be neonates and most vulnerable to cold, are seen within groups of whales in the pack ice (Braham et al. 1984). At Cunningham Inlet in the Canadian Arctic many belugas, including those with neonate calves, concentrate at the mouth of a cold, fresh river which is fed by snow melt. In the Bering Sea, which is strongly influenced by water of North Pacific origin, summer surface water temperatures are comparatively warm throughout. Any thermal advantage that might occur from calving in coastal waters would probably be slight. In contrast, as the ice moves offshore in the Chukchi Sea, radiant warming and flow from rivers may increase nearshore temperature substantially. In July water temperatures in plumes flowing out of Kasegaluk Lagoon through passes were as much as 2° C warmer than in adjacent marine waters, and belugas occurred most commonly in the plumes (Seaman et al. 1988).

In at least some parts of their range, belugas congregate during during the molt in shallow areas, where they are observed to crowd together in flowing fresh water and rub on the bottom (T. G. Smith, Arctic Biological STATION, pers. comm.). Warmer waters may be important for rapid cell growth during the molt (Finley 1982; St. Aubin et al. 1990). Alternatively, or in combination, warm temperatures and the presence of fresh water may attract belugas to areas such as Kaselaguk Lagoon for molting. Turbid conditions in most parts of Alaska preclude observations of rubbing behavior such as have been made in other coastal concentration areas.

It is clear that beluga whales feed along the coast of western Alaska during summer months (Seaman et al. 1982). However, the importance of summer concentration areas for feeding appears to differ among regions. In Bristol Bay a series of very abundant anadromous and nearshore fishes (smelt, salmon smolt, adult salmon) provides continuous feeding opportunities for belugas during the open water season. A similar situation seems to occur in the Norton Sound/Yukon Delta region with somewhat different species of prey (herring, capelin, adult salmon, saffron cod). Although some feeding does occur near coastal concentration areas in the Chukchi Sea, there is no evidence that nearby food resources are unusually abundant or suitable during the 2–3 wk that belugas are present. Most belugas leave Kotzebue Sound before the salmon arrive in July and August.

Belugas are sensitive to disturbance in certain circumstances and airborne and waterborne noise may influence their distribution and behavior (e.g. Fraker 1977; Stewart et al. 1983; Finley and Davis 1984). The principal disturbances to which they are presently exposed in coastal Alaska are associated with beluga hunting, commercial fishing, coastal traffic, industrial development, and the proximity of settlements. The intense activity associated with the Bristol Bay red salmon fishery has had no obvious effect on beluga distribution and movements in that area (Frost et al. 1984b). Belugas move and feed in proximity to both fixed nets set from shore and drift nets set from boats, and commonly approach anchored but noisy processors and freighters. Their behavior appears little affected by transiting boats or aircraft, except in narrow river channels when they will flee from approaching outboard motorboats (Frost and Lowry, unpubl. observation). We have less information on how fisheries and other activities in the Northon Sound/Yukon Delta region have affected belugas, although whales are reported to be less easy to approach since the widespread use of outboard motors (Seaman and Burns 1981). Residents of Norton Sound have suggested that belugas are less common nearshore in spring since the local herring fishery intensified in the mid-1980's. A major source of disturbance in Kotzebue Sound and Kasegaluk Lagoon is that associated with hunting. Whales nonetheless continue to return to traditional hunting areas. Near Point Lay, a village of about 120 people, the period of beluga hunting is brief, as an adequate number of whales can be taken in 1 or 2 drives (in 1 or 2 d). Residents have noticed no recent changes in distribution or abundance, although they do report that belugas do not reappear in a specific area for several days after they are hunted. In contrast, residents of Kotzebue, a settlement of over 3 000, think that increased traffic and noise in their area have caused fewer whales to remain for shorter periods in northeastern Kotzebue Sound. Small boat traffic and low-flying aircraft have been blamed by hunters for preventing whales from entering Eschsholtz Bay (Burns and Seaman 1988). Some residents cite the introduction of underwater exhaust on outboard engines as the reason for increased avoidance of heavily travelled areas (Pete Shaeffer, pers. comm.).

Local residents frequently state that movements of belugas in their areas are being affected by killer whales. Killer whales occur off western Alaska and they are known to prey on beluga whales (Lowry et al. 1987b). Fish and Vania (1971) demonstrated the effectiveness of killer whale calls in changing beluga whale movement patterns. Occupancy of coastal areas by belugas may somewhat reduce such interactions, especially in relatively confined estuaries where killer whales rarely occur.

We conclude that beluga whales concentrate in coastal waters of the eastern Bering Sea primarily because of the availability and abundance of forage fishes. In these areas belugas are not particularly responsive to disturbance, and movements appear to relate mostly to changes in prey distribution. In the eastern Chukchi Sea, coastal areas may be important to belugas for other reasons, such as for molting. In these areas whales appear to be more sensitive to disturbance and, at least in the Kotzebue Sound area, their distribution and movements may be affected by human activities.

We think it is likely that in Bristol Bay and Norton Sound, where during May–September there are abundant prey in shallow, low-salinity areas, belugas feed and molt in the same locations. Along the Chukchi Sea coast, belugas may feed offshore where prey are more abundant and move into shallow coastal waters for relatively short periods in order to facilitate the molt.

Acknowledgments

It is impossible to list the many people who contributed the data included in this study. We thank them all, especially John Burns, Bob Nelson, Dick Russell, Glenn Seaman, Bob Uhl, and Craig Whitmore. Support for our field studies of beluga whales was provided by the U.S. National Oceanic and Atmospheric Administration and the U.S. Minerals Management Service. Preparation and printing of this manuscript were supported by the Alaska Department of Fish and Game and the Department of Fisheries and Oceans Canada.

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Age–Length and Length–Weight Comparisons in the Beluga, *Delphinapterus leucas*

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DOIDGE, D. W. 1990. Age–length and length–weight comparisons in the beluga, *Delphinapterus leucas*, p. 59–68. *In* T. G. Smith, D. J. St. Aubin, and J. R. Geraci [ed.] Advances in research on the beluga whale, *Delphinapterus leucas*. Can. Bull. Fish. Aquat. Sci. 224.

Examination of published and new data of age-length and length–weight support the hypothesis that adult belugas, *Delphinapterus leucas*, vary in body size between regions, but not to the large extent reported previously. Age–length relations differ between sexes and regions. Adult males are slightly longer than females. Length–weight relations were similar among the sexes and regions. Belugas from Hudson Bay tend to be shorter, and presumably lighter than those from Alaska, W. Greenland, the St. Lawrence River, and the MacKenzie Delta. These differences are generally too small to classify individuals to region on the basis of size. In eastern Hudson Bay belugas, body weight (kg) can be predicted from length (cm) and maximum girth (cm) using the relationship

Weight = $10^{-4.33}\text{Length}^{2.46}\text{Girth}^{0.36}$ (R^2=0.96, n=17) for males, and

Weight = $10^{-3.95}\text{Length}^{1.08}\text{Girth}^{1.71}$ (R^2=0.95, n=20) for females.

Lack of data on seasonal changes in food intake and energy reserves prevents testing of the hypothesis that the small differences observed in belugas from different regions is due to differences in winter productivity.

Une analyse de données publiées et de nouvelles données sur le rapport âge – longueur et longueur–poids viennent appuyer l'hypothèse que l'on retrouve une variation régionale de taille chez les marsouins blancs adultes, *Delphinapterus leucas*, mais d'une échelle moindre que rapportée antérieurement. Le rapport âge – longueur varie entre les sexes et les régions. Les mâles adultes sont légèrement plus longs que les femelles. Le rapport longueur-poids est similaire entre les sexes et les régions. On note que les marsouins blancs de la baie d'Hudson ont tendance à être plus courts, et, présumément, plus légers que ceux de l'Alaska, de l'ouest du Groenland, du fleuve St-Laurent et du delta du Mackenzie. En prenant en considération les données sur la taille, les écarts sont généralement trop faibles pour classifier les individus par provenance géographique. Chez les marsouins blancs de l'est de la baie d'Hudson, le poids (kg) peut-être calculé à partir de la longueur (cm) et du tour de taille maximal (cm) en utilisant l'équation

Poids = $10^{-4.33}\text{Longueur}^{2.46}\text{Tour de taille}^{0.36}$ (R^2=0.96, n=17) pour les mâles, et

Poids = $10^{-3.95}\text{Longueur}^{1.08}\text{Tour de taille}^{1.71}$ (R^2=0.95, n=20) pour les femelles.

Un manque de données sur la variation de l'alimentation saisonnière et des réserves énergitiques ne permet pas la vérification de l'hypothèse que les petits écarts observés chez les marsouins blancs des diverses régions sont dûes à une différence dans la productivité hivernale marine.

Introduction

The possibility of stock recognition based on body size has important management implications for belugas, *Delphinapterus leucas*, since whale numbers and harvest intensity vary greatly between regions. In the eastern subarctic, belugas that summer in Hudson Bay, Ungava Bay and Cumberland Sound appear to overwinter together in Hudson Strait (Finley et al. 1982; Reeves and Mitchell 1987). Presently, the degree of exchange between these proposed stocks is unknown. Differences in body size would imply genetic discreteness and lack of interchange between these regions.

Based on differences in extrapolated body weight, which can vary threefold for adult males, Sergeant and Brodie (1969) conclude that three different beluga populations inhabit eastern North America: small animals in (western) Hudson Bay, medium sized animals in the Canadian Arctic and the St. Lawrence River, and large animals along the West Greenland coast. They suggest winter productivity is the most important factor in determining body size in belugas. Although Sergeant and Brodie were working with the best data available at the time, recent data and an error in the published regression equation for Hudson Bay belugas (D.E. Sergeant, 555 St. Pierre Blvd., Ste-Anne de Bellevue, Qué., H9X 3R4, pers. comm.) warrant a reexamination and interpretation of body weight differences in beluga.

Here, I compare both age–length and length–weight relations for beluga by sex and region and develop equations for predicting body weight in the eastern Hudson Bay stock based on length and maximum girth.

Methods

Age – length data were gathered in 1980 and between 1983–87 as part of a wider study of beluga population ecology in N. Quebec centred at the Nastapoka estuary, eastern Hudson Bay (56°55'N, 76°33'W). These data also include a small number of whales harvested on the southern side of Hudson Strait and Ungava Bay. Teeth were removed by boiling and were stored dry. A longitudinal mid-section 0.3 mm thick was removed from the most anterior tooth of the lower jaw (usually the left) using a Buehler Isomet slow speed saw (Buehler Ltd., 41 Waukegan Rd., Lake Bluff, IL., USA, 60043). Sections were stored in absolute ethanol. Growth layer groups (GLGs, terminology of Perrin and Myrick 1980) were counted in unstained sections using 6–10 power of a binocular microscope. Two GLGs were considered to represent an annual increment (Sergeant 1973; Goren et al. 1987). Teeth were regarded as unworn if the neonatal line was present in the dentine.

Age–length data, based on unworn teeth, from N.W. Alaska (Burns and Seaman 1985, Fig. 2), Churchill[1] (D.E. Sergeant, 555 St. Pierre Blvd., Ste-Anne-de-Bellevue, Qué., H9X 3R4, unpubl. data) and N. Quebec (this study) had adequate sample sizes ($n > 30$ of each sex) for regression-based comparisons. Logistic, parabolic, von Bertalanffy and Gompertz growth curves (Kaufmann 1981; Innes et al. 1981; Roff 1980) were fitted to the age – length data from each of the above sites using the NLIN procedure of PC–SAS (Ver. 6.03, Statistical Analysis Systems, Cary, NC, USA). The Richards model was considered to be too sensitive to imprecision in the small datasets available (Zach 1988) so was not fitted. Whales having unworn teeth from the St. Lawrence River (Sergeant 1986, table VIII, $n = 16$), Bristol Bay, Alaska (Burns and Seaman 1985, fig. 3, $n = 18$), the Mackenzie Delta[2] (D.E. Sergeant, 555 St. Pierre Blvd., Ste-Anne-de-Bellevue, unpubl. data) and West Greenland (R. Dietz, Greenland Environment Research Institute, Tagensvej 135, 1. sal. 2200, Copenhagen, Denmark, unpubl. data, $n = 9$) were compared to the 95% confidence intervals of asymptotic length for N.W. Alaska, Churchill and N. Quebec.

[1] Sergeant (1973, fig. 10) shows mean values.

[2] Sergeant (1973, fig. 6) contains worn and unworn teeth.

Thirty-seven beluga (17 male, 20 female) shot by Inuit between late June and early September of 1985 and 1986 in the Nastapoka estuary were weighed using a 2 500 lb. capacity scale (Model S-250, Dillon, 14620 Keswick St. Van Nuys, Ca, USA) attached to a tripod by a 5 t capacity chain hoist. Weights were recorded to the nearest 5 lb then converted to the nearest kg. Sex, reproductive status (pregnant, lactating or barren), standard length (Amr. Soc. Mammal 1961) and maximum girth (which occurs near the umbilicus) were noted.

Length – weight data from the St. Lawrence River (Vladykov 1944, n = 10), Churchill, Manitoba (Doan and Douglas 1953, n = 16), Seal River, Manitoba (Geraci, unpubl. data, n = 9) and Cumberland Sound, Baffin Island (Brodie 1989, n = 10) had inadequate sample sizes for regression-based comparisons. Data from these regions were compared to the 95% confidence intervals of the length – weight relationship found for eastern Hudson Bay (n = 36).

Statistical analysis generally followed the procedure and philosophy put forth by Peters (1983, Chapter 2). When sample size was judged adequate, within region comparisons of the regression parameters of males and females used standard F tests (Snedecor and Cochran 1967). Most other comparisons were based on confidence intervals because sample mean, range, variance or size often differed between data sets. Confidence intervals show the degree of uncertainty associated with the data and facilitate assessment of practical and statistical significance associated with any differences (SAS Institute 1987). The level of statistical significance for Type I error was 0.05.

Results

In the age–length analyses, Gompertz and von Bertalanffy models consistently produced the smallest and similar residual sum of the squares. Because the von Bertalanffy curves severely underestimated body length at young ages, I chose the Gompertz equation to describe beluga age–length relationships (Fig. 1).

Sexual dimorphism is apparent from the non-overlapping of the 95% confidence intervals of asymptotic length for N.W. Alaska and Churchill belugas (Table 1, Fig. 2), males being slightly longer than females. This difference was not significant in the N. Quebec sample where confidence intervals of asymptotic length of males and females overlap.

Regional comparisons of age–length relationships are shown graphically (Fig. 2) where the fitted curves represent larger datasets (See Table 1 for growth coefficients) and age – length is plotted individually for the smaller datasets. Belugas from Churchill and N. Quebec (henceforth termed Hudson Bay) show similar changes in length with age and attain similar adult body lengths. Beluga from N.W. Alaska are significantly longer when fully grown than beluga from Hudson Bay, the absolute difference being greater in males. Male and female beluga from Hudson Bay also appear slightly shorter than their counterparts from Bristol Bay (Alaska), Greenland and the St. Lawrence, but the small sample size prevents meaningful statistical comparison.

Length–weight relationships from the Nastapoka River showed no sexual dimorphism (comparison of slopes $F_{1,33}$ 2.09 intercepts $F_{1,34}$ 4.05, P>0.05) so a single regression line was fitted. Body weight (kg) of either sex of beluga from eastern Hudson Bay can be estimated from body length (cm) using the equation

$$\text{Weight} = 10^{-3.84}\ \text{Length}^{2.58} \quad (R^2 = 0.92,\ n = 36)$$

Length – weight data from W. Hudson Bay and the St. Lawrence lie within the 95% C.I. of E. Hudson Bay (Fig. 3) demonstrating that beluga do not differ significantly in length–weight relationships between those regions. The Churchill animals were known to have been gutted (Doan and Douglas 1953) which explains their low values (Fig 3).

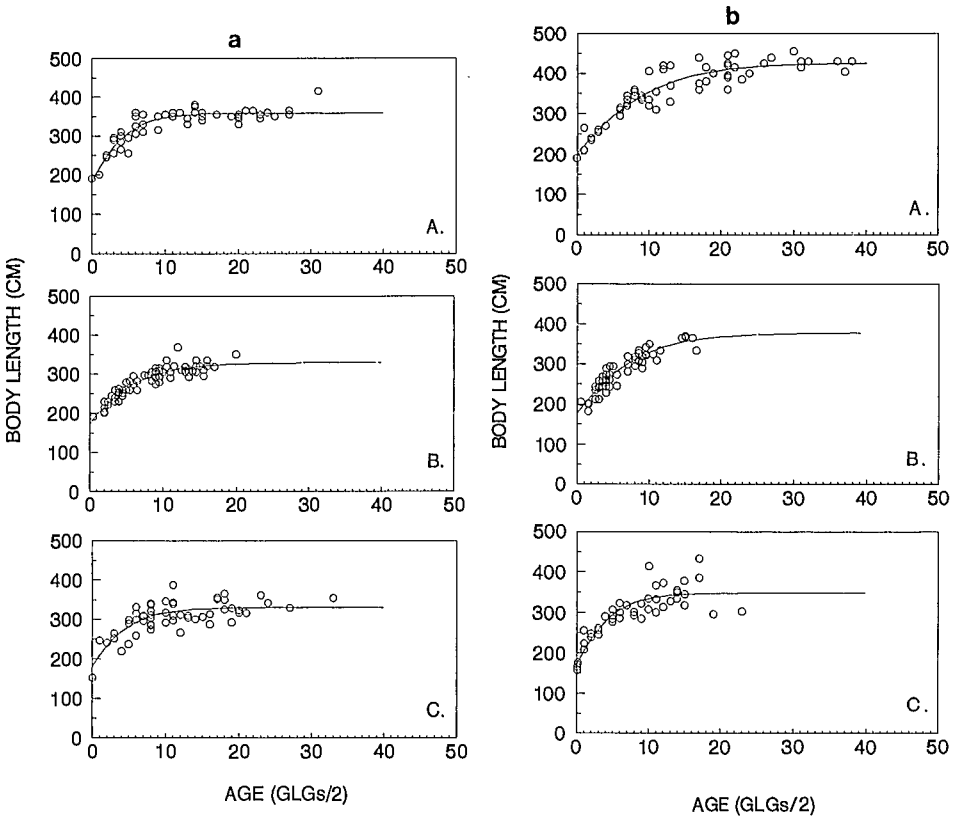

FIG. 1. Gompertz growth curves fitted to age–length data of beluga whales from various regions. A. NW Alaska, B. Churchill, Manitoba, C. N Quebec. (a) females, (b) males. Data sources given in text. Circles represent individual data points.

For the Nastapoka River data (Table 2), least squares regression showed significant relationships between $\log_{10}$ standard length and $\log_{10}$ body weight in males (R^2=0.95) and females (R^2=0.80). The addition of a maximum girth term improved the fit of the female regression model (R^2=0.95), but did not noticeably change the explained variance in the male regression model (R^2=0.96). Lactation did not affect female weight (ANOVA $F_{1,19} = 0.05$, $P>0.05$). Body weight (kg) can be estimated from length (cm) and girth (cm) for females by

$$\text{Weight} = 10^{-3.96}\ \text{Length}^{1.71}\ \text{Girth}^{1.08} \quad (R^2 = 0.95,\ n = 20)$$

and males by

$$\text{Weight} = 10^{-4.33}\ \text{Length}^{0.36}\ \text{Girth}^{2.46} \quad (R^2 = 0.96,\ n = 17).$$

Discussion

The hypothesis that belugas differ in body size between regions is supported by re-examination of the data (Fig. 1, 2, 3), but not to the degree reported previously (Sergeant and Brodie 1969). The conclusion that male belugas can differ by up to threefold in body weight likely results from extrapolations made from the St. Lawrence power curve describing body length and mass (Sergeant and Brodie 1969), and the application of an incorrect gutting factor to Hudson Bay animals.

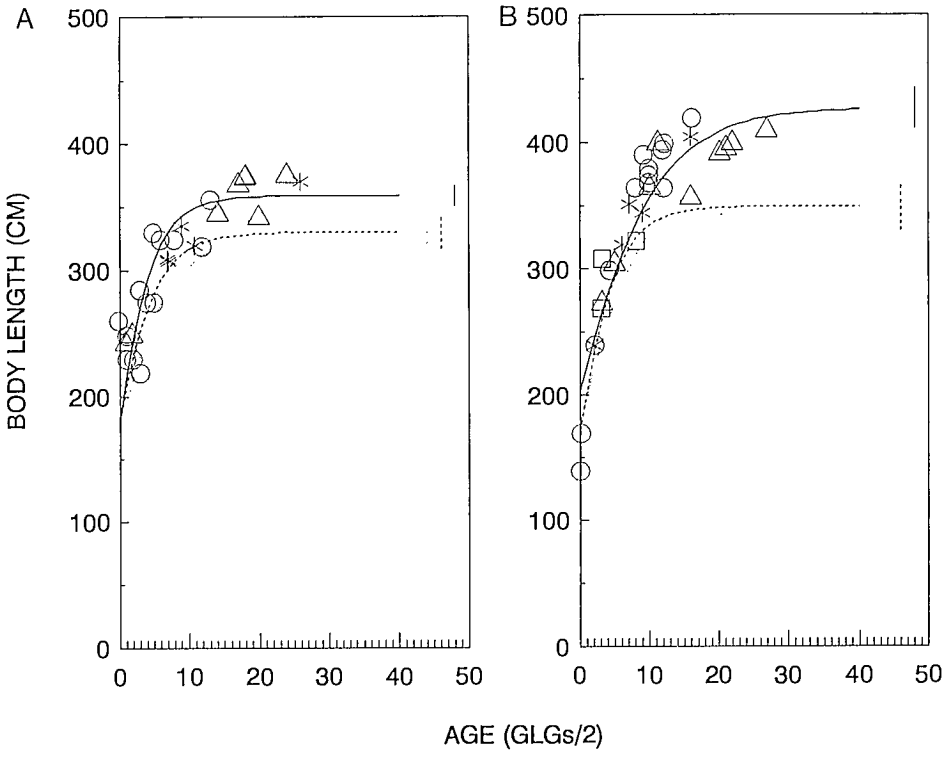

FIG. 2. Gompertz growth curves fitted to age–length data of beluga whales from NW Alaska (solid line), Churchill, Manitoba (dots) and N Quebec (dashes) with individual data points from Bristol Bay, Alaska (circles), the St. Lawrence River (triangles), West Greenland (squares) and the MacKenzie Delta (asterisks). A. females, B. males. Vertical lines represent asymptotic 95% confidence intervals. Data sources and curve coefficients given in text.

TABLE 1. Growth parameters ($X \pm$ asymptotic SE) of the Gompertz growth equation fitted to age–length data from beluga whales from various sites where Body length (cm) = A·(exp(-b·exp(-k·age))) and age is GLGs/2.

Region	Sex	*A*	SE	*b*	SE	*k*	SE	*n*
NW Alaska[a]	F	359	4	0.30	0.04	0.68	0.07	51
	M	427	8	0.14	0.02	0.74	0.06	56
Churchill[b]	F	328	6	0.21	0.03	0.64	0.04	77
	M	377	14	0.17	0.03	0.75	0.04	65
N Quebec[c]	F	330	6	0.27	0.06	0.60	0.10	55
	M	349	10	0.28	0.05	0.71	0.07	44

[a] Burns and Seaman (1985).
[b] D.E. Sergeant, pers. comm.
[c] This study.

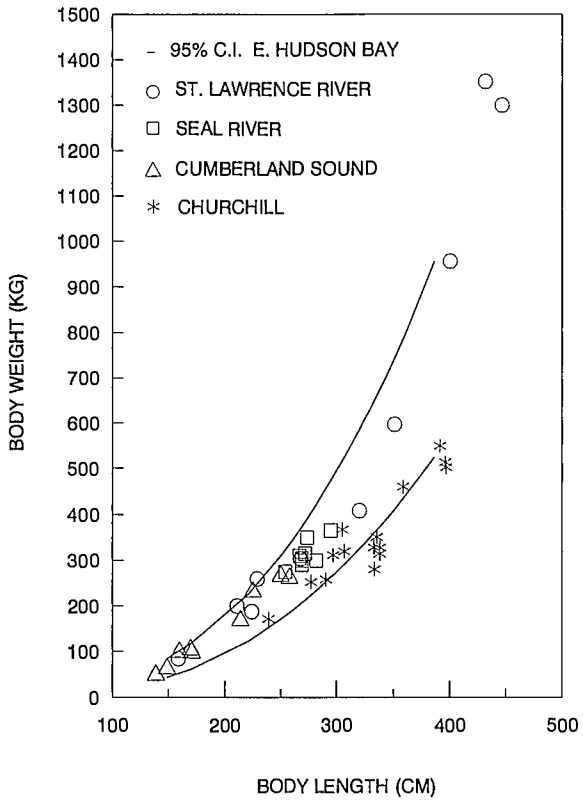

FIG. 3. Body length–weight relationships of beluga whales from various regions. Data sources given in text. Confidence intervals are asymmetric due to the log–log transformation of the data.

Age – length comparisons of N. Quebec and St. Lawrence animals showed slight differences between sites. Mean predicted lengths of adults from N.W. Alaska are ca. 30 – 50 cm longer than Hudson Bay animals. The limited data from W. Greenland, the St. Lawrence, the MacKenzie Delta, and Bristol Bay show a similar trend, but individuals generally cannot be assigned to stocks on the basis of body size because of overlapping confidence intervals of length between regions (Fig. 2).

The long body lengths attributed to Greenlandic beluga (Degerbol and Neilsen 1930) and used for weight extrapolations by Sergeant and Brodie (1969) are not evident in present Greenlandic harvests (R. Dietz, Greenland Environment Research Institute, Tagensvej 135, 1. sal. 2200, Copenhagen, Denmark, unpubl. data). Vladykov (1943) remarked on the lower fluke width to body length ratios for West Greenland (Degerbol and Neilsen 1930) compared to St. Lawrence belugas. He suggested this difference could be real or due to differing precision of measurement. A decrease in the abundance of older age classes or possible use of either snout to fluke tip or curvilinear lengths by Degerbol and Neilsen (1930) could explain this discrepancy. The similarity of recent fluke width to body length ratios from W. Greenland (R. Dietz, Greenland Environment Research Institute, Tagensvej 135, 1. sal. 2200, Copenhagen, Denmark, unpubl. data) to those of N. Quebec and St. Lawrence beluga (Fig. 4) implies Degerbol and Neilsen's (1930) body lengths were longer than the present accepted

TABLE 2. Weight, length and maximum girth of beluga whales taken at the Nastapoka River, N. Quebec.

Sex	Weight kg	Length cm	Girth cm	Sex	Weight kg	Length cm	Girth cm
F	345	324	176	M	681	350	118
	402	319	188		375	284	172
	275	252	168		518	330	200
	336	273	172		284	268	152
	513	319	200		885	386	254
	306	262	172		341	284	178
	456	332	189		438	322	190
	558	338	208		552	344	188
	415	339	174		304	320	100
	486	334	182		470	319	204
	361	316	171		388	316	162
	304	293	164		238	262	137
	470	320	196		459	344	178
	375	299	170		363	303	160
	440	301	190		64	149	100
	409	310	186		290	282	161
	445	347	174	F	1000+[a]	394	224
	179	221	140				
	427	323	184				
	600	360	210				

[a] Incomplete weight, D.M. Albright, Dept. Fisheries and Oceans, Ste-Anne-de-Bellevue, Quebec, pers. comm., 85.08.13.

standard measurement. Any bias in length measurement is further amplified in the weight estimate because of the power nature of the curve (Fig 3).

Sergeant and Brodie (1969) assume only abdominal viscera, representing 5% of body weight, were lost when the Churchill beluga were gutted and thus divide the original weights (Doan and Douglas 1953) by 0.95. Comparison of the uncorrected Churchill data with the larger sample from the Nastapoka (Fig. 3) indicates a larger than 5% difference in body weight. Since Doan and Douglas (1953) do not explicitly state what organs were removed by gutting, their weight data has little use in body comparisons between localities.

Comparison of Seal River and Nastapoka length – weight relationships indicate belugas are similar in body size between western and eastern Hudson Bay. Small differences in length – weight relations may exist between Hudson Bay belugas and belugas from other regions, but sample sizes are presently too limited to allow meaningful statistical testing. I believe the use of extrapolated weights for Greenlandic animals and the more than 5% gutting factor for Churchill belugas led Sergeant and Brodie (1969) to conclude erroneously that belugas differed greatly between region in body length – weight relationships.

Comparisons of body size between populations or stocks must consider several factors. Differences in average body size between populations may only reflect disparity among samples in age or sex composition rather than a true change in body size at a given age (Scheffer 1955). Body weight without length or age data is a poor body size criterion since it is subject to bias related to sampling technique. Hunters tend to select large animals

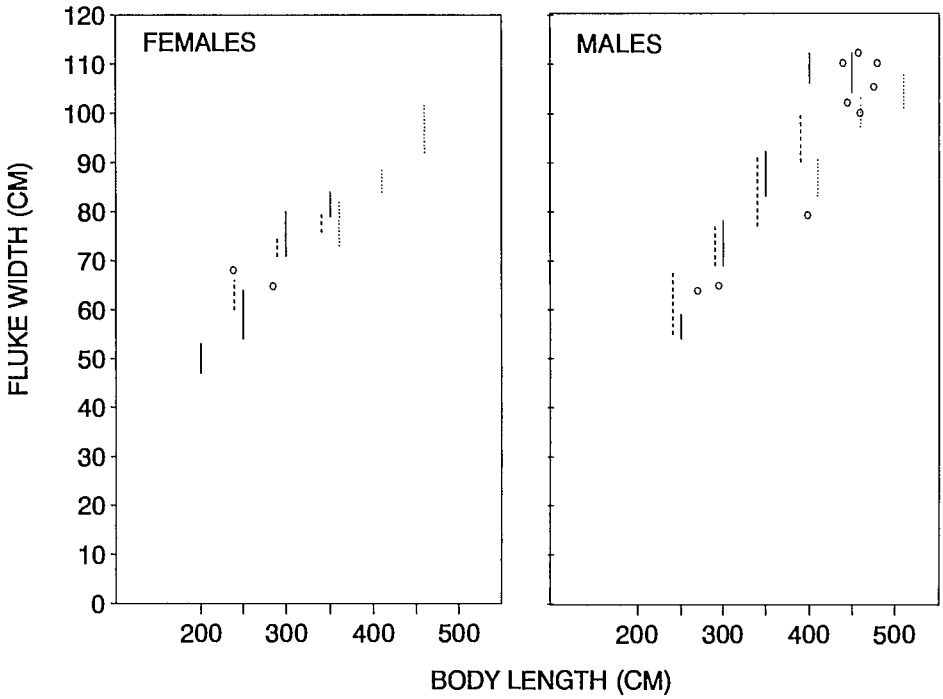

FIG. 4. Body length versus fluke width of beluga whales from the St. Lawrence River (solid line, Vladykov 1943), W. Greenland (dotted line, Degerbol and Neilsen 1930, open circles, R. Dietz unpubl. data) and N. Quebec (dashed lines, this study). Vertical bars represent mean ± 2 SE.

(Caughley 1977), whereas shore-tethered nets catch greater numbers of females and calves (Sergeant and Brodie 1969; Sergeant 1973). Time of sampling may influence weight relationships through seasonal changes in body condition, so inclusion of body girth in weight analyses is desirable. Length–weight relations are useful for comparisons of size and shape, but similar growth dynamics do not dictate that whales of different stocks attain the same maximum weight or, depending on the age structure, have the same population mean weight. In the ecological context, age–weight or age–length comparisons may be more useful since weight at a particular age should on average reflect food availability, but tooth wear and small harvest sizes limit the size of age based samples of beluga whales.

The similarity of length–weight and the slight differences in age–length relations between regions implies that body mass per unit length is fairly constant, but that the rate of body growth (per unit time) varies between regions. Levels of thyroid hormones in the blood indicate that body growth is accelerated in the summertime when belugas frequent warmer estuarine waters (St. Aubin and Geraci 1988). Although girth had a significant effect on body weight in females, seasonal changes in blubber reserves are not well enough documented to indicate if body growth is fuelled by summer feeding or mobilization of reserves built up on the wintering grounds. Thus the data are still not adequate for testing the hypothesis that winter productivity is responsible for *small* body size differences in belugas between regions.

Acknowledgments

I thank the beluga hunters of N. Quebec for access to their catch and personnel from Dep. Fisheries and Oceans, Makivik Corp., and the University of Guelph who helped examine it.

Data gathered in N. Quebec in 1980 by K. Finley and others of LGL Ltd., Toronto, was made available for analysis. R. Dietz, J.R. Geraci and D.E. Sergeant supplied unpublished data on body size. C. Hudon and M. Hammill offered advice on SAS programming and statistics. G.G. Beck, R. Dietz, J.R. Geraci, M.O. Hammill, L. Lowry, D.E. Sergeant, T.G. Smith and two anonymous reviewers suggested improvements to the manuscript.

This work was supported by the Dept. of Fisheries and Oceans Canada, World Wildlife Fund Canada's "Whales Beneath the Ice" project, the Centre for Northern Studies, McGill University and an NSERC postgraduate scholarship.

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Philopatry and Site Tenacity of Belugas, *Delphinapterus leucas*, Hunted by the Inuit at the Nastapoka Estuary, Eastern Hudson Bay

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CARON, L. M. J., AND T. G. SMITH. 1990. Philopatry and site tenacity of belugas, *Delphinapterus leucas*, hunted by the Inuit at the Nastapoka estuary, eastern Hudson Bay, p. 69–79. *In* T. G. Smith, D. J. St. Aubin, and J. R. Geraci [ed.] Advances in research on the beluga whale, *Delphinapterus leucas*. Can. Bull. Fish. Aquat. Sci. 224.

Observations were made of white whales, *Delphinapterus leucas*, in the Nastapoka River estuary of eastern Hudson Bay during the summers of 1983 and 1984. The highest herd counts in 1983 and 1984 were 245 and 260 whales. The location of belugas was found to be strongly influenced by the tide, the total number of whales in the estuary, the state of the water surface, and the total time spent by the whales in the estuary. Of the five size classes that could be discerned based on lengths of grey immatures relative to adult length, neonates (≥ 1/3 length of adult) represented 16.3% of the estuarine herd in 1983 and 19.1% in 1984. All non-white size classes totalled 61.5% of the 1983 herd and 60.5% of the 1984 herd. In the 1984 season, the adult male to adult female sex ratio was estimated as 1:4.3. Some whales identified by their scars were seen both years, and throughout the same season. In 1984, an average daily presence of 30% was calculated for 24 of the most conspicuously marked whales. Average periods of 40 and 24 h were required for the whales to reoccupy the estuary after disturbances from hunts or motor traffic.

Les marsouins blancs, ou bélugas, *Delphinapterus leucas*, de l'estuaire de la rivière Nastapoka, située sur la côte est de la baie d'Hudson, ont été observés au cours des étés 1983 et 1984. Les plus grands troupeaux dénombrés en 1983 et 1984 comprenaient de 245 et 260 bélugas respectivement. La répartition des individus à l'intérieur de l'estuaire était influencée par la marée, le nombre total de bélugas dans l'estuaire, l'amplitude des vagues et le temps écoulé depuis leur arrivée dans l'estuaire. Cinq classes de tailles relatives ont été identifiées, dont celles des nouveau-nés mesurant 1/3 ≥ de la longueur des adultes, représentait 16.3 % des dénombrements en 1983 et 19.1 % en 1984. Les classes bélugas gris prises globalement totalisaient 61.5 % et 60.5 % respectivement des dénombrements de 1983 et 1984. En 1984, l'estimé du rapport mâles adultes sur femelles adultes était de 1:4,3. Des individus identifiés à l'aide de marques naturelles et de cicatrices ont été vus chaque année et de façon répétitive au cours d'une même saison. Un taux de la présence journalière de 30 % en 1984 a été calculé pour 24 des individus les plus facilement reconnaissables. Des périodes moyennes de 40 et 24 h étaient nécessaires pour le retour des bélugas dans l'estuaire après les évacuations causées par les chasses et le déplacement des embarcations motorisées.

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Introduction

White whales or belugas are the most abundant of the odontocete species occupying Canadian arctic waters. During the summer months, belugas congregate in certain estuaries. The occupation of traditional sites along with indications of differences in the body size of belugas from different areas has led to the delineation of several separate stocks in Canada (Sergeant 1986; Smith et al. 1985; Brodie et al. 1981; Sergeant 1981; Finley et al. 1982; Fraker 1980; Vladykov 1944).

In the 19th century, herds of belugas in eastern Hudson Bay occupied the Great Whale and Little Whale rivers by the "thousands" during the summer months, and there were reports of herds of similar size farther north in Richmond Gulf and in the "Nistabucky" River (probably the Nastapoka River) (Francis 1977). Richmond Fort, on Richmond Gulf, was the first beluga hunting site used by the Hudson Bay Company in 1750, where there was a harvest of whale skins valued for their high quality leather. Native whale hunting continued for the next 100 yr or so along the eastern Hudson Bay coast. Then, from 1854 to 1870, newer whaling techniques using nets decimated the Great Whale and Little Whale River herds to the point where the remaining whales would no longer use the estuaries, and the "porpoise fishery" had to be abandoned (Francis 1977).

The Nastapoka River estuary is currently the main major summer concentration area of beluga whales in eastern Hudson Bay, and it is also an important site of Inuit whale hunting. Approximately 30 whales are taken at this site every year from a population on which there is still limited information. The earliest coastal aerial survey conducted in 1978 in the Great Whale area (Breton-Provencher 1980) counted between 242–254 belugas; subsequent nearshore counts in 1982 showed only 162 belugas along the whole eastern Hudson Bay coastline (Finley et al. 1982). More recent comprehensive systematic surveys including the whole of James Bay and areas offshore as far as the Belcher Islands have yielded estimates of some 1124–1904 belugas for the eastern Hudson Bay stocks (Smith and Hammill 1986). In their survey the coastal concentrations alone totalled 474, of which 139 individuals were seen at the Nastapoka estuary.

The persistent habit of estuarine aggregation makes the beluga one of the most vulnerable arctic marine mammal species to overharvesting and destruction of critical habitat. Here we describe the numbers and age structure of the Nastapoka belugas and their tenacity to site in the face of hunting and human disturbance.

Materials and Methods

The Nastapoka estuary, on the east coast of Hudson Bay (56°55'N, 76°36'W) is 1.3 km long from the river mouth to the 30 m high waterfalls and 0.2 km wide in an east–west orientation. Observations were made from a 6 m high aluminium tower located on the north shore of the river mouth (Fig. 1). The study was conducted from 20 July to 13 August 1983 and 21 June to 2 September 1984. In 1983 the observations were non-systematic and selective of individuals with identifying marks. In 1984, scan samples (Altmann 1974) were taken every 2 h from 09:00 to 21:00 daily for a total of 48 d. More detailed focal samples concentrating on individuals or groups were also made on 82 occasions totalling 390 min of observations.

The estuary was divided into four quadrats from which we recorded the frequency of the different size classes of whales along with time, tidal height, water temperature, wind speed and direction, surface conditions and clarity (ordinal scale 1 to 4; choppy to calm and clear) and light conditions (scale 1 to 4; strong glare to diffuse light).

The ages of different size classes were verified by analysis of carcasses, which had been aged by tooth sections, in the catches from Whale Cove, western Hudson Bay from 1962 to 1964 (Sergeant 1973) and catches from Cumberland Sound, eastern Baffin Island (Brodie 1967). Data were also obtained from carcasses of belugas taken in eastern Hudson Bay

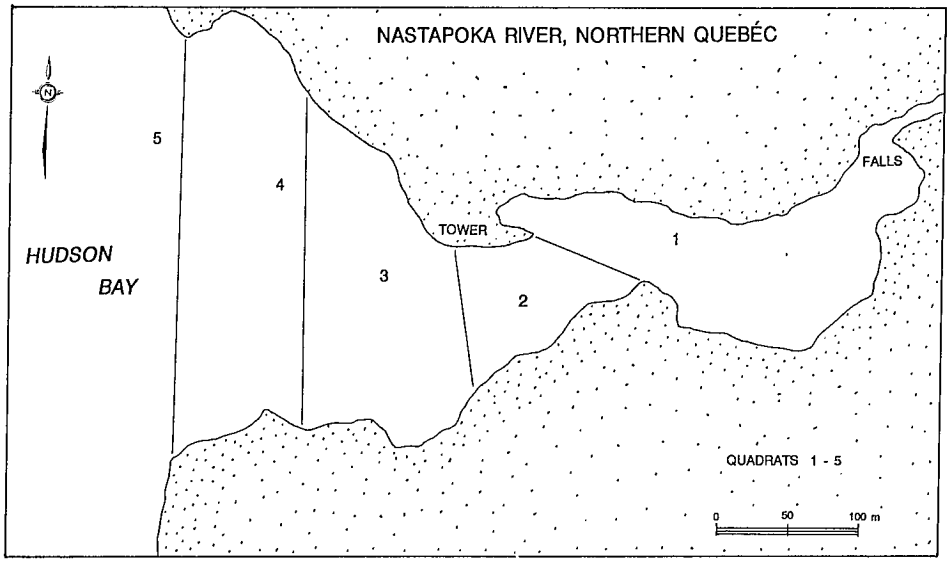

Fig. 1. The study area at the Nastapoka River estuary showing the different quadrats observed from the tower.

(Breton-Provencher 1980). Ages were assigned to the carcasses based on counts of two dentinal layers per year (Goren et al. 1987). Mean lengths of different age classes were calculated as proportions of the mean lengths of adult (white) females in the catch (Table 1).

Individual belugas were identified from scars which appeared for the most part to have been old bullet wounds. Only scars located on the left side of the individual were used to minimize error in re-identification.

Spearman rank correlations were used to test the relationship between the distribution of belugas in the estuary and physical factors. Chi square tests were performed on the contingency tables of the age structures, and a deviation statistic Z (Legendre and Legendre 1984) was calculated for each cell to verify which observed frequency deviated significantly from the expected one. Mann–Whitney U tests were used to compare the means of recovery times of whale numbers in the estuary after hunting to the recovery times after motor traffic.

Results

Numbers, Distribution, and Population Structure

In 1983, whales were present in the estuary both before and after the period of observations. In 1984, however, the first whales of the season were seen on 23 June, but were still present after observations ended. Numbers of belugas fluctuated daily throughout both seasons. Some fluctuations were caused by boat traffic and whale hunting, while others were unexplained. The highest count for 1983 was 245 and occurred on 27 July. In 1984, the highest count, 260 belugas, was made on 25 August. During the 1984 season, the herd size gradually increased in July and August, then started to decrease in early September (Fig. 2.)

On 22 July 1984, low altitude aerial photos taken from helicopter showed that there were 160 whales at the surface and between 20 and 30 whales visible below the water surface. Counts made from the observation tower two hours before and one half hour after this flight showed 175 and 145 whales in the study area respectively, closely in agreement with the aerial estimates.

TABLE 1. Measured nose to tail length (cm) of belugas taken in three Canadian arctic areas with calculated proportional mean lengths of different age calves (sexes lumped) to a mean lengths of white adult females (%) in the same catches.

	Mature female	Neonate	Yearling	2 yr old grey	3 yr old grey	4 yr old grey	5 yr old grey	6 yr old grey	References
	$\bar{x}$ n	$\bar{x}$ n %	$\bar{x}$ n %	$\bar{x}$ n %	$\bar{x}$ n %	$\bar{x}$ n %	$\bar{x}$ n %	$\bar{x}$ n %	
Western Hudson Bay (Whale Cove 1962-1964; July 31 to 5 Sept.	310.5 57	151.9 9 48.9	198.4 16 63.9	225 16 72.5	242 6 77.9	260.7 19 84.0	273.7 15 88.1	280.1 14 90.2	(Sergeant 1973)
Eastern Hudson Bay (24 June to 25 Nov.)	327.2 75	155.6 5 47.6	228.3 6 69.8	243.3 4 74.4	260.5 6 79.6	255.5 2 78.1	281.3 7 86.0	296 9 90.5	(Breton-Provencher 1980)
Cumberland Sound (July and Aug.)	363.8 13	166.6 10 45.7	249.0 2 68.4	— — —	290.8 5 80.0	318.8 5 87.6	331 7 91.0	352 7 96.8	(Brodie 1967)

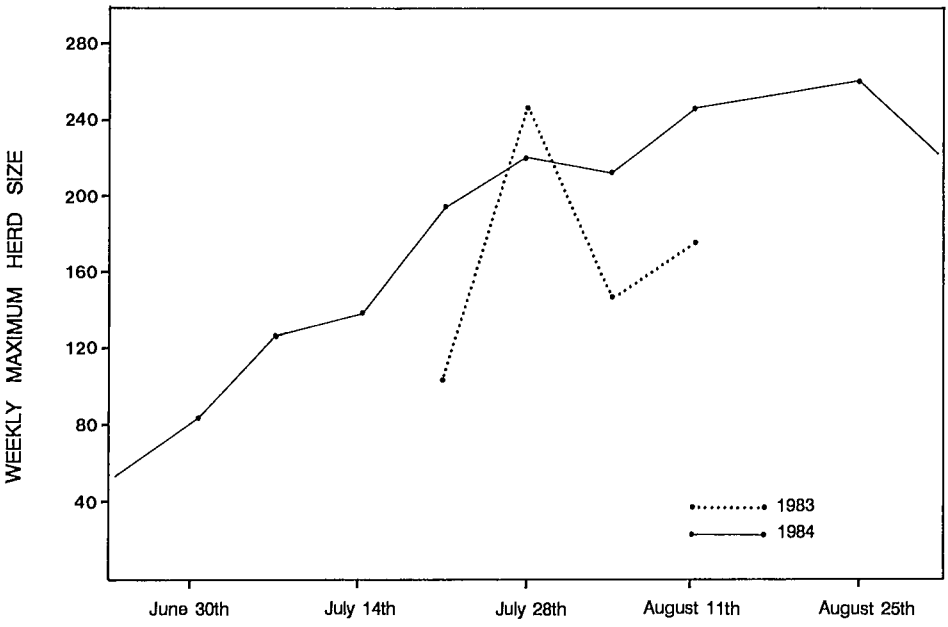

Fig. 2. Seasonal change in the weekly peak number of belugas seen in the Natapoka River estuary.

In the estuary, groups of belugas were observed to swim upstream and downstream displaying various behaviors. Spearman rank correlation between physical factors and the median of the distribution of whales in the estuary showed that the median position of the herd advanced and receded with the flow and ebb of the tide ($R = 0.4, P = 0.0001$). It also indicated that large herds ($R = 0.34$, $P = 0.0001$), long periods without disturbances ($R = 0.23$, $P = 0.0001$), high waves ($R = 0.32, P = 0.0001$), strong northerly winds ($R = 0.15, P = 0.005$), high river water temperature ($R = 0.11$, $P = 0.0332$), and clear water ($R = 0.12$, $P = 0.0224$) favored the occupation of the upper reaches of the estuary.

We are easily able to recognize neonate (0+) and yearling (1+) calves by their shape and size proportional to their accompanying white adult females. Neonates which are born prior to entering a high arctic estuary, Cunningham Inlet, N.W.T., probably from mid-June to the first week of July, are initially very thin, light grey to slightly pink in coloration and measure from > 1/3 to < 1/2 of the length of their accompanying white adults. Yearling calves are much bulkier in appearance, are the darkest of the grey immature age classes and measure > 1/2 to 70% of the length of the white adult females. Both neonates and yearlings remain very close to their presumed mothers, rarely ever leaving their side. The remaining immature grey age classes, from 2+ to 6+ yr old, range from > 2/3 to < 3/4 (73 – 97%) of the length of adult females; they are loosely associated with adults and cannot be reliably separated by visual observation into definite age categories (Table 1).

In 1984, the size class structure was estimated using scan and focal sampling techniques. Results did not differ significantly. Scan sampling showed that 19.20% of the herd was composed of neonates (> 1/3 lengths), 15.39% were > 1/2 length yearlings, 11.37% were > 2/3 length greys, 12.73% were > 3/4 length greys, and 41.31% were white individuals.

The size class distribution was found to vary slightly, but significantly, with the season (Table 2). The age class contributing the most to the total variation was the > 2/3 length. The abundance of this age class was high at first, then sharply decreased after the first quarter of the season, and increased only during the last quarter. The proportions of > 1/3 lengths and

TABLE 2. Contingency table of the age structure variation from scan samples of the Nastapoka herd over the 1984 season ($n = 33\,027$). The dates listed are mean values of dates for blocks of equal sample size. Asterisks note the values significantly different from the average. (Chi Square = 703.7002, df = 12, $P < 0.005$.)

	17 July	7 Aug.	20 Aug.	29 Aug.	Total
Size class	Percent	Percent	Percent	Percent	Average
1/3 (neonate)	* 17.4	20.4	20.0	18.9	19.2
1/2 (yearling)	* 13.7	* 17.4	15.1	15.4	15.4
2/3	* 17.8	* 8.7	* 6.6	12.5	11.4
3/4	* 10.9	* 14.4	12.3	13.2	12.8
White	40.2	* 39.0	* 46.1	40.0	41.2

> 1/2 lengths were slightly below the mean value during the first quarter of the season, but their numbers increased and stabilized later on.

Only an indirect calculation of the sex ratio could be made. Observations of > 1/3 and > 1/2 length calves were equated with the presence of an adult female. White animals accompanying > 2/3 length calves were also counted as adult females. From this it was calculated that 0.322 of the Nastapoka herd was composed of adult white female animals. By subtraction this left 0.0742 adult males, yielding a maximum sex ratio of 1:4.33. This is unreliable since it does not include large grey animals that are known to be mature and with calves nor does it identify the lone females which at the Nastapoka make up 16% (5/31) of the white adult females as indicated by whales shot by Inuit. The sex ratio from killed white animals at the Nastapoka is indicated to be unity 32:32 (Arctic Biological Station, unpublished data). However, this is probably biased towards males since the Inuit select for large animals unaccompanied by calves both by preference and as a conservation measure.

Philopatry and Reaction to Human Disturbance

A measure of philopatry or site fidelity was derived from individually identified belugas. In 1983 of a total of 18 individually marked animals, 14 were resighted on 2 or more days and 9 of those were again seen the following year. In 1984 over a period of 59 d, 46 individuals, mainly white adults or large grey individuals, were recognized individually and resighted from early July to late August.

From the resighting of identified individuals in 1984, a mean daily presence in the Nastapoka estuary was calculated to be about 30% of the total number of days in the season (Table 3). This average frequency of daily occupation is considered a minimal estimate because of the difficulties inherent in reliably resighting the relatively small number of well-marked individuals.

The Nastapoka estuary is well known among native communities as a good whale hunting area, and at the time of this study, it was regularly visited throughout the season by hunters of Inukjuak and Kuujjuarapik located approximately 200 km north and south respectively of the study site. The shoreline of the estuary was also used as camping sites for caribou and waterfowl hunters travelling in the area.

In 1984 during a period of 59 d of observations, the estuary was vacated 7 times for a total of 170 h because of whale hunting and 6 times for 84 h because of motor boat traffic. The estuary was vacated 18% of the time in 1984 and to 15% of the total time observed in 1983.

In the usual pattern of hunting disturbance, Inuit motor boats would suddenly arrive at the beginning of weekends in a direction parallel to the coast at top speed and head into the estuary in an effort to push the whales as far as possible into the shallow waters. Each boat would then select its targets.

TABLE 3. Occupation rates of the Nastapoka estuary by belugas individually identified using scars and natural markings during 1984.

Whale ID #	Total observation period (days)	Number of days of occupation	Percent estuary occupation
[a] * 1	26	10	38
* 3	26	14	54
* 4	25	7	28
7	25	7	28
8	25	6	24
* 10	24	11	46
11	23	4	15
12	24	2	8
* 15	23	11	48
* 17	24	8	33
19	21	2	10
20	18	8	44
22	19	5	26
* 23	19	5	26
26	18	2	11
28	12	5	42
30	19	3	16
31	13	2	15
37	13	3	23
39	11	5	45
41	13	3	23
42	10	4	40
* 44	7	5	71
* 45	6	1	17

[a] Whales also identified in 1983.
Mean minimum estuary occupation = 30.46% ± 15.89%.

The majority of whales reacted to approaching motor boats by quickly leaving the estuary. However, some whales which were further into the estuary (quadrats 1 or 2, Fig. 1) would continue to swim upstream and would only react overtly when the boats were as close as 500 – 1 000 m away.

When small groups of whales were pursued, some whales would leap out of the water during their escape, whereas others would lift their heads out for a brief moment before resuming their flight. Others tried to escape by remaining motionless close to the shores, or by swimming far upstream almost to the Nastapoka falls.

Motor boats passing approximately 1 km or more outside the estuary only caused the whales to recede into the downstream portion, whereas motor traffic within quadrats 1 to 4 and each hunt caused the whales to completely desert the area. On a few occasions, however, the whales were seen to depart on their own when there was no apparent disturbance. Once, the whales left from the upstream quadrats (1 and 2) at the precise moment when an observer was walking close to the adjacent sandy north shore of quadrat 2. On one occasion, a bullet hitting the water in quadrat 2 was apparently the cause of a mass whale exodus from the

upstream quadrats. Low altitude air traffic (less than 100 m), such as helicopters, caused whales to rapidly swim away from the aircraft. Aircraft flying higher than approximately 300 m did not appear to cause any change in swimming direction of the whales.

The effect of disturbance was measured by noting the time required for whales to return to the estuary. We defined a partial recovery as the time required for the first whales to appear. Total recovery was arbitrarily defined as the time required for there to be 70% of the pre-disturbance numbers of whales in the estuary. This was done to allow for seasonal attrition of numbers in animals that were using the estuary and to adjust for random movements away to another area. There did not appear to be any significant differences in the mean times it took for whales to first reappear after hunting disturbance or motor disturbance ($U = 25.5, P > 0.10$) (Tables 4 and 5). However, it did on the average take significantly longer (40.1 h) for full recovery after hunts than after simple disturbance by motor boats (24.6) ($U = 13.0, P = 0.015$).

The reaction of individually recognized whales appeared to vary greatly in response to either type of disturbance. Individuals were seen to return in as little as 33 h and stay away for as long as 574 h. For the 18 resightings of individuals after disturbances of any kind, the average period of absence was 185 h or 7.7 d.

TABLE 4. Recovery time of whales in the Nastapoka estuary as a result of hunting activities during the 1983 and 1984 seasons. Recovery time: Partial = return of first whale to estuary, Total = return of > 70% of the pre-disturbance count to estuary.

Date of hunt	Pre-disturbance count	Partial recovery (hours)	Total recovery (hours)	Recovery time of identified whales # of hours (ID no.)
23/07/83	100	35	48	—
09/07/84	88	19	50	—
12/07/84	51	36	35	380(8), 117(10,11)
15/07/84	35	2	25	—
15/07/84	25	26	48	—
29/07/84	114	4	45	—
08/08/84	31	48	58	144(3), 56(39)
18/08/84	209	11	12	48(15)

TABLE 5. Recovery time of whales in the Nastapoka estuary as a result of motor traffic activities during the 1983 and 1984 seasons. Recovery time: Partial = return of first whale to estuary, Total = return of > 70% of the pre-disturbance count to estuary.

Date of disturbance	Pre-disturbance count	Partial recovery (hours)	Total recovery (hours)	Recovery time of identified whales # of hours (ID no.)
25/07/83	70	24	33	—
03/08/83	105	28	28	—
07/07/84	101	28	36	165(1), 372(3,4) 574(7), 106(8)
10/07/84	40	20	22	—
25/07/84	117	16	41	42(10), 236(20) 169(19), 177(26)
20/08/84	129	3	5	123(23)
22/08/84	14	2	5	—
24/08/84	207	15	27	33(1), 104(3)

TABLE 6. Contingency table of the age structure variation over increasing periods of time elapsed since the return of belugas to the estuary after disturbance during the 1984 season (n = 33 027). Cell values which are significantly different from the expected value are marked with an asterisk. (Chi Square = 161.6074, df = 12, $P < 0.005$.)

	< 30 h	30 – 75 h	75 – 135 h	> 135 h	
Size class	Percent	Percent	Percent	Percent	Average
1/3	19.4	19.6	18.7	19.3	19.2
1/2	15.1	14.8	15.8	16.0	15.4
2/3	* 9.8	10.6	* 13.9	11.4	11.4
3/4	* 10.9	12.9	12.6	* 14.2	12.8
White	41.3	42.0	* 39.0	* 39.1	41.2

The size class distribution of the first groups of whales to reoccupy the estuary after a disturbance was found to be significantly different from the size composition of whales arriving later (Table 6). Adults accompanied by neonates and yearlings were among the first whales to reoccupy the estuary after disturbances, while > 2/3 and > 3/4 length greys appeared later. The adults with the smallest immatures were more abundant throughout recovery periods.

Discussion

Certain estuaries appear to attract belugas each summer. Until recently the function of these summer areas of aggregation was unknown. Recent findings indicate that belugas use the warmer waters and abrasive substrates of the estuary during a period of epidermal cell growth which is physiologically equivalent to a real molt (St. Aubin et al. 1990). Previous hypotheses defining them as calving (Sergeant 1973) or feeding areas (Seaman and Burns 1981) have not proven correct for Canadian arctic summer aggregations. Females and young calves probably use the more protected nearshore areas for suckling and nurturing activities and possibly for shelter from the elements and aquatic predators.

At the Nastapoka our average proportion of neonates was 19.2% which is one of the highest reported so far for belugas. In other estuaries or coastal concentrations the percentages of neonates usually range between 8 and 14% (Sergeant 1973; Heyland 1974; Davis and Finley 1979; Breton-Provencher 1980; Finley et al. 1982), and exceptionally it was reported as 18 – 23.8% (Norton and Harwood 1985). Most of those observations came from aerial photographs in which neonates might have been underestimated because of their position under the female during suckling. Our higher proportions made from shore observation posts could be upwardly biased because of the more rapid breathing rhythm of neonates, and greater time spent at the surface.

Sergeant (1973), for the western Hudson Bay beluga populations, calculated a gross annual reproduction rate of 0.13 based on reproductive tract analyses, which represents slightly less than one calf per female every three years. While we have no independent data base with which to compare our eastern Hudson Bay population, it seems that the high neonate representation in the Nastapoka is likely an indication of the estuarine habitat preference of females with newborn rather than a real difference in the reproductive rates. The lower representation of adult males could also point to a summer segregation of sexes which possibly utilize different feeding strategies in the inshore and offshore areas (Smith and Hammill 1986). However, Sergeant (1973), from a consideration of various netted and shot beluga catches, concluded that the true sex ratio was close to unity and that mortality rates were comparable for both sexes.

The return in 1984 of 9 of 14 belugas recognized in 1983 is the first positive proof of site fidelity in this species. All but two of those individuals were white animals and five of those were females accompanied by neonate calves. Two of the others were lone white animals of undetermined sex and the two others were > 3/4 length grey individuals accompanied by neonates.

The tenacity to site displayed by the Nastapoka herd is the most striking and important result of this study. Belugas, including individually recognizable whales, reoccupied the estuary after hunting. This indicates a strong physiological dependance or behavioral fixation on the particular site which is undaunted by heavy human predation. The vulnerability of the stock to overharvesting especially because of the strong representation of sexually mature females is clearly underlined by this pattern of behavior.

Recent analyses using mitochondrial DNA markers of belugas (Helbig et al. 1990) and humpback whales (Baker et al. 1990) show that there is a geographic segregation of haplotypes. Both species migrate over long distances and share common wintering grounds with conspecifics which have spent the summer in other regions. The segregation of haplotypes is probably a consequence of fidelity of maternal lineages to specific summer sites, supporting the hypothesis that stocks of belugas can be defined by their summer estuarine aggregations.

Belugas must be managed with strong consideration given to protection of the possibly distinct stocks occupying estuaries in the summer. Protection of the estuaries as critical habitats follows as a logical priority in the future conservation of the species. This is particularly important in relation to management of exploited stocks since, as in the case at the Nastapoka, a large number of belugas, possibly members of the same putative stock, are killed there each year.

Acknowledgments

T.G. Smith would like to acknowledge the efforts made by the late Louise Caron. This would have been her first published paper from a project in which she displayed remarkable industry and persistence. We would also like to thank Dr. P. Legendre, Université de Montréal, for help with statistical matters. Dr. B. White, Queen's University, provided us with information on the results of the genetic analyses of this and adjacent beluga stocks. The World Wildlife Fund, "Whales Beneath the Ice" Project provided financial support. Mimi Breton, Pêches et Océans Canada, critically reviewed the manuscript and helped with the French translation.

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Cutaneous Response to Implants, Tags, and Marks in Beluga Whales, *Delphinapterus leucas*, and Bottlenose Dolphins, *Tursiops truncatus*

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GERACI, J. R., AND G. J. D. SMITH. 1990. Cutaneous response to implants, tags, and marks in beluga whales, *Delphinapterus leucas*, and bottlenose dolphins, *Tursiops truncatus*, p. 81–95. *In* T. G. Smith, D. J. St. Aubin, and J. R. Geraci [ed.] Advances in research on the beluga whale, *Delphinapterus leucas*. Can. Bull. Fish. Aquat. Sci. 224.

To assess the value of metallic and plastic substances for tagging cetaceans, we examined the cellular response to small test rods implanted through the skin of beluga whales, *Delphinapterus leucas*, and bottlenose dolphins, *Tursiops truncatus*. One material, a porous high density polyethylene, was retained in the dolphins for the 12-wk duration of the study when used alone. This, and a porous composite, Proplast I, remained in the belugas for 8 wk. When these materials were coated on metal rods, the implants were rejected in 3–35 d. All other materials were expelled in 3–39 d. To gain insight into the cutaneous response to tag configurations, we implanted various prototypes; all were expelled in 0–44 d. Our findings indicate the need to develop a composite implant using materials that initiate only a mild inflammatory reaction, and permit rapid formation of a viable biological seal by fibrous tissue growth into a porous material. Such implants would increase mechanical stability and provide a barrier to invasive pathogens. We also investigated the use of dye-marking in beluga whales, and found it to be unsatisfactory.

Afin de juger de la valeur de substances métalliques et plastiques pour l'étiquetage de cétacés, nous avons examiné les réactions cellulaires aux petites tiges de contrôle implantées chez les marsouins blancs, *Delphinapterus leucas*, et chez les dauphins, *Tursiops truncatus*. Un matériel, le polyéthylène poreux de haute densité, est resté en place chez les dauphins pour les douze (12) semaines de la durée de l'étude, si utilisé seul. Ce dernier et un composite poreux, Proplast 1, ont été retenus chez les marsouins blancs pour huit (8) semaines. Lorsque ces matériaux ont été appliqués sur des tiges de métal, les implantations ont été rejetées dans 3–35 jours. Tous les autres matériaux ont été rejetés dans 3–39 jours. Pour une meilleure compréhension de la réponse cutanée aux configurations de l'étiquetage, nous avons implanté des prototypes de designs variés; tous ont été rejetés dans 0–44 jours. Les résultats obtenus pointent au besoin de développer une implantation composite utilisant des matériaux qui initient seulement une légère réaction inflammatoire, et permettent une formation rapide d'un scellant biologique viable par une croissance de tissus fibreux dans un matériel poreux, assurant ainsi une stabilité mécanique, prévenant le repliement épidermale, et érigeant une barrière aux pathogènes envahisseurs. Nous avons aussi étudié la réaction des tissus au marquage par la teinture et au poinçonnage par gel chez les marsouins blancs. Les deux ont donné des résultats peu satisfaisants, d'une part dûe à l'épaisseur de l'épiderme et de l'autre à cause d'une cicatrisation indistincte sur le fond blanc.

Introduction

A cetacean that can be individually identified becomes a resource for studies on behavior, abundance, distribution and movements. Such identification can be achieved through the use of natural pigment patterns and scars, artificial marks, visible tags, and radio transmitters. A variety of tags and marking techniques has been tested, as recently reviewed by Scott et al. (1990). Some tags are implanted in the body wall (spaghetti and arrowhead types) or dorsal fin (disks and clips) (Evans et al. 1972; Perrin et al. 1979); others encircle the caudal peduncle (White et al. 1981). With some exceptions (Scott et al. 1990), these devices are not dependable enough to be used routinely. They are either too difficult to apply, are rejected, cause inordinate tissue damage, or fail because the materials are not durable or the marks distinctive (White et al. 1981; Hobbs and Goebel 1982; Irvine et al. 1982).

We undertook this investigation to determine the tissue reactions leading to rejection of materials embedded through cetacean skin. We had previously characterized the inflammatory response and rate of healing in the skin of belugas, *Delphinapterus leucas* (Geraci and Bruce-Allen 1987) and bottlenose dolphins, *Tursiops truncatus* (Bruce-Allen and Geraci 1985). In this study, we examined the reaction to eight metals and nine plastic materials that have been used successfully as implants in human surgery. These materials, either metal, plastic, or plastic-coated metal, were inserted as rods. We also tested three types of "spaghetti" tags, with dart points embedded in the blubber and streamers fully exposed. In addition, we examined the cutaneous reaction to dye-marking (tattooing) which, though of marginal value in other cetaceans (White et al. 1981), might be particularly distinctive on the white skin of *D. leucas*.

Materials and Methods

Animals

Ten belugas were kept at a temporary camp on the shore of western Hudson Bay, 7 km north of the Seal River, Manitoba, in pools 8.2 m in diameter and 1.2 m deep, containing natural seawater at a temperature of 10–12°C and salinity of 25–30 o/oo. The pools were drained and refilled with clean water every 1–3 d. The whales were fed thawed Pacific herring (*Clupea harengus pallasi*) and fresh cisco (*Coregonus artedii*), providing 1.7 to 2.1 x 10^5 J • kg body wt^{-1} • d^{-1}.

Three female bottlenose dolphins were maintained at the New England Aquarium, Boston, in a 6.7 x 13.7 x 1.8 m deep pool containing chlorinated (<0.05 ppm free chlorine) seawater at a temperature of 17–18°C, salinity of 32 o/oo, and a pH of 8.0. The dolphins were fed thawed herring (*Clupea harengus*) and capelin (*Mallotus villosus*) providing 1.4 to 2.4 x 10^5 J • kg body wt^{-1} • day^{-1}. During the study period, the animals were in good health as judged by appetite, general appearance, and results of hematologic and blood chemical analyses.

The belugas were immobilized by lowering the water level in the pool until they grounded on the vinyl pool liner. Sufficient water remained in the pool to keep the whales moist during the hour it took to apply the tags or marks. For the study on dolphins, each animal was captured, restrained in a standard dolphin transport stretcher, and placed on a foam pad at poolside, where it was kept moist by sponging during the 30 min required to complete the procedures.

Dye-Marking

Dye-marks were applied on beluga whales, using a small hand-held applicator fitted with six 20-mm-long scored pins spaced 5 mm apart, that were coated with either black, red, or purple tattoo ink (Spaulding & Rodgers Mfg., Inc., Voorheesville, NY). The marks were

applied in one of three ways: on untreated skin; on untreated skin that was then freeze-branded; or on a site first prepared by freeze-branding to devitalize the epidermis.

The first approach was done simply by pressing the ink-coated pins perpendicularly and to their full length into skin that had been scrubbed with alcohol and dried. To freeze the site, either before or after applying the dye, a bronze block with a facial surface of 0.8 x 3.5 cm was cooled in liquid N_2 to -196°C, and applied to dry skin for periods of up to 240 s.

Percutaneous Rods

Plastic and metal materials (Table 1), were prepared in the form of rods either 1.5 mm or 3.0 mm in diameter for direct insertion in skin. Other metal rods (1.5 and 2.9 mm in diameter) of copel, inconel, 316 L stainless steel, Stellite, and titanium, all resistant to corrosion by seawater (Fig. 1), were coated with various plastics. Rods with a 1-mm-thick coating of Proplast I were prepared by Vitek, Inc., Houston, TX. A 1-μm-thick layer of ultra low temperature isotropic carbon was vapor-deposited on rods by CarboMedics, Austin, TX. The remaining implant rods were prepared in our laboratory: metal rods were inserted in blocks of HDPE-70 and HDPE-120 which were then machined on a lathe to a thickness of about 1 mm; Gore-Tex, in the form of a vascular prosthesis 3 mm in diameter, was slipped over rods and fastened with a small amount of Tecoflex 1 MP adhesive; Dacron, in the form of double velour cardiovascular patch material 1.5 mm thick, was glued with Tecoflex 1-MP adhesive to rods previously prepared with Tecoflex primer; and medical grade polyurethane was applied to rods primed with Tecoflex primer, by dip-coating with a 5.5% solution of SG-60D Tecoflex dissolved in *n,n*-dimethylacetamide.

The uncoated metal rods were cleaned in 100% acetone, stored in 100% ethyl alcohol, and then rinsed in a sterile 0.9% saline solution. All other implants were placed in a steam sterilizer for 20 min, then stored dry in sealed containers. Uncoated rods were inserted in the dorsal fin of the bottlenose dolphins and in the dorsal ridge of the beluga whales. After scrubbing the site with alcohol, channels spaced 2 cm apart were made 1 cm from the leading edge of the dorsal fin of the dolphins and 2 cm from the apex of the dorsal ridge of the whales. A 14-gauge needle was used to core channels for materials 1.5 mm in diameter, and a laboratory cork borer was used for materials 3 mm in diameter. One implant was inserted to the full depth of each channel, flush with both surfaces of the fin or ridge. Control channels, without implants, were also made in each dorsal fin.

To implant the coated rods, sites 5 cm apart on the dorsal ridge of the whales were scrubbed with alcohol, then injected with 2% lidocaine hydrochloride, a local anesthetic. Channels were cut through the ridge with custom-made stainless steel coring tools 3 or 5 mm in diameter. One rod was inserted through each channel and held in place with a nylon nut on both ends (Fig. 1).

Tags

"Spaghetti" tags were made in eight different configurations from three basic designs (Fig. 2): flat head/tubing, flat head/wire, and cone head. A flat head/tubing tag had a head stamped from 316 L stainless steel, 0.64 mm thick, to which was glued a 1.5 cm length of 80A Tecoflex tubing with an outside diameter of 4.5 mm and a wall thickness of 0.4 mm. A vinyl reward message was glued inside the tube and the end heat-sealed. Some of these tags had 15-mm-wide collars of Proplast I, Gore-Tex, or Dacron glued around the base of the tubing where it joined the tag head. The collars were intended to provide a substrate for tissue-bonding that would seal the surface. The flat head/wire tag used the same flat head, to which was attached a 1.5-cm-long strand of 316 L stainless steel wire 0.76 mm in diameter, to anchor a 9-cm-long piece of 80A Tecoflex tubing containing a reward message. Cone head/tubing tags were made using cone-shaped heads machined from 316 L stainless steel. Like the flat head/tubing

TABLE 1. Materials implanted percutaneously in three bottlenose dolphins and ten beluga whales.

Material	Description	Supplier
HDPE-70 -120 -250	porous high density polyethylene; pore size: 70, 120, 250 μm	Porex Technologies, Fairburn, GA
Proplast I & II	porous composite of polytetrafluoroethylene combined with carbon (I) or aluminum oxide (II); pore size: 100-400 μm	Vitek, Inc., Houston, TX
Gore-Tex	expanded polytetrafluoroethylene; pore size: 40 μm	Wm. Blair Medical Specialties, Ltd. Toronto, Ontario
Dacron	woven polyethylene terephthalate	USCI International, Billerica, MA
Isotropic Carbon	turbotratic form of vapor deposited ultra low temperature carbon	CarboMedics, Inc., Austin, TX
Tecoflex	aliphatic, polyether-based linear polyurethane	Thermedics, Inc., Woburn, MA
Urethane	polyether urethane	BrandoFlex, Ltd., Brantford, Ontario
Aquaplast	low temperature plastic	WFR/Aquaplast Corp., Ramsey, NJ
Polyform	low temperature plastic	Rolyan Medical Products, Menomonee Falls, WI
Copper	99% pure Cu	Lewis Tool & Die, Ltd., Guelph, Ontario
Copel	copper-nickel alloy	Lewis Tool & Die, Ltd.
Inconel 671	nickel-chromium alloy	Lewis Tool & Die, Ltd.
Monel 400	nickel-copper alloy	Lewis Tool & Die, Ltd.
316 L Stainless Steel	—	Lewis Tool & Die, Ltd.
416 Stainless Steel	—	Lewis Tool & Die, Ltd.
Stellite	cobalt-chromium alloy	Lewis Tool & Die, Ltd.
Titanium	99.7% pure Ti	Johnson Matthey, Inc., Seabrook, NH

tags, these also had 80A Tecoflex tubing containing a reward message attached, and some had 15-mm-wide collars of Proplast I or Gore-Tex glued to the base of the tubing.

Five of the tags were selected at random and tested for durability. Four were clamped to a spring balance and subjected to tension stress up to 1 600 g; two of these were submerged in a 3% solution of NaCl and tested daily for 5 d. The fifth tag was clamped in a customized tensiometer, submerged in a 3% NaCl solution, and stressed repeatedly to 300 g at 1.2 cycles • s^{-1} for 100 000 cycles.

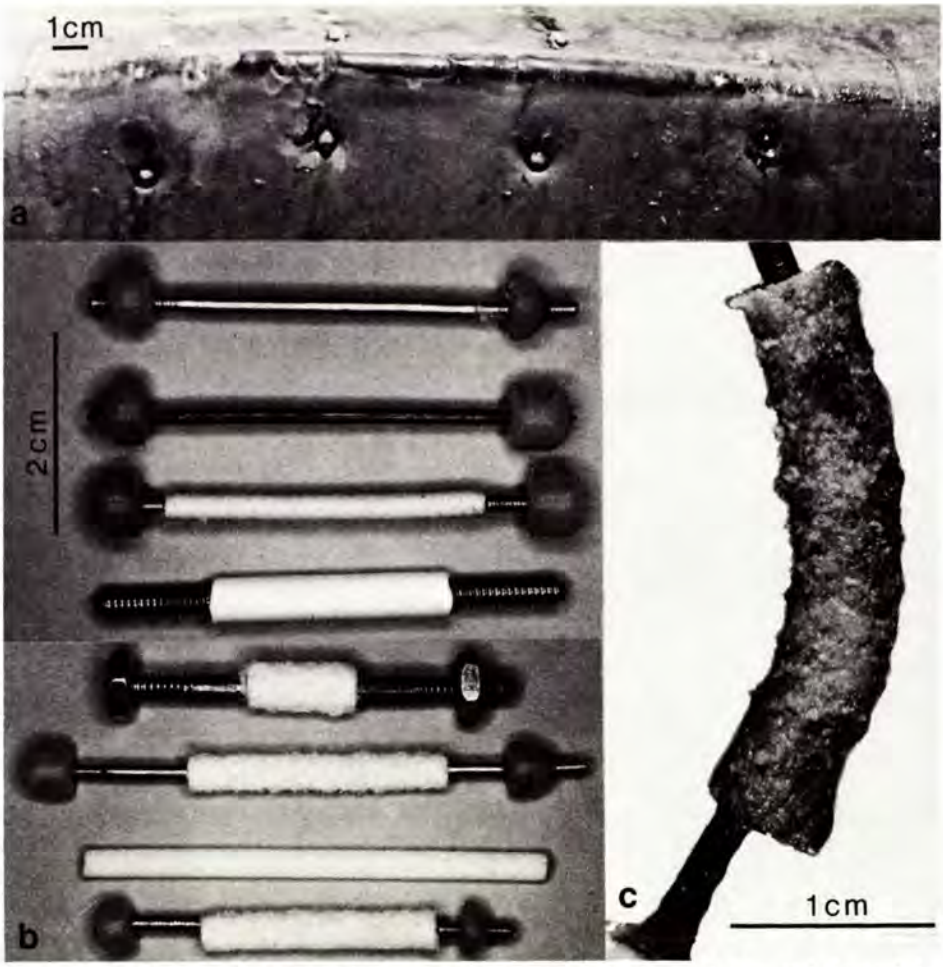

FIG. 1. (a) Plastic-coated rods immediately after being implanted in the dorsal ridge of a beluga whale. (b) Representative rods coated with, from the top: Tecoflex, isotropic carbon, Dacron, Gore-Tex, HDPE-120/carbon, HDPE-120/Tecoflex, HDPE-250, HDPE-70; bolts were made of nylon. (c) This monel rod coated with HDPE-120 was removed surgically after 26 d.

In vivo trials were conducted by inserting the tags through the skin on the flanks of the captive whales, using custom-made tag applicators. Tags were tested in groups of four, and some were replaced following structural failure or rejection. Each whale received 8 or 12 tags; in all, 64 tags were applied.

One flat head/tubing and one flat head/wire tag were implanted in each of 13 whales that were captured in shallow water for that purpose, restrained long enough to apply the tag, and released. This operation to test methods for applying tags was complemented by an *in vitro* study to examine the orientation of tags in the integument. Nine tags with either flat or cone heads, and a commercially manufactured tag (model FH-69A stainless steel dart tag, Floy Tag and Manufacturing, Inc., Seattle, WA), were inserted through the skin of a freshly killed beluga whale taken by Inuit from Wakeham Bay, Quebec. The skin and underlying blubber surrounding the tags was removed and transported frozen to the laboratory for dissection.

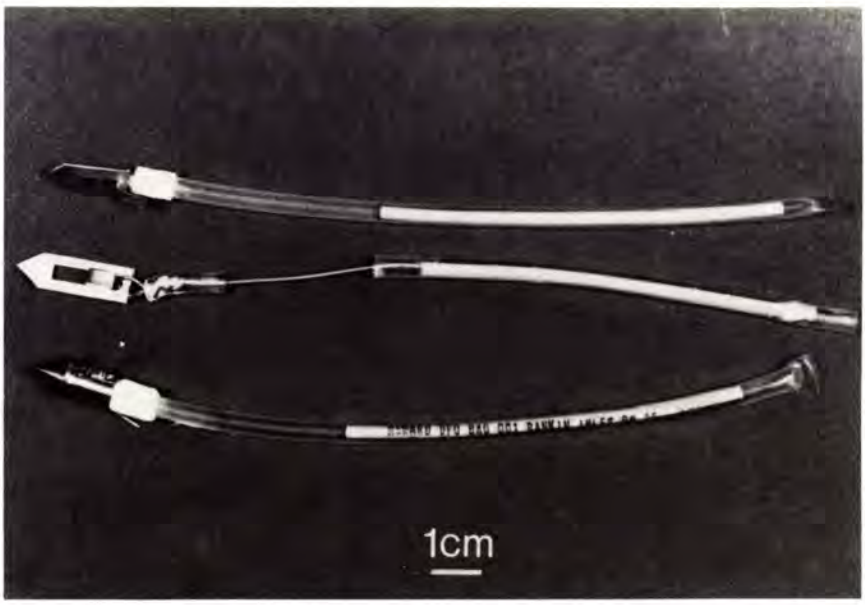

FIG. 2. The three basic "spaghetti" tag designs: flat head/tubing (*top*), flat head/wire (*middle*), and cone head/tubing (*bottom*).

Evaluation

The appearance of marks and implant sites was recorded daily, and a photographic record was maintained. At prescribed intervals, tissue samples were taken for histological evaluation. Each biopsy site was prepared by scrubbing with 95% ethyl alcohol, then injecting into the dermis a surrounding pattern of 1% lidocaine hydrochloride anesthetic. From dye-marked and freeze-branded sites on beluga whales, a scalpel was used to remove 1 x 2 cm wedge-shaped sections, incorporating epidermis and dermis, at the transition zone between the site and adjacent normal tissue. From implant sites, small sections of channel openings were excised immediately after an implant was expelled or removed. A sample of tissue adherent to each plastic or plastic-coated rod was removed with the rod, so that the point of union could be examined. Biopsy specimens from the dolphins were placed in 5 mL of universal fixative for 72 h, then dehydrated in a graded series of ethyl alcohol, infiltrated with methacrylate for 7 d, and embedded in methacrylate in a vacuum desiccator. Sections 2–5 μm thick were stained with hematoxylin and eosin. Sub-samples from the dolphins and samples from the whales were placed in 10% phosphate-buffered formalin and stored for several weeks. The fixed tissues were then processed through alcohol and xylene and embedded in paraffin blocks. Sections 10–12 μm thick were stained with hematoxylin and eosin.

Results

Animals

No difficulty was encountered during the application of any of the cryogenic or dye marks, or implantation of the materials and tags. All the animals quickly resumed normal behaviour patterns following the procedures.

Dye-Marking

Five sites on beluga whales were dye-marked, seven sites were dye-marked then frozen, and 10 other sites were frozen, allowed to thaw for 10 min, then dye-marked. The results were similar in all cases. All sites were mildly elevated and pale 24–48 h after the procedure. The ink was visible in the puncture marks immediately after application, but effectively disappeared by 24 h.

Freeze-branding, whether applied before or after the dye, resulted in shallow depressions with normal coloration for 3 or 4 wk. Histologically, coagulation necrosis was evident in the cells within the entire epidermal column, from the tips of the dermal papillae to the stratum. externum. By the second week, surface layers of epidermis were sloughing, resulting in a shallow (2–4 mm) erosion of the site. A new s. externum was forming at the junction of this and the healthy lower layer of s. spinosum, and the s. germinativum was restored. By the third and fourth weeks, new epidermal tissue bridged the sites, and within 7 wk, the healing process was nearly complete.

Percutaneous Rods

Bleeding caused by the implant procedures stopped within 30 min in the dolphins, and 24–48 h in the whales. In the dolphins, the skin surrounding each implant developed a pale gray halo up to 12 mm in diameter, which persisted for 12 wk. In the belugas, the skin immediately surrounding the implant sites was elevated after 24 h and remained so for 1 or 2 wk.

All uncoated metal rods became loose within the first few days after being implanted. All were extruded within 10 d in the whales, and 21 d in the dolphins (Table 2).

The plastic rods fared better. One material, HDPE-120, remained in the dolphins and the whales for the duration of the study (Table 2). Proplast I also remained in the whales throughout the study, but an analogue, Proplast II, was expelled from the dolphins within 7 d. Tissue response to HDPE-120 and Proplast I was similar for both materials. However, the sequence of events in the whales was delayed by about 2 wk, the inflammatory response was more intense and persistent, and bacteria were present in the implant sites. Polyform remained in the whales for the 39-d duration of the study, but histological examination revealed bacteria, a chronic inflammatory cell infiltrate composed mainly of macrophages, and mature s. externum surrounding the implant. These were signs that the material would soon be expelled.

Most of the coated rods became loose within 3 to 5 d, and were expelled from 3 to 35 d after implantation (Table 2). One of the rods was removed surgically after 26 d (Fig. 1b), just before the whale was released.

The following is a composite description of the inflammatory response to the implants, based on serial biopsy samples from whales and dolphins. Histologically, each metal-implant site showed an acute inflammatory response within the first week. Openings left by expelled implants were filled with exfoliated s. externum cells, neutrophils, bacteria, and erythrocytes within a fibrin matrix. Where implants were still present, hemorrhage and a neutrophilic infiltrate filled the space between the s. intermedium and the implant. Cells of the s. germinativum within 1 mm of the implants were mitotically active. The dermis contained a marked inflammatory cell infiltrate composed mainly of neutrophils. By the end of the third week, the tissue response had become chronic. The s. externum in the implant sites was thickened due to proliferation and hyperplasia of the epidermal cells. The mild inflammatory cell infiltrate in the dermis was composed of neutrophils and a few macrophages. By the end of the sixth week, a slightly hyperplastic s. externum and some maturing scar tissue were the only evidence that an implant had been present.

TABLE 2. Summary of retention of materials implanted percutaneously.

Material	Maximum retention time (days)	
	Dolphins	Whales
Plastic rods:		
HDPE-120	84[a]	57[a]
HDPE-250	—	35
Proplast I	—	58[a]
Proplast II	<7	—
Urethane	<7	<20
Aquaplast	—	14
Polyform	—	39[a]
Metal rods:		
Copper	<21	—
Copel	<21	—
Inconel 671	<7	<10
Monel 400	<21	3
416 Stainless Steel	<21	6
Titanium	<7	<3
Coated rods:		
HDPE-70	—	20
HDPE-120	—	26[a]
Proplast I	—	27[a]
Proplast I/Isotropic Carbon	—	35
Proplast I/Tecoflex	—	35
Dacron	—	31[a]
Gore-Tex	—	25
Isotropic Carbon	—	10[a]
Tecoflex	—	28

[a] Implant removed surgically.

The histological reaction to plastic and plastic-coated metal was, for the most part, less severe. After 1 wk, the s. externum was hyperplastic and edematous and, in the whales, contained bacteria within microabscesses. The pores of the implant material contained bacteria, exfoliated cells, and inflammatory exudate. Neutrophils were scattered throughout the s. spinosum. Cells of the s. germinativum were mitotically active and migrating down the surface of the implant towards the dermis. The inflammatory response in the dermis was confined within a radius of 7 to 10 dermal papillae from the implant, and was characterized by congestion and an infiltrate of neutrophils. Early fibroplasia was seen in the immediate area of the implant.

At the end of 3 wk, the s. externum adjacent to the implant was thickened due to hypertrophy and hyperplasia (Fig. 3). S. spinosum cells in contact with the implant had begun differentiating into s. externum-like cells, and coated the surface of the implant in a layer 10 to 20 cells thick. Mitotic figures were common within the s. germinativum. Pores of the plastic within the epidermis remained filled with exfoliated cells and bacteria. In the dermis, the implant was surrounded by granulation tissue and an inflammatory cell infiltrate composed of neutrophils and a few macrophages.

By 6 wk, the cells of the s. externum adjacent to the implant were mature, while those of the s. spinosum remained undifferentiated. Cells of the s. germinativum continued to divide actively. The dermis contained a bed of maturing, well-vascularized scar tissue. Exfoliated

epidermal cells and fibroblasts were present in the peripheral pores of the implant, while deeper pores contained macrophages, giant cells, fibrocytes, and a few budding capillaries.

Over the next 6 wk, the reaction to the implant approached a steady state (Fig. 4). Cells of the s. externum and upper two-thirds of the s. spinosum were mature where they contacted

FIG. 3. (a) An HDPE-120 implant in dolphin skin *in situ* after 3 wk illustrating the histological appearance of the implant and the response of the surrounding tissue (H&E). (b) Epidermal growth had advanced down to the level of the bed of granulation tissue (H&E). (c) At the level of the dermis, the pores of this implant contained newly forming fibrous tissue with few neutrophils and macrophages (H&E).

the implant; the lower third of the spinous cells were not fully differentiated. Mitotic figures in the s. germinativum became less common, and there was more maturing fibrous tissue within the implant.

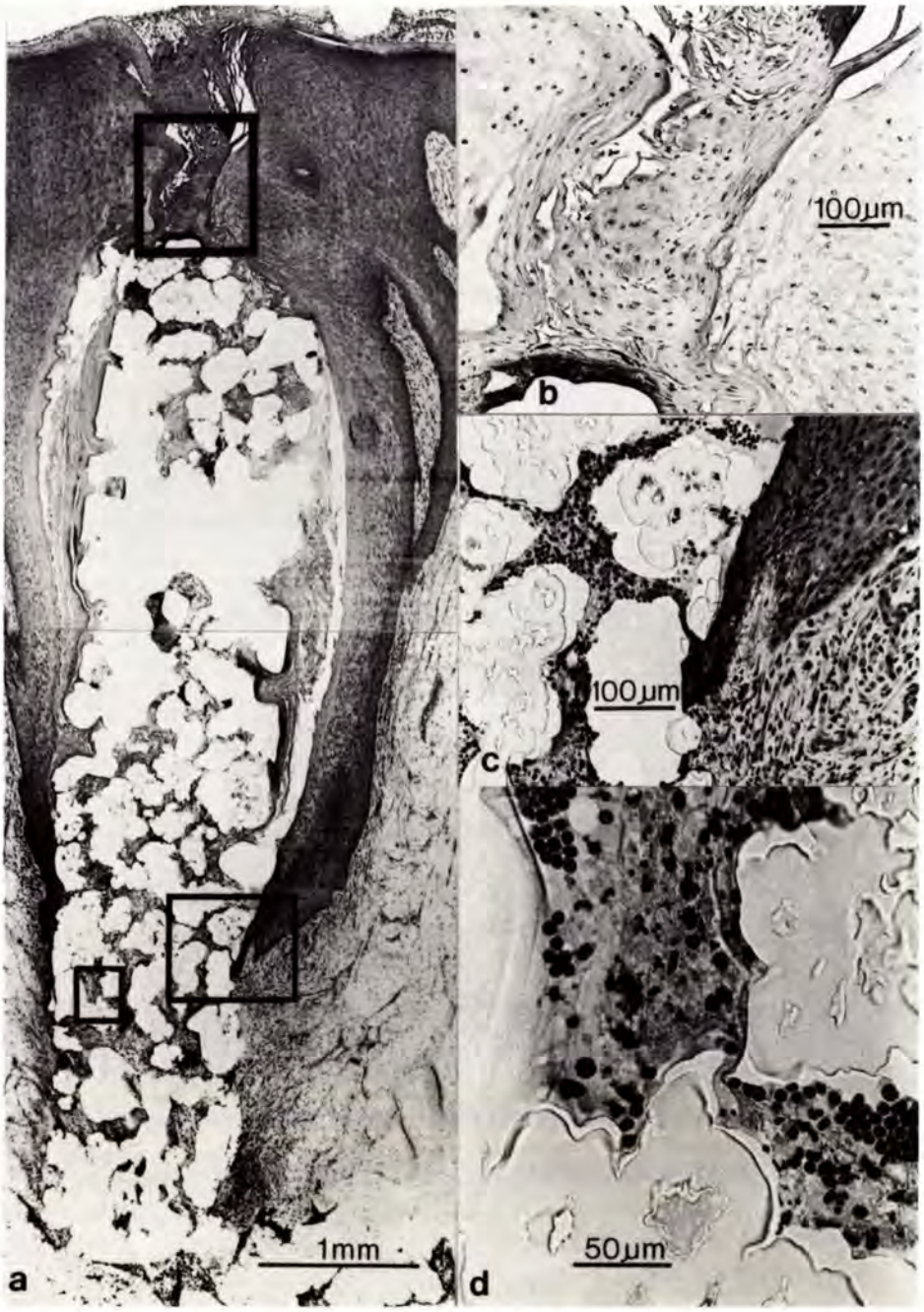

FIG. 4. (a) A completely buried HDPE implant in dolphin skin *in situ* after 12 wk (H&E). (b) Epidermal cells were bridging the opening (H&E). (c) Some pores of the implant contained an inflammatory infiltrate (H&E) composed of (d) neutrophils, tissue debris and red blood cells (H&E).

Tags

In laboratory tests to examine the durability of the tags, the adhesive on three of the five tags failed at 800 to 1 000 g of stress, allowing the tubing to separate from the head. Tecoflex 1-PP adhesive did not provide a good bond, whereas Tecoflex 1-MP did when used as prescribed by the manufacturer. This required cleaning the tag head, applying multiple coatings of adhesive, and final activation of the adhesive by wiping both surfaces with methyl ethyl ketone prior to bonding. The Tecoflex tubing did not break in any of the tags tested, although a stress of 1 600 g stretched the tubing from 138 to 265 mm, an elongation of 192%.

During the *in vivo* trials, we found that the flat head/tubing and flat head/wire tags inserted easily, whereas the cone head/tubing tags required that the dermis first be punctured with the tip of a scalpel blade. In a few cases, bleeding occurred after tag insertion and appeared to stop within 24 h, but recurred intermittently for 4–7 d with cone head/tubing or flat head/wire tags. Tags fabricated with Tecoflex 1-PP adhesive were rejected or suffered adhesive failure 0 to 11 d (average 5 d with flat head/tubing tags) and 5 to 41 d (average 20 d) (cone head/tubing tags) after insertion. Tags fabricated with 1-MP adhesive remained intact and were rejected 3–10 d (average 5 d with flat head/tubing tags) and 3–44 d (average 20 d with cone head/tubing tags) after insertion. Flat head/wire tags were extruded 4–13 d after implantation.

Ten of the cone head/tubing tags were monitored for movement within the integument by measuring the length of tubing exposed immediately after insertion, and at 2–12 d intervals thereafter. Initially, the cone head tags without a collar of porous material moved about 5 mm deeper into the body during the first 5–10 d, and then were extruded at a rate of up to 2 mm • d^{-1}. Cone head tags with a collar of Proplast I also moved in and out as much as 2.3 mm • d^{-1}. The most stable cone head tags were those with a collar of Gore-Tex, with net extrusion rates of 0.17 to 0.54 mm • d^{-1}, but even one of these tags moved outward at a rate of 4 mm • d^{-1}.

Field trials on live whales showed that flat head/wire tags were easy to apply and that the applicator could be removed from the animal without dislodging the tag. Flat head/tubing tags with Dacron collars were more difficult to apply because of problems keeping the tag loaded on the applicator, and, once applied, in removing the applicator from the whale without dislodging the tag. Following application, all tags were tested with a gentle (300 g) pull; none came out (Fig. 5). However, some could be pushed deeper into the body. There was little bleeding and no visible reaction from the whales. We were able to observe the tags in two of the whales after release. Hydrodynamic drag folded the Tecoflex tubing of the flat head/tubing tags back against the skin, and caused the stiffer flat head/wire tags to vibrate.

A whale carcass was used to evaluate mechanical damage to tissue associated with the implant procedure. The anchoring flange on the flat head tags was compressed during insertion, reducing the effectiveness of the anchors. The tops of the anchor flange of the flat head/tubing tags and the flat head/wire tags were situated about 5 and 25 mm, respectively, below the non-papillary dermis (16 mm from the surface) (Fig. 5). One prong of the spring wire of the cone head tags was anchored against the base of the dermis (Fig. 5). The epidermis was pressed against the tubing, and there was some tissue destruction at the level of the dermis, so that very little tissue was in contact with the band of porous material. The single Floy tag tested was anchored in the blubber about 4 cm below the non-papillary dermis. The head was designed to flip over and lie parallel to the surface after implantation, although in the tag examined, the head was resting at a 45° angle.

Discussion

We were unable to produce a visible dye-mark in beluga whales using procedures that can reasonably be carried out in the field. Beluga epidermis is so thick that it hid the tattoo pigments from view; pre-treatment by freezing did not have the desired effect of replacing

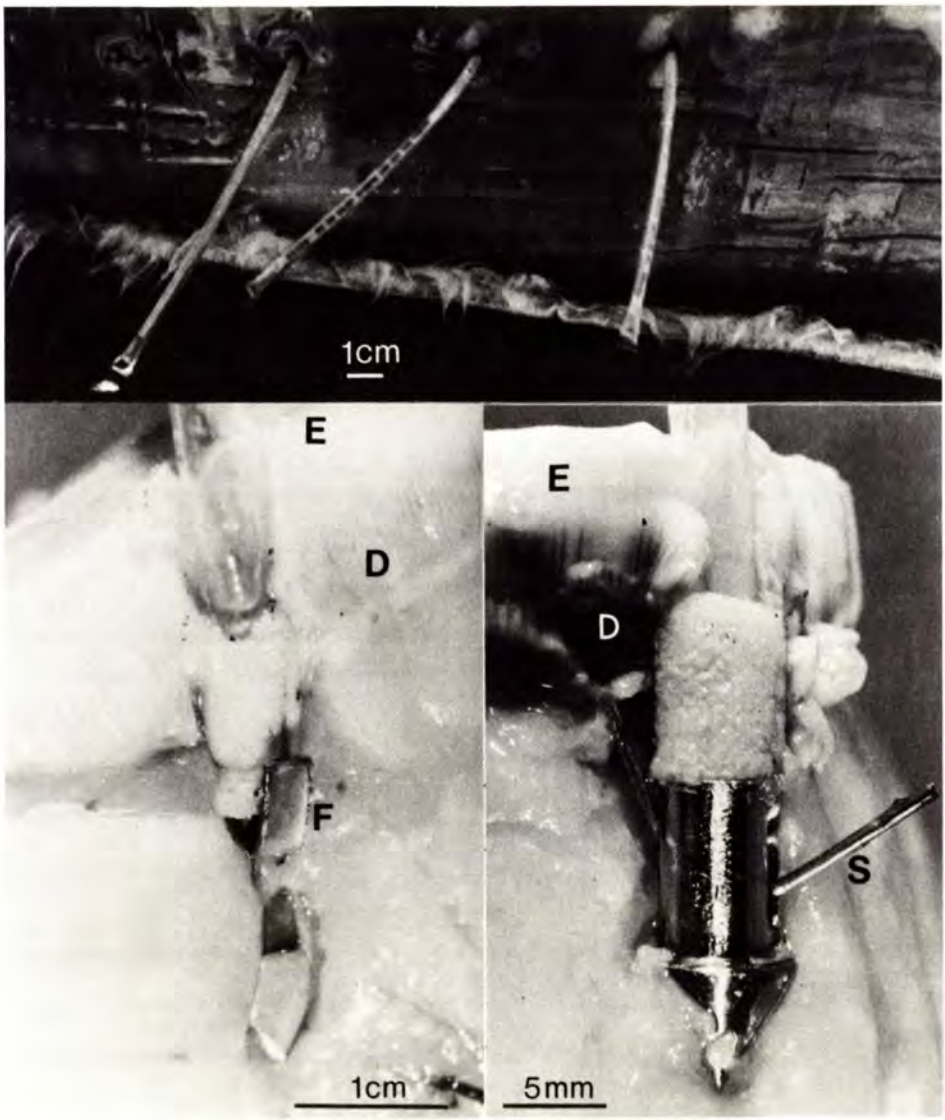

FIG. 5. *Top*: Tags 4 d after insertion through the skin of the flank of a beluga whale. The holes slowly widened around the streamers. No tag remained beyond 44 d. *Lower left*: Flat head tag from *in vitro* study. The anchor flange (F) was loose in the blubber and not anchored against the dermis (D): E epidermis; B blubber. *Lower right*: Cone head tag from *in vitro* study. The spring wire barbs were positioned at (S) the base of the dermis and appeared to be insecure anchors.

the epidermis with a translucent scar, as it does on odontocetes with a thin epidermis (White et al. 1981; Irvine et al. 1982). We conclude that dye-marking is not a practical technique to identify beluga whales.

Implanted rods and tags, whatever the material or configuration, and whether on whales or dolphins, lasted only long enough to be of value as a marking tool for short-term monitoring. One material, porous polyethylene HDPE-120, was retained in the dolphins for the 12-wk study. This polymer, and the porous composite Proplast I, remained in the belugas for 8 wk.

However, all metal rods coated with the same materials were rejected within 35 d. Metals alone lasted for even shorter periods. The prototype tags used in the pilot study of free-ranging whales were rejected in 0–44 d in the captive animals.

We anticipated that some of the materials would be rejected. Corroding copper, for example, releases products that impede healing (Williams 1981a). The urethane was of industrial grade and may have released plasticizers and other toxic substances (Peppas 1982). All of the metallic implants were lost, less because of their physical properties than the location in which they were placed. Titanium resists corrosion, as do Inconel, monel, and copel (American Society for Metals 1980), and is used in surgical prostheses that are deeply implanted with no surface exposed (Williams 1981b). In this study, all were rejected within 3 wk, partly because the skin reacts naturally to sequester and expel foreign objects (Daly and Dasse 1983), and partly because the surrounding tissue was weakened by infection with bacteria that were carried into the wound with the implant (Dasse 1984) or deposited there from water bathing the opening. Infection following the 416 stainless steel implant evolved into an abscess. Thus, the corrosion-resistant property of a metal seems to be less important to the permanence of a percutaneous implant in cetaceans than the opening it leaves behind as a gateway for infectious organisms from the sea.

For this reason, we tested porous plastics used in surgical implants, hoping that a coating of such material would effectively serve as a gasket to reduce the wound opening, yet recognizing that bacteria can gain entrance through the same materials (Hall et al. 1975). We also thought that the pores would serve their intended role to attract fibroblasts from the dermis and blubber, eventually bonding the tissue to the implant (von Recum 1984). The experiments were marginally successful. Some of the sites became infected; in others, the plastics such as Proplast II became compressed when introduced and lost their vital porous characteristics. However, the results with HDPE-120 and Proplast I showed the sequence of tissue reactions one might ideally expect when these substances are implanted in odontocete skin.

The HDPE-120 and Proplast I remained in place for 8 wk until the whales were released, and the HDPE-120 implants were still present in the dolphins after 12 wk. By the end of the first week in the dolphins and third week in the whales, fibroblasts began crowding the pores of the implants; these cells were part of a mild inflammatory response. Two weeks later, fibrous tissue was growing into the pores of the implants, and after 5 additional weeks, the fibrous tissue was maturing. Our study ended at this point, so we were unable to determine whether scar tissue ultimately developed, marking the final stage of maturation and the formation of potentially sound anchoring tissue. But the findings were encouraging.

Porous plastics lack the tensile strength required of a tag. That is why we coated them onto metal rods for another series of experiments. The results were discouraging; infection ensued, and the mechanical forces on the rods, great enough to cause bending in some cases, collapsed the pores. All coated rods were rejected within 5 wk.

To determine how a small tag with an exposed streamer might endure, we tested some prototypes in the whales. All of the tags failed for a number of reasons. The bare metal was as poor an anchor as might have been predicted from the reactions to the same materials used as embedded rods. Furthermore, the flange intended to secure the flat head tags bent during insertion through the tough dermis. The cone head tags were more effective, but only extended the retention time by about one week; the tag heads continually shifted in the soft blubber and underlying moving muscle, thereby preventing encapsulation of the head by fibrous tissue. Tag heads with a collar of Gore-Tex were more stable, perhaps due to friction between the collar and surrounding tissues. Bacterial infection inevitably played a role in rejection of these tags, as well. The wire attaching the Tecoflex polyurethane tubing streamers (which endured well) kept the wounds open, thereby promoting infection. Conditions in the wild will undoubtedly influence the biological processes involved with retention of implants, but it is not likely that the tags, as constructed, would be useful for long-

term monitoring studies. However, for tags that need not be permanent, configurations using HDPE-120 or Proplast I may have the edge over other materials.

From these observations, we suggest the following measures to improve the effectiveness of percutaneously implanted tags and other devices. Minimize the diameter of the head, hence the size of the hole for access by bacteria. Embed the head deeply enough and with enough anchors to minimize movement within the tissue. Avoid the use of sharp edges, including wire, that can cut through tissue. Include in the design of the head a series of circular channels for inlaying porous plastic "O" rings (we would choose HPDE-120 or Proplast I) which, when in place, would be flush with the surface of the metal and therefore less apt to be crushed between the anchor and the tissue. Devise a collar that provides a tight seal at the surface of the skin to prevent bacteria from reaching the porous component. Include a slow-release, broad spectrum antibiotic in the implant, and take measures to prevent contamination while embedding the device.

These suggestions are intended to minimize infection and movement in tissue, two principal forces that reduce the life of an implant. The permanence of bolts and other percutaneous devices that anchor electronic packages might also be improved by applicable changes in design (Grosse-Siestrup and Affeld 1984). None of these modifications will with certainty prevent the channel in the skin from delivering the organisms that usually undermine the attachment. That problem should be addressed in the next generation of studies.

Acknowledgments

The studies on captive dolphins were made possible through the cooperation of J. Prescott (Director), G. Early, J. Pearson, P. Fiorelli, J. Boggs and the "Discovery" crew at the New England Aquarium, Boston, MA. Funding for this portion of the study came from the U.S. Department of the Interior, Minerals Management Service contract no. 14-12-0001-29169. We gratefully acknowledge the generous logistic and laboratory support provided by the Department of Fisheries and Oceans (DFO), Winnipeg, Manitoba. We thank R. Moshenko, DFO, for facilitating the field operations, and J.Orr, DFO, for supervising the camp set-up. D. Jacobs, Ministry of Natural Resources, provided helpful advice and assistance in Churchill. J. Hickes and his capture crew demonstrated considerable skill and patience while selecting whales that met our requirements. For their capable assistance in the field and laboratory, we thank K. Baker, J. Batstone, G. Beck, K. Brown, T. Friesen, L. Joe, L. Latta, C. Thomson, and S. Waters. Drs. B. Hicks and N. Palmer helped with interpretation of the histological findings. We are grateful to the following companies for advice, free samples, and goods and services supplied at cost: CarboMedics, Inc., Porex Technologies, Rolyan Medical Products, Thermedics, Inc., USCI International, Vitek, Inc., WFR/Aquaplast Corp., and Wm. Blair Medical Specialties, Ltd. The study was supported in part by a "Whales Beneath the Ice" grant from the World Wildlife Fund Canada.

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Reactions of Belugas, *Delphinapterus leucas*, and Narwhals, *Monodon monoceros*, to Ice-Breaking Ships in the Canadian High Arctic

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FINLEY, K. J., G. W. MILLER, R. A. DAVIS, AND C. R. GREENE. 1990. Reactions of belugas, *Delphinapterus leucas*, and narwhals, *Monodon monoceros*, to ice-breaking ships in the Canadian High Arctic, p. 97–117. *In* T. G. Smith, D. J. St. Aubin, and J. R. Geraci [ed.] Advances in research on the beluga whale, *Delphinapterus leucas*. Can. Bull. Fish. Aquat. Sci. 224.

The responses of belugas and narwhals to ice-breaking ships in the Canadian high Arctic were studied over a 3–yr period. Belugas and narwhals exhibited very different behavioral responses to ship approaches and ice-breaking activity. Typically, belugas moved rapidly along ice edges away from approaching ships whereas narwhals showed no overt panic reaction. Presumed alarm vocalizations of belugas indicated that they were aware of an approaching ship over 80 km away and they showed strong avoidance reactions to ships approaching at distances of 35 – 50 km when received noise levels ranged from 94 to 105 dB re 1 μPa in the 20 – 1 000 Hz band. The "flee" response of the beluga involved large herds undertaking long dives close to or beneath the ice edge; pod integrity broke down and diving appeared asynchronous. Belugas were displaced along ice edges by as much as 80 km; the degree of displacement depended on the proximity of ice edges to coastal areas. Narwhals showed subtle responses to approaching ships; they did not form large herds, their movements were slow or they remained motionless near the ice edge, and they huddled together in pods, often engaging in physical contact. Rather than actually diving, they tended to sink during submergence and dispersed slowly along the ice edge in front of advancing ships. Ship approaches caused narwhals to cease vocalizing temporarily. Narwhals returned to disturbance areas much faster than belugas and resumed normal activities when received noise levels from ice-breaking operations were as high as 120 dB. The responses of both species at unprecedented ranges may be explained in part by the fact that no similar field studies have been conducted in pristine marine environments with industrially-naive populations of marine mammals.

Les réactions des marsouins blancs et des narvals aux navires brise-glaces dans le grand nord de l'Arctique canadien ont été contrôlées sur une période de 3 ans. Les marsouins blancs et les narvals ont exhibé des réaction très différentes de comportement à l'approche des navires et des activités de brise-glaces. Typiquement, les marsouins blancs se sont déplacés rapidement le long du bord des glaces en s'éloignant des navires qui s'approchaient, tandis que les narvals n'ont manifesté aucune réaction évidente de panique. Des vocalisations d'un signal présumé

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d'alarme des marsouins blancs ont démontré qu'ils étaient conscients de l'approche d'un navire à plus de 80 km de distance et laissèrent voir de fortes réactions d'évasion aux navires approchant à des distances de 35–50 km quand l'enregistrement des niveaux de bruit était de 94 à 105 dB rel µPa (20–1 000 Hz). La réaction d'évasion des marsouins blancs impliqua de gros troupeaux s'engageant dans de longues plongées près ou dessous le bord des glaces; l'intégrité du troupeau se rompit et la plongée semblait asynchrone. Les marsouins blancs étaient dispersés le long du bord des glaces allant jusqu'à 80 km des navires; le degré du déplacement était rattaché à la proximité du bord des glaces aux régions côtières. Les narvals ont exhibé des réactions subtiles au rapprochement des navires; ils ne se sont pas regroupés en gros troupeaux; leurs mouvements étaient lents ou ils restèrent immobilisés près du bord des glaces; ils se serraient les uns contre les autres en bandes, résultant à des contacts physiques fréquents. Plutôt que de plonger directement, ils avaient tendance à se laisser câler et se dispersaient tranquillement le long du bord des glaces en avant des navires qui s'approchaient. L'approche de navires provoquait un arrêt temporaire de vocalisation chez les narvals. Les narvals sont retournés plus vite dans les zones de perturbation que les marsouins blancs et ont résumé les activités normales quand l'enregistrement des niveaux de bruits de brise-glaces étaient aussi hauts que 120 dB. Cette réaction sans précédent des deux espèces peut, en partie, être expliquée puisqu'aucune étude similaire en chantier n'a été effectuée dans des environnements marins avec des populations de mammifères marins industriellement-naïves.

Introduction

Ever since the controversial cruise of the ice-breaking tanker *Manhattan* through the Northwest Passage in 1969, there has been concern regarding the effects of increased marine traffic on the people and wildlife of the region. In the past two decades, there have been proposals to ship hydrocarbons in large ice-breaking carriers operating year-round in the passage. The most significant new development in the region is the expansion of the traditional summer shipping season by using reinforced carriers to serve mine sites.

One of the major environmental concerns associated with increased vessel traffic in the arctic is the potential for deleterious effects on marine mammal populations. The effects of excessive underwater noise levels is of particular concern since the acoustical sense of marine mammals is of vital importance in their navigation, communication and feeding. Lancaster Sound, the entrance of the Northwest Passage, is a major migration corridor for several species of marine mammals, including belugas, *Delphinapterus leucas*, narwhals, *Monodon monoceros*, and bowhead whales, *Balaena mysticetus*.

In 1982, Canarctic Shipping Limited announced plans to send the ice-breaking ore carrier MV *Arctic* through Lancaster Sound to the Nanisivik lead–zinc mine situated in Admiralty Inlet, northern Baffin Island. The purpose of this exploratory voyage was to examine the feasibility of increasing the length of the commercial shipping season to the mine by breaking through the fast ice of Admiralty Inlet. The voyage raised concerns among local Inuit hunters who hunt narwhals in spring along the ice edge across the mouth of Admiralty Inlet. The hunters were worried that ship traffic would cause displacement of the narwhals and interfere with their hunt. In response to the concerns of the hunters and to broader concerns about arctic shipping, the present study was initiated in June 1982 to obtain preliminary data on the responses of narwhals and belugas to the Arctic. The study was continued in June of 1983 and 1984 to take advantage of additional probes through Lancaster Sound and Admiralty Inlet by the Arctic and accompanying ice-breakers of the Canadian Coast Guard. This paper is a synthesis of the main findings of the study, the results of which are presented in more detail in a technical report by LGL (1986).

Methods and Materials

The spring distribution of whales in Lancaster Sound is strongly influenced by the extent of fast ice. In "heavy" ice years such as occurred during this study, the fast ice may cover most of the sound with a solid ice edge extending across its entrance. Since the position of the ice edge changed from year to year, the location of study area and procedures also varied.

Our approach was to document the undisturbed behavior and distribution of the whales along ice edges before the arrival of ships in Lancaster Sound. Whale behavior and distribution were monitored during the ships' arrival, during periods when there was ship activity in the area, and during a post-disturbance period. Information was collected by aerial surveys, ice-based observations and underwater recordings.

Study Areas and Protocol

The positions of the ice edge in each year are shown in Fig. 1. Changing circumstances — weather, ice and ship — often necessitated extemporization of the planned study design. The setting and study protocols are reviewed briefly here.

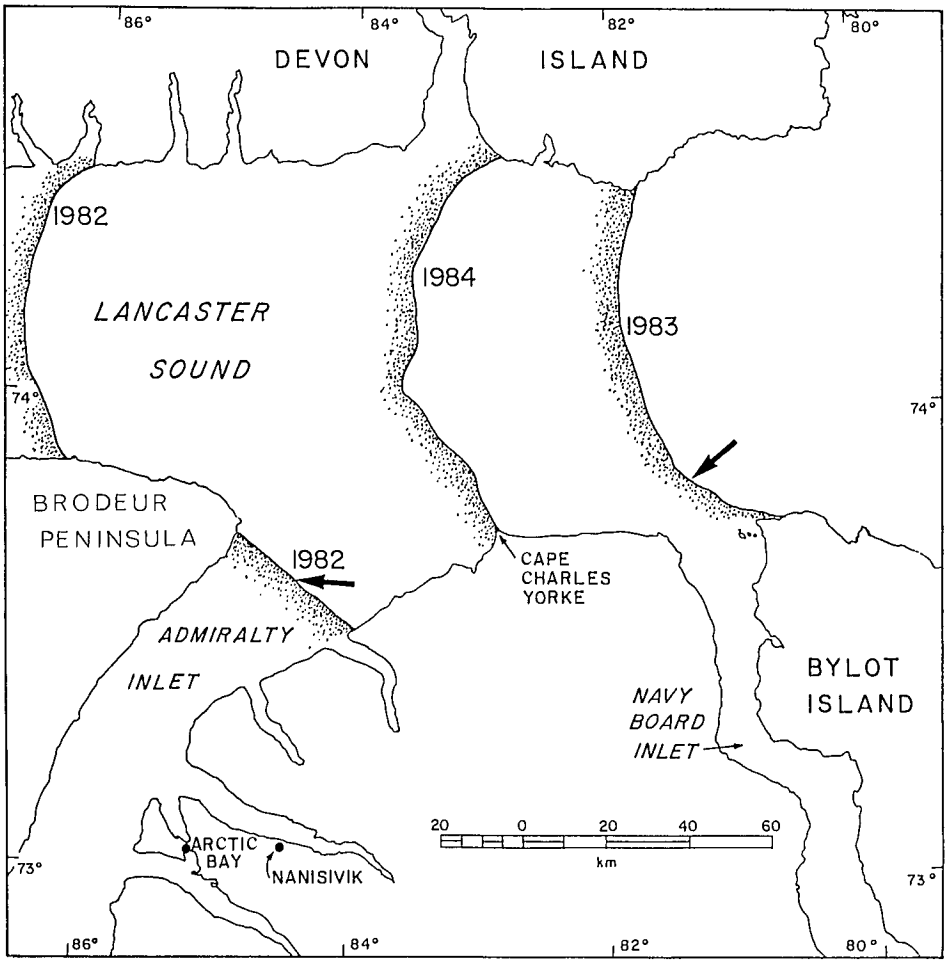

FIG. 1. Locations of the major ice edges in Lancaster Sound during the study periods in 1982–84. Principal ice-based study areas are indicated by arrows.

1982: The ice edge across Lancaster Sound was located west of Admiralty Inlet. Fast ice covered the inlet, creating another ice edge across the mouth of the inlet. The *Arctic* arrived at the Admiralty Inlet ice edge on 28 June. The ice-breaker CCG *John A. MacDonald* remained offshore in Lancaster Sound because the *Arctic* encountered little difficulty in breaking through the fast ice.

The 1982 study was a prototype project organized at short notice; we had only one day to study the pre-disturbance distribution and behavior of the whales. Continuous observations of whale behavior and regular underwater recordings were made from camps along the ice edge during the ship's approach and were continued until after the ship reached Nanisivik mine on 30 June. Helicopter surveys of the ice edge were conducted 22 h before, and 28 and 52 h after, the *Arctic* contacted the ice edge. Survey procedures are described by LGL (1986). For safety reasons, the helicopter could not be flown over open water, and because it was not equipped with an accurate navigation system, it was not possible to determine the positions of whales along the ice edge accurately.

1983: The ice edge was located near the eastern entrance of Lancaster Sound and ice conditions were severe. The *Arctic* arrived at the ice edge on 24 June but had great difficulty penetrating the fast ice. The CCG *John A. MacDonald* arrived 2 d later and broke ice for the *Arctic* into Admiralty Inlet. The ships did not reach Nanisivik until 9 July.

Information on pre-disturbance whale distribution and behavior was obtained on 5 d prior to the arrival of the *Arctic*. Because the ice was so thick, the ships made very slow progress through Lancaster Sound. Thus, levels of underwater noise remained high at the point of entry into the ice edge for the week following the *Arctic*'s arrival. This, coupled with the fact that both ships ceased operations every night, created a series of disturbance periods and quiet intervals during which the behavior and distribution of the whales were monitored. Attempts to monitor post-disturbance behavior and distribution were complicated by the development of major cracks in the Lancaster Sound ice sheet and the beginning of a whale hunt by local Inuit.

Eighteen helicopter surveys of the Lancaster Sound ice edge were flown in 1983. The surveys covered the entire width of the sound plus a small section of the adjacent coast. Some of these surveys were incomplete due to local weather conditions. A snow storm prevented a survey on the day that the *Arctic* arrived.

1984: The Lancaster Sound ice edge was again located east of Admiralty Inlet about 60 km west of the 1983 position. The *Arctic* arrived at the ice edge on 28 June accompanied by the ice-breaker CCG *Louis St. Laurent*. The ice-breaker accompanied the ore carrier into the ice but the *Arctic* was able to break its own track into Nanisivik mine.

The 1984 study consisted of aerial surveys by fixed-wing aircraft equipped with a GNS-500 navigation system to provide better coverage of the distributional responses of belugas and narwhals to ships. Seven surveys were flown: the first was on the day before the ships arrived; four surveys were flown when levels of ship activity were high at the ice edge; and the final two surveys were flown after the ships had moved west into the ice but were probably still audible to whales at the ice edge. The survey procedures are described by LGL (1986).

Ice-Based Observations and Underwater Recordings

Observations of whale behavior and numbers were conducted from ice-edge camps in 1982 and 1983. We recorded species and numbers of marine mammals, their general activity, direction of movement, distance from ice edge, and sex and relative age.

Hydrophones were deployed at the ice-edge camps to record ambient noise levels in the water, animal calls, and ship noise. Ten-minute underwater recordings were obtained every 2 h when ships were absent and usually continuously when the ships were operating nearby. A total of 4 h of underwater recordings was obtained in 1982 and 45 h in 1983.

Hydrophones were deployed at two depths, 3 and 20 m, so that any depth-related differences in the received sounds could be measured. We used U.S. Navy model H56 standard reference hydrophones, which are wideband (to 50 kHz), low-noise hydrophones with built-in preamplifiers. We also used low-noise bender hydrophones sensitive at frequencies below 2 kHz. Each hydrophone had a post-amplifier with selectable gain (in 10 dB steps) up to 60 dB. Two types of tape recorders were used. The simplest was a Sony model TC - D5M two-channel cassette recorder with a calibrated response of 10 to 16 000 Hz. Most recordings were made with a four-channel Fostex model 250 cassette recorder with a frequency response of 10 Hz to 32 000 Hz.

Analyses of Ambient and Ship Sounds

Analysis of ambient and ship sounds was based on the use of a Hewlett-Packard model 9816 computer with an analog-to-digital converter. Several programs were used to analyze the data. Power spectral density estimation was based on computing discrete Fourier transforms.

For convenience and consistency, received noise levels in this paper are presented in terms of dB re 1μPa in the 20 – 1 000 Hz band at a depth of 20 m, unless specified otherwise. Most of the sound energy of ships occurs below 1 kHz; noise levels in higher frequency bands tend to have a stable and predictable relationship to the level in the 20 – 1 000 Hz band. Hence, the level in this lower frequency band is a useful index to higher frequency ship noises. Most of the communication signals of belugas and narwhals occur between 500 – 5 000 Hz (Ford and Fisher 1978; Sjare and Smith 1986a).

Analyses of Whale Vocalizations

The basic vocal repertoire of the narwhal has been described by Watkins et al. (1971) and Ford and Fisher (1978). Narwhals emit primarily two types of sounds in the frequency range audible to the human ear: clicks and pulsed-tone calls. *Clicks* are relatively narrow-band pulses of constant frequency generated in series at regular, slow (mostly < 10 s) repetition rates with most audible energy in the 3–7 kHz band. *Pulsed-tone calls* are rapidly-pulsed emissions ranging from slower ratchet-like growls to higher-pitched creaking sounds, generated primarily at frequencies from 0.5 - 6.5 kHz. Narwhals occasionally emit tonal sounds (whistles) with changing pitch.

The basis vocal repertoire of the beluga in the high Arctic has been described by Sjare and Smith (1986a). Tonal sounds are the predominant vocalizations and exhibit a complex array of characteristics. Less frequently, belugas emit pulsed-tone calls including higher-frequency screams and buzzy sounds to lower-frequency squawks, barks and blaring sounds.

Both narwhals and belugas produce broad-band clicking sounds for echolocation purposes; much of the energy of these signals occurred at frequencies beyond the recording sensitivity of our equipment and were not considered in this study.

In June, the underwater environment at ice edges in Lancaster Sound is usually saturated with the vocalizations of narwhals, belugas and bearded seals (*Erignathus barbatus*). Because both whale species were often present at the same time during this study, vocalizations were often intermixed on recordings. After listening to some recordings on which only one species was present, it was possible to "predict" from all recordings which species was present and to roughly gauge its proximity to the recording station.

In 1983, predictions of absence or presence of narwhals and belugas were tested for accuracy by comparison with independent observations of the ice-based observers. In 86 recording sessions obtained when synchronized ice-based observations were obtained, we correctly "predicted" which species was present in the immediate area 96% of the time. In five cases, belugas (2 cases) or narwhals (3), were audible on the tape but the observers did not see any animals nearby. However, in each of these cases the species in question was seen

in the area during recording sessions immediately preceding or following. Incorrect predictions of absence occurred on two occasions when narwhals were present but apparently silent.

Detailed analysis of whale vocalizations was conducted on the recordings obtained in 1983. Taped 30-s segments were randomly selected for spectral analyses from 10-min recording sessions with adequate signal: noise ratios. In some sessions where ship noise predominated, it was necessary to select quieter moments when the ship shifted between ramming and backing modes. The selected segments were analyzed using a Spectra Color real-time spectrum analyzer for the frequency bandwidths of 60 – 6000 Hz and 60 – 12000 Hz. Vocal activity was evaluated from 77 30-s spectrographic segments; 24 of these came from the pre-disturbance period, 33 from disturbance periods, and 20 from intervening quiet intervals. Attempts to quantify the level of vocal activity were difficult. For example, it was seldom possible to distinguish individual click series from the general "clatter" when narwhals were present, but pulsed tones tended to be distinctive, allowing enumeration. Belugas often created a cacophony that was difficult to decipher. Overlapping signals could usually be separated on the basis of relative intensity and close attention to the real-time spectral display but it was often impossible to discern how many components constituted a single call. At close quarters, belugas usually produced a bewildering array of sounds that we did not attempt to quantify.

Results

Ship and Ambient Noise Levels

The *Arctic* is an ice-breaking ore carrier of about 20 000 deadweight tonnes and is 209 m long with a draft of 11 m. The ship is powered by a single diesel engine producing 14, 770 HP on a single shaft with a variable pitch propeller. The *John A. MacDonald* is a Canadian Coastguard ice-breaker of about 3 685 deadweight tonnes and is 96 m long with a draft of 8.6 m. The ship is powered by nine diesel electric engines producing 15 000 HP on three propellers.

Figure 2 shows the received noise levels of the two ships at various ranges from the Lancaster Sound ice edge during their approaches and subsequent ice-breaking operations in 1983. The *Arctic* was first detectable by a tonal peak at 105 Hz on noise spectrographs when the ship was at a range of about 130 km. This tone was probably the second harmonic of the major 53 Hz tone that became evident as the ship approached closer. The fundamental tone

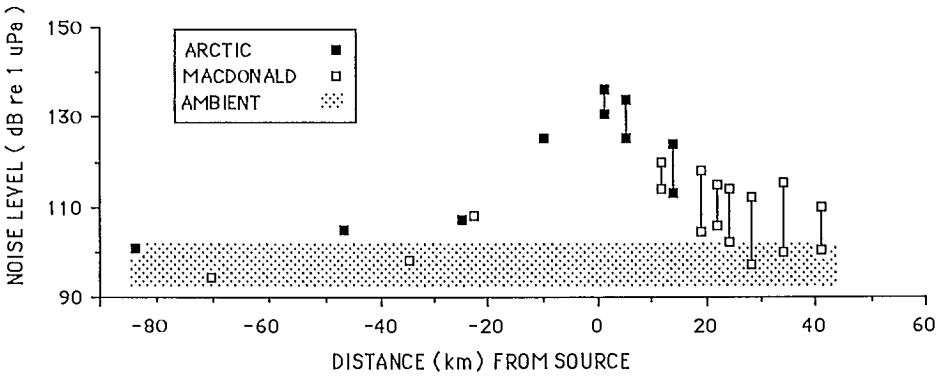

FIG. 2. Received noise levels (20–1 000 Hz band) at various ranges during the approach of the MV *Arctic* and the CCG *John A. MacDonald* to the Lancaster Sound ice edge and during ice-breaking operations in 1983. Vertical lines show the maximum noise levels during backing and minimum levels during ramming. The typical range of ambient noise at the ice edge is shown.

was related to the cylinder firing rate of the *Arctic*. The ship was distinctly, though faintly, audible to the human ear by listening to the hydrophone signal when it was at a range of 85 km and the 20 – 1 000 Hz band level was 101 dB. At a range of 47 km the noise level was 105 dB. At its closest point of approach (672 m) during ice-breaking operations, the noise levels from the *Arctic* reached 136 dB. Noise levels of both ships during backing were usually 10–15 dB higher than during ramming. Ship noise during ramming often merged with background noise at ranges > 25 km but was intermittently strong during backing operations at ranges > 45 km.

In 1982 the approach of the *Arctic* to the Admiralty Inlet ice edge was first indicated in the noise spectra by a tonal peak at 205 Hz. This tone and another at 53 Hz became more prominent as the *Arctic* approached closer. The ship was plainly audible (noise level 94 dB) on the hydrophone signal as it worked its way through a small pack ice field at a range of about 46 km.

Source levels for the *Arctic* during ice-breaking operations were estimated from recordings obtained in 1982 when the closest distance between the ship and the hydrophone was 463 m. Maximum received noise levels at a depth of 20 m during backing attained 138 dB in the 10–1 000 Hz band. Estimated source levels, assuming spherical spreading, in the backing-up mode (191 dB re 1 μPa at 1 m) were consistently higher than in the ramming mode (184 dB). Prominent tones occurred at 53, 106 and 205 Hz during ramming; the first two were associated with the cylinder firing rate of the diesel engine (the fundamental and second harmonic) and the latter, to the bubbler system that functions to reduce friction between the ship's hull and sea ice. Cavitation noise dominated the sound spectra during backing operations. Noise levels at a depth of 3 m averaged 12 dB lower than at 20 m due to the Lloyd Mirror Effect.

Ambient noise levels at the Lancaster Sound ice edge in 1983 ranged from 93 to 104 dB re 1 μPa in the 20–1 000 Hz band at a depth of 20 m. Noise levels at 3 m depth averaged 9 dB lower. Noise levels at the Lancaster Sound ice edge were higher than at the Admiralty Inlet ice edge in 1982 (85–92 dB) due to higher sea states and more animal calls. Figure 2 shows the typical range of ambient noise levels at the Lancaster Sound ice edge. The quietest periods occurred after the ships had arrived at the ice edge and displaced the belugas and narwhals from around the recording station.

Normal Distribution Patterns of Belugas and Narwhals

The chronology of spring migration of whales in Lancaster Sound is dictated by ice conditions, particularly the position of the fast ice edge. When the whales arrive in June and early July, coastal areas are still bound in fast ice and, in some years, Lancaster Sound may be covered by fast ice. The position of the ice edge tends to be stable in any one season but it is highly variable from year to year; most often it occurs west of northern Baffin Island. The present study was conducted during a period when the ice edge was located close to the entrance of Lancaster Sound, unusually far east of its normal position (Fig. 1). The presence of this ice barrier caused high concentrations of whales. Figures 3 and 5 show the typical distribution patterns of belugas and narwhals along the Lancaster Sound ice edge.

In normal ice years, when Lancaster Sound is not covered by fast ice, the peak beluga migration occurs in late June and early July, and the whales closely follow the north shore of the sound toward their summering grounds in the central archipelago (LGL 1983). In ice-barrier years, many belugas congregate along the ice edge. They distribute themselves more or less evenly along the ice edge, although they tend to concentrate along the coast of Devon Island (Fig. 3, 5). In offshore areas, belugas remain close to the ice edge and their movements are usually parallel to it; they appear to be waiting for breakup and their movements tend to be causal and exploratory. Herd movements are often coordinated in one direction over a large area. The belugas along the ice edge in June tend to be predominantly adults, often occurring in distinctive all-white pods, believed to consist of males.

Unlike belugas, which follow coastal routes or ice edges during spring migration, narwhals are more pelagic in habit, arriving in a broad-front migration through the pack ice of northern Baffin Bay (Davis et al. 1978). Although some narwhals move west through Lancaster Sound as ice conditions permit, the major summering grounds of the narwhal are in the fiord complexes of northern Baffin Island, particularly Admiralty Inlet. Thus, the existence of an ice edge across the sound does not constitute such a barrier to migration as it does for belugas. In mid to late June small numbers of narwhals, primarily adult males, occur along ice edges — particularly in the southern half of the Sound adjacent to their summering areas (Fig. 3, 5) Most of the narwhals remain widely distributed in the offshore pack ice of Baffin Bay until the fast ice begins to disintegrate.

Thus, in most years there is relatively little intermingling of narwhals and belugas because their migration routes are segregated — belugas keeping mainly to the north shore of the sound and the narwhals keeping to the south side and offshore. During the three years of this study both species intermingled along the ice edge. This provided an unusual opportunity to compare their responses to ships in the same environmental setting.

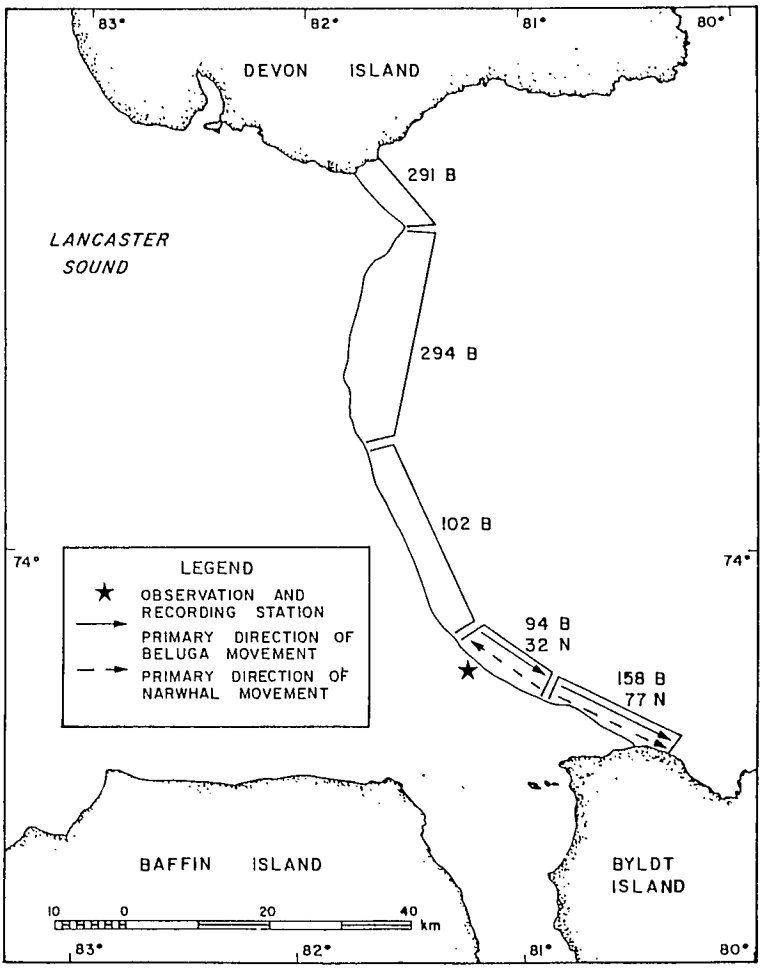

FIG. 3. Normal distribution pattern of belugas (B) and narwhals (N) along the Lancaster Sound ice edge, 23 June 1983.

Whale Responses in 1982

A total of 42 narwhals and 18 belugas were observed during an aerial survey along the Admiralty Inlet ice edge on 27 June prior to the arrival of the *Arctic*. Underwater recordings obtained from the center of the ice edge were saturated with calls of both species although none were seen within 3 km of the recording station. Whale calls still dominated the ambient noise at 12:15 on 28 June but a small peak in the noise spectra at 205 Hz indicated the presence of the *Arctic* at about 105 km. At 14:31 the ship was 46 km from the ice edge and the noise level was 94 dB. At this time, tonal calls of belugas dominated the higher frequencies. However, between 14:40 and 14:50, the type of calls changed noticeably: more distinctive pulsive calls were emitted. These calls occurred just prior to a notable movement of belugas at the ice edge and the calls were tentatively attributed to them. Although the ice-edge observers had not seen any whales until this time, at 15:00 many belugas were seen moving rapidly westward along the ice edge. Approximately 200–300 whales passed between 15:00 and 16:25, most of them in the first 15 min. The belugas closely followed the ice edge, often diving under the ice. Their swimming behavior appeared abnormal; they rose unusually high out of the water and the surface-dive cycle of individuals appeared to lack synchrony with other whales in the same pod. After 16:25, the movements of a few belugas along the ice edge became erratic and turned eastward, apparently "cut off" from the major westward movement. At this time the ship was about 13 km to the north of the ice edge and approaching rapidly.

Small numbers of narwhals were observed at the ice edge from 16:34 until after the ship struck the ice at 17:14. Their behavior was notably different than that of the belugas. Their movements were slow and they frequently rested motionless close to the ice edge. In contrast to the rapid forward-rolling dives of the belugas, narwhals tended to sink quietly beneath the surface with little audible respiratory sound. Pods of narwhals appeared more cohesive than those of belugas, and individuals in pods were seen contacting each other with their tusks or flippers. Narwhals were seen within 5 km of the ship at 17:49 when it was breaking ice.

Whales and whale sounds were absent from the Admiralty Inlet ice edge throughout 29 June as the *Arctic* continued to break ice 10–26 km from the ice edge. An aerial survey of the ice edge late in the day found no whales, although 1 072 belugas and 118 narwhals were observed along the north coast of the Brodeur Peninsula and a short section of the Lancaster Sound ice edge. Some belugas were moving back toward Admiralty Inlet at 23:00, and by noon on 30 June a mixed herd of 200 belugas and narwhals was observed in a "feeding frenzy" at the centre of the ice edge. The *Arctic* was about 48 km from the ice edge at this time. Ship noise was intermittently audible to the human ear on hydrophones (102 dB). Thus within 43 h of the arrival of the *Arctic*, both narwhals and belugas had resumed apparently normal activities along the ice edge although the ship was still audible.

Whale Responses in 1983

Although we were unable to conduct strictly controlled disturbance experiments in 1983, ship activity occurred on an intermittent basis, permitting observations of the reactions of narwhals and belugas to ship sounds during discrete intervals following quiet periods. Seven disturbance periods were recognized, varying in intensity from ship approaches to the ice edge to subsequent start-ups and ice-breaking operations as the ships moved over 40 km into the fast ice away from the ice edge.

Pre-Disturbance Conditions

Aerial surveys were conducted on five days prior to the arrival of the *Arctic* at the Lancaster Sound ice edge in late June. Belugas were widely distributed along the ice edge with a

maximum count of 939 on 23 June (Fig. 3). Narwhals were consistently found along the southern third of the ice edge where a maximum of 115 was counted on 21 June. Typically both species were associated strongly with the ice edge; the majority occurred within 400 m of the edge and their movements were generally parallel with it. Over 90% of the narwhals were adult males and 61% of the belugas were thought to be males (i.e., either in distinctive all-white "bachelor" pods or adults not accompanied by immatures).

Ice-based observers recorded movements of belugas and narwhals throughout a 45 h period prior to the arrival of the *Arctic*. During this period, movements were back and forth: 108 narwhals passed north and 117 passed south; 241 belugas moved north and 299 south. Underwater recordings during the pre-disturbance period were saturated with vocalizations of both species along with the calls of bearded seals.

Reactions of Whales to Ship Approaches

At 02:00 on 24 June, the *Arctic* was in northwest Baffin Bay about 250 km from the ice-edge recording station in Lancaster Sound. It was not a factor in the ambient noise which was dominated by water and ice noise, and bearded seal calls. The earliest indication of the presence of the ship was at 06:00 when the Arctic was 132 km away and a weak tone at 105 Hz was present in the noise spectra.

The first evident changes in whale behavior were noted at 08:00 when the ship was 84 km from the ice edge. Although no whales were seen in the immediate vicinity of the recording station, several distinctive vocalizations, identical to those heard at 14:40 on 28 June 1982, were heard. At this time, the *Arctic* was faintly audible on recordings although the noise level (101 dB) was within the range of ambient noise levels during the pre-disturbance period.

Between 09:35 and 10:22 when the *Arctic* was 55 – 40 km to the northeast, 44 belugas moved rapidly north past the observation site along the ice edge, showing the same "flight" reaction as in the previous year. During this period many harsh pulsive calls, presumed to be beluga calls, were heard. Small groups of adult narwhals were observed during this period and their behavior, as in the previous years, was notably different from that of the belugas: the narwhals exhibited a "freeze" response to the oncoming ship. The observers were unaware of the proximity of the *Arctic* which was not expected until later in the day. The *Arctic* entered the ice edge at 12:20 about 4 km south of the observation site but visibility was limited to <1 km in a heavy snowfall.

Because of poor weather and unstable ice, we were unable to determine how far the whales were displaced or when they returned to the disturbance area. The *Arctic* continued breaking ice until 09:07 on 25 June without making much progress. An aerial survey, conducted 2 h after the ship shut down less than 10 km into the ice, showed that narwhals had already returned and, in fact, were concentrated in the bight at the ship's entry point. Belugas were just arriving in the area from the north along the ice edge.

The *Arctic* remained idle in the ice until 07:56 on 26 June when it began ice-breaking. Noise levels at the ice edge reached 124 dB. The reaction of belugas to the ship's start-up was dramatic: over 225 belugas passed the ice-edge observer in 9 min, all showing a typical "flee" response. A few narwhals that were present in the area exhibited a "freeze" response and eventually disappeared. Strong ship noise masked many of the whale sounds but several distinctive pulsed calls were heard during brief lulls between ramming and backing modes of the ship.

An aerial survey beginning 1.5 h after the ship started up showed that belugas had been displaced 49 km north along the ice edge and were still moving rapidly away from the ship (Fig. 4). About 1 100 northbound belugas were counted but this figure is imprecise because the whales were tightly clumped and many were undertaking long dives beneath the ice edge. Narwhals had also been displaced; none remained within 18 km north of the ship track. Narwhals and belugas that departed south of the ship track had ceased travelling when they

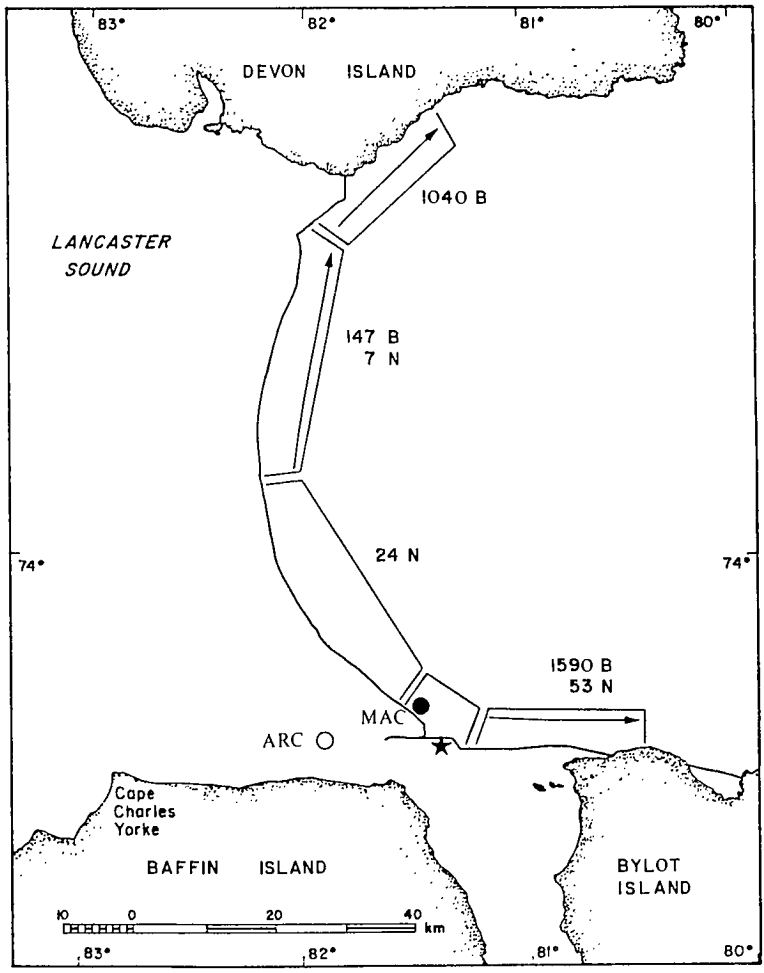

FIG. 4. Distribution and movements of belugas and narwhals following the arrival of the CCG *John A. MacDonald* (MAC) on 26 June 1983. The position of the MV *Arctic* (ARC) is also shown.

reached the coast of Bylot Island, 20 km away, and many were milling at the ice – land interface. Undoubtedly the whales first responded to the start-up of the *Arctic* but, by the time of the survey, they may also have been influenced by the approach of the *MacDonald*. The *MacDonald* arrived at the ice edge at 13:30 and proceeded to assist the *Arctic* which had shut down after being unable to make headway.

An aerial survey beginning 1 h after the arrival of the *MacDonald* showed that belugas had continued their rapid northward movement along the ice edge and were over 80 km from the ship track near the coast of Devon Island. The closest narwhals were 37 km north of the ship track and it was apparent, from reduced numbers, that some had dispersed offshore. Large numbers (1 590) of belugas remained milling at the land-ice interface on the south side of the ship track.

After their departure, belugas were not seen or heard at the observation site as the *MacDonald* continued breaking ice throughout the day. However, narwhals returned to the ship track by 19:30 when the ship was operating at a distance of 15 km. Received noise levels

at 20:00 were 120 dB and, during quieter intervals, a few narwhal click series were audible. At 21:00, the maximum received noise level was 118 dB when the ship was 19 km away; narwhal click "clatter" was strong in the quieter intervals.

Reactions of Whales to Intermittent Ice-breaking Operations of Diminishing Intensity

From 27 June to 1 July, the *MacDonald* and the *Arctic* progressed slowly westward through the fast ice, averaging just over 4 km per day. The *Arctic* operated intermittently, following the track created by the *MacDonald.* Although noise levels diminished, they were not insignificant; received levels at the ice edge reached 115 dB during backing operations on 1 July when the *MacDonald* was about 40 km from the edge.

Except for one instance on 29 June when *MacDonald* returned to within 18 km of the ice edge to assist the *Arctic*, we did not discern any notable influence of ship start-ups or operations on the behavior of narwhals. On this occasion the maximum noise level, with both ships operating, reached 121 dB, and although the narwhals left the area near the ship track they returned 8 h later when both ships had returned westward (noise levels 111 dB). In fact, following the arrival of the ships at the ice edge on 25 and 26 June, narwhals appeared to be attracted to the rubble-filled ship track, and many engaged in dives directed toward the track, possibly exploring for a westward passage. This "exploratory" activity appeared to wane following their initial interest; fewer narwhals appeared sporadically around the track. On 30 June, most of the narwhals had moved to a feeding area along the Navy Board Inlet ice edge. Belugas and narwhals, along with many harp seals (*Phoca groenlandica*), remained in a large feeding aggregation at this location until 2 July.

Belugas continued to react as the ships slowly progressed away from the ice edge. Although aerial survey coverage was incomplete after 27 June, due to poor weather, belugas appeared to avoid the southern part of the Lancaster Sound ice edge until 2 July. Belugas reacted by emitting distinctive pulsive calls during most ship start-ups, and at other times during ice-breaking operations their vocal activity suggested a heightened level of excitement.

Whale Responses in 1984

An aerial survey on 27 June, the day before the ships arrived, documented normal patterns of whale distribution (Fig. 5). Belugas were distributed more or less evenly along the length of the ice edge and narwhals were distributed along the southern half of the ice edge. Both species were widely distributed in small numbers on the offshore transects.

Major changes in whale distribution had occurred when the next survey was conducted at 08:00 on 28 June, 2 h after the Arctic arrived at the ice edge (Fig. 6). The CCG *Louis St. Laurent* was approaching the ice edge; it arrived at 09:00. Virtually all the whales had vacated the offshore waters in a large zone around the vessels. No belugas and only four narwhals were found along a 27 km stretch of the ice edge centered in the position of the *Arctic*.Belugas and narwhals 20 – 80 km north of the ships were moving rapidly north along the ice edge. Whales over 80 km north of the ships were milling or resting, apparently not reacting to the ships.

By 16:00 on 28 June, 9 h after the arrival of the *St. Laurent*, whales had begun to return toward the area. The ships had been drifting since their arrival with their main engines off but some shipboard machinery was operating. Narwhals had advanced substantially farther south than had belugas but both species were moving south toward the ships.

During the night, the two ships moved into the ice a short distance and again stopped. An aerial survey on the morning of 29 June showed that narwhals had re-occupied the ice edge near the ships. However, the distribution of belugas along the ice edge was still affected by the ships; most remained > 10 km north of the ships. The offshore distribution of both species had returned to pre-disturbance patterns.

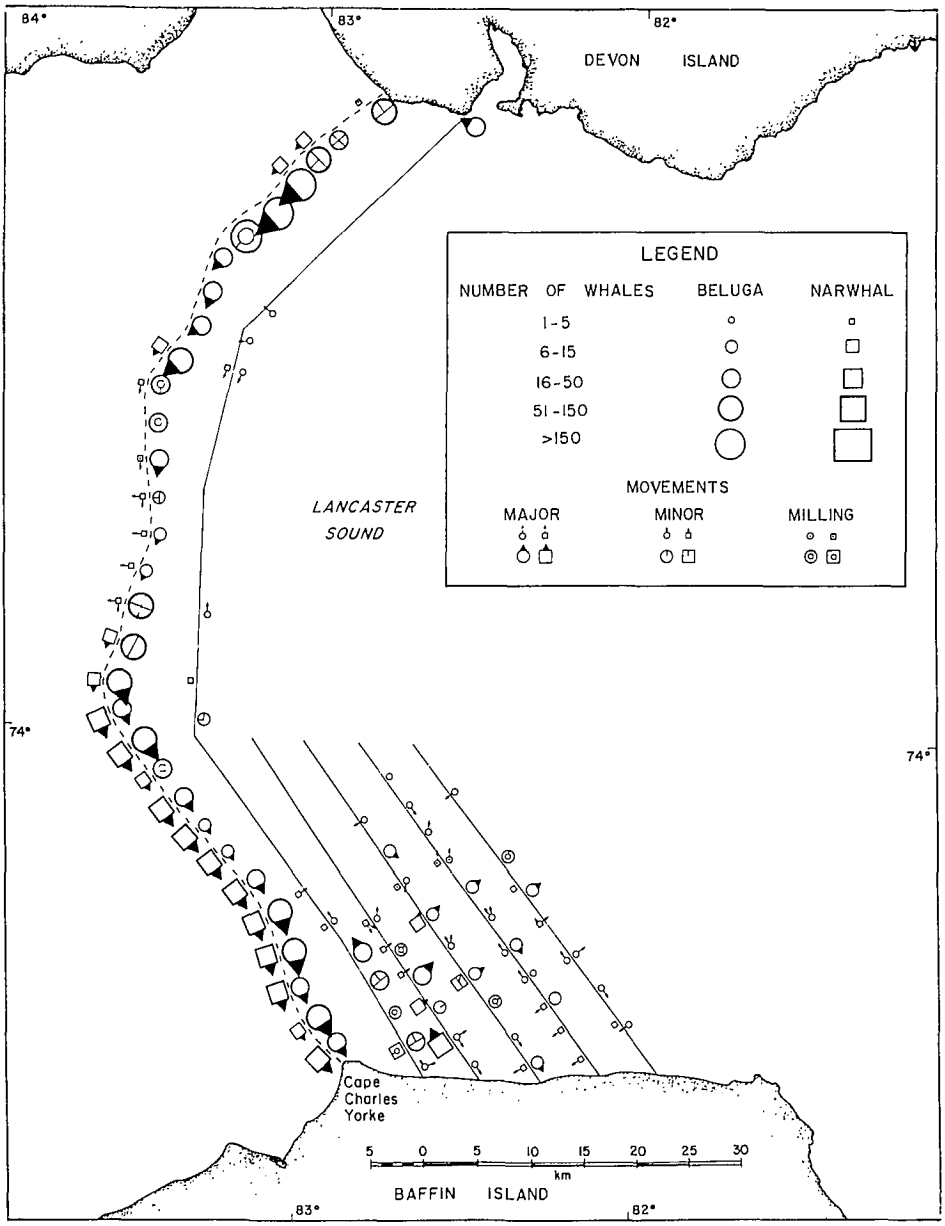

FIG. 5. Normal distribution patterns and movements of belugas and narwhals before the arrival of ships, 27 June 1984. Symbols indicate the number of whales observed in each 1–min period. "Major" movements were indicated when > 75% of the whales observed in a time period were moving in a given direction, "minor" movements indicated 25–75% of the whales. When > 50% of the whales were not showing directed movement, the whales were considered to be "milling."

In the early evening of 29 June, both ships started up and moved south along the ice edge, then turned west into the ice, beginning ice-breaking operations. We were surveying the easternmost transect line (20 – 25 km from the ice edge) when the ships started moving. The reactions of the whales were immediate and striking. Virtually all whales began moving away very rapidly, exhibiting porpoising behaviour and spending little time underwater. Belugas

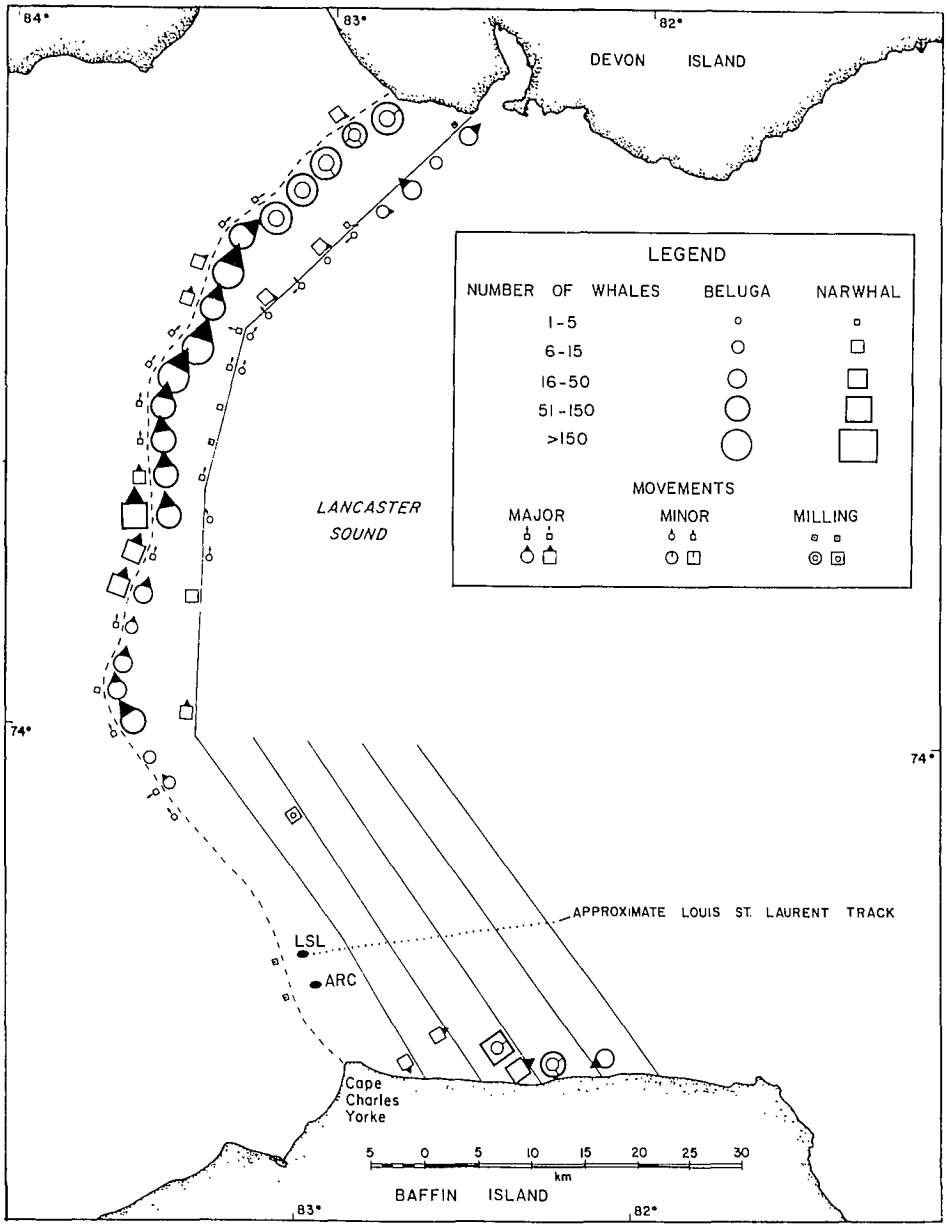

FIG. 6. Distribution and movements of belugas and narwhals following the arrival of the MV *Arctic* (ARC) and CCG *Louis St. Laurent* (LSL) on 28 June 1984 (08:00–10:00).

were moving faster than narwhals but even the latter species was moving faster than previously observed. When we surveyed the ice edge an hour later, narwhals and belugas were moving quickly north away from the ships at distances > 20 km, nearly all the way to the Devon Island coast 80 km away. South of the advancing ships, narwhals were moving rapidly toward the coast of Bylot Island.

Documentation of a return to normal conditions was hindered by fog on 30 June and was complicated by the appearance of cracks in the fast ice on 1 July. The cracks caused many

whales to move into the ice away from the ice edge. Nevertheless, it was apparent that 45 h after the ships had started up, beluga distribution along the ice edge and offshore had not returned to normal. The ships were 45 – 50 km into the ice at this time. The ship noise reaching the ice edge was unmeasured but no doubt rather weak. Beluga distribution was close to normal 16 h later on the morning of 2 July. The distribution of narwhals on 1 July appeared to be fairly normal, but so few whales were present that the situation was difficult to evaluate.

Influence of Ships on Whale Vocalizations

In June, the underwater environment at ice edges in Lancaster Sound is usually saturated with the vocalizations of narwhals, belugas and bearded seals. The presence of narwhals is evident by their click "clatter" and pulsed calls, of belugas by their bird-like whistles and trills, and of bearded seals by their long, descending trills.

Table 1 shows the frequency of different call types of the beluga during undisturbed situations and during periods when ships were operating at the Lancaster Sound ice edge in 1983. This repertoire is similar to that recorded at Cunningham Inlet (Sjare and Smith 1986a) and corresponding call types are cross-referenced where possible in the table. Tonal calls accounted for the majority of vocalizations during undisturbed periods (96% of all calls) and during periods when ships were operating (84%). Most notable was the increase in the occurrence of pulsed tone calls, descending tonals and chirp trains during disturbance periods. Pulsed tone calls and descending tonals were most obvious during initial stages of disturbance whereas chirp trains were heard during later disturbance periods. Also notable was the decrease in the occurrence of rising and stepped tonals during disturbance periods. In addition to changes in call types in response to disturbance, belugas also appeared to alter the frequency emphasis or duration of some of their signals. During disturbance periods,

TABLE 1. Frequency of occurrence of various beluga vocalizations during the presence and absence of ship ice-breaking noise at the Lancaster Sound ice edge, 1983.

	% Occurrence		% Composition	
Call Type	in quiet periods (n = 31)	in noisy periods (n = 26)	in quiet periods (n = 313)	in noisy periods (n = 352)
Tonal				
constant (1a)[a]	68	62	21	12
broken (1b)	48	50	12	15
stepped (3a)	52	19	11	1
falling (4a)	19	46	5	13
rising (2a)	32	23	10	3
undulating regular (6a)	26	31	6	5
undulating irregular (6b)	23	54	7	9
chirp	32	31	11	7
yelp	16	35	4	5
chirp train (7)	23	69	4	13
up trills	13	4	6	2
Pulsed tones				
buzz (Grp 1d)	10	31	4	6
tonal scream (Grp 1a)	0	23	0	7
noisy scream (Grp 3i)	0	12	0	3

[a] Number in parentheses refers to designation by Sjare and Smith 1986a.

undulating tonals began at lower frequencies (2.5 kHz ± SD 1.0 vs 5.0 ± 2.9, $n = 16, 16$; $P < 0.01$) and covered a wider frequency range than during quiet periods. Generally, the durations of many tonal signals increased during ship disturbance (0.9 s ± SD 0.6 vs 0.7 ± 0.5, $n = 254, 235$; $P < 0.01$). These quantifiable changes in frequency range and duration, along with distinctive call types, gave a distinct aural impression of alarm or excitedness among belugas in situations of disturbance.

Except for three occasions on which narwhals temporarily ceased producing click emissions and pulsed-tone calls during initial phases of disturbance (ship approach and start-ups), there was no evidence that they changed the type or structure of their signals in response to ship noise. Pulsed-tone calls accompanied click "clatter" in 68% of 25 spectrographic segments during disturbance periods, 80% of 20 segments in the pre-disturbance period, and 71% of 14 segments in intervening quiet periods. The mean number of pulsed calls per 30-s segment was similar in disturbance periods (5.2 ± SD 5.8), predisturbance periods (3.8 ± SD 3.9) and quiet intervals (4.2 ± SD 4.0). There was no evidence of any change in the median frequency or duration of pulsed calls in response to ship noise. Similarly, there was no evidence that ship noise influenced click emissions.

Discussion

Responses of Whales to Ships

The results from this study demonstrate that narwhals and especially belugas, in the high Arctic, are extraordinarily sensitive to shipping activity in the spring. However, the two species responded in surprisingly different ways, considering their supposed relatedness. We refer to these different behaviors as the "flee" response of the beluga and the "freeze" response of the narwhal. The following behaviors constitute the general observable or audible responses of belugas and narwhals to vessels:

Belugas	Narwhals
— rapid movement	slow movement or motionless
— herd formation, loss of pod integrity	no herd formation; pod cohesion, body contact
— asynchronous, shallow dives	sinking submergence
— pagophilic, littoral	pagophilic, pelagic
— "alarm" calls	silent

The Inuit recognize these combinations of behavioral traits as "ardlingayuk" — fear of killer whales. The primary fear/avoidance responses of these species have probably evolved in response to predation by killer whales (*Orcinus orca*). The killer whale is probably the only significant natural predator of belugas and narwhals in the high Arctic. It may be reasonable to view the responses of belugas and narwhals to potentially threatening situations, such as ships, from this perspective. The narwhal's strategy seems to be to remain inconspicuous — visibly and audibly, whereas the beluga's strategy is to flock and flee.

In the particular offshore setting of this study, belugas showed much stronger apparent reactions to ship disturbances than did narwhals. The beluga tends to be more of a shallow water species than is the narwhal (at least in summer). The stronger reactions of belugas to ship traffic may be indicative of their sense of vulnerability in an offshore situation. It is interesting that the degree of displacement of belugas by ships appeared to depend on the

proximity of coastal waters and ice cover; animals on the side of the ship closest to shore stopped travelling when they reached the shore – ice edge interface (e.g., 18 km in 1983), whereas those on the offshore side of the ship continued to travel (as much as 80 km) until they reached the opposite shore. Although narwhals initially sought cover along the ice edge during the approaches of ships, they later tended to disperse offshore, perhaps toward pack ice fields in Baffin Bay, their habitat for much of the year. The widespread displacement of narwhals observed in offshore Lancaster Sound in response to ship approaches in 1984 may have been due to lack of adequate pack ice cover. During most of the year, narwhals and belugas inhabit areas of dense ice cover (Finley et al. 1982; LGL 1983). Ice edges provide only limited potential for protective cover as compared to pack ice, which killer whales tend to avoid.

The major displacement of belugas from the Lancaster Sound ice edge may also have been due, in part, to their lack of a vested interest in remaining in the area. The ice edge acts as a barrier to belugas and their activities in such ice-barrier years might best be described as "passing time"— waiting for the ice to breakup so they can proceed to traditional summering areas in the central arctic archipelago. Their normal movements along the ice edge appear casual and exploratory. There is no evidence that ice edges constitute significant feeding habitat for belugas, so they may have no vested interest in remaining in an area when a ship approaches. Later in the summer, in their traditional estuarine habitat, belugas often show persistence in using certain estuaries in spite of vessel traffic, suggesting that they have a vested interest in remaining in specific areas (Finley et al. 1982, 1987). Belugas may then tolerate excessive noise because there are no alternative areas that meet their ecological requirements.

The long-range responses shown by both species to the approach of the *Arctic* in 1982 and 1983 are unprecedented in the marine mammal literature. This may be largely explained by the fact that no similar field studies have been conducted in pristine marine environments with industrially naive populations of marine mammals. High Arctic populations of whales may be especially naive because they are exposed to very low levels of shipping activity; their responses may be exaggerated relative to populations that are exposed to more frequent ship traffic. Also, it is generally agreed that marine mammals are more likely to show strong avoidance reactions to vessels if there are sudden changes in course, speed and noise levels (see review by Richardson et al. 1989). The relatively rapid approach of the ships to the ice edge and the sudden start-ups and variable noise levels associated with ramming and backing modes of the ice-breakers may have evoked stronger reactions than if the noise source had been constant. Belugas and narwhals returned to the disturbance area when noise levels were higher than those to which they initially reacted. This suggests that their initial responses were startle responses, and that their sensitivity to ship noise declined subsequently. In fact, apart from their initial reactions to ship aproaches, narwhals showed little or no reaction to ship activities such as start-ups or ice-breaking when the ships were operating within the fast ice away from the edge; we could not discern any influence of received noise levels as high as 120 dB on the level of narwhal vocal activity or on their surface behavior.

Vocal Responses of Whales to Ships

When this study began, we were not familiar enough with the vocal repertoire of either whale species to be able to ascribe call types with certainty to one or the other. Nonetheless, during the approach of the Arctic to the Admiralty Inlet ice edge, a marked change was evident in the type and quality of whale vocalizations. A large proportion of the calls were of a noisy pulsive type (screams) that were not heard outside the disturbance period. These calls were tentatively attributed to belugas which at the time were moving rapidly along the ice edge in response to the approaching ship. In 1983 these pulsive "screams" were first heard when the Arctic was approaching the ice edge at a range of 85 km and they were heard in

the initial stages of virtually all ship disturbances when belugas were present and showing "fleeing" reactions. In most cases narwhals were also present when pulsive "screams" were heard but on one occasion only belugas were visible when these calls were heard. This, and the association of these calls with belugas exhibiting a fleeing response in 1982 and 1983, strongly suggests that belugas were the source; their coincidence with the panic movement suggests that these calls represent an alarm signal. These calls are similar to the pulsed tone sounds of belugas described by Sjare and Smith (1986a) in Cunningham Inlet. Sjare and Smith (1986b) found no evidence that these calls were used more often in situations of alarm; they were also heard during social behavior and herd movements. However, pulsed tone calls show much variation in amplitude and frequency emphasis making them difficult to categorize, let alone assign a functional value. It is likely that the alarm situations observed at Cunningham Inlet (e.g. polar bears swimming in water, aircraft overflights) are not comparable to an ice-breaker. Sjare (per. comm.) suggests that there may not be a specific alarm call as such; rather, there may be a tendency for the noise component or harshness of a certain call to increase when an animal is under stress. This is a common characteristic of mammalian vocalizations.

Tonal vocalizations are widely used by odontocete whales in communication and probably find their greatest expression in belugas. Tonal signals tend to be species-specific (Steiner 1981), and in some species tonal signals are believed to function as signature calls, i.e., to identify individuals and their location (Caldwell and Caldwell 1965). The Caldwells believed that the emotional state of individuals was transmitted through variations of rapidity, repetition rate, loudness and/or duration of the basic signal contours. For example, dolphins (*Tursiops truncatus*) recorded in a variety of stressful situations produced only "excited" variants of their signature whistles. The Caldwells concluded that there was no special alarm signal. However, Dreher and Evans (1964), who studied the tonal vocalizations of four species of dolphins, found that one general call, common to all, was the downswept tonal, a signal that was "definitely associated with great fright and disturbance." We heard similar tonal calls along with pulsed screams in the initial phases of ship disturbance in 1983. These calls were heard along with "excited" variants of other tonal vocalizations. The spectrum of tonal calls used in the context of disturbance was also distinctive by the absence of certain calls heard during undisturbed situations (e.g. rising and stepped tonals). In general, the measurable characteristics of wider frequency excursions and longer durations of certain tonal calls, the absence of some call types, and the use of pulsed tone sounds gave a distinct aural impression of excitement or alarm by belugas in situations of disturbance.

The vocalizations of narwhals and belugas are surprisingly different considering that they are in the same family. Low-frequency (< 10 kHz), narrow-band click signals are the prevalent sounds produced by narwhals in Lancaster Sound along with pulsed tone calls. Indeed, dense click "clatter" contributes significantly to the high ambient noise levels at the Lancaster Sound ice edge. It is uncertain whether these clicks function in echolocation or in the maintenance of social organization. Ford and Fisher (1978) suggested that low-repetition rate click series could function in range finding and topographic analysis and that individual identity, emotional state and position were communicated through pulsed-tone calls. Watkins et al. (1971), noting the similarity between narwhal and sperm whale (*Physeter catodon*) sounds, suggested that individual click series may contain information about individual identity and position. Three properties of low-frequency clicks — regularity of repetition rate, apparent omnidirectionality and signal locatability — might be appropriate attributes of a communication signal. Often at the Lancaster Sound ice edge, click signals were heard for several minutes duration in the absence of pulsed-tone calls, suggesting that the narwhals were maintaining contact by the one mode alone. Like the sperm whale, the narwhal is a pelagic species and appears to be a deep-diving teuthophage (squid-eater); such behavioral and habitat similarities might favour the development of similar acoustic behavior for maintenance of spatial organization.

The only audible response of narwhals that we could discern during ship disturbance was a brief cessation of sound (both clicks and pulsed tones), but this occurred only in the initial phases of disturbance when the ship was approaching the ice edge in 1982 and 1983. A shot fired into the water by hunters located about 2 km from our recording station in 1983 had the same transient effect on dense click "clatter" of narwhals. In fact, following the shot, the noise level dropped from 110 dB to 103 dB. The same effect has been heard in an underwater recording of narwhals that were being pursued by hunters in a Baffin Island fiord in late summer of 1984 (Finley, unpubl. data). The silent behavior of narwhals corresponds to their "freeze" reaction in situations of distress. In our experience with narwhals in stressful situations (e.g. Finley et al. 1980; Finley and Miller 1982), we have never observed a rapid, mass-movement of animals like belugas that might require a herd-coordinating signal. These observations fit the "ardlingayuk" model if the narwhal's primary survival strategy is to remain undetected by its underwater predators.

Potential for Acoustic Interference

When considering the potential effects of industrial noise upon hearing among whales, it is important to estimate the zone of influence around the noise source. Richardson (1990) has suggested several different criteria for defining the zone or radius of influence: (1) the radius of detection, within which the industrial noise is detectable; (2) the radius of masking, within which the noise affects the ability of the animal to detect other sounds; and (3) the radius of behavioral responsiveness, within which the behavior of animals changes overtly. Several factors are important in determining the zone of noise influence; these include the noise frequency and source level, rate of attenuation, ambient noise levels, the hearing sensivity of the animal at different frequencies and "critical ratio," (i.e, the intensity by which a signal must exceed background noise in order to be heard). Because of the many sources of variability, the radius of influence of an industrial activity will vary widely with location and time. Also, very little is known about the function of various communication calls of whales and the range at which the calls are used, so it is difficult to evaluate the effects of increased noise levels on their effective communication range.

Toothed whales can hear sounds over a very wide frequency range from about 40 Hz to 150 kHz but certain bandwidths are utilized by whales for different functions; in general, high frequency sounds are used for echolocation, and low-frequency sounds (within the human audible range) are used in communication. At high frequencies, the beluga's echolocation abilities are likely to be little affected by vessel noise. It is at the lower frequencies that sound detection may be limited by vessel noise.

The audiology of the beluga has been conducted with captive animals using tonal frequencies between 40 Hz and 125 kHz (White et al. 1978; Awbrey et al. 1988; Johnson et al. 1989). Beluga hearing was found to be most sensitive at frequencies between 20 and 75 kHz, with an upper limit of hearing of 125 kHz. Like other odontocete whales, their peak sensitivity correlates well with the high frequency character of their echolocation signals. At frequencies below 10kHz, the absolute tonal thresholds of belugas steadily decline (e.g., 81 dB at 4 kHz, 102 dB at 1 kHz, Johnson et al. 1989) parallel with an increase in natural ambient noise.

Using the audiogram of the beluga produced by White et al. (1978) and estimated noise attenuation rates for an ice-breaking tanker, Mansfield (1983) calculated that a beluga with an absolute auditory threshold of 75 dB at 3.85 kHz (an estimated average frequency of its communication sounds) would first be able to detect a tanker breaking ice at full power at a distance of 5 km. This simple calculation did not take into account the critical ratio, calculated by Johnson et al. (1989) to be an additional 17 dB at this frequency. By similar deduction, using Johnson et al.'s test results, we can calculate that, with an absolute auditory threshold of 104 dB at 1 kHz and a critical ratio of 17 dB, a beluga would be unable to detect ships ice-

breaking at full power at ranges > 20 km, judging from the received noise levels shown in Fig. 2. However, the present study suggests that belugas were aware of a ship's approach at a distance of 85 km and certainly they showed overt behavioral responses at ranges > 40 km. There are many factors which contribute to noise attenuation but these would not account for the disparity between our field observations and theoretical calculations. We can only suggest that the disparity is due to the application of laboratory audiograms to natural situations. It is possible that the estimated auditory thresholds of belugas and other species are too high, especially at frequencies below 1kHz (see review by Richardson et al. 1989). Almost all studies of audition and auditory masking of toothed whales have employed tonal signals against a background of white noise. Relatively few of the sounds produced or received by whales are pure tones and presumably the cetacean brain is finely tuned to modulated signals of broader frequencies.

In their natural environment, belugas and narwhals presumably depend on passive listening to low-level, low-frequency ambient sounds of moving and solid ice to obtain information that is critical to their navigation and survival in ice-covered waters. Artificially increasing the background noise could presumably interfere with this information-gathering process. Masking by industrial noise could conceivably result in reduced navigational and foraging capabilities in whales, thereby leading to physiological stress and reduced fitness of populations. Such an effect would be difficult to demonstrate.

To some degree the acoustic system of belugas and narwhals must be adapted to deal with relatively high levels of ambient noise in a pack ice environment. Studies by Au et al. (1985) and Turl et al. (1987) have demonstrated that belugas are adept at tuning the frequency and duration of their echolocation signals in response to changing levels of ambient noise. Our studies suggest that belugas may also change the frequency and duration of their social signals during periods when ship noise predominates. We are just beginning to appreciate the sophistication of the acoustic processing system of these remarkable animals.

Acknowledgments

Principal funding and support for this study was provided by the Northern Environmental Protection Branch of the Department of Indian Affairs and Northern Development. Additional funding and support was provided by Canarctic Shipping Ltd., Canadian Coast Guard (Ministry of Transport), Arctic Pilot Project, Dome Petroleum Ltd., Gulf Canada Resources Inc., Consolidex-Magnorth Ltd. and Environment Canada. We thank D. Stone, R. Hurst and T. Langtry of DIAND and Captain I. Marr of the CCG for their major roles in planning and coordinating the study. Mr. M. Luce of Canarctic Shipping was supportive in many aspects of the field program.

G. Silber operated recording equipment in the field. Logistic support on the ice was provided by D. Kalluk, O. Nakitavak, Tuktu and G. Williams of Arctic Bay. B. Hough of Polar Continental Shelf Project coordinated aircraft support and radio communications. J. Ford of the Vancouver Public Aquarium provided advice and assistance in the analysis of whale vocalizations. R. Ferraro of the Institute of Applied Physiology and Medicine, Seattle, assisted in the production of real-time spectrographs. Dr. W. J. Richardson, B. Sjare, L. Darling and an anonymous reviewer provided constructive comments on the manuscript.

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Echolocation Abilities of the Beluga, *Delphinapterus leucas*: A Review and Comparison with the Bottlenose Dolphin, *Tursiops truncatus*

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TURL, C. W. 1990. Echolocation abilities of the beluga, *Delphinapterus leucas*: a review and comparison with the bottlenose dolphin, *Tursiops truncatus*, p. 119–128. *In* T. G. Smith, D. J. St. Aubin, and J. R. Geraci [ed.] Advances in research on the beluga whale, *Delphinapterus leucas*. Can. Bull. Fish. Aquat. Sci. 224.

Belugas (*Delphinapterus leucas*) can navigate under the ice, locate food, and find areas of open water. The results of echolocation experiments suggest that the echolocation capabilities of belugas may be well suited to the high noise and reverberation levels that are found in the Arctic. The beluga has a narrow transmitted beam pattern that would be useful in under-ice navigation. The beluga can detect targets that are masked by noise and reverberation at low signal levels. The ability of belugas to detect echoes from a surface-reflected path may be a strategy they have developed in an Arctic environment.

Some experiments have directly compared the beluga and the bottlenose dolphin (*Tursiops truncatus*) in the same echolocation task. The results of these experiments show that the beluga and bottlenose dolphin have different capabilities, and may have different echolocation strategies. The beluga's bioacoustic abilities are not fully known, but the information that is available suggests that their echolocation system is well suited to function in the Arctic environment.

Le béluga (*Delphinapterus leucas*) peut naviguer sous la glace, localiser de la nourriture et trouver des étendues d'eau libre de glace. Les résultats d'expérience d'écholocation portent à croire que le pouvoir d'écholocation du béluga est bien adapté aux niveaux de bruit et de réverbération que l'on retrouve dans l'Arctique. Le béluga transmet un faisceau étroit qui serait utile pour naviguer sous la glace. Il peut détecter des cibles de faibles niveaux qui sont masquées par le bruit et les réverbérations. Le béluga peut détecter des échos réfléchis de la surface, et c'est peut-être là une stratégie développée dans le milieu arctique.

Certaines expériences ont comparé directement le béluga et le dauphin à gros nez (*Tursiops truncatus*) dans la même activité d'écholocation. Elles démontrent que le béluga et le dauphin à gros nez ont différentes capacités et peut-être différentes stratégies d'écholocation. Les capacités bioacoustiques du béluga ne sont pas parfaitement connues, mais l'information disponible porte à croire que son système d'écholocation est bien adapté au milieu arctique.

Introduction

Kleinenberg et al. (1969) suggested that belugas (*Delphinapterus leucas*) have a well developed "echo-sounding" ability that helps them to orient under the ice and locate areas of ice-free water. Several experiments have been conducted to quantify the echolocation abilities of belugas, including underwater hearing sensitivity, critical ratio thresholds, the transmitted beam pattern and echolocation signal characteristics. The target detection capabilities of the beluga's sonar system have been measured in a variety of ways including target detection in masking noise, target detection in reverberation, and maximum range detection. Measurements of source level of echolocation signals, target strength and noise or reverberation level were made so that the echo-to-noise ratio (E/N) or the echo-to-reverberation ratio (E/R) at threshold could be determined. The beluga's ability to discriminate between two complex planar targets has also been reported. Some echolocation experiments have directly compared the beluga and the bottlenose dolphin (*Tursiops truncatus*). The results of these experiments show some striking differences between these two species. Here I will review the results of the beluga sonar experiments and compare experimental data from *Tursiops* when possible.

Results

Underwater Hearing and Critical Ratio

White et al. (1978) measured the underwater hearing thresholds of a male and a female beluga using pure tone signals between 1 and 123 kHz. They reported that the maximum hearing sensitivity was at 30 kHz for both animals. Other frequencies with thresholds below 40 dB re 1 μPa were 42.5, 60 and 85 kHz. The authors noted that the frequencies of maximum hearing sensitivity were similar to the peak frequencies of beluga echolocation click trains reported by Gurevich and Evans (1976) for a shape discrimination experiment. Johnson (1964) reported that the maximum underwater hearing sensitivity of the bottlenose dolphin was at 50 kHz (45 dB re 1 μPa). Above 50 kHz the threshold increased to about 55 dB re 1 μPa at 100 kHz.

Johnson et al. (1989) measured the masked auditory thresholds of a beluga between 40 Hz and 115 kHz. They report that the beluga's critical ratios were about 3 dB lower than critical ratios reported for the bottlenose dolphin (Moore and Au 1982). A low critical ratio suggests a good frequency discrimination ability. The term critical ratio is used to quantify the effects of noise on detection. The critical ratio is the ratio of signal power to noise spectrum level at masked threshold.

Transmitted Beam Pattern and Echolocation Signals

Au et al. (1987) measured the transmitted echolocation beam pattern of a beluga while the animal performed a target detection task. The animal was trained to station on a bite plate so that its transmission beam could be measured in the vertical and horizontal planes using a hydrophone array. The major axis of the vertical beam was directed approximately 5° above the plane defined by the animal's teeth. The 3-dB beamwidth, in both the vertical and horizontal plane, was approximately 6.5°. The directional character of sound emitted by a projector can be described by its directivity index, defined as the ratio between levels produced by a directional and omnidirectional transducer emitting equal power. The beluga's calculated directivity index was 32.1 dB. Au (1980) reported that the 3-dB beamwidth of a bottlenose dolphin transmitted beam was approximately 11.7° in the vertical plane and 10.7° in the horizontal plane. The calculated directivity index of *Tursiops* was 26.5 dB (Au and Moore 1984).

Au et al. (1985) suggested that *Delphinapterus* and *Tursiops* (Au 1980) may change the peak frequency and peak amplitude of their echolocation signals depending on the ambient noise spectrum in their environment. Au et al. (1985) measured the echolocation signals of a beluga in San Diego Bay, California and the same beluga after it had been moved to Kaneohe Bay, Oahu, Hawaii. In San Diego Bay, the beluga emitted echolocation signals with peak frequencies from 40 to 60 kHz and 3-dB bandwidths between 15 and 25 kHz. In Kaneohe Bay, the beluga shifted its signals about an octave higher in frequency with peak frequencies between 100 and 120 kHz, and 3-dB bandwidths between 30 and 40 kHz. Signal intensities measured were about 18 dB higher than in San Diego Bay.

Au et al. (1974) measured echolocation signals of two bottlenose dolphin in Kaneohe Bay. They reported that the animals were using echolocation signals with peak energies at frequencies between 120 and 130 kHz compared to 30 to 60 kHz reported for *Tursiops* in pools. The average peak-to-peak source levels were 30 dB higher in Kaneohe Bay.

Target Detection in Masking Noise

Turl et al. (1987) trained a beluga and a bottlenose dolphin to detect targets in masking noise. Targets were stainless-steel, water-filled spheres 7.62 and 22.86 cm in diameter. Target ranges of 16.5 and 40 m were used with the 7.62-cm sphere and 80 m with the 22.86-cm sphere. Masking noise with a flat spectrum from 40 to 160 kHz was projected from a spherical transducer located in front of the animal hoop station in line with the target. Target detection performance was determined as a function masking noise level at each target range. Each animal's target detection performance, as a function of the masking noise level for both targets and three distances, is shown in Fig. 1. The beluga matched the dolphin's performance in noise levels 8–13 dB higher.

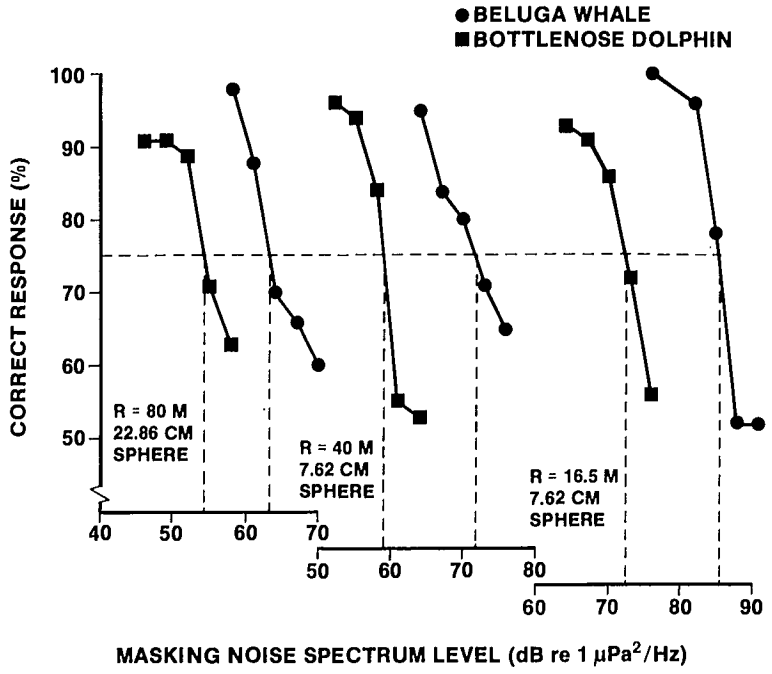

FIG. 1. (a) Beluga and bottlenose dolphin's performance data as a function of masking noise levels at 16.5, 40 and 80 m (after Turl et al. 1987).

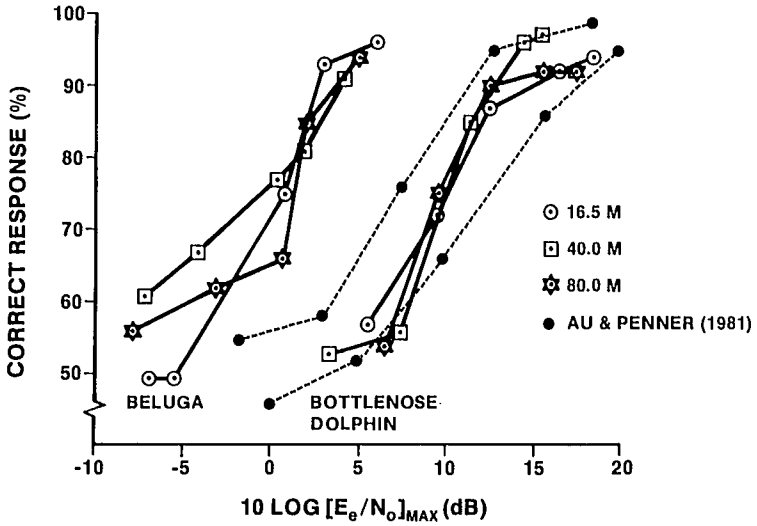

FIG. 2. Beluga and bottlenose dolphin's performance data at three distances replotted as a function of the maximum echo signal-to-noise ratio (from Turl et al. 1987).

The beluga's and dolphin's performance data in Fig. 1 are replotted in Fig. 2 as a function of echo-to-noise ratio. The average value of the maximum source energy flux density (E_s) per trial was used in the calculation. Such a technique will provide the upper limit of the E_s/N_o, that is, the maximum E_s/N_o available to the animal. The data of Au and Penner (1981) for two *Tursiops* are also included in Fig. 2. At the 75% correct response threshold, the $(E_s/N_o)_{max}$ was approximately 1.0 dB for the beluga at the three target distances. For the bottlenose dolphin (Turl et al. 1987), $(E_s/N_o)_{max}$ was approximately 10 dB, consistent with the data of Au and Penner (1981) for *Tursiops*.

Target Detection in Reverberation

Turl and coworkers (unpubl. data) measured a beluga's ability to detect targets placed in front of a clutter screen. The clutter screen consisted of 400 5.1 cm diameter cork balls spaced 15.2 cm apart in a 20 × 20 array. The clutter screen was 8 m from the animal's hoop station. Targets were hollow stainless steel cylinders (3.2-cm diameter and 0.38-cm wall thickness), 14.0, 10.0, 7.0, 5.0 and 3.0 cm long. Using cylinders with the same wall thickness and diameter, but of different lengths, the amplitude of the target echoes could be varied without changing the echo structure.

Backscatter measurements of the clutter screen and targets were made using the procedures given in Au and Snyder (1980). The backscatter measurements of the clutter screen were made with the transducer located so that its 3-dB beamwidth covered approximately the same area of the clutter screen that the beluga's beam (Au et al. 1987) would at a distance of 8 m. The clutter screen was used in two positions: perpendicular to the beluga (90° grazing angle) and rotated 22° (68° grazing angle). Values of the target strength based on energy (TS_e) and on maximum peak-to-peak amplitudes ($TS_{p\text{-}p}$) are shown in Table 1 for the clutter screen and the five targets. To include the entire echo, the TS_e for the clutter screen was measured for 1 ms. At 68° grazing angle, the backscatter from the clutter screen was 2 dB lower than at 90° grazing angle.

TABLE 1. Results of the target strength measurements of the clutter screen and cylinder targets. The E/R_{pp} based on the peak-to-peak amplitudes and on the energy of the incident and echo signals are shown for clutter screen grazing angle of 90°. E/R_E values were measured over a 1 ms time interval.

Target	Length (cm)	TS_{p-p} (dB)	TS_E (dB)	E/R_{pp} (dB)	E/R_E (dB)
Screen					
90°	—	-25.8 ±1.7	-19.9 ±1.0	—	—
68°	—	-27.8 ±1.3	-20.3 ±0.6	—	—
Targets					
1	13.0	-17.6 ±.2	-16.8 ±.2	+8.2	+3.1
2	10.0	-19.3 ±.2	-18.3 ±.2	+6.3	+1.5
3	7.0	-22.0 ±.2	-21.1 ±.2	+3.8	-1.2
4	5.0	-25.1 ±.3	-23.9 ±.5	+0.7	-3.0
5	3.0	-29.3 ±.3	-27.6 ±.9	-3.6	-7.7

The beluga's detection results when the targets were located within the plane of the clutter screen are shown in Figure 3 as a function of E/R. The E/R based on energy represents the lowest estimate of the E/R since the entire clutter screen echo occurred within the 1 ms integration time used. The E/R based on the peak-to-peak amplitude represents the highest estimate of E/R. The results indicate that at the 50% detection threshold the echo-to-reverberation ratio was -1.0 dB, based on the peak-to-peak measurements, and -5.1 dB based on the energy measurement.

Au and Turl (1983) trained a bottlenose dolphin to detect different length cylinders in front of a clutter screen similar to the experiment for the beluga. The results of this experiment (Fig. 3) show that when the targets were located within the plane of the clutter screen, the bottlenose dolphin's 50% correct detection was 2.6 dB, based on the peak-to-peak measurements, and 0.25 dB based on the energy measurement. The results of these two experiments suggest the beluga can detect targets in 3.6 to 5.4 dB more reverberation than *Tursiops*.

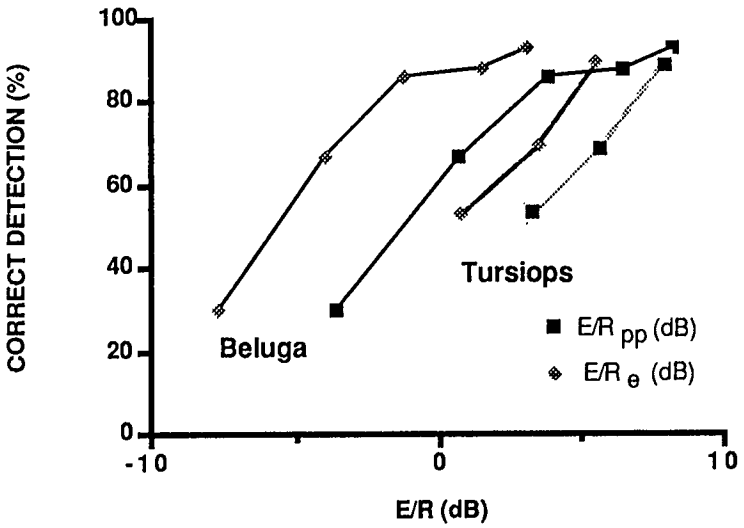

FIG. 3. Beluga and bottlenose dolphin (after Au and Turl 1983) performance data as a function of the echo-to-reverberation ratio. In this case, the targets were within the plane of the clutter screen. The squares indicate echo-to-reverberation ratios based on peak-to-peak amplitudes and the triangles indicate echo-to-reverberation ratios based on energy.

Maximum Target Detection

Turl and Penner (unpubl. data) trained a beluga to detect a 7.62 and a 15.24 cm diameter stainless steel, water-filled sphere between 40 and 120 m. The target strength of the 7.62 and 15.24 cm spheres was -30.8 and -21.4 dB, respectively. At the 50% correct detection threshold, the beluga's performance for the 7.62 and 15.24 cm spheres is 116 and 117 m, respectively. The target strength difference between the 7.62 and 15.24 cm spheres is approximately +9 dB and yet the difference of the detection threshold is 1 m. At target distance <115 m, the beluga's performance was greater than 90% correct detection for both spheres. At 120 m, the beluga's performance was at chance for the 7.62 and 15.24 cm spheres. Au and Snyder (1980) reported that a bottlenose dolphin's maximum range detection with a 7.62 cm sphere on the same target range was 113 m. The results of these two experiments indicate that the beluga and *Tursiops* have about the same detection range.

Echolocation Strategies

Turl and Penner (1989) reported that a beluga emitted different patterns of echolocation click trains than the bottlenose dolphin while performing the same echolocation task. The beluga emitted three different patterns of echolocation clicks. A Pattern I (Fig. 4A) click train started with low amplitude clicks, followed by packets of clicks. A packet contained several clicks with interclick intervals less than the two-way travel time (TWT) to the target; the interpacket intervals were greater than the TWT. A Pattern II (Fig. 4B) click train consisted of a combination of individual clicks, with some intervals less than and some greater than the TWT. This pattern did not contain packets. Pattern III (Fig. 4C) click trains consisted of individual clicks with interclick intervals less than the TWT.

Pattern I and II click trains always started with an initial series of clicks that were less than the TWT. This implies the beluga transmits signals and receives echoes simultaneously which may provide the beluga with information about target presence or absence, but probably does not provide information about target range. In Pattern I click trains the interpacket interval is longer than the total packet duration and greater than the TWT. The beluga may be processing all echoes in a packet before the next echo packet returns to the animal. Beyond 80 m target distance, the beluga emitted Pattern I and Pattern II click trains.

Pattern III click trains had a constant repetition rate of 40 to 57 ms and were emitted by the beluga at target distances of 40 and 60 m. This suggests the beluga may be processing echoes between the transmission of echolocation signals and that this repetition rate might optimize the analysis of information.

The bottlenose dolphin typically emits an echolocation signal and waits until the echo returns before emitting the next signal. The bottlenose dolphin changes the pulse repetition rate as the target distance changes so that the signal echo is during the interclick interval (Morozov et al. 1972; Penner and Kadane 1980).

Turl et al. (1987) reported that a beluga and a bottlenose dolphin emit different echolocation click patterns in the same masking noise experiment. The beluga and bottlenose dolphin were the same animals that were the subjects used in Turl and Penner (1989). The targets were at three distances from the animal (16.5, 40 and 80 m). At 16.5 and 40 m, the average interclick intervals of beluga click trains were about the same as the TWT (21 to 52 ms), whereas at target distance of 80 m, the beluga average interclick interval was less than the TWT (≈55 ms). The bottlenose dolphin's interclick interval was greater than the TWT at the three distances.

Target Discrimination

Gurevich and Evans (1976) trained a beluga to discriminate between two complex planar targets. The targets were three-step pyramids constructed of polyvinyl chloride sheets each

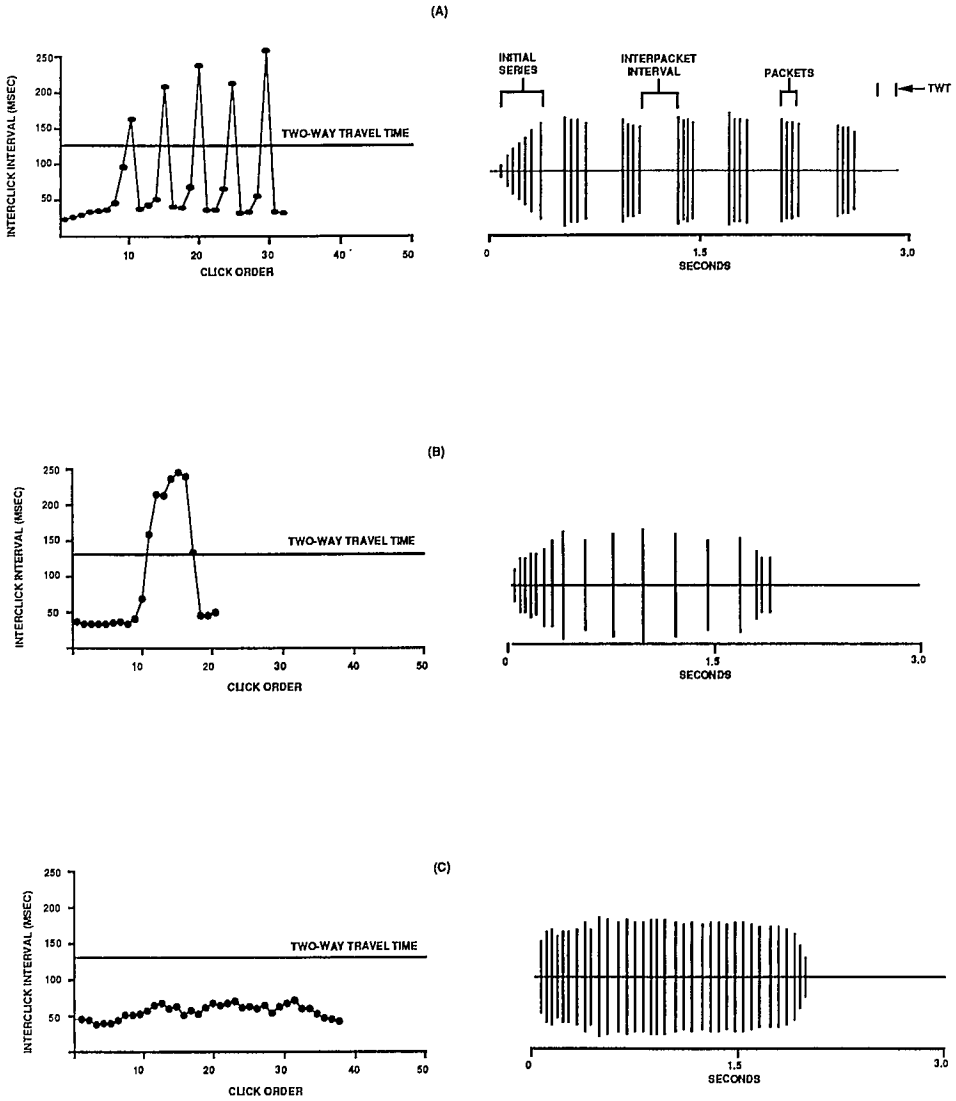

FIG. 4. Examples of the three patterns of beluga echolocation click trains for targets at 100 m are shown in click order (*left*) and in the time domain (*right*). A beluga pattern I click train [see (A)] plotted in the time domain showing the relationship of the initial series, interpacket interval, and packets (after Turl and Penner 1989). A Pattern II click train is shown in 4B and Pattern III in 4C.

13 mm thick. For the standard target, the first step was 10 × 10 cm, the second step was 7 × 7 cm and the third step was 3 × 3 cm. A selection of the standard target was considered a correct response. The comparison targets (incorrect response) differed from the standard targets in the size (surface area) of the third step. In a comparison of a third step of 2.9 × 2.9 cm versus the standard of 3.0 × 3.0 cm, the beluga's average correct response was 81%. When presented with two standard or identical targets, the beluga's response dropped to 50%. A bottlenose dolphin tested with similar targets was at chance performance on a comparison of 2.7 × 2.7 cm versus 3.0 × 3.0 cm.

Target Detection Using Surface-Reflected Path

Penner et al. (1986) reported that during the initial stages of a masking noise experiment (Turl et al. 1987) with a beluga and bottlenose dolphin, the beluga's performance did not decrease with increasing noise. The beluga's detection performance was 85% even when the noise level was 15 dB greater than the noise threshold level of the dolphin. Since the interfering noise came from a point source, Penner et al. reasoned that the beluga might realize a gain in the signal-to-noise ratio by projecting and receiving signals off the surface as depicted in Fig. 5. The beluga's signals were measured along the whale-target axis and these were similar to "off-axis" signal reported for the bottlenose dolphin (Au 1980). Measurements using the initial test geometry (Fig. 6) showed that maximum amplitude of the echolocation signals was approximately 7° above the animal-hydrophone-target mid-line axis. Two methods were used to test the surface-reflected path hypothesis. First, the noise projector was raised from 1.0 to 0.4 m, placing it directly in the surface-reflected path; two sessions were conducted with this geometry. Second, a screen was used to block the surface path. The screen was a 60- × 91-cm doormat lined on one side with 0.3-cm-thick corprene and on the other side with a loose weave fiber packing material (commonly called horsehair). The screen was placed 3 m from the hoop station. The screen extended to a depth of 0.6 m below the surface of the water. Twenty test sessions were conducted with the screen in place.

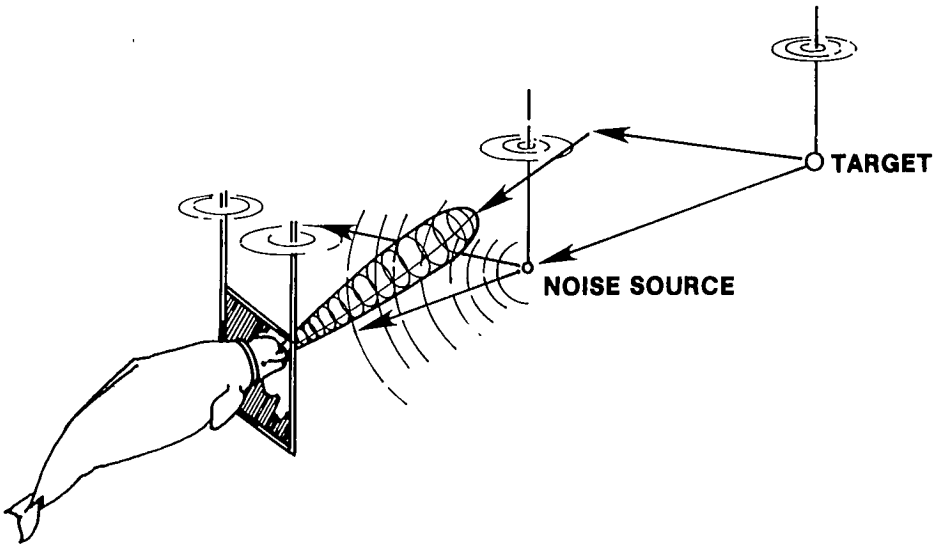

FIG. 5. Drawing showing how the beluga might achieve a higher signal-to-noise ratio using a surface-reflected propagation path in the original test condition (from Penner et al. 1986).

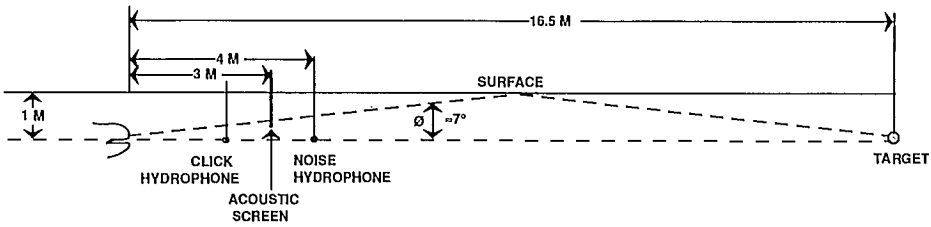

FIG. 6. Side view of the beluga, the noise projector, and the test geometry showing a direct and surface-reflected path (after Penner et al. 1986).

In the first session, after the noise projector was raised to a depth of 0.4 m, the beluga's correct detection decreased as the noise level increased. However, in the second session, the beluga's detection performance increased to the level previously measured with the noise projector at a depth of 1 m. The signal measuring hydrophone at 1 m measured higher amplitude signals for the second session. Penner et al. said that the beluga had abandoned the surface-reflected path and was using the direct path to maximize performance.

The beluga's detection performance was altered when the screen was used to block the surface-reflected propagation path and the noise projector was at 1.0 m. The beluga's detection performance sharply decreased as the noise level increased from 79 to 91 dB. Without the screen, the beluga's performance was relatively constant (>85% correct response) between these two levels. Penner et al. concluded that the initial test geometry used in this experiment enabled the beluga to echolocate via a surface-reflected propagation path.

Discussion

Comparing the results of the experiments for the beluga and the bottlenose dolphin suggests that there are differences in the sonar characteristics and target detection sensitivity of these two species.

Kleinenberg et al. (1969) suggested that belugas locate "areas of ice-free water, finding directions by active echo sounding of water lapping in the polynya." The edge of an ice sheet is a source of noise caused by wave impact upon the ice floe (Urick 1984). Belugas have good directional underwater hearing. Since maximum range detection would probably be limited by either noise or reverberation it would seem more likely that belugas might use passive orientation to detect the direction to open water.

Au et al. (1987) suggested that the beluga's narrow transmitted beam should provide good spatial localization and target resolution capabilities. They further say that "by scanning over the extent of an elongated target with a narrow beam, the animal should be able to discriminate various echo highlight producing reflectors. Such a capability would be useful in under-ice navigation and to find air pockets under an ice pack." Beluga's can discriminate between targets that differ by 1 cm in test conditions; however, the cues used by this animal to differentiate targets is not known.

The results of experiments show that belugas differ from bottlenose dolphins in their ability to (1) detect targets in noise, (2) detect targets in reverberation, and (3) use surface-reflected signals. Belugas also seem to differ in hearing ability and pulse production patterns. These differences might be the result of beluga's adaptation to the Arctic acoustic environment. The results from acoustic tests show a beluga can detect targets in masking noise about 8-13 dB higher than the bottlenose dolphin. A beluga can detect targets in 3.6 – 5.4 dB more reverberation than *Tursiops* in test conditions in which the targets are normal to the animal's echolocation beam (e.g., looking up into the ice). The beluga's ability to receive and use surface-reflected echoes may be useful when passing through areas of extensive ice coverage. The beluga's critical ratio is lower than that for bottlenose dolphin by approximately 3 dB. The beluga emits packets of clicks, bottlenose dolphins do not.

Experimental results suggest that the beluga's echolocation system is well suited to function in the Arctic environment. The ability of the beluga to detect low amplitude echoes in high levels of masking noise and reverberation may reflect an adaptation to the high ambient noise and reverberation levels of acoustic interference found in the Arctic. Further investigation, including measuring the receiving beam pattern and signal processing characteristics of the beluga, is required in order to isolate the mechanisms which account for the belugas's increased detection sensitivity. Belugas may have different signal processing capabilities than those measured for other species of odontocetes. Additional information concerning the temporal resolving capability of the beluga could help isolate mechanisms used by the beluga that might be relevant in this type of click emission strategy.

Acknowledgments

I would like to thank the following co-workers at the Naval Ocean System Center (Hawaii Laboratory) for their assistance in the preparation of this paper, Dr. Jeanette Thomas for her helpful comments and P.W.B. Moore, William F. Friedl, Dr. Whitlow Au and Dr. Paul E. Nachtigall for their review of the manuscript. The many discussions with Ralph H. Penner are greatly appreciated.

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Integumentary Heat Loss and Blubber Distribution in the Beluga, *Delphinapterus leucas*, with Comparisons to the Narwhal, *Monodon monoceros*

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The minimum metabolic rate necessary for thermostasis was estimated from integumentary heat loss using skin and blubber thicknesses, thermal conductivities and body girths from beluga, *Delphinapterus leucas* (n=22), and narwhal, *Monodon monoceros* (n=5). Blubber is not uniformly distributed over the body, but forms a thickened saddle posterior to the dorsal ridge, and smooths the outline of tendons in the caudal region. The thinnest blubber and the thickest skin occurred on a neonate. Thickened skin serves as a thermal buffer at birth. Standard measures of girth at the axilla or umbilicus are highly correlated with blubber volume (R^2=0.98), indicating girth is an excellent index of body condition.

Thermal conductivity of beluga blubber was 0.102 ± 0.011 $W \cdot m^{-1} \cdot {}^{o}C^{-1}$ (n=6); skin was 0.249 ± 0.019 $W \cdot m^{-1} \cdot {}^{o}C^{-1}$ (n=7). For eastern Hudson Bay belugas of body lengths 149 to 401 cm, the thermostatic energy requirement (Watts) in 15°C water equals 0.238 body length$^{1.136}$. Beluga and narwhal are equally insulated, but only beluga exhibit seasonal occupation of warmer estuarine waters.

Le taux métabolique minimum nécessaire pour maintenir la thermoneutralité a été estimé à partir de la perte de chaleur intégumentaire en se servant des épaisseurs de peau et de graisse, des conductibilités caloriques et des tours de taille des marsouins blancs, *Delphinapterus leucas* (n = 22), et narval, *Monodon monoceros* (n = 5). La graisse n'est pas distribuée uniformément sur la superficie du corps, mais forme une selle plus épaisse postérieure à l'épine dorsale, et égalise le contour des tendons dans la région caudale. La graisse la plus mince et la peau la plus épaisse se trouvent chez les néo-natals. Une peau épaissie sert de tampon thermique à la naissance. Des mesures standards de tour de taille à la hauteur axillaire ou ombélicale sont fortement correlées avec le volume de graisse (R^2 = 0.98) indiquant que le tour de taille est un excellent index de condition corporelle.

La conductibilité calorique de la graisse de baleine était 0.102 ± 0.011 $W \cdot m^{-1} \cdot {}^{o}C^{-1}$ (n=6); la peau était 0.249 ± 0.019 $W \cdot m^{-1} \cdot {}^{o}C^{-1}$ (n=7). Pour les marsouins blancs de l'est de la baie d'Hudson, d'une longueur de 149 à 401 cm, la demande d'énergie thermostatique (Watts) dans l'eau de 15°C égale 0.238 de la longueur du corps $^{1.136}$. Le marsouin blanc et le narval sont également isolés mais seul le marsouin blanc démontre une occupation saisonnière d'estuaires aux eaux plus chaudes.

Introduction

Estimates of metabolic rates of marine mammals, especially cetaceans, have supported the impression that these animals have high metabolic rates relative to terrestrial animals of comparable size (Brodie 1975). Yet these estimates remain controversial since few published studies meet the criteria for measuring basal metabolism (Lavigne et al. 1986). These criteria, which set standard conditions for comparisons with other mammals, require that metabolic rates be measured on mature, resting animals in a postabsorptive state at a metabolically indifferent temperature (Kleiber 1975). Since it is often difficult or impossible to meet these criteria when studying cetacean energetics, an alternative (but little used) approach is to determine the thermostatic energy requirement. Kleiber (1975) defined this as the heat production needed to maintain a constant mammalian body temperature above that of the environment. In marine mammals, the thermostatic energy requirement equals the heat lost by conduction through the integument when the loss via evaporative cooling in the lungs (ca. 5%, Kanwisher and Sundnes 1966) is ignored.

The properties and function of whale blubber were explored by Parry (1949) in a study of the structure and heat flow through fin whale (*Balaenoptera physalus*) and harbour porpoise (*Phocoena phocoena*) blubber. He suggests blubber functions as an energy store and as insulation. Others, notably Kanwisher and Sundnes (1966) and Brodie (1975), have estimated energy requirements of cetaceans using surface area and blubber thickness. In these studies, the term blubber is used in the commercial whaling sense which lumps blubber and skin as one; or considers only fat thickness and not skin in the heat loss equations. However, the thermal properties of skin and blubber are quite different, their thermal conductivities differing by about a factor of 2 (See Results section, p. 133.). Given the thick skin of cetaceans, especially the polar adapted species (Geraci et al. 1986), I have considered separately the roles of skin and blubber on integumentary heat loss.

The distribution of blubber over the body affects heat loss, streamlining and buoyancy. When coupled with measurements of body length and girth, blubber thickness data can be used to estimate a whale's blubber volume, and if blubber density is known, blubber mass. The correlation between standard field measurements of blubber thickness and body girth (Am. Soc. Mammal. 1961) and blubber volume (or mass) indicates how suitable these measures are as indices of body condition.

I examined the topography and thermal conductivity of blubber and skin and evaluated integumentary heat loss in beluga (*Delphinapterus leucas*) and narwhal (*Monodon monoceros*), two related species with distinct ecological niches. The similarities observed in integumentary heat loss challenge the view that niche separation depends on differences in thermal adaptation.

Methods

Specimens

Standard measurements (Am. Soc. Mammal. 1961), and detailed skin, blubber and girth data, were obtained from 16 beluga specimens of various sizes and reproductive status in the summers of 1984 and 1985 on the coast of eastern Hudson Bay, primarily at the Nastapoka River (56°55'N, 76°33'W). Two neonate and two adult belugas were examined at Cunningham Inlet, N.W.T. (74°07'N, 93°50W') in July, 1977; one adult at Winton Bay, N.W.T. (64°28'N, 64°42'W) in August, 1978; and one neonate at Wakeham Bay, Quebec (61°36'N, 71°56'W) in November, 1985. Two near-term fetuses, a neonate, a calf and an adult narwhal from the north Baffin Island harvest were examined in summer during the mid-1970's.

Blubber and Skin Thickness, Volume and Mass

Whales from eastern Hudson Bay were measured by making 7 transverse cuts equally spaced along the total length of each animal (Fig. 1). Half girth was recorded to the nearest centimetre at each interval. Skin and blubber thickness were measured *in situ* to the nearest millimetre at 7 equally spaced points dorsal-ventrally at each interval on one side of the animal, except in the genital slit region where the most ventral measurement was not made.

Sampling protocol for the other specimens depended on time available for blubber and skin measurements and ranged from 5 to 13 transverse intervals. These data were linearly interpolated to yield 7 by 7 evenly spaced data matrices as described above. Only the un-interpolated data from eastern Hudson Bay beluga were used to assess blubber and skin distribution. Both the un-interpolated and interpolated data of narwhal and beluga were used in the estimation of integumentary heat loss.

Whales were considered circular in cross-section for all computations of volumes and heat loss. The cross-sectional area of skin, blubber and core at each interval was calculated using the interval girth and mean skin and blubber thickness. Skin, blubber and core volumes were then estimated using Simpson's Rule (Boyce and DiPrima 1969) to evaluate the numerical integral of the respective cross-sections over the animal's length. Blubber and skin density were determined by dividing the weight of a sample by the volume it displaces in water.

The General Linear Models procedure of PC-SAS (SAS Inc, Cary, NC, USA) fitted least square regressions to the length, girth and blubber data to predict blubber, core and skin volume. The distribution patterns of skin and blubber were established by determining areas of similar (relative) thickness using Friedman's test (ANOVA based on ranked data, See Conover 1981).

Heat Loss

The thermal conductivity of beluga blubber and skin was estimated using a heat flux plate (Model S387, Geneq, Montreal) to measure the heat flow through samples of known thickness and temperature gradient. The heat source, a 4 L beaker of water, was maintained

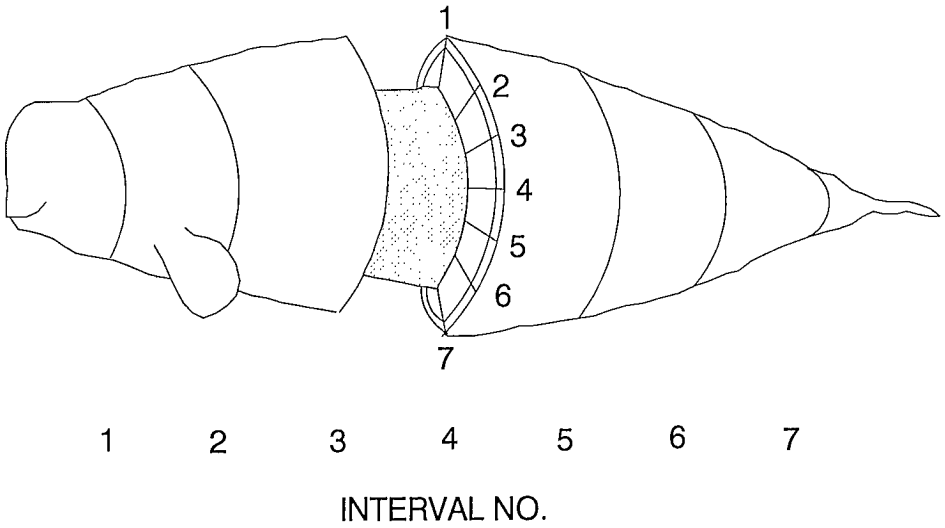

FIG. 1. Skin and blubber sampling points spaced equally, dorso-ventrally at each of 7 equally spaced girth intervals. Interval width is 1/8 of standard body length.

at 45°C by a laboratory heater pump. Water at an ambient temperature of 5°C circulated from a 10 L water bath through a 800 cm^3 metal box which acted as the heat sink. Temperature gradient and heat flux were recorded at 10 min intervals. After allowing a 20 min period for the temperature profile to stabilize, the thermal conductivity of each sample was calculated using the thickness of the sample at the end of the test and the mean ($n > 10$) of temperature gradient and heat flux records. No correction was made for reduction in thermal efficiency due to blood flow in live tissue (Kanwisher and Sundnes 1966).

The equations used to determine heat loss are given in Table 1. Equation (1) states Fourier's law of heat conduction between the surface of a body and its environment (Kleiber 1975). Due to the law of conservation of energy, the total heat loss across the skin equals the loss across the blubber (Eq. 2). Using the above relationships, the temperature at the junction of the skin and blubber layers can be determined (Eq. 3). This simplifies the heat transfer problem from that of two layers (blubber and skin) to that of one layer (blubber or skin). The heat flux at a given interval is governed by Eq. (4). Total heat loss is calculated using Simpson's rule (Boyce and DiPrima 1969) to evaluate the numerical integral of these fluxes over the length of the animal (Eq. 5).

TABLE 1. Equations governing integumentary heat loss.

Fourier's law of heat conduction

(1) $$Q = K \cdot A \cdot \delta T \cdot D^{-1}$$

Heat loss through the blubber equals the loss through the skin

(2) $$K_b \cdot G_b \cdot L \cdot (T_c - T_{sb}) \cdot B^{-1} = K_s \cdot G_s \cdot L \cdot (T_{sb} - T_e) \cdot S^{-1}$$

Solving for temperature at the blubber - skin junction

(3) $$T_{sb} = \frac{G_s \cdot K_s \cdot B \cdot T_e + G_b \cdot K_b \cdot S \cdot T_c}{G_s \cdot K_s \cdot B + G_b \cdot K_b \cdot S}$$

Unit flux per cm length at interval$_i$

(4) $$F_i = \frac{K_b \cdot G_{bi} \cdot (T_c - T_{sbi})}{B_i}$$

Integumentary heat loss

(5) $$H = \int_{\text{snout}}^{\text{tail}} F_i \, dL$$

where

Q	Rate of heat flow per unit time
K	Thermal conductivity of insulating layer
A	Surface area
δT	Temperature difference across insulating layer
D	Thickness of insulating layer
S	Skin thickness
B	Blubber thickness
G	Body girth

Subscripts

b	blubber
c	inner core
s	skin
sb	skin-blubber junction (the base of the dermis)
i	interval number

Results

Integumentary Heat Loss

The thermal conductivity of beluga blubber (summer samples) was 0.102 ± 0.011 $W \cdot m^{-1} \cdot {}^{o}C^{-1}$ ($n = 6$) and skin was 0.249 ± 0.019 $W \cdot m^{-1} \cdot {}^{o}C^{-1}$ ($n = 7$). The minimum integumentary heat loss for thermostasis in eastern Hudson Bay belugas (body length 149–401 cm) ranged from 70 to 207 *W*, for an ambient water of 15°C (Table 2). In the same temperature regime, high arctic belugas and narwhals had similar heat losses to those of eastern Hudson Bay belugas (Fig 2).

Heat loss is directly proportional to surface area (constant·length·girth) and inversely proportional to the thickness of insulation (in this case blubber or skin). However, length alone predicts heat loss well (R^2 0.95). This relationship in eastern Hudson Bay belugas is:

$$H = 0.238\text{Length}^{1.1357} \qquad (n=16, P<0.001)$$

where *H* is heat loss (*W*) and length is straight-line distance (cm) from the tip of the snout to the fluke notch.

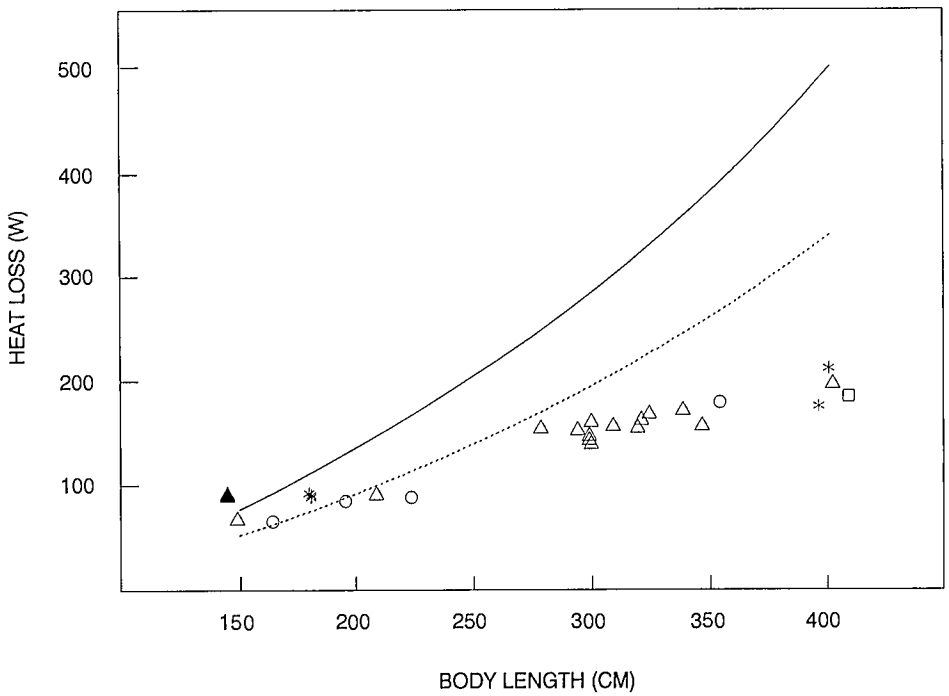

FIG. 2. Comparison of theoretical basal heat production based on body mass and integumentary heat loss in 15°C water with core temperature of 35°C. Beluga: Open triangle — eastern Hudson Bay; Asterisk — Barrow Strait, NWT; Solid triangle — Hudson Strait, N. Quebec; Open square — E. Baffin. Narwhal: Open circle — N. Baffin. Basal metabolic heat production based on total mass (solid line) 70 $Mass^{.75}$; Basal metabolic heat production based on mass excluding blubber (dashed line) 70 $(0.6Mass)^{.75}$ where $W(kg) = 0.000182\ L(cm)^{2.56}$ (Doidge 1990).

TABLE 2. Body morphometrics, integumentary heat loss in 15°C water, body surface area and status of Monodontids from various sites.

	Standard length cm	Max. girth cm	Lateral[a] blubber mm	Lateral[a] skin mm	Heat loss[c] W	Surface area[d] m^2	Status[b]
Beluga							
E. Hudson Bay							
Male	149	100	24	13	70	1.0	N
	208	156	55	11	95	2.4	—
	278	172	40	13	161	3.4	—
	293	182	37	12	159	3.7	—
	401	210	52	14	207	5.9	—
Female	298	194	52	12	148	3.7	P
	298	184	50	13	151	3.9	L
	299	176	47	12	145	3.6	R
	299	164	39	14	166	3.5	L
	308	196	50	13	164	4.1	L
	319	200	57	12	162	4.4	P
	320	182	48	14	170	4.3	L
	320	196	51	11	170	4.4	L
	324	176	43	13	176	4.1	L
	337	184	44	12	180	4.4	L
	346	207	63	14	164	4.8	B
Cunningham Inlet							
Male	179	106	24	12	97	1.3	N
	180	113	26	11	94	1.4	N
	399	252	58	12	224	6.6	—
Female	395	242	66	12	186	6.3	L
Wakeham Bay							
Male[e]	145	98	13	25	92	1.1	N
Winton Bay							
Male	407	300	82	10	194	8.0	—
Narwhal							
N. Baffin							
Male	164	110	34	5	70	1.2	F
	195	138	38	11	89	1.8	N
Female	223	142	45	11	93	2.1	—
	353	210	41	11	188	4.6	L
Sex ?	182	114	30	10	85	1.4	F

[a] Measured mid-length.

[b] F fetus, N neonate, P pregnant, R resting, L lactating.

[c] When maintaining body core at 35°C in 15°C water.

[d] Not including flippers and flukes.

[e] Sampled in November; all other whales sampled between late June and late August.

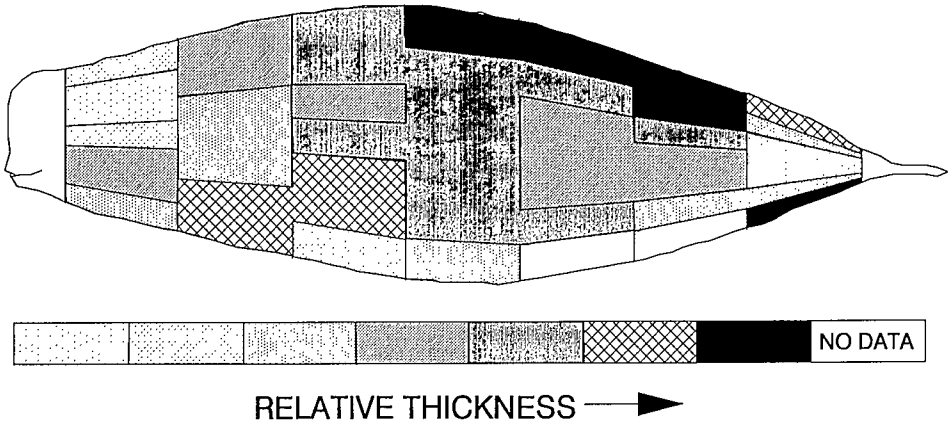

FIG. 3. Blubber distribution in belugas showing areas of significantly different relative thickness based on Friedman's test (n = 16).

Blubber Thickness

The general pattern of blubber distribution (Fig. 3) of eastern Hudson Bay belugas appeared similar regardless of sex or reproductive status. The thickest blubber occurred dorsally from mid-length posteriorly to the caudal peduncle, broadening as a slight lateral saddle. A smaller pad of equivalent thickness lay ventrally at the caudal peduncle. The next thickest blubber occurred laterally just behind the flipper. Behind this "flipper pad" and ventral to the thick blubber of the dorsal ridge lay a wide region of intermediate thickness. Blubber was thinnest in the dorso-lateral region of the neck and the lateral area of the caudal peduncle. No measurements were made in the region of the melon or jaw.

Skin Thickness

Figure 4 shows the variation in relative skin thickness (epidermis and dermis) over the body surface. Skin is thinnest at the caudal peduncle and in the region of the axilla, followed by the neck (Intervals 7, 2 & 1, respectively). The thickest pad covers the anterior end of the

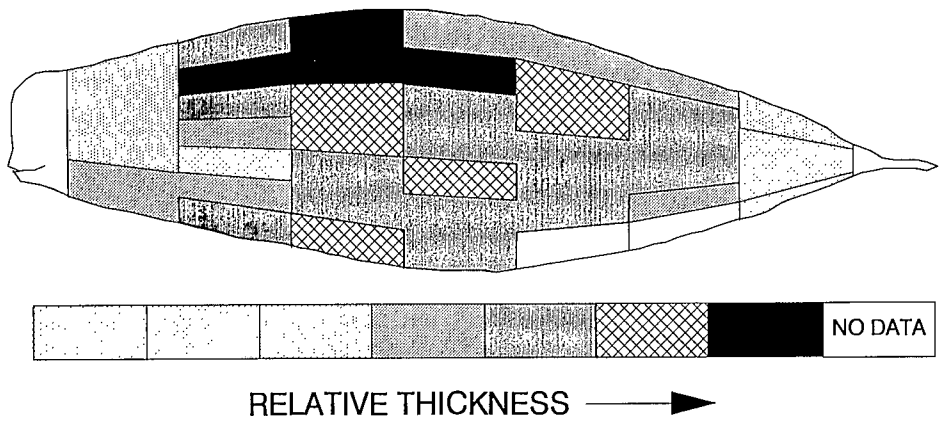

FIG. 4. Skin distribution in belugas showing areas of significantly different relative thickness based on Friedman's test (n = 16).

dorsal ridge extending as a slight lateral saddle. Skin on the animal's side is slightly thicker than intermediate thickness. Skin on the dorsal ridge posterior to mid-length is intermediate in thickness. The dorsal ridge is more a product of steeply sloping sides of the animal rather than of thickened skin.

Body Composition and Condition

Skin, blubber and core volume can be predicted from body girth or body length. Girths at intervals 1 to 5 (see Fig. 1) and body length each explain at least 95% of the variance in volume when cubed and multiplied by the appropriate coefficient (Table 3). The density of blubber (hypodermis) was 0.92 ± 0.09 g · cm^{-3} (n = 6) and that of skin 1.07 ± 0.02 g · cm^{-3} (n = 4). Direct measurements of the density of the body core were not made.

Discussion

The aquatic existence of homeotherms is generally thought to be energetically demanding because of the high thermal conduction of water compared to air (Scholander et al. 1950). This led many early investigators to assign high metabolic rates to marine mammals (Brodie 1975). Since the high thermal losses caused by an aquatic existence can be reduced by a thickened blubber layer, metabolic rate need not be increased above the expected rate of terrestrial mammals. If the warmest waters inhabited by whales are within their thermal neutral zone, integumentary heat loss should represent the lower boundary of metabolic rate.

Heat loss through the integument depends, in part, on the mass transfer of heat via blood flow. The heat transfer model assumes a negligible amount of heat is lost through flippers and flukes. However, these appendages are not at environmental temperature so some additional heat is lost even when blood flow is restricted. Bel'kovich (1961) reported belugas had the ability to regulate blood flow through the integument using well-developed muscles in the arterial walls, but the effect on thermal conductivity has not been quantified in belugas. The thermal conductivity of live blubber is 35 – 65% greater than dead tissue (Kanwisher and Sundnes 1966; Irving and Hart 1957) so the heat losses reported here for beluga are conservative.

TABLE 3. Coefficients for estimating blubber, skin and core volume of Nastapoka belugas (n=16) from the cube of body girths or body length.

	Volume = $A \cdot 10^{-5} \cdot \text{Girth}^3$ or $A \cdot 10^{-6} \cdot \text{Length}^3$								
	(L)			(cm)			(cm)		
	Blubber			Skin			Core		
Girth Interval	A	SE	R^2 10^{-2}	A	SE	R^2 10^{-2}	A	SE	R^2 10^{-2}
1	6.03	0.35	95	1.77	0.10	96	11.00	0.55	96
2	2.77	0.13	96	0.81	0.04	96	5.02	0.22	97
3	2.37	0.08	98	0.68	0.03	96	4.27	0.16	98
4	2.50	0.10	98	0.73	0.03	98	4.52	0.17	98
5	4.66	0.16	98	1.35	0.06	97	8.38	0.33	98
6	12.00	0.87	92	3.48	0.28	90	21.50	1.75	90
7	39.50	6.17	71	11.40	1.83	70	70.80	11.33	70
Length	5.00	0.20	98	1.46	0.06	97	9.06	0.31	98

The thermal conductivity of blubber (hypodermis) of beluga whales lies at the lower end of the three-fold range reported for marine mammals (Table 4). Most published values of blubber conductivity are from samples which include dermis, epidermis, and, in the case of seals, the pelage. These heterogeneous samples thus bias heat flow estimates based solely on blubber (fat) thickness. Thermal conductivity may vary with body location since fatty acid composition is stratified with blubber depth (at least in fin and sei whales *B. borealis*, Lockyer et al. 1985) and thermal conductivity appears to vary with fatty acid chain length (Table 4). In belugas, the connective tissue content of blubber (and presumably the lipid content) was fairly homogeneous over most body regions, as judged by ease of cutting and visual appearance. The thermal conductivity of the mid-dorsal blubber is used here in the absence of more widespread measurements and is thought to be representative of most body regions with the exception of the head and caudal peduncle. The extent to which fatty acid composition and thermal conductivity may vary with body location in belugas is not known.

Brodie (1975) argued that only a whale's inner core should be considered as the metabolically active mass. In belugas, up to 40% of body mass can be blubber (Sergeant and Brodie 1969, pers. obs.). For thermostasis in a given environment, heat loss must be balanced by heat production. The integumentary heat loss of belugas in the estuarine waters of Hudson Bay (15°C) and their theoretical basal heat production based on either total or metabolically active body mass (Fig. 2) are approximately equal for calves whereas adults are overinsulated. Even in high arctic waters of 0°C in which the thermostatic energy requirement is increased by 75%, Kleiber's prediction for adult basal metabolism appears sufficient to meet this demand. Larger animals may have to dissipate heat through blood vessels in the flippers and the flukes (Bel'kovich 1961).

Basal metabolic rates based on O_2 consumption reported by Kasting et al. (1989) for three captive belugas are 1.5 – 1.8 times those predicted by Kleiber's relation. These values, however, should be viewed with caution. The heat loss reported for the beluga named Churchill (estimated weight 324–340 kg) was 236 *W* in 12 – 18°C water (Kasting et al. 1989, p. 695), a value slightly lower than the basal heat production of 263 *W* predicted by Kleiber's relation, but higher than the 161 *W* integumentary loss which I determined for a similar sized

TABLE 4. Thermal conductivity of lipids from various sources.

	Conductivity $W \cdot m^{-1} \cdot °C^{-1}$	Species	Source
Blubber	0.07[a]	*Mirounga leonina*	Bryden (1964)
	0.06[a, b]	*Phocoena*	Yasui and Gaskin (1986)
	0.18[a]	*Phoca groenlandica*	
		Phoca vitulina	
		Halichoerus grypus	Worthy (1985)
	0.20[a,c]	*Phoca hispida*	Scholander et al. (1950)
	0.21[a]	*Balaenoptera physalus*	Parry (1949)
Fat	0.21	human	Hensel et al. (1973)
	0.33	?	Stolwijk and Hardy (1977)
Fatty	0.16	stearic acid	CRC (1967)
acids	0.17	palmitic acid	CRC (1967)
	0.23	oleic acid	CRC (1967)

[a] Includes epidermal, dermal and hypodermal layers.

[b] Flux of 133.07 $kcal \cdot m^{-2} \cdot h^{-1}$ through 1.7 cm thickness having 14°C gradient.

[c] Average of 4 measured in water.

beluga (length 278 cm) in 15°C Hudson Bay water (Table 2). The average heat flux of 47 $W \cdot m^{-2}$ (161W/3.4 m^{-2}) over the skin surface of the 278-cm male beluga from Hudson Bay is similar to the 50 $W \cdot m^{-2}$ on the body of the whale called Churchill (Kasting et al. 1989). The O_2 metabolic estimates of Kasting et al. (1989) may be biased due to the short time interval over which expirations were collected and to the use of an assumed RQ of 0.80 rather than the measured values.

Stromberg (1985) judged the thermogenic effect of the oxidation of fatty acids and lipogenesis in the skin to be a useful adaptation especially in polar species of cetaceans. Because heat flow is directly related to temperature gradient, the maintenance of higher than ambient skin temperatures would be metabolically expensive regardless of the process used (mass transport of heat via the blood or thermogenesis of fat oxidation). If skin is thermally tolerant (possibly through high glycerol levels, Stromberg 1985), then temperatures in the skin could drop, thereby reducing heat loss. The non-saturation of fatty acids in the blubber would allow it to cool without the fat setting (Sokolov 1962). Muscle temperatures below 30°C in a net-entrapped narwhal in Tremblay Sound, Baffin Is., NWT, and a stranded beluga at Cunningham Inlet (Doidge, unpubl. data) indicates shell cooling similar to that found in fin whales (Brodie and Paasche 1985). The superior ability of fat to cool without losing physiological function may be the reason that it rather than muscle is deposited subcutaneously. Thus the fat acts as an insulative layer as a "consequence of its presence" (Pond 1978). Its insulative value does not appear to be maximised since blubber thickness (Fig. 3) relative to body radius (girth / 2π) is not constant (Ryg et al. 1988). Blubber distribution must therefore be influenced by additional factors, or the temperature distribution on the surface of the inner shell must also vary within girth interval.

Bel'kovich (1961) suggested the thick horny layer (*stratum externum*) of perinatal belugas was characteristic of all neonatal cetaceans. A 187 cm beluga from northern Soviet waters had skin 22 mm thick and blubber on the mid-back of 30 mm (Kleinenberg et al. 1969). Two beluga neonates examined in northern Quebec in 1985 had similarly thickened epidermis. A 160 cm calf had mid-lateral skin of 22 mm and blubber of 24 mm. Mid-lateral skin and blubber thicknesses of a 145 cm neonate was 25 and 10 mm, respectively. The observed color changes of neonates (Bel'kovich 1961; Sergeant 1973) suggests the outer layer of the *stratum externum*, which accounts for this extra thickness, is shed soon after birth. The outermost cells lack the cohesiveness to remain attached to the underlying layers (D. J. St. Aubin, OVC, University of Guelph, Guelph, Ont., pers. comm.).

Heat loss is related to the thermal conductivity and thickness of skin and blubber, but skin has only one half the insulative value. Epidermal thickness in neonates compensates for the reduced blubber layer. Thickened skin thus serves as a thermal buffer at birth, which is shed and replaced by blubber. No evidence of thickened skin was observed in the two narwhal near-term fetuses. However, the small number of animals examined precludes speculation on how widespread the phenomenon of perinatal pachydermy is in cetaceans.

The thermal benefit of estuaries is directly proportional to the temperature gradient across the skin and blubber to the animal's body core. Since narwhals and belugas appear to be equally insulated (Fig. 2) and yet only beluga have an estuarine habit, estuarine use must offer more than simply reducing heat loss. Elevated temperatures encountered by belugas in river mouths enhance the molting process of the skin and allow for other metabolic adjustments (St. Aubin and Geraci 1989; St. Aubin et al. 1990). It is not known if narwhal undergo the same rapid skin turnover without the benefit of higher water temperatures.

Although the thermostatic approach can give only an approximation of metabolic rate under the specific conditions mentioned earlier, this method allows comparison between individuals and species of cetaceans. Coupled with heat flow data and ultrasound measurements of blubber and skin, more detailed studies of the dynamics of cetacean energetics and thermoregulation can be undertaken using this approach on live specimens in captivity.

[1] Kasting et al. (1989), Table 2 report 28 $W \cdot m^{-2} \cdot °C^{-1}$ and $T_{skin} - T_{water}$ of 1.8°C which is equivalent to $W \cdot m^{-2}$.

Acknowledgments

D.E. Sergeant and P.F. Brodie sparked my initial interest in whale blubber and heat loss. P. Schuepp of Macdonald College provided heat flow equipment and advice on thermal matters and numerical methods. H. Silverman with the aid of S. Attagootak supplied the Pond Inlet narwhal data. R. Greendale, M. Hammill, I. Inookie and T. Smith helped with data collection in the high arctic. D. Albright, L. Caron, G. Horonowitsch, P. Inukpuk and D. St. Aubin provided assistance in N. Quebec. Hunters from the high arctic and N. Quebec kindly allowed their catch to be examined. Criticism from D. Albright, G. Beck, J. Geraci, M. Hammill, C. Lockyer, D. Sergeant, T. Smith, D. St. Aubin and two anonymous reviewers improved the manuscript.

Funding was provided by Fisheries and Oceans Canada, World Wildlife Fund Canada's "Whales Beneath the Ice" project, the Centre for Northern Studies of McGill University, and an NSERC postgraduate scholarship.

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Dynamics of Tooth Growth in Beluga Whales, *Delphinapterus leucas*, and Effectiveness of Tetracycline as a Marker for Age Determination

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Seven subadult beluga whales (*Delphinapterus leucas*) were captured in Hudson Bay, Canada, and held in captivity for up to 10 wk after receiving an intramuscular injection of oxytetracycline. Sections from teeth, extracted prior to their release, were examined under a microscope using ultraviolet light. Fluorescent marking was evident in the teeth of all the experimental animals, and provided a time reference from which tooth growth could be measured. After taking into account the age-specific changes in thickness of Growth Layer Groups (GLGs), the ratio of pre- to post-injection tooth growth provided an estimate of age. Calculated age was in agreement with a deposition rate of two GLGs per year. The strict seasonality of an arctic habitat is considered as a potential factor in explaining this phenomenon. The study also demonstrated that the teeth of beluga can be effectively marked by dosages of tetracycline lower than previously used in cetaceans.

Sept marsouins blancs subadultes (*Delphinapterus leucas*) ont été capturés dans la baie d'Hudson, au Canada, et gardés en captivité jusqu'à 10 semaines, après avoir reçu une injection intramusculaire d'oxytétracycline. Avant de les remettre en liberté, des sections de dents extraites furent examinées sous microscope utilisant une lumière ultraviolette. Un marquage fluorescent était évident dans les dents de tous les animaux expérimentaux, et a fourni une référence temporelle par laquelle la croissance dentaire pouvait être mesurée. Après avoir pris en considération les changements spécifiques à l'âge dans l'épaisseur des Groupes de Croissance en Couches (G.C.C.), le ratio de la croissance dentaire donna un estimé de l'âge entre la pré-injection et la post-concordance avec la cadence de dépositions de deux G.C.C. par année. Le précis des saisons de l'habitat arctique est considéré comme un facteur potentiel pour expliquer ce phénomène. Cette étude a aussi démontré que les dents des marsouins blancs peuvent être marquées efficacement avec des dosages de tétracycline moins élevés que ceux utilisés au préalable chez les cétacés.

Introduction

Aging belugas by counting tooth layers is controversial because of disagreement as to whether single or multiple growth-layer-groups (GLGs) (Perrin and Myrick 1980) are deposited annually. In belugas, as many as four GLGs are deposited before the tooth erupts and is exposed to wear. Erosion of the record of early growth can begin after as few as 15 GLGs have been laid down (Brodie 1969). Body growth rates of known-age animals have been difficult to obtain, and have so far been limited to measurements from long-term captive animals (Brodie 1982; Goren et al. 1987). Ideally a reference point within the calcified tissue is required in order to establish the rate at which the tooth grows and therefore what portion of the year is represented by a GLG.

Tetracycline administered to an animal binds with free body calcium, and is incorporated into hard tissue that is forming at the time the drug is introduced. This becomes detectable as fluorescence under ultraviolet illumination. Cetacean teeth have been so marked using tetracycline in dosages of 40–60 mg/kg of body weight (Best 1976; Gurevich et al. 1980) and 25 mg/kg (Myrick et al. 1984). The technique was first applied to beluga whales in Western Hudson Bay in 1968 by Sergeant and Brodie (1969a) who administered approximately 20 mg/kg to 93 tagged free-ranging specimens; however, none of the animals could be recovered for subsequent analysis because of reduced hunting from that large population. In 1984 and 1985 the experiment was repeated, but in a setting that guaranteed retrieval of teeth after a suitable period of time following administration of the drug.

Materials and Methods

Subadult beluga whales were captured in the estuary of the Seal River, Manitoba, on the western side of Hudson Bay, and held for up to 10 wk in 8.2 m diameter pools. The whales were fed thawed Pacific herring (*Clupea harengus pallasi*) and fresh cisco (*Coregonus artedii*), providing $1.7 - 2.1 \times 10^5$ J·kg body $wt^{-1} \cdot d^{-1}$.

Four individuals in July 1984 and three in August 1985 were given intramuscular injections of oxytetracycline (100 mg/mL), at a dosage of 10–20 mg/kg (Table 1). To achieve the desired dose, multiple injections of up to 10 mL each were administered using a 10 cm, 18 gauge needle directed into the epaxial musculature. After 3–7 wk, one tooth was extracted from each of six whales; three teeth were collected post mortem from the seventh. Prior to extracting a tooth, 3–4 mL of lidocaine was injected into the gum tissue. A dental gouge was used to free the teeth from the soft tissue attachment. Teeth were stored in NaCl, embedded in plastic and sectioned using a Gillings-Hamco thin sectioning machine (Hamco, Rochester, NY) and further handground on 600 grit wetpaper. The 40-50 μm thick sections were examined using a microscope equipped with an ultraviolet light source.

Results and Discussion

In view of the small number of animals available for study, we chose not to designate any of the whales as sham controls for the drug injections. We interpreted any fluorescent mark as the result of tetracyline labelling. Such are the limitations of field-based research on large marine mammals.

All teeth showed some degree of fluorescent marking, though there was variation in the degree of marking between individuals and in different teeth from the same individual. There was less intense deposition of tetracycline in the cementum, from the base of the tooth to within 3 – 5 mm of the tip, the portion of the tooth that was protruding from the gum and was not available to deposition. Teeth from animals with the lowest dosage of tetracycline (10 mg/kg) were as intensely marked as those from whales receiving twice the dosage.

TABLE 1. Age estimates of beluga based on tooth layer counts and the ratio of dentine deposition before and after tetracycline injection.

Whale ID#	Sex	Length (cm)	Time (d) between injection and tooth extraction	GLG counts		Age estimate (yr) indicated by tetracycline mark/ total dentine
				Dentine	Cement	
SR0384	M	254	24	4	4	2.17
SR0284	F	267	51	5 – 6	4	2.10
SR2385	M	272	48	6	5	2.00
SR0184	F	269	26	8 – 9	8	4.27
SR1685	M	274	44	8 – 9	9 – 10	2.77
SR2185	F	295	48	10 – 12	10	4.82

To use post-injection tooth growth as an index of age, the cumulative, median widths of previous GLGs were compared with the thickness of substrate deposited after the tetracycline mark. Since the post-injection period was known precisely, the ratio provided an age estimate. This approach will underestimate the age of younger animals because GLG thickness in beluga increases with age to about physical maturity, then declines (Fig. 1), a trend which is apparently not found in many of the other odontocetes (Myrick 1988). The magnitude of the error decreases with the age of the animal. Based upon the growth trend in Fig. 1, the correction would bring the estimates more into agreement with ages based upon dentine and cementum laminae at a ratio of two GLGs per year. In order for single GLGs to represent annual growth, a correction of 100% would be required.

A particularly unusual finding in three of the whales was the occurrence of distinct double bands in the dentine and, though less well defined, in the cementum (Fig. 2). One band was deposited within the collagen matrix containing the tubule extensions of the odontoblasts, sometimes referred to as Tomes' fibres (Miles 1967; Brodie 1970). The other was at the base of the tubules, adjoining the pulp cavity.

Tomes' fibres are part of the mechanism by which mineralization proceeds (Miles 1967; Brodie 1970). These tubules appear to be formed coincidentally with the extrusion of collagen

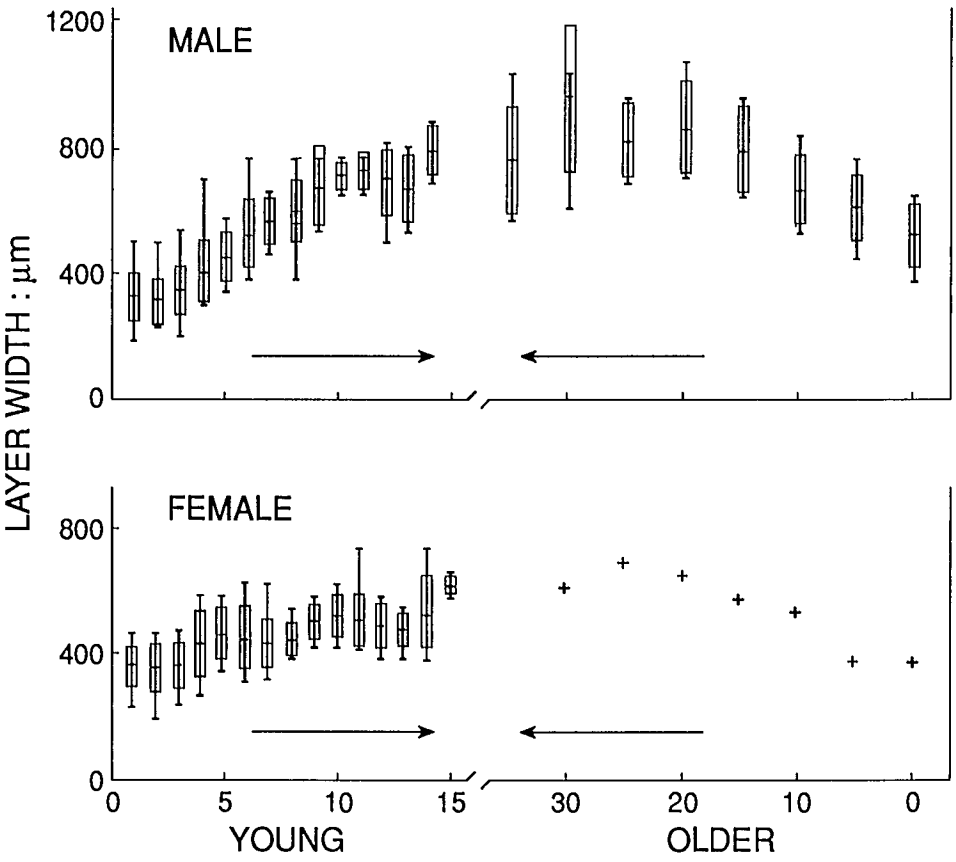

FIG. 1. Thickness measurement of GLGs of male and female belugas, measured as shown in Fig. 2B. Arrows indicate the direction in which the GLGs were measured. Teeth of younger animals, with prenatal teeth still discernible, provided thickness measurement for the first 15 GLGs. Older animals, with much of the tooth worn away, provided GLG thicknesses counting from the pulp cavity, towards the worn tip. Only one older female was included in the sample. (from Brodie 1970)

and are pinched off in unison from the odontoblasts (Fig. 2). The collagen substrate continues to be produced and carries with it this sheet of tubules. In unstained, longitudinal sections of teeth it is this sheet of tubules which appears as a dark layer in transmitted light and as white layer in reflected light. Fine laminations within the collagen, running parallel to the edge of

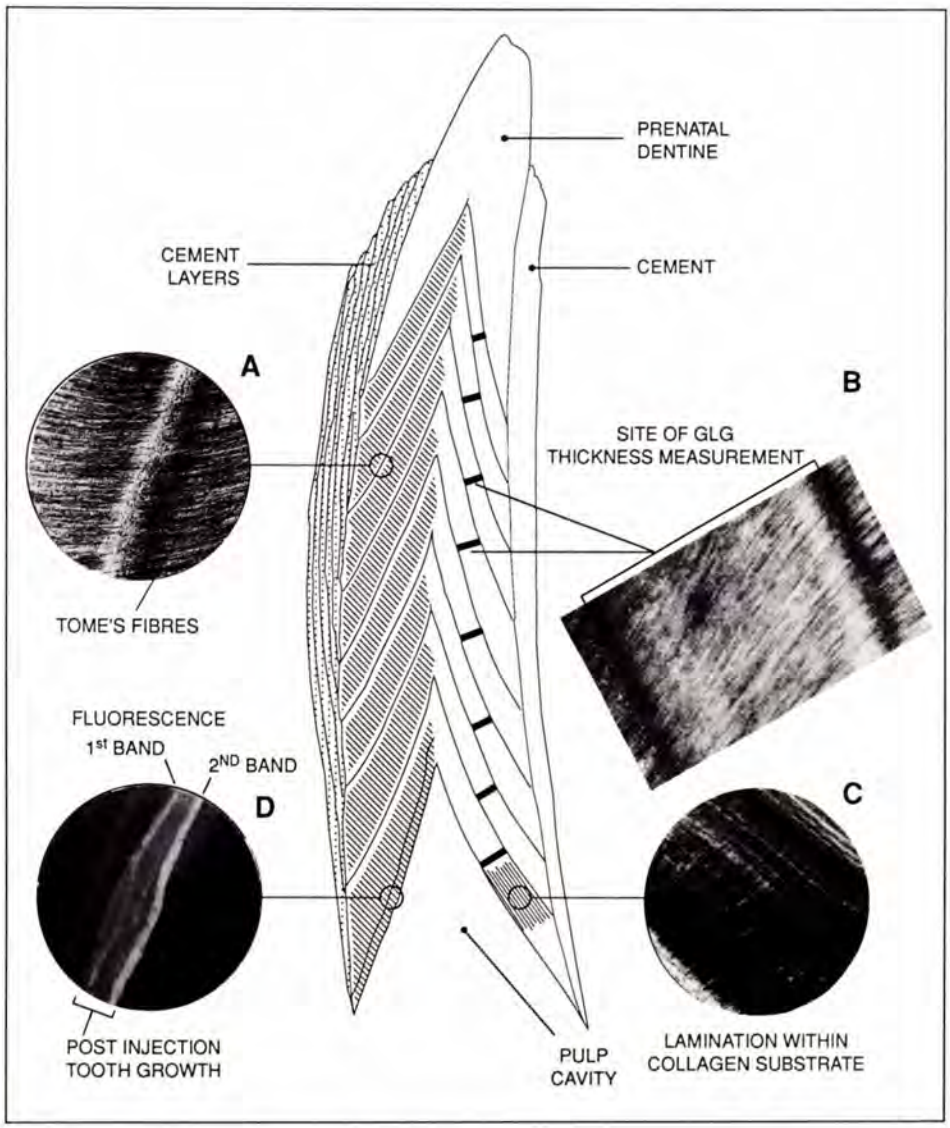

FIG. 2. General structure of a beluga tooth in long section, with microphotographs of features. Eight Growth Layer Groups are depicted here. (A) Tomes' fibres as seen with transmitted light, showing the cessation and continued extrusion of the tubules. (B) Growth Layer Group (GLG) as seen by reflected light, which includes one dark and one light layer within the dentine. (C) Collagen substrate within the GLG, which appears to be extruded in pulses. Tome's fibres are seen here by transmitted light, perpendicular to the pulp cavity. (D) Fluorescent bands formed after injection of tetracycline. Two bands are seen here: the first being deposited immediately after injection. while the second band is formed at the interface with the pulp cavity.

the pulp cavity (Fig. 2), suggest that this substrate may be extruded in pulses and, relative to post-injection deposition as indicated by the tetracycline mark, each pulse may represent 1–2 wk. There is evidence that tooth mineralization was in progress among the experimental animals at time of capture, since the Tomes' fibres seem to have been in various stages of extrusion when the drug was administered. Single fluorescent bands were observed at the distal ends of the tubules in some animals and mid-way along the tubule formation in others, indicating that there were sites of mineralization along the tubules and intertubular spaces.

A simple test was conducted to ascertain whether the band at the proximal end of the Tomes' fibres, in contact with the pulp cavity, was an "edge effect," with the tubules acting as optic fibres, conducting fluorescence back to the surface. Under a microscope using UV light, small pieces of the tooth section containing the proximal band were broken off. The broken pieces continued to fluoresce, while the newly exposed edge on the tooth section did not. This eliminated the possibility of an edge effect and indicated that the proximal band was real.

We do not know if the inner band at the pulp cavity would have eventually fused with the outer one, or would have formed a separate fluorescent band within the extruded substrate, because the experimental animals were released. We also cannot exclude the possibility that the pattern might simply have been an artifact of captivity, even though only three of the experimental animals had evidence of double banding. It is possible that some tetracycline may have been withheld, by bonding with calcium in the bloodstream, causing a delay in complete deposition within bones and teeth. Such an artifact might also complicate interpretation of a series of tetracycline injections administered over a long period in captivity (Myrick et al. 1988).

The occurrence of double bands suggests an unusual pattern of dentine deposition in this species. Their teeth appear to grow continuously via collagen extrusion, punctuated by regular periods of mineralization (Brodie 1969). These periods may coincide with seasonal cycles in hormone secretion, such as has been observed for thyroid activity in these animals (St. Aubin and Geraci 1989). Normal calcium deposition may be interrupted by episodes of hypocalcemia, perhaps associated with reproduction or stress (Myrick 1988) from physical injury (for example, from massive bullet wounds) which result in resorption and mobilization of minerals that have already been deposited (Brodie 1970).

We do not propose that the observed artifact of double lamination of tetracycline bands is argument for double GLGs per annum, simply that the initial mark indicates the rate of tooth growth and the relative age. The rate at which the tooth grows, as indicated by tetracycline marking, adds to a body of evidence that in this species, there is the potential for multiple, rather than single, laminations to be deposited annually. Tentative classification of calves by year class in the field, using several parameters — body growth rate (Brodie 1971) and skin color change of a captive animal (Brodie 1982) — have provided evidence for multiple, rather than single, GLGs as annual deposits; the reason for this continues to be elusive.

The natural lamination sequences may reflect temporary consistent activities, in which the entire herd participates, such as an early winter movement out from the coasts to feeding areas in ice-free waters (Kleinenberg et al. 1964) and a return in early summer, half a year later, to coastlines and estuaries. The beluga is one of the few circumpolar odontocetes subject to the extremes of strict seasonality imposed by such a high latitude, where the year is clearly divided into two parts (Brodie 1969). The Gulf of St. Lawrence population, the most southerly habitat for this species, is subject to essentially the same subarctic conditions. This predictable seasonality in belugas raises the question as to whether other species, with cyclical patterns, for example, its cohabitant, the narwhal (*Monodon monoceros*) or the highly migratory sperm whales (*Physeter catodon*), are similarly affected.

The study demonstrated that the teeth of beluga whales can be effectively marked by dosages of tetracycline lower than previously used in cetaceans. The higher proportion of blubber (as much as 40%, Sergeant and Brodie 1969b) on this arctic-adapted species may suggest that body tissue composition should be taken into account when estimating effective

dosages in marine mammals. Still, even in its most concentrated form (100 mg/mL), the volume of tetracycline solution to mark a 500-kg whale would be in the order of 50 to 100 mL, considerably more than the 10 mL volume regarded as the safe limit for injection into a single site. Thus, any marking program for belugas would require that the animals be temporarily restrained for multiple injections.

Acknowledgments

We thank T. Friesen and C. Thomson (University of Guelph) and J. Orr and S. Waters (Dept. of Fisheries and Oceans) for field assistance and maintenance of the whales. R. Moshenko, Section Chief (DFO), coordinated logistic support for the whale capture and field camp. Tooth sections were prepared by D. W. Doidge. The authors wish to thank the referees for their very constructive comments. Funding for the study was provided by the Department of Fisheries and Oceans, The World Wildlife Fund ("Whales Beneath the Ice" Program), and the Natural Sciences and Engineering Research Council (Grant A6130 to JRG).

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Adrenal Responsiveness to Stimulation by Adrenocorticotropic Hormone (ACTH) in Captive Beluga Whales, *Delphinapterus leucas*

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The effect of 75 IU of bovine adrenocorticotropic hormone (ACTH) on circulating adrenal hormones and white blood cells was assessed in two beluga whales, *Delphinapterus leucas*, immediately after capture, and in five others on seven occasions during the course of 10 wk in captivity. Five control studies using saline were carried out on four of the whales held for at least 6 wk; a sixth control injection was performed on one whale immediately after capture. Blood samples were collected prior to, and 0.25, 0.5, 1, 2, 3, 4, 5, 6, 12, and 24 h after, injection with ACTH or saline solution. Stimulation by ACTH significantly elevated circulating levels of cortisol and aldosterone, and depressed total eosinophil counts. The increase in aldosterone was proportionately greater and more consistent than for cortisol. Peak response for aldosterone occurred 2 h after stimulation, and normal values were restored after 6 h. Eosinophil counts declined steadily during the first 12 h after ACTH stimulation, and were within the normal range after 24 h. The pattern of hormonal and cellular changes in acclimated whales was comparable to that observed in whales tested immediately after capture.

L'effet de 75 IU de l'hormone adrénocorticotropic bovine (ACTH) sur les hormones circulatoires surrénales et les cellules blanches sanguines fut évalué chez deux marsouins blancs, *Delphinapterus leucas*, immédiatement après les avoir capturés, et chez cinq autres, à sept occasions, au cours des 10 semaines de captivité. Cinq études de contrôle utilisant une saline furent effectuées chez quatre des baleines gardées pendant au moins 6 semaines; une sixième injection de contrôle fut administrée chez une baleine immédiatement après la capture. Des échantillons de sang furent recueillis avant, et 0.25, 0.5, 1, 2, 3, 4, 5, 6, 12, 24 h après une injection avec l'ACTH ou une solution saline. La stimulation par l'ACTH éleva d'une façon significative les niveaux circulatoires de cortisol et d'aldostérone, et a abaissée la numération éosinophile totale. L'augmentation d'aldostérone était proportionnellement plus forte et plus uniforme que pour le cortisol. La réaction de pointe pour l'aldosterone se produisit 2 h après la stimulation, et les valeurs normales furent rétablies après 6 h. Le décompte d'éosinophiles déclina d'une façon régulière durant les 12 h après la stimulation par l'ACTH, et était dans le champ normal après 24 h. L'échantillonage des changements hormonaux et cellulaires chez les baleines acclimatées était comparable à celle observée chez les baleines examinées immédiatement après la capture.

Introduction

An integral part of the mammalian stress response is the release of steroid hormones from the adrenal cortex. Secretion is controlled principally by adrenocorticotropic hormone (ACTH) produced by the anterior pituitary, which in turn is regulated by corticotropin-releasing hormone (CRH) from the hypothalamus. Exogenous ACTH or CRH can be used as a controlled stimulus to determine the responsiveness of the adrenal cortex *in vivo*. This protocol has broad applications as a diagnostic tool and in experimental studies on a variety of species (Paape et al. 1977; van Mourik and Stelmasiak 1984; Willard et al. 1987), including marine mammals (St. Aubin and Geraci 1986; Thomson and Geraci 1986).

Continuous infusion of ACTH produces a biphasic response from the adrenal. Initially, plasma levels of cortisol and aldosterone are increased, but after 48–72 h, the aldosterone response is attenuated, an adaptation referred to as "aldosterone escape" (Gaillard et al. 1983; Oelkers 1985). The adjustment is associated with morphologic and enzymatic changes in the zona glomerulosa of the adrenal, reducing its capacity to synthesize and secrete aldosterone (Mazzocchi et al. 1986; Riondel et al. 1987). We used ACTH stimulation to indirectly assess whether a similar transformation was associated with acclimation to captivity in beluga whales, *Delphinapterus leucas*.

Materials and Methods

Eight beluga whales were captured in the Seal River estuary during July, 1985 (Table 1). Three were studied immediately after capture, then released. The others were transported to holding facilities, where they were maintained for 10 wk in two 8.2-m-diameter pools containing 3.8×10^4 L of water renewed daily from Hudson Bay. The whales were fed Pacific herring, *Clupea harrengus pallasi*, supplemented with vitamins, but were fasted for 12 h before, and for the first 6 h of, each study.

During the latter 5 wk of the holding period, seven ACTH stimulation tests and five sham controls were conducted (Table 1). All of the trials were begun between 07:45 and 10:15 h. For a test, the pool was drained to a depth of less than 30 cm, a procedure that required approximately 1 h. A sample of venous blood from the caudal peduncle or the flukes of each beluga to be studied was drawn into chemically clean sterile syringes then transferred to vacuum tubes containing heparin for plasma chemical analysis, and EDTA for hematological determinations. A 15-cm needle was used to deliver 75 IU (0.2–0.28 IU/kg) of Cortrosyn (Organon Canada Ltd., Toronto, Ont.) or 3 mL of saline (control) into the dorso-lateral musculature, in line with the middle of the dorsal ridge. Thereafter, samples were nominally taken at 15 and 30 min, and 1, 2, 3, 4, 5, 6, 12, and 24 h. Specimens were held on ice until further processed. The holding pool was refilled following the 6 and 12 h samplings, and drained again to collect samples at 12 and 24 h post injection.

TABLE 1. Schedule of ACTH stimulation tests and saline controls, expressed as the number of weeks after capture.

Whale	Sex	Length (cm)	Weight (kg)	ACTH Test	Control
DL7	M	246	—	0	—
DL8	M	345	—	0	—
DL24	M	269	—	—	0
DL4	M	269	275	6	—
DL14	F	269	270	9	7
DL16	M	274	330	10	6,10
DL21	F	295	370	5,9	10
DL23	M	272	350	6,8	10

Eosinophil determinations were made within 24 h of blood collection; blood smears and total leukocyte counts were made within 48 h. Duplicate counts of eosinophils and total leukocytes were performed using Unopette system (Becton-Dickinson) and a Neubauer hematocytometer. Differential white blood cell counts were performed by counting 200 cells on a Wright's stained peripheral blood smear using the cross-sectional method. To maintain uniformity when calculating percentages, total white blood cell (direct) counts and blood smears were made at the same time.

In the field camp, blood for hormonal and chemical analysis was centrifuged within 1 h of collection; the plasma was transferred to sterile culture tubes and immediately frozen. Samples from the three whales studied at the capture site were held on ice for up to 24 h before processing. Plasma chemical constituents, including electrolytes (Na, K, Cl, Ca, P, and Fe), metabolites (glucose, cholesterol, triglycerides, urea, uric acid, and creatinine), enzymes (creatine kinase, alkaline phosphatase, aspartate aminotransferase, alanine aminotransferase, lactate dehydrogenase, and γ- glutamyl transpeptidase), protein, and steroid hormones were analysed as previously described (St. Aubin and Geraci 1989).

Statistical comparisons were made by univariate analysis of repeated measures, according to the Statistical Analysis System (SAS Institute, Cary, N.C.).

Results

Cortrosyn, a synthetic peptide containing 24 of the amino acids of natural ACTH, was effective in eliciting the release of adrenal hormones in beluga whales. No attempt was made to use graded doses to establish whether the observed response represented maximal stimulation. We present the findings in terms of the peak response for each animal, and, in the interest of establishing an abbreviated sampling protocol for future studies, at intervals selected to demonstrate the most consistent changes in each of the hormonal and cellular constituents (Tables 2 and 3). Samples collected 2 h after stimulation showed maximal or near maximal release of aldosterone and cortisol, whereas changes in eosinophils and lymphocytes were most evident in the 6 h sample.

Immediate Response

The stress of chase and capture alone elicited a characteristic adrenal response. Blood samples obtained from whale DL24 during the first 6 h after capture showed rising concentrations of cortisol (190% after 2 and 6 h) and aldosterone (400% after 2 h) (Fig. 1, Table 2). During this time, circulating eosinophils declined by 55% (Fig. 1), from an initial count of 2.88 x 10^9 cells/L, and lymphocytes by 81%, from 5.8 x 10^9 cells/L.

In the two whales injected with ACTH within 1 h after capture, cortisol showed a similar incremental increase of 100–120 nmol/L, but because the initial values were lower than in DL24, the proportional change (360% and 420% after 3 and 5 h, respectively) was greater (Fig. 1, Table 2). Peak concentrations of aldosterone were noted at 2 h after capture, and reached 570% and 1280% of initial levels in the two ACTH-stimulated whales. After 6 h, counts of circulating eosinophils had declined by 80% from 6.25 x 10^9 cells/L in DL7, and by 30% from 2.28 x 10^9 cells/L in DL8 (Fig. 1, Table 3). Lymphocyte counts decreased from 4.0 to 0.8 x 10^9 cells/L in DL7, but in DL8 showed no consistent change from a relatively low initial count of 1.1 x 10^9 cells/L.

Response in Acclimated Whales

The findings in whales studied 5–10 wk after capture are shown in Fig. 2, and summarized on Tables 2 and 3. On average, the maximum percent response was lower for cortisol and greater for aldosterone in the four ACTH trials conducted after 8–10 wk in captivity,

TABLE 2. Hormonal response to saline (CONT) or ACTH injection in beluga whales. Peak concentrations are expressed as percent of the value at the start of each trial. Numbers in parentheses show the time, in hours, when the highest steroid concentrations were observed.

		Cortisol			Aldosterone		
Whale no.	Treatment schedule[a]	Initial level[b]	2 h sample[b]	Max % Inc. (time)	Initial level[c]	2 h sample[c]	Max % Inc. (time)
Immediate Response							
DL7	ACTH - 0	41	116	420 (5)	100	1340	1280 (2)
DL8	ACTH - 0	39	135	360 (3)	140	820	570 (2)
DL24	CONT - 0	132	246	190 (2)	230	950	400 (2)
Response after Acclimation							
DL4	ACTH - 6	135	223	310 (6)	70	300	470 (4)
DL14	CONT - 7	94	119	210 (1)	70	70	320 (1)
	ACTH - 9	36	210	590 (3)	70	820	1180 (2)
DL16	CONT - 6	113	77	90 (1)	260	70	50 (1)
	CONT - 10	218	105	70 (1)	80	70	110 (1)
	ACTH - 10	102	80	190 (1)	70	150	2160 (2)
DL21	CONT - 10	28	69	420 (1)	200	70	35 (1)
	ACTH - 5	28	39	220 (12)	70	590	850 (2)
	ACTH - 9	163	201	150 (3)	70	710	520 (1)
DL23	CONT - 10	138	28	80 (1)	100	70	70 (1)
	ACTH - 6	72	221	460 (3)	70	970	1410 (3)
	ACTH - 8	119	174	190 (4)	70	680	970 (2)

[a] Time, in weeks after capture, when the whale was tested.
[b] Cortisol concentration in nmol/L.
[c] Aldosterone concentration in pmol/L.

compared with the three earlier trials. However, in whales DL21 and DL23, which were injected with ACTH on two occasions, the maximum change for both steroids was less during the later trials (Table 2). The timing of the sham control injections had no apparent effect on the hormonal response in the whales.

A mild adrenocortical response was associated with the manipulation required to conduct the tests. In whales receiving a control injection of saline, mean cortisol levels ranged between 120 and 135 nmol/L during the first hour of sampling, and thereafter declined to roughly half of the initial values. Concentrations greater than 100 nmol/L were again noted in samples collected after 12 and 24 h, as a further response to draining the holding pool. Aldosterone concentrations initially followed a similar pattern; samples collected during the first hour had concentrations of 120–170 pmol/L, whereas subsequent specimens averaged 70 pmol/L or less. In contrast to cortisol, aldosterone levels showed no further increase in the 12 and 24 h samples. Mean eosinophil counts remained within 30% of initial values ($2.95 \pm 1.50 \times 10^9$ cells/L) throughout the sampling period. Circulating lymphocytes were affected only in the three animals with counts greater than 2.0×10^9 cells/L in samples drawn at time 0; in these animals, a 35–60% decrease in cell counts occurred after 5–6 h. Initial counts in these whales ranged from 2.5 to 3.4×10^9 cells/L, whereas in the other two trials the values were 1.4 and 1.9×10^9 cells/L.

Table 3. Changes in circulating eosinophil and lymphocyte counts following saline (CONT) or ACTH injection in beluga whales. Minimal counts are expressed as percent of the value at the start of each trial. Numbers in parentheses show the time, in hours, when the lowest cell counts were observed.

		Eosinophils			Lymphocytes		
Whale no.	Treatment schedule[a]	Initial level[b]	6 h sample[b]	Max % Dec. (time)	Initial level[c]	6 h sample	Max % Dec. (time)
Immediate Response							
DL7	ACTH - 0	6.25	1.32	21 (6)	4.0	nd	19 (5)
DL8	ACTH - 0	2.28	1.59	69 (5)	0.9	0.8	89 (4)
DL24	CONT - 0	2.88	1.26	44 (6)	5.8	1.1	19 (6)
Response after Acclimation							
DL4	ACTH - 6	1.74	0.47	9 (12)	2.8	1.9	39 (5)
DL14	CONT - 7	4.92	3.78	60 (12)	1.4	1.5	93 (3)
	ACTH - 9	4.80	1.74	28 (12)	1.7	1.1	24 (3)
DL16	CONT - 6	1.22	0.87	64 (4)	2.5	1.0	40 (6)
	CONT - 10	1.33	1.09	75 (12)	1.9	2.2	89 (3)
	ACTH - 10	1.55	0.46	30 (6)	3.1	2.0	39 (5)
DL21	CONT - 10	4.24	4.48	82 (3)	3.4	3.4	59 (5)
	ACTH - 5	4.99	2.50	22 (12)	1.9	1.3	58 (3)
	ACTH - 9	3.73	2.33	51 (5)	2.2	3.1	73 (12)
DL23	CONT - 10	3.05	2.35	77 (6)	3.5	2.1	66 (5)
	ACTH - 6	2.74	1.17	31 (12)	2.3	2.4	74 (3)
	ACTH - 8	2.02	1.29	59 (12)	1.8	2.0	67 (2)

[a] Time, in weeks after capture, when the whale was tested.

[b] Cell counts in 10^9 cells/L

Injection of ACTH significantly increased circulating levels of aldosterone ($F_{1,8} = 8.43$, $P < 0.05$) (Fig. 2). On average, peak aldosterone concentrations were 10-fold greater than in controls at each time interval; the greatest relative increase was 2140% in DL16. The large individual variation in cortisol response obscured any significant effect of ACTH treatment on the group as a whole ($F_{1,8} = 1.67$). In most of the trials, a two- to three-fold increase was observed, although cortisol levels were elevated nearly six-fold in DL14. Because of the wide variation in initial eosinophil counts ($3.08 \pm 1.33 \times 10^9$ cells/L) among the whales, statistical comparisons using actual counts at each sampling revealed no significant effect of ACTH. However when the data were expressed as a percentage of initial values for each whale, the changes in relative values were readily apparent and highly significant ($F_{1,8} = 10.05$, $P < 0.01$). Pre-test levels were restored in the 24-h sample. In four of seven trials, lymphocyte counts decreased by at least 30% after 5–6 h, and in two of these, did not recover by 24 h.

There were few significant changes in any of the other plasma chemical constituents or hematological elements analysed in samples collected during the stimulation tests. In the 6-h sample, glucose concentrations had significantly ($P < 0.05$) increased in the test animals (7.0 ± 0.8 mM/L, n=7, vs. 6.1 ± 0.3 mM/L at time 0, n=7), and decreased in the controls (6.0 ± 0.3 mM/L, n=5, vs. 6.6 ± 0.5 mM/L at time 0, n=5); comparison of test vs. control for the 6-h sample showed a similar statistical difference ($P < 0.05$). In the control group, iron

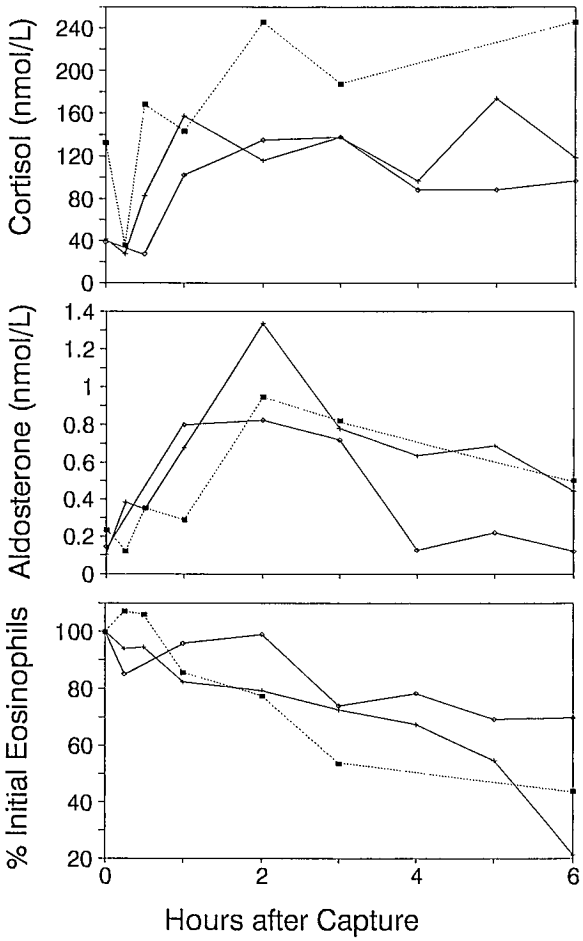

FIG. 1. Plasma cortisol and aldosterone concentrations and relative changes in circulating eosinophil counts in 3 beluga whales during the first 6 h after capture. Two whales (DL7 —+; DL8 —⁄) were given 75 IU of ACTH; DL24 (■ – – – ■) received a control injection of saline.

concentration decreased from 47.2 ± 12.1 μM/L (n=5) at time 0 to 28.3 ± 2.1 μM/L at 12 h, and 17.3 ± 4.7 μM/L at 24 h (n=3 for each), though statistical comparisons are not possible because of the small sample size. A similar trend was apparent in ACTH stimulated whales, but wide variation in initial levels (34.3 ± 15.8 μM/L) obscured the significance of the findings.

Discussion

The adrenocortical response to a single injection of ACTH in belugas was comparable to that in bottlenose dolphins (Thomson and Geraci 1986). The most consistent feature of the response, which distinguishes it from that in terrestrial mammals, is the large proportional increase in aldosterone (Johnson-Kocal 1985; St. Aubin and Geraci 1986). We have previously suggested that this pattern, which is shared to some extent with seals, is an adaptation to the marine environment (St. Aubin and Geraci 1986).

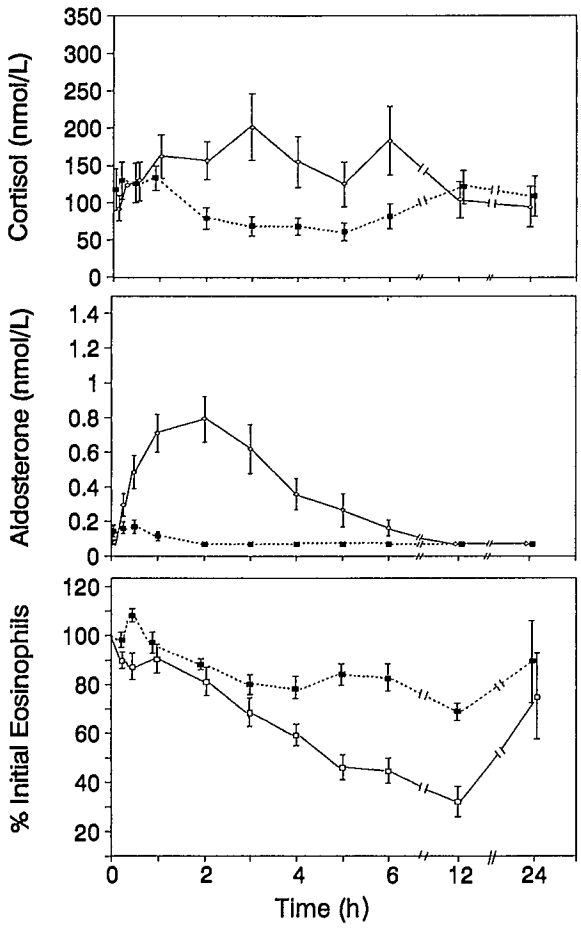

FIG. 2. Plasma cortisol and aldosterone concentration, and relative change in circulating eosinophil counts (mean and se) in 7 tests on 5 whales given 75 IU of ACTH (□), and in 5 control tests on 4 whales (■).

The influence of ACTH on aldosterone secretion, though evident in other species including people (Nicholls et al. 1975; Chan 1979; Seely et al. 1989), is particularly well developed in cetaceans. The mechanism underlying this adaptation is unclear. Chu and Hyatt (1986) isolated from rat adrenal a population of zona glomerulosa cells that is highly responsive to ACTH, and perhaps similar cells are abundant in the outer cortex of the cetacean adrenal. A directed study is clearly needed to address this hypothesis.

By comparison, the cortisol response was variable and comparatively weak, making this hormone an unreliable index of the degree of adrenal stimulation in these animals. We assumed that cortisol is the predominant glucocorticoid in this species, as it was shown to be in bottlenose dolphins (Thomson and Geraci 1986), and therefore we did not examine changes in other cortical secretions, such as corticosterone. Perhaps larger doses of ACTH would have produced greater elevations in cortisol, but in our experience higher levels have only been observed under pathological conditions such as terminal shock associated with stranding. Forewarned by the deaths of two bottlenose dolphins given slightly higher doses

of ACTH in a previous study (Thomson and Geraci 1986), we selected a more conservative dose for this investigation. We felt it would be imprudent to place other animals at such risk by conducting a dose–response trial simply to establish maximal hormone release.

The systemic effects of even modest changes in plasma cortisol are reflected in the consistent decline in circulating eosinophils, the brief elevation in glucose, and suggestion of reduced plasma iron. In the same whales, we also noted a concurrent decline in triiodothyronine levels (St. Aubin and Geraci 1988). Perhaps the metabolic systems regulating these constituents are particularly sensitive to cortisol. Alternatively, cetacean plasma may have a lower capacity to bind the hormone, and consequently is less able to buffer changes in free hormone concentration. Studies in progress in our laboratory suggest that the latter may apply.

Lymphopenia has been associated with corticosteroid administration in bottlenose dolphins (Medway et al. 1970), but not in those stressed by handling or stimulated by ACTH (Thomson and Geraci 1986). In belugas, circulating lymphocytes appear to be more sensitive to adrenocortical activity associated with initial capture (St. Aubin and Geraci 1989) than to injection of ACTH. One consistent pattern in both control and experimental groups was that little change occurred when basal counts were low. These low values suggest that in some individuals lymphocyte reserves were already depleted, perhaps as a consequence of episodic glucocorticoid secretion as the animals acclimated to captivity. Fauci and Dale (1974) observed that hydrocortisone selectively affects T-lymphocytes, and it is possible that these cells were already depleted in some of the initally lymphopenic animals. We made no attempt to distinguish between T- and B-cell populations in the belugas.

Within the latter four weeks of the holding period, the two whales tested twice with ACTH showed some attenuation of the peak aldosterone response, but not enough to suggest an "escape" from ACTH control. It remains to be established whether continuous stimulation by ACTH does in fact result in loss of response from the zona glomerulosa in these animals. In view of the peculiar demands on electrolyte balance in the marine environment, such a mechanism would appear to be maladaptive in marine mammals.

Acknowledgments

We thank T. Friesen and C. Thomson (Univ. of Guelph), J. Orr and S. Waters (Department of Fisheries and Oceans), and J. Batstone (Churchill, Manitoba) for invaluable assistance in the field. C. Thomson (Univ. of Guelph) performed the laboratory analyses, and M. Cattet (Univ. of Guelph) and D. W. Doidge (McGill University) assisted with data analysis. R. Moshenko (Section Chief, DFO) coordinated logistic support for the whale capture and field holding facilities. This study was funded by the Department of Fisheries and Oceans, The World Wildlife Fund ("Whales Beneath the Ice" Program), the Natural Sciences and Engineering Research Council (Grant A6130 to JRG), and the United States Office of Naval Research (Grant N00014-87-G-0114).

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Assessment of Immunological Function in Captive Beluga Whales, *Delphinapterus leucas*: Humoral Response to Sheep Red Blood Cell Antigens

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The humoral response to sheep red blood cells (SRBC) was examined in six beluga whales, *Delphinapterus leucas*, captured and maintained for 10 wk near Seal River, Manitoba. Three were sensitized by intraperitoneal injection of the antigen immediately after capture, and challenged by the same route 12 d later. The others were similarly tested after 45 and 57 d, respectively, in captivity; one of the whales in this group was released prior to receiving a challenging dose of SRBC. A weak antibody response (1/2 dilution) to the sensitizing dose was noted in only one of the first whales tested. Rapidly rising titers (up to 1/256) were demonstrated after challenge in all five whales. The findings from this limited first attempt to probe humoral immunity in a cetacean demonstrate the suitability of the approach, and suggest that this component of the whales' immune system was unaffected by the stress associated with acclimation to captivity.

La réaction humorale aux cellules rouge du sang d'agneau (SRBC) fut examinée chez six marsouins blancs, *Delphinapterus leucas*, capturés et retenus pendant 10 semaines près de la rivière Seal au Manitoba. Trois furent sensibilisés par injection intrapéritonéale d'un antigène immédiatement après la capture et provoqués par la même voie 12 jours plus tard. Un contrôle similaire a été fait chez les autres en captivité après 45 et 57 jours, respectivement; une baleine de ce groupe fut relâchée avant d'avoir reçu une dose provocatrice de SRBC. Une faible réaction anticorps (dilution 1/2) à la dose de sensibilisation a été notée seulement chez une des premières baleines provoquées. Une augmentation rapide de la titrimétrie (jusqu'à 1/256) fut notée après provocation chez les cinq baleines. Les résultats de ce premier essai préliminaire d'exploration d'immunité humorale chez un cétacé démontre le bien fondé de cette approche et suggère que cette composante du système immunitaire des baleines n'a pas été affectée par le stress associé avec une acclimatisation à la captivité.

Introduction

The immune response to foreign antigens is a complex of cellular and chemical events. The ability of an individual to mount such a response can vary according to nutritional (Sheffy and Williams 1982) and hormonal status (Grossman 1984), and prior exposure to a given

challenge. A number of indirect approaches are used to gauge immune competence (Dean et al. 1979; Muneer et al. 1988), including analysis of lymphocyte subpopulations, lymphocyte response to mitogenic stimulation, measurement of specific immune mediators, assessment of antibody levels, and resistance to infectious challenge. With little of such information for cetaceans, and none for belugas, we are at a loss to determine immunocompetence in free-ranging individuals and populations.

As a first remedial step, we undertook this study to determine the antibody response in captive beluga whales injected intraperitoneally with sheep red blood cells (SRBC). The whales were challenged at different times after capture to assess their ability to mount an immune response in the face of ongoing physiological and hormonal adjustments to captivity (St. Aubin and Geraci 1988, 1989). The study thus provides some insight into the sensitivity of the immune system to a foreign antigen in beluga whales during early confinement.

Materials and Methods

Six beluga whales (3M, 3F) were captured in the Seal River estuary in early July, 1985, and transported to nearby holding facilities where they were maintained for 10 wk in two 8.2-m diameter pools containing 3.8×10^4 L of seawater drawn and replaced daily from Hudson Bay. The whales were fed Pacific herring, *Clupea harrengus pallasi*, supplemented with thiamine and α-tocopherol, to provide an average of 40 $kcal \cdot kg^{-1} \cdot d^{-1}$.

Blood samples drawn from veins in the caudal peduncle or tail flukes were obtained from four whales at the time of capture, and from all six 3–4 h later after transport to holding facilities. Thereafter, the whales were sampled at irregular intervals, as part of a routine health assesment. Blood for hematology was collected into tubes containing the sodium salt of ethylenediaminetetraacetic acid (EDTA), for plasma chemical analysis into heparinized tubes, and for antibody tests into untreated vials. Hematological and plasma chemical constituents were analyzed as previously described (St. Aubin and Geraci 1989).

On arrival at the field camp, three of the whales (Group A) were injected intraperitoneally, with a 10-cm 18-gauge needle, containing 6.3 mL of a 30% (v/v) solution of SRBC. Twelve days later, they received a second injection of 5.0 mL of an 18% solution. The other three whales (Group B) were given the same doses, 45 and 57 d after capture.

The antigen was prepared from whole sheep blood, diluted 1:1 with Alsever's solution and stored at 4°C for up to 1 mo. After centrifugation for 10 min at 1 000 g, the supernatant and buffy coat were removed. The red cells were resuspended in an equal volume of phosphate buffered saline (PBS, pH 7.4, 0.15 M), centrifuged again, and the supernatant discarded. An appropriate volume of PBS was added to produce the final SRBC solutions.

Antibody titers were determined by the hemagglutination technique (Herbert 1978). To inactivate complement system proteins, the serum samples were held in a water bath at 56°C for 1 h. Duplicate serial dilutions of test serum in PBS (total volume — 49 μL) were made in U-bottom microtiter plates, to which 25 μL of a 1% solution of SRBC was added. Serum from a rabbit immunized against SRBC was assayed concurrently as a positive control; fetal calf serum and PBS served as negative controls. The plates were incubated at room temperature overnight on a shaker, then examined for evidence of hemagglutination. Antibody titer is reported as the most dilute preparation yielding at least 50% hemagglutination.

Results

A weak antibody response (1/2 dilution) to SRBC was detected in one of the three whales in Group A 5 and 7 d after the first injection; all three animals showed a humoral reaction after

a challenging injection on day 12 (Fig.1). Two of the whales achieved titers of at least 1/256, 9 after challenge, whereas the third showed a more gradual rise to a titer of 1/32.

The whales in Group B, tested after more than 6 wk in captivity, reacted similarly to those in Group A (Fig. 1). No antibodies were detected following the initial sensitizing dose in any of the animals. At this time, one of the whales was released due to inappettance and weight loss. In the other two, the challenging dose of SRBC produced an antibody response comparable to that in the whales tested immediately after capture.

Circulating lymphocytes, calculated from total and differential white cell counts, fluctuated widely (Fig. 2 and 3), with no evidence of lymphopenia. No attempt was made to distinguish between T- and B-cell subpopulations. Counts in Group B animals at the time of the first SRBC injection were comparable to or exceeded those at capture.

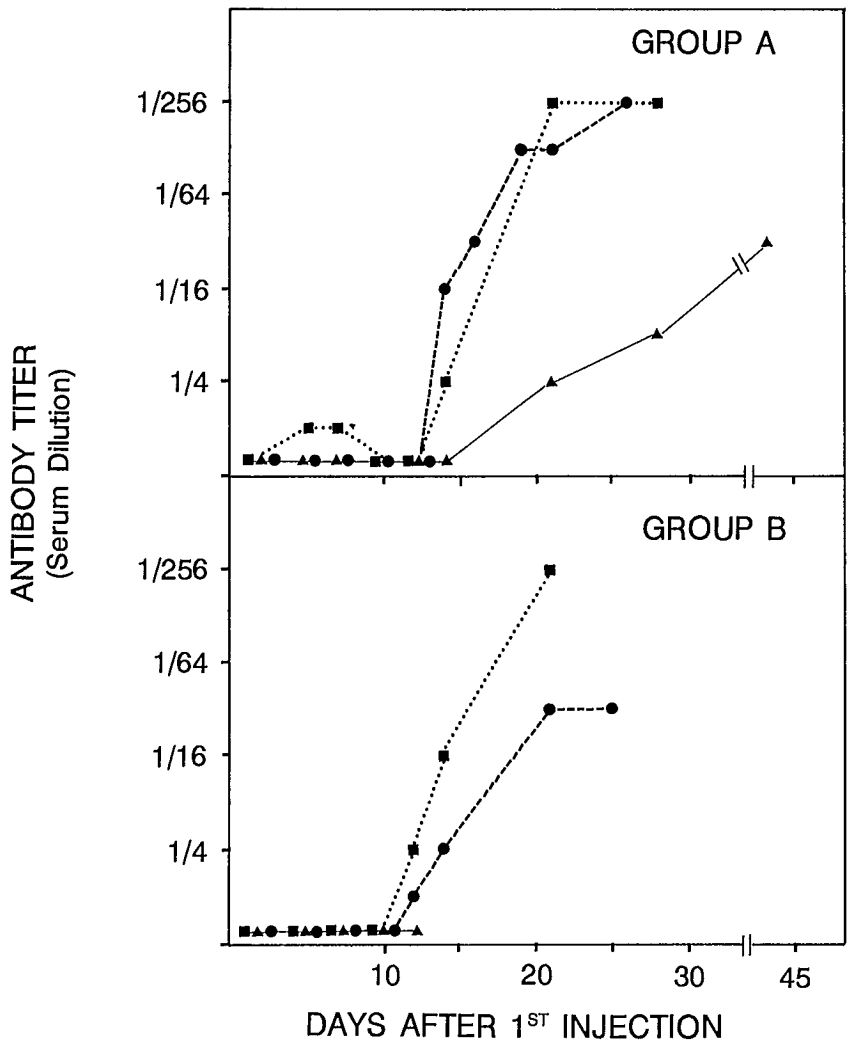

FIG. 1. Hemagglutinating antibody titers in serum from beluga whales injected with sheep red blood cells 0 and 12 d (Group A) or 45 and 57 d (Group B) after capture. One whale in Group B was released prior to the second SRBC injection.

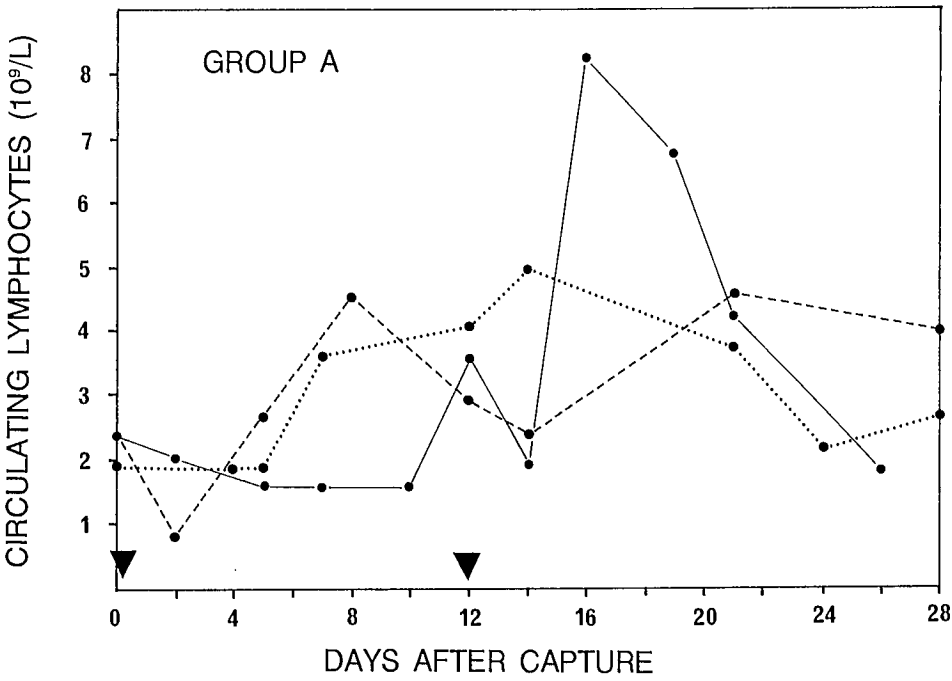

FIG. 2. Circulating lymphocyte counts in three belugas injected with sheep red blood cells within 12 h after capture, and again 12 d later (arrows).

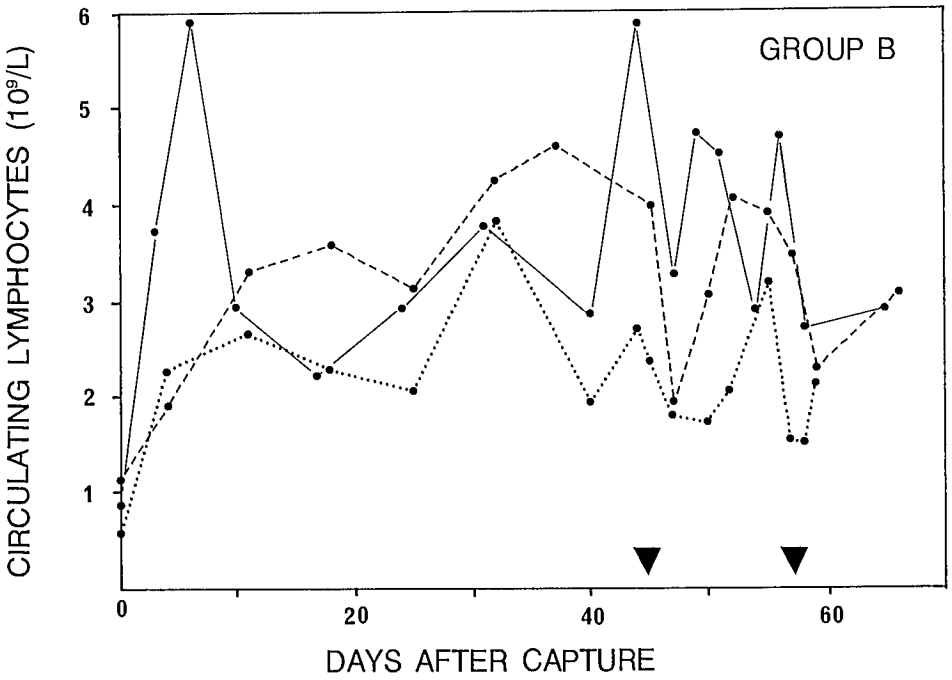

FIG. 3. Circulating lymphocyte counts in three belugas injected with sheep red blood cells after 45 d in captivity, and again 12 d later (arrows).

Discussion

Sensitization and challenge with SRBC, a T-cell dependent antigen, was effective in eliciting an immune response from the whales. Although six weeks in captivity did not appear to diminish the whales' ability to mount an antibody response, it would be premature to suggest that the cumulative stress associated with a novel environment, altered diet, and intensive handling for concurrent studies had no effect on their immune system. The small sample size available does not permit statistical comparison of the two groups, and the test itself measures only one aspect of immune function.

The suppressive effect of the glucocorticoid component of the stress response on the immune system has been documented extensively (Munck et al. 1984). Cortisol and its various analogs depress circulating lymphocyte counts, particularly T-cells (Fauci and Dale 1974). This mechanism also functions in odontocetes, including belugas (Medway et al. 1970; St. Aubin and Geraci 1989). In blood samples obtained from four whales immediately after capture and 3-4 h later after transport to holding facilities, we observed a marked decline in circulating lymphocytes (St. Aubin and Geraci 1989). Apparently normal levels were restored within a week. Throughout the 10-wk period in captivity, lymphocyte counts fluctuated, perhaps reflecting the opposing influences of antigenic stimulation and the glucocorticoid response to confinement and handling.

Glucocorticoids also enhance the rate of gamma globulin catabolism (Levy and Waldman 1970). In the captive whales, we noted no significant change in serum concentrations of gamma globulins (data not shown), though routine electrophoretic analysis would not have revealed changes in immunoglobulin fractions involved in primary and secondary responses to specific antigenic stimulation.

This preliminary study was undertaken to address the issue of stress-related immunosuppression in a cetacean. Further research is clearly needed on more subjects before the question may be answered. Nevertheless, the technique of sensitization to SRBC antigen proved to be effective in generating a response from the immune system of belugas, and with continued application, should produce a pattern of expected responses that will be useful in assessing the immunocompetence of captive and free-ranging whales.

Acknowledgments

We thank T. Friesen and C. Thomson (University of Guelph) for field and laboratory assistance. Valuable field logistic support was provided by R. Moshenko (Section Chief), J. Orr, and S. Waters (Department of Fisheries and Oceans). Funding for the study was provided by the Department of Fisheries and Oceans, the World Wildlife Fund ("Whales Beneath the Ice" Program), the Natural Sciences and Engineering Research Council (Grant A6130) and the United States Office of Naval Research (Grant N00014-87-G-0114).

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Organochlorine Contaminants in Belugas, *Delphinapterus leucas*, from Canadian waters

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Concentrations of organochlorine compounds were compared in blubber samples from the six stocks of beluga whales (*Delphinapterus leucas*) in Canadian waters. Highest concentrations of PCB congeners (ΣPCB), DDT-group (ΣDDT), polychlorinated camphenes (PCCs), chlordane-related compounds (ΣCHLOR), mirex and dieldrin were found in animals from the St. Lawrence estuary. Mean concentrations of hexachloro-cyclohexane isomers (ΣHCH), total chlorobenzenes (ΣCBz), and ΣCHLOR in females, showed few significant differences between any of the stocks. Mean concentrations of ΣPCB in arctic male belugas ranged from 2.53 ± 0.57 µg/g in animals from Jones Sound to 4.65 ± 0.94 µg/g (wet wt) at Cumberland Sound. ΣPCB, ΣDDT and mirex concentrations were 25, 32 and 100-fold higher, respectively, in males from the St. Lawrence than average levels in arctic males. The St. Lawrence animals are clearly exposed to higher levels of PCBs as well as other pollutants than the arctic animals. Continued study of the St. Lawrence animals is needed because toxicological effects of organochlorines are more likely to occur in this stock before becoming apparent in other beluga stocks.

Les concentrations de certains composés organochlorés ont été comparés dans des échantillons de tissus adipeux des six cheptels de bélugas (*Delphinapterus leucas*) des eaux canadiennes. Les concentrations les plus fortes des congenères de BPC (ΣBPC), du groupe DDT (ΣDDT), des camphènes polychlorés (CPC), des

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composés apparentés au chlordane (ΣCHLOR) de mirex et de dieldrine furent retrouvés dans les animaux de l'estuaire du Saint-Laurent. Les concentrations moyennes des isomères de l'hexchlorocyclohexane, des chlorobenzenes totaux (ΣCBz) et des ΣCHLOR pour les femelles présentèrent peu d'écarts significatifs entre les divers cheptels. L'écart des concentrations moyennes de ΣBPC chez les bélugas mâles de l'Arctique a varié de 2,53 ± 0,57 µg/g (poids humide) au détroit de Jones à 4,65 ± 0,94 µg/g au détroit de Cumberland. Les concentrations de ΣPBC, de ΣDDT et de mirex étaient 25, 32 et 100 fois, respectivement, plus élevées chez les bélugas mâles du Saint-Laurent par rapport au niveau moyen noté chez les mâles de l'Arctique. Il est évident que les bélugas du Saint-Laurent sont exposés à des teneurs plus élevées de BPC et d'autres éléments polluants que les animaux de l'Arctique. Le cheptel de bélugas du Saint-Laurent doit donc faire l'objet d'études poursuivies étant donné qu'il est plus probable que les indicences toxicologiques des organochlorés se manifesterant en premier chez ces animaux.

Introduction

As top predators in marine food chains, belugas (*Delphinapterus leucas*) are an excellent species for studying the presence and geographic variation of lipophilic organochlorine chemicals such as polychlorinated biphenyls (PCBs) and chlorinated pesticides. At the same time belugas, like other predatory mammals and birds, may be vulnerable to ecotoxicological effects of some organochlorines such as reproductive failure (Reijnders 1986; Peakall 1975) and hepatic mixed function oxidase enzyme induction (Walker 1983; Safe 1984). Analysis of stranded belugas from the Gulf of St. Lawrence estuary has shown accumulation of PCBs and DDT-related compounds (Sergeant 1980; Martineau et al. 1987) at levels suggested to cause the low reproductive rate of this population (Martineau et al. 1987; Sergeant and Hoek 1988).

There has been little study of the levels or geographic variation of organochlorine contaminants in belugas, or other small, toothed whales, inhabiting Canadian Arctic waters. The four Arctic beluga stocks (Hudson Bay, Cumberland Sound, High Arctic (Jones Sound) and Beaufort Sea)(Stewart 1986) could conceivably be exposed to different levels of organochlorine pollutants depending on the remoteness of the marine and estuarine environments that they inhabit. Norstrom et al. (1988) found that polar bears in Hudson Bay had generally higher levels of organochlorine contaminants in fat and liver tissues than did animals further north, which they found consistent with expected greater loadings via continental runoff and atmospheric deposition to this region. In the only report to date on organochlorine contaminants in Arctic belugas, Addison and Brodie (1973) found 3.9 µg/g total DDT and low levels of PCBs (<0.5 µg/g detection limit) in Beaufort Sea belugas.

This survey of organochlorines in Arctic belugas was undertaken to examine possible geographic variations of the pollutants in the various stocks and to compare the levels of types of contaminants in Arctic animals with those in the St. Lawrence population. An additional objective of this study was to provide information on the dietary exposure of native people in the Arctic who utilize whale tissues as part of their traditional diet.

Materials and Methods

Samples

Beluga tissues were obtained from animals taken by Inuit hunters at five locations in the Canadian Arctic between 1983 and 1987 (Table 1). Samples were packaged in polyethylene bags, frozen and held at -40°C until analysis. Blubber samples from the carcasses of stranded

TABLE 1. Sampling location and characteristics of beluga blubber samples.[a]

Stock	Sampling site	Sex	*N*	Date	Age (yr)	Length (cm)	% Lipid[b]
E. Hudson Bay	Nastapoka R. & Belcher Is.	M	8	1984, 85	12.0 ± 9.5 5.0 - 33.0	311 ± 41 278 - 401	86.5 ± 2.2 83.9 - 89.4
		F	8	1984, 85	11.9 ± 6.4 3.0 - 20.0	314 ± 31 252 - 346	86.4 ± 3.0 80.7 - 89.6
E. Hudson Bay	Nastapoka R.	M	6	1987	15.6 ± 3.0 12.0 - 20.0	347 ± 22 324 - 387	85.8 ± 5.9 81.7 - 97.2
		F	6	1987	17.0 ± 6.3 8.0 - 24.0	316 ± 18 307 - 342	88.7 ± 2.9 84.5 - 91.6
Cumberland Sound	Pangnirtung	M	6	1983	7.3 ± 6.5 0 - 16	415 ± 40 335 - 438	83.9 ± 6.2 77.6 - 88.0
		F	6	1983	8.1 ± 7.3 0 - 17	375 ± 15 361 - 395	87.7 ± 1.5 86.4 - 90.4
W. Hudson Bay	Eskimo Point	M	4	1986	13.0 ± 4.8 8.0 - 19.0	351 ± 33 309 - 385	66.1 ± 3.1 62.7 - 70.2
		F	4	1986	10.3 ± 4.1 5.0 - 15.0	312 ± 18 285 - 325	74.1 ± 12.7 56.5 - 85.4
Beaufort Sea	Mackenzie Bay	M	10[c]	1983, 87	17 13 - 20.0	431 ± 25 390 - 472	74.1 ± 10.0 60.4 - 88.0
		F	2[d]	1983, 87	18 —	361 —	81.7 77.9 - 85.6
Jones Sound	—	M	8	1984	4.4 ± 2.2 1.0 - 7.5	331 ± 71 253 - 432	88.4 ± 2.8 84.3 - 92.8
		F	7	1984	4.6 ± 2.9 1.5 - 10.5	308 ± 56 254 - 424	87.5 ± 1.9 84.5 - 90.1
St. Lawrence estuary	—	M	4	1986, 87	17.5 ± 9.1 4.0 - 23.5	416 ± 68 315 - 453	86.8 ± 2.7 83.2 - 89.6
		F	5	1986, 87	15.6 ± 10.4 2.5 - 29.0	352 ± 43 277 - 382	86.6 ± 3.9 80.4 - 91.4
Retrospective Samples	Baffin Is.	F	1	1966 or 67	adult	—	100
		M	1	1966 or 67	<1	—	100
	Churchill	—	1[e]	1966 or 67	—	—	100

[a] Mean ± standard deviation and range.
[b] Hexane extractable lipids.
[c] Ages available for 2 animals only.
[d] Age and length available for 1 animal only.
[e] Blubber oil — not fresh tissue — from male and female whales.

belugas in the St. Lawrence estuary were collected and preserved as described by Martineau et al. (1987). Prior to analysis, samples were partially thawed and subsampled taking care to exclude the exterior portion of tissue in contact with plastic.

Analyses for organochlorines were performed on blubber samples from all locations. Liver from Cumberland Sound animals and muscle from the eastern Hudson Bay stock where also analysed. Ages (years or growth layer groups), sex, length and maximum girth were available for most of the animals.

In addition to fresh tissue samples, one sample of crude beluga oil obtained from the commercial harvest of whales at Churchill (MB) and two samples of beluga blubber from Baffin Island collected in 1966/67 (provided by Dr. R.G. Ackman, Technical University of Nova Scotia, Halifax, N.S.) were included to provide retrospective organochlorine analysis. The sample from Churchill was taken from the whale oil manufacturing process and had therefore been subjected to heat whereas the two samples from Baffin Island had been extracted at room temperature to recover fats.

Extraction and Separation

Determinations of organochlorines in blubber tissues followed the procedures described by Muir et al. (1988a). Briefly: samples of blubber (2 g) were mixed with anhydrous sodium sulfate and ball-milled (30 min) with hexane. The extract was centrifuged and a portion (1/10) removed for lipid determination. The extract was chromatographed on a gel permeation column (GPC) to separate chlorinated hydrocarbons from co-extractive lipids, and then fractionated on Florisil into three eluates — hexane (F1), hexane:DCM (85:15) (F2), and hexane:DCM (1:1) (F3) (Norstrom and Won 1985). The chromatography on Florisil separated PCBs, chlorobenzenes, 4,4'-DDE and mirex in F1 from most polychlorinated camphenes (PCCs), chlordane-related compounds and 4,4'-DDT in F2. F3 contained heptachlor epoxide and dieldrin.

Twelve blubber and muscle samples from E. Hudson Bay were analysed by the method of Addison et al. (1986). Samples were extracted by blending with hexane and the extracts were "cleaned up" on Florisil. PCBs were confirmed by treatment of the Florisil eluates with KOH.

Liver samples were homogenized, mixed with anhydrous sodium sulfate and extracted with hexane. The hexane extract was evaporated to small volume and a portion removed for lipid determination. Liver extracts were subjected to GPC and Florisil chromatography as described above.

Blubber and liver extracts were chromatographed on a 60 m x 0.25 mm DB-5 column with H_2 carrier gas using gas chromatographic (GC) conditions described in previous studies (Muir et al. 1988a). Muscle and blubber extracts from E. Hudson Bay animals were chromatographed on a 30 m x 0.25 mm DB-5 column with He carrier gas.

Organochlorines were confirmed by GC-mass spectrometry (GC-MS) on a 30 m x 0.25 mm DB-5 column using HP-5970 mass selective detector (MSD). Additional mass spectrometry was performed on an HP 5987B, operated in electron impact mode at 15 eV, at the National Wildlife Research Centre of the Canadian Wildlife Service. GC-MS conditions were identical to those of Norstrom et al. (1988). The presence of chlordane-related compounds, PCCs and mirex was also confirmed by treatment of samples with HNO_3:H_2SO_4 (1:1) to destroy chlorinated aromatics (PCBs, DDT, HCB) (Musial and Uthe 1983).

PCBs and organochlorine pesticides were identified and quantified as described previously (Muir et al. 1988a). Total PCB (ΣPCB) was the sum of all congeners. Total chlordane (ΣCHLOR) was the sum of all chlordane-related compounds including heptachlor epoxide. PCCs were quantified by a modification of previous procedures (Muir et al. 1988a): response factors for individual PCC peaks were calculated from the weight percent of each peak in the total ion chromatogram of a toxaphene standard. Total PCCs was the sum of the areas of up to 20 peaks (8 major peaks were generally observed) (Muir et al. 1990a).

Data Analysis

Organochlorine concentrations in beluga blubber samples were $\log_{10}$ transformed prior to calculation of means, standard errors and correlation coefficients. The general linear models procedure of SAS (SAS Institute 1987) was used with an analysis of covariance (ANCOVA) model to examine the main effects of location and sex, and regressor effects of length and age on organochlorine concentrations. Comparisons between mean concentrations of each organochlorine, ratios of various compounds, length and age at each location were made with Tukey's test using the mean square error from the ANCOVA. Comparisons between mean concentrations in males and females were made with the Student's *t*-test.

Results

Samples

A total of 88 samples of beluga blubber from six locations were analysed for organochlorine contaminants in this survey (Table 1). Ages were available for samples from Jones Sound, Cumberland Sound, Hudson Bay and the St. Lawrence; lengths were available for almost all animals. The St. Lawrence belugas were generally older than the Arctic animals, with a mean age of 15.6 ± 10.4 yr for females and 17.5 ± 9.1 yr for males. However, there was wide variation in ages within all groups, and only the animals from Jones Sound were significantly younger ($P < 0.05$) than those from the St. Lawrence estuary. The St. Lawrence animals included here were similar in age to the group analysed by Martineau et al. (1987). The Beaufort Sea belugas that were analysed were significantly larger ($P < 0.05$) than the Hudson Bay and Jones Sound animals. Unfortunately, ages were available for only three of the 12 Beaufort Sea animals; they were significantly older than the Jones Sound group and were similar to the average age of the St. Lawrence animals.

Identification of Individual Contaminants in Blubber

The major organochlorine contaminants in beluga blubber from all six locations surveyed were ΣPCBs, PCCs, ΣDDT and ΣCHLOR (Table 2). Positive identification of all major components in blubber extracts from the Western Hudson Bay stock and from the St. Lawrence was made by full scan mass spectrometry and by use of multiple ion chromatograms (Fig. 1 and 2).

A total of 60 PCB peaks (approximately 65 congeners because some co-eluted) could be routinely determined in beluga blubber samples from all locations (Fig. 1). To facilitate discussion, the PCB congeners are referred to by their IUPAC number (Ballschmiter and Zell 1980). Twelve congeners accounted for >50% of ΣPCB in all samples: tetrachloro-52 and -66, pentachloro-95, -101, -99, and -118, hexachloro-149, -151, -153 and -138; heptachloro-187/182 and -180 (Fig. 3 and 4).

PCC was the major organochlorine contaminant detected in blubber of Arctic belugas (Table 2). Mean PCC concentrations were about 2-fold higher than ΣCHLOR and 1.5 fold-higher than ΣPCB and ΣDDT in the Arctic animals. Fourteen PCC peaks could generally be distinguished in beluga blubber extracts (Fig. 2). Two peaks, T2 and T12 in Fig. 2, predominated in all samples. T2 eluted mainly in F1 along with PCBs but is shown together with other PCC peaks in the multiple ion chromatogram because both fractions were combined for GC-MSD analysis. Peaks T2 and T12 were previously identified in dolphin blubber extracts as octa- and nonachloro- camphenes, respectively (Muir et al. 1988a).

The major DDT component in beluga blubber was 4,4'-DDE which represented 66% and 57% of total DDT-group compounds (ΣDDT) in male and female St. Lawrence belugas, respectively, and from 47 to 57% of ΣDDT in Arctic belugas (Table 2). Other major DDT

TABLE 2. Mean concentrations (μg/g wet wt ± SD) of major organochlorine pesticides in beluga blubber from Canadian waters.[a]

Stock	Sex	HCB	ΣCBz	γHCH	ΣHCH	*t*-nona-chlor	ΣCHLOR	4,4'-DDE	ΣDDT	PCC	mirex	dieldrin
E. Hudson Bay 1984/85	M	0.30 ± 0.19 0.15 - 0.66	0.32 ± 0.20 0.17 - 0.70	0.16 ± 0.05 0.10 - 0.23	0.21 ± 0.06 0.14 - 0.30	0.59 ± 0.11 0.44 - 0.72	1.86 ± 0.35 1.46 - 2.41	1.28 ± 0.42 0.65 - 1.97	2.27 ± 0.68 1.23 - 3.27	4.13 ± 0.82 3.24 - 5.67	0.02 ± 0.01 0.02 - 0.04	0.28 ± 0.09 0.18 - 0.45
	F	0.14 ± 0.12 0.05 - 0.39	0.16 ± 0.13 0.07 - 0.46	0.11 ± 0.03 0.07 - 0.15	0.15 ± 0.04 0.09 - 0.21	0.28 ± 0.18 0.12 - 0.55	0.87 ± 0.58 0.38 - 1.79	0.56 ± 0.42 0.15 - 1.33	0.98 ± 0.73 0.30 - 2.25	1.99 ± 1.10 1.07 - 3.99	0.01 ± 0.01 0.01 ± 0.02	0.14 ± 0.10 0.07 - 0.34
E. Hudson Bay 1987	M	0.29 ± 0.17 0.19 - 0.64	—[b]	0.21 ± 0.07 0.12 - 0.34		—	—	3.09 ± 0.54 2.27 - 3.94	5.53 ± 0.67 4.36 - 6.33	—	—	0.26 ± 0.13 <0.01 - 0.33
	F	0.14 ± 0.08 0.09 - 0.29	—	0.16 ± 0.05 0.10 - 0.24		—	—	0.88 ± 0.99 0.18 - 2.68	1.96 ± 2.05 0.35 - 5.64	—	—	0.11 ± 0.16 <0.01 - 0.40
W. Hudson Bay	M	0.61 ± 0.05 0.58 - 0.68	0.66 ± 0.05 0.61 - 0.72	0.16 ± 0.05 0.12 - 0.24	0.24 ± 0.07 0.18 - 0.34	0.90 ± 0.14 0.79 - 1.09	2.33 ± 0.26 2.03 - 2.67	1.80 ± 0.23 1.46 - 1.98	3.13 ± 0.20 2.96 - 3.38	5.10 ± 0.42 4.66 - 5.63	0.03 ± 0.00 0.02 - 0.03	0.36 ± 0.07 0.25 - 0.40
	F	0.19 ± 0.18 0.08 - 0.46	0.23 ± 0.20 0.11 - 0.53	0.11 ± 0.02 0.09 - 0.14	0.15 ± 0.04 0.12 - 0.21	0.30 ± 0.30 0.13 - 0.75	0.85 ± 0.80 0.36 - 2.05	0.49 ± 0.57 0.11 - 1.34	0.85 ± 0.96 0.18 - 2.25	1.77 ± 1.41 0.69 - 3.83	0.01 ± 0.00 0.00 - 0.01	0.14 ± 0.12 0.07 - 0.32
Retrospective samples[c]	F	0.06	0.07	0.03	0.04	0.05	0.13	0.24	0.93	0.66	<0.01	0.05
	M	0.07	0.09	0.03	0.04	0.04	0.11	0.13	0.54	0.55	<0.01	0.05
	M&F	0.30	0.35	0.06	0.09	0.16	0.44	1.81	3.77	0.66	<0.01	0.17
Cumberland Sound	M	0.96 ± 0.18 0.74 - 1.26	1.05 ± 0.18 0.83 - 1.34	0.23 ± 0.08 0.10 - 0.32	0.39 ± 0.11 0.23 - 0.56	1.05 ± 0.27 0.79 - 1.48	2.38 ± 0.40 1.99 - 3.05	3.38 ± 1.02 2.22 - 4.93	6.83 ± 1.89 4.19 - 9.73	5.78 ± 5.39 1.61 - 12.7	0.01 ± 0.01 0.01 - 0.01	0.91 ± 0.26 0.61 - 1.19
	F	0.18 ± 0.04 0.13 - 0.24	0.24 ± 0.06 0.17 - 0.32	0.23 ± 0.05 0.14 - 0.26	0.24 ± 0.06 0.19 - 0.32	0.18 ± 0.15 0.07 - 0.29	0.62 ± 0.15 0.39 - 0.78	0.40 ± 0.28 0.16 - 0.95	0.93 ± 0.55 0.45 - 1.96	1.77 ± 1.76 0.49 - 4.61	0.01 ± 0.00 0.00 - 0.01	0.20 ± 0.33 0.15 - 0.24
Beaufort Sea	M	0.59 ± 0.13 0.40 - 0.78	0.65 ± 0.15 0.43 - 0.85	0.13 ± 0.04 0.06 - 0.20	0.23 ± 0.06 0.14 - 0.32	0.53 ± 0.12 0.32 - 0.72	1.75 ± 0.41 1.28 - 2.56	1.03 ± 0.44 0.15 - 1.76	2.20 ± 0.83 1.47 - 3.73	3.83 ± 1.16 2.55 - 6.62	0.04 ± 0.01 0.02 - 0.06	0.23 ± 0.05 0.16 - 0.34
	F[d]	0.29 0.16 - 0.41	0.33 0.19 - 0.47	0.10 0.09 - 0.12	0.17 0.17 - 0.17	0.21 0.11 - 0.31	0.67 0.44 - 0.89	0.35 0.19 - 0.52	0.67 0.46 - 0.88	1.38 1.12 - 1.63	0.02 0.01 - 0.03	0.10 0.07 - 0.14

TABLE 2. (continued)

Stock	Sex	HCB	ΣCBz	γHCH	ΣHCH	*t*-nona-chlor	ΣCHLOR	4,4'-DDE	ΣDDT	PCC	mirex	dieldrin
Jones Sound	M	0.50 ± 0.21	0.55 ± 0.22	0.12 ± 0.07	0.19 ± 0.09	0.59 ± 0.13	1.87 ± 0.44	1.07 ± 0.21	1.96 ± 0.32	4.25 ± 1.02	0.01 ± 0.00	0.34 ± 0.11
		0.27 - 0.83	0.30 - 0.87	0.06 - 0.29	0.11 - 0.40	0.44 - 0.76	1.34 - 2.53	0.74 - 1.36	1.42 - 2.34	2.96 - 5.40	0.01 - 0.02	0.21 - 0.48
	F	0.39 ± 0.21	0.44 ± 0.23	0.10 ± 0.05	0.16 ± 0.08	0.58 ± 0.35	1.84 ± 1.13	1.26 ± 1.08	2.19 ± 1.69	3.74 ± 2.12	0.01 ± 0.01	0.33 ± 0.23
		0.08 - 0.70	0.11 - 0.79	0.06 - 0.18	0.10 - 0.28	0.29 - 1.32	0.97 - 4.25	0.56 - 3.69	1.13 - 5.95	1.77 - 8.08	0.01 - 0.03	0.09 - 0.81
St. Lawrence estuary	M	1.34 ± 0.44	1.34 ± 0.44	0.10 ± 0.01	0.37 ± 0.11	3.67 ± 0.30	7.43 ± 0.63	65.8 ± 19.1	101 ± 32.6	14.7 ± 2.46	1.00 ± 0.64	0.93 ± 0.12
		0.82 - 1.90	0.82 - 1.90	0.09 - 0.12	0.28 - 0.51	3.25 - 3.91	6.54 - 8.02	38.5 - 80.6	52.4 - 123	11.7 - 17.6	0.19 - 1.54	0.81 - 1.06
	F	0.60 ± 0.43	0.60 ± 0.43	0.11 ± 0.03	0.24 ± 0.10	1.86 ± 0.86	3.55 ± 1.99	13.9 ± 11.3	23.0 ± 17.3	6.34 ± 3.51	1.11 ± 0.99	0.56 ± 0.31
		0.22 - 1.27	0.22 - 1.27	0.08 - 0.14	0.12 - 0.32	0.87 - 2.82	1.50 - 6.38	1.73 - 26.8	3.95 - 42.7	2.05 - 10.3	0.38 - 2.66	0.21 - 0.87

[a] Arithmetic mean ± standard deviation and range of concentration.
[b] Not determined.
[c] Consisting of 1 adult female, 1 newborn male and a sample of beluga oil (Table 1).
[d] No standard deviation, N=2.

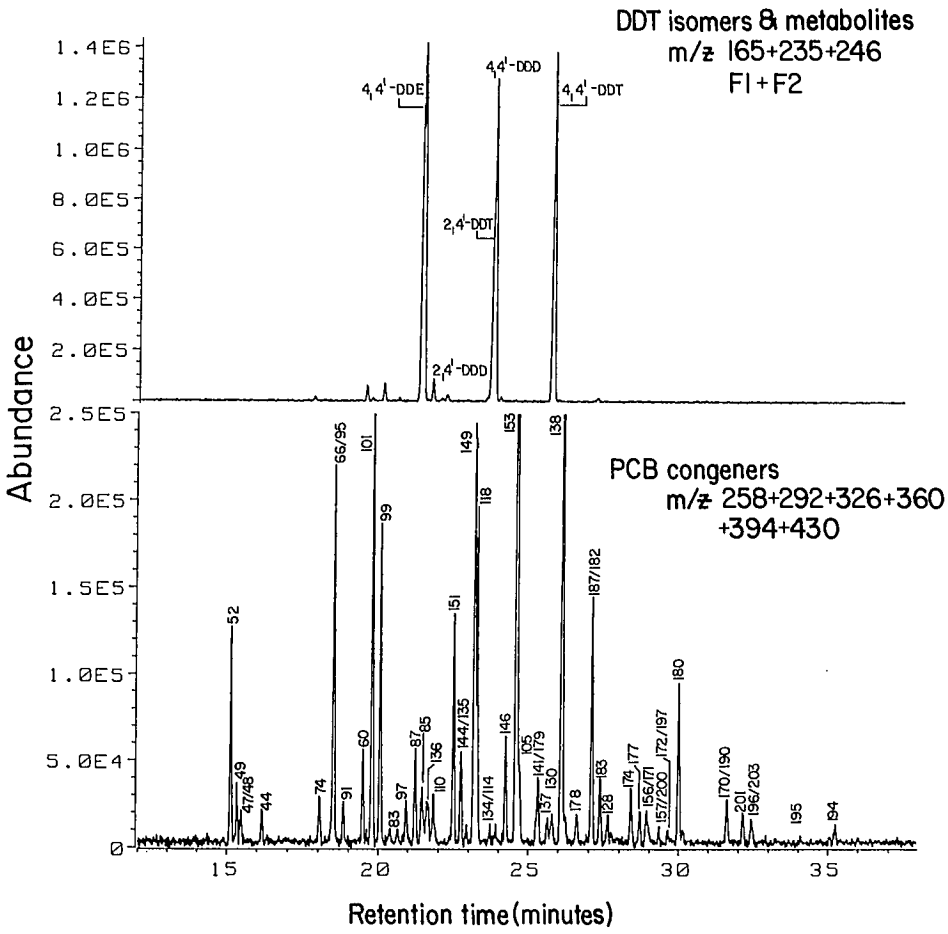

FIG. 1. Capillary GC-MSD multiple ion chromatograms (30 m x 0.25 mm i.d. DB-5 column) of a beluga blubber extract from Western Hudson Bay showing characteristic ions of tri- to octachloro biphenyls (lower chromatogram) and DDT-related compounds. Major PCBs are identified by their IUPAC numbers.

components quantified in all beluga samples were 4,4'DDT, 4,4'DDD and 2,4'-DDT (Fig. 1). 2,4'-DDT and 4,4'-DDD are not separated in the chromatogram because F1 and F2 were combined for the GC-MSD analysis; however, the 2,4'-isomer was quantified by GC because it eluted mainly in F1. 2,4'-DDD was also detected (Fig. 1) but was not determined by GC.

Fourteen chlordane-related compounds were routinely determined in beluga blubber extracts from all locations (Fig. 2 and 5). Trans-nonachlor was the major chlordane-related compound accounting for 30 – 40% of ∑CHLOR in Arctic animals and for 50 – 52% of ∑CHLOR in the St. Lawrence stock. Cis-nonachlor and nonachlor III (1,2,2,4,5,6,7,8,8-nonachlor; Norstrom et al. 1988) were also major chlordane components especially in Arctic animals (Fig. 2). U1 or photoheptachlor was also more prominent in Arctic samples (Fig. 5). The extent of transformation of chlordane is evident by the fact that cis-and trans- chlordane were minor peaks although they form a major proportion of technical chlordane (Fig. 5). Nonachlor III and cis-chlordane co-elute in Fig. 2 but they were separated by chromatography on Florisil, with nonachlor III eluting in F1, and determined separately by GC. Metabolites oxychlordane and heptachlor epoxide also formed a significant fraction of

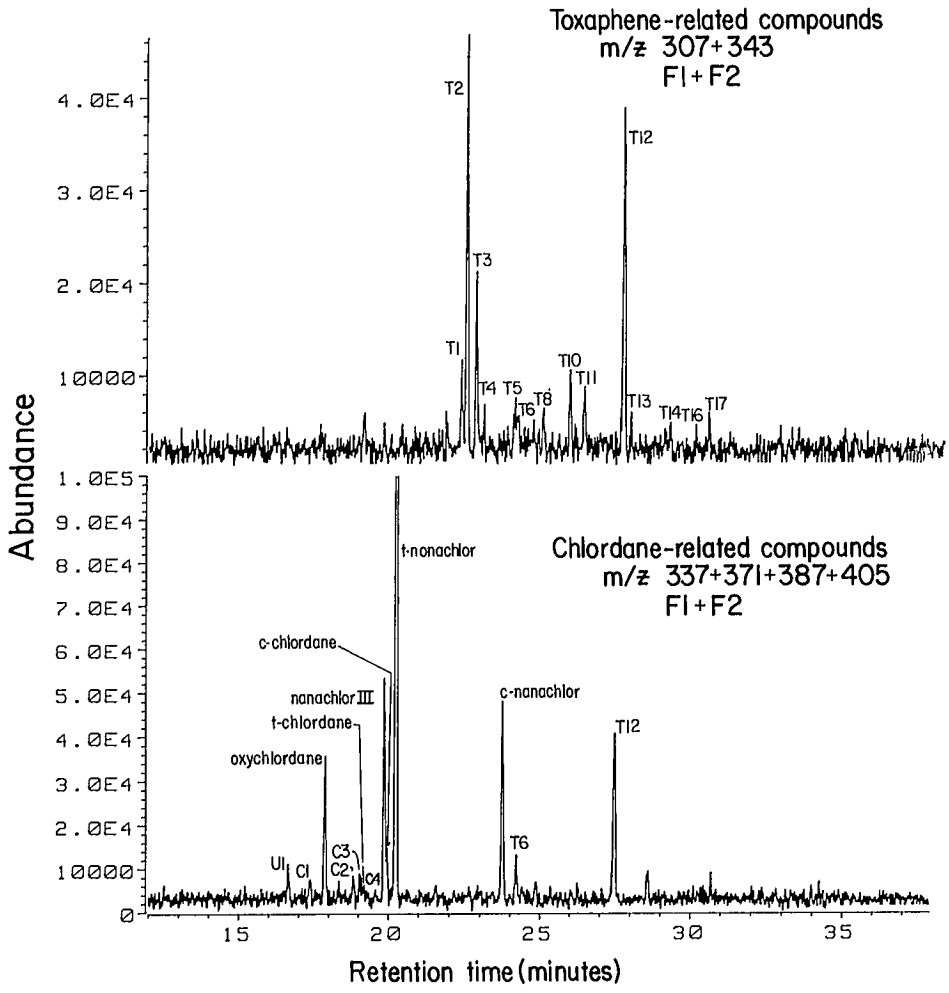

FIG. 2. Capillary GC-MSD multiple ion chromatograms of a beluga blubber extract from Western Hudson Bay showing characteristic ions of chlordane-related compounds (lower chromatogram) and polychlorinated camphenes (toxaphene). GC conditions as in Fig. 1.

ΣCHLOR (Fig. 3). C1 is a monohydro analog of trans-chlordane while C2 and C3 are heptachloro- compounds with mass spectra having a base peak at m/z 339 (Norstrom et al. 1988). C4 is a 5-hydro analog of trans-nonachlor. Compound "C," a heptachloro component of technical chlordane (Fig. 5) (Miyazaki et al. 1985), is not shown in Fig. 2, but was identified by its correct retention time and characteristic ions.

Hexachlorocyclohexane isomers (α-, ß-, γ-HCH) were detected in all beluga blubber samples at relatively low levels compared to PCBs, PCCs, ΣCHLOR and ΣDDT (Table 2). Hexachlorobenzene (HCB) was the major form of total chlorobenzenes (ΣCBz) in all beluga samples surveyed (Table 2). In St. Lawrence animals, tetra and pentachlorobenzenes were undetectable (<0.01 μg/g). However the detection limits were set relatively high because of the high levels of PCBs in the same Florisil eluate. Tetra- and pentachlorobenzene isomers constituted <10% of ΣCBz in Arctic beluga blubber. Mirex and dieldrin were also detected in all samples (Table 2).

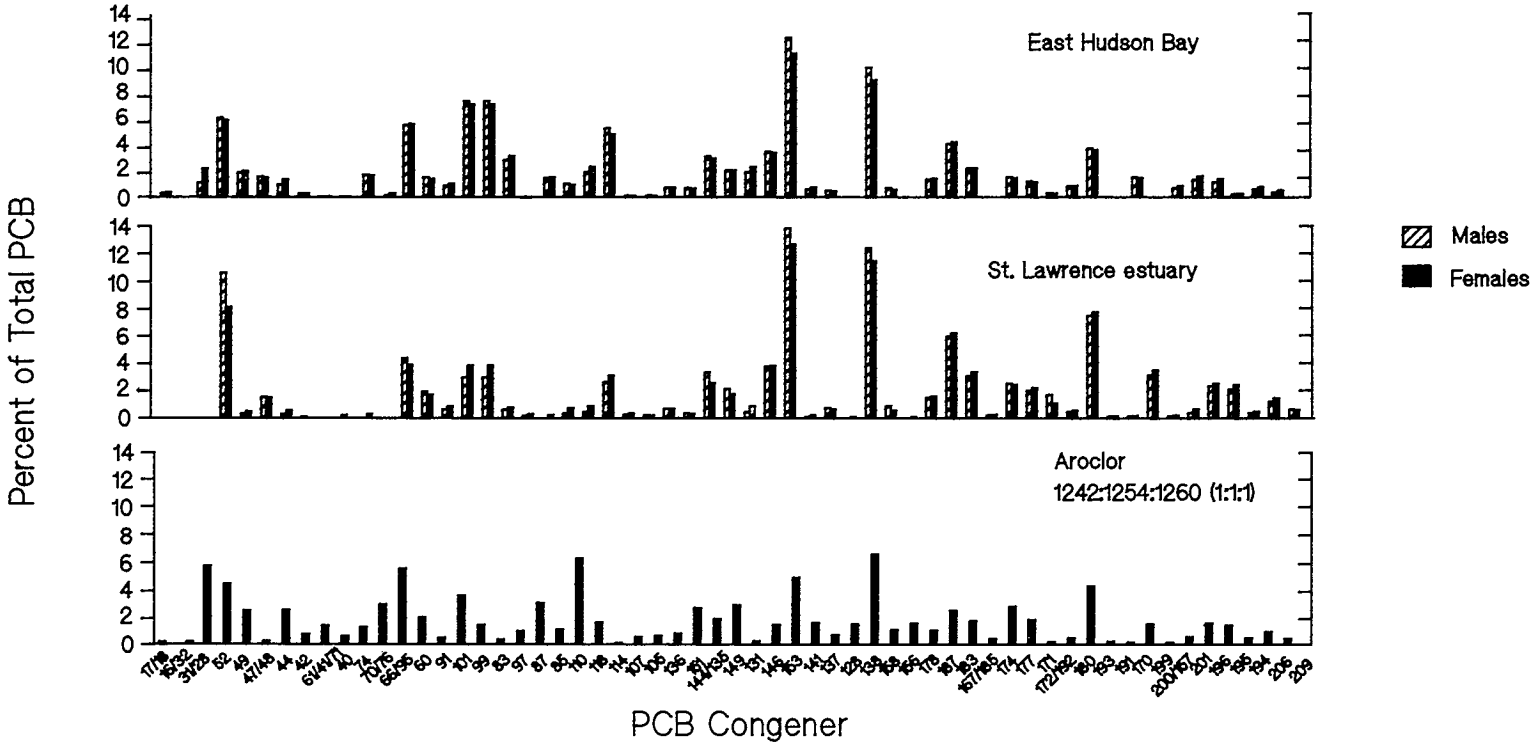

FIG. 3. PCB congeners as a percent of ∑PCB in an Aroclor standard mixture and in beluga blubber from Hudson Bay and the St. Lawrence estuary.

Comparisons Among Stocks

In all beluga stocks, except for the animals from Jones Sound, mean ΣPCB levels were significantly higher (*t*-test at $P < 0.01$) in males than in females (Table 3). Statistical comparisons between the stocks for PCBs and other organochlorines were therefore done by sex. As expected from the work of Martineau et al. (1987), male and female belugas from the St. Lawrence had significantly higher mean ΣPCB and ΣDDT levels (Tukey's test, $P < 0.05$) than mean levels in any Arctic stocks. Mean ΣPCB levels were 25-fold higher, for both males and females, in the St. Lawrence animals than in the Arctic animals while for ΣDDT the differences were 32-fold and 19-fold, respectively. Although only a limited number of St. Lawrence animals are reported here, mean PCB concentrations as Aroclor equivalents (119 ± 25.5 μg/g; Table 3) were similar to those reported for a set of 26 animals by Martineau et al. (1987), who found 185 ± 79 μg/g in blubber of males and 88 ± 165 μg/g in females. The high standard deviation for females was due to one very high result (576 μg/g). With this result omitted, the mean for females reported by Martineau et al. (1987) reduces to 43 ± 31 μg/g which is not significantly different from the mean (54.2 ± 37.6 μg/g Aroclor equivalents) for 5 females reported in Table 3. ΣDDT levels reported by Martineau et al. (1987) of 91 ± 58 μg/g (15 males) and 21 ± 28 μg/g (11 females) were virtually identical to those reported here although 2,4'-DDT was not determined in the latter study. Among Arctic stocks, ANCOVA showed a significant effect of location, but not of length or length-location interaction for ΣPCBs and ΣDDT in males, while female belugas showed no effects for these factors. Comparisons of mean ΣPCB and ΣDDT levels in males showed samples from Cumberland Sound had significantly higher PCBs ($P < 0.05$) than those from E. Hudson Bay or Jones Sound. ΣDDT levels in males from Cumberland Sound were also significantly higher than males from the Beaufort Sea.

The ΣPCB/DDE ratio of 5.1 for the Beaufort Sea males was significantly higher than that for the St. Lawrence or Hudson Bay stocks while the ratio for the Jones Sound stock was significantly higher ($P < 0.05$) than for the St. Lawrence stock (Table 4). No significant differences for the ΣPCB/DDE ratio were observed for females. The mean DDE/ΣDDT ratios for both males and females in the St. Lawrence stock were significantly higher ($P < 0.05$) than means for the Arctic stocks.

The large differences in concentrations observed for ΣPCB and ΣDDT between Arctic and St. Lawrence animals were not observed for PCC and ΣCHLOR. PCC levels in male and female St. Lawrence belugas (means of 14.7 ± 2.5 and 6.3 ± 3.5 μg/g, respectively) were significantly higher ($P < 0.05$) than the mean levels at all Arctic locations, but differences were only 2 to 3 fold (Table 2). Mean levels of ΣCHLOR in male St. Lawrence belugas (7.4 ± 0.6 μg/g) were significantly higher ($P < 0.05$) than concentrations in all Arctic stocks by 2 to 3 fold (Table 2). ΣCHLOR levels in female St. Lawrence belugas (3.5 ± 2.0 μg/g) were not significantly different from those in females from Jones Sound (1.8 ± 1.1 μg/g).

There were no significant differences ($P < 0.05$) in PCC levels among locations for Arctic belugas. There was no significant effect of location, age or length using either the entire set of data for ΣCHLOR in females or on separate analysis of the Arctic animals. ΣCHLOR/PCB ratios for St. Lawrence belugas were 5- to 7-fold lower than those for Arctic animals (Table 4). Mean values of ΣCHLOR/PCB were not significantly different among Arctic stocks.

In males, ΣHCH levels in St. Lawrence animals were not significantly higher than in mean levels in Cumberland Sound, Beaufort Sea and West Hudson Bay animals. Highest levels of α-HCH were found in Cumberland Sound males. Females from Cumberland Sound had significantly higher levels of α-HCH than St. Lawrence and Jones Sound animals. There were no significant differences among stocks of females for ΣHCH.

α-HCH accounted for a much higher proportion of ΣHCH in Arctic stocks (63% in males; 70% in females) than in St. Lawrence animals (27% in males; 45% in females). There were no significant differences in levels in mean α-HCH or ΣHCH concentrations between males

TABLE 3. Mean concentrations of total PCB congeners (ΣPCB) and homologs (μg/g wet weight) in blubber of beluga from Canadian waters.[a]

Stock		ΣPCB	Cl_3	Cl_4	Cl_5	Cl_6	Cl_7	Cl_8	Cl_9	Arochlor 1254:1260
E. Hudson Bay 1984/85	M	2.77 ± 0.51 2.10 - 3.70	0.03 ± 0.01 0.01 - 0.05	0.51 ± 0.09 0.40 - 0.68	0.76 ± 0.15 0.57 - 1.03	0.92 ± 0.19 0.65 - 1.24	0.44 ± 0.10 0.31 - 0.58	0.10 ± 0.02 0.06 - 0.12	0.008 ± 0.003 0.005 - 0.011	3.45 ± 0.83 2.26 - 4.78
	F	1.23 ± 0.84 0.44 - 2.43	0.03 ± 0.02 0.02 - 0.07	0.23 ± 0.19 0.06 - 0.52	0.33 ± 0.25 0.10 - 0.70	0.39 ± 0.27 0.13 - 0.82	0.19 ± 0.11 0.08 - 0.39	0.05 ± 0.02 0.03 - 0.08	0.007 ± 0.004 0.003 - 0.014	1.38 ± 1.00 0.45 - 3.04
E. Hudson Bay 1987	M	—[b]	—	—	—	0.98 ± 0.23 0.76 - 1.42	—	—	—	7.99 ± 1.99 5.48 - 11.1
	F	—	—	—	—	0.38 ± 0.38 0.08 - 1.09	—	—	—	2.53 ± 2.95 <0.01 - 7.58
W. Hudson Bay	M	3.12 ± 0.34 2.75 - 3.47	0.02 ± 0.01 0.01 - 0.02	0.65 ± 0.14 0.53 - 0.81	0.95 ± 0.13 0.76 - 1.07	0.89 ± 0.04 0.86 - 0.95	0.49 ± 0.02 0.46 - 0.51	0.11 ± 0.01 0.10 - 0.13	0.016 ± 0.005 0.010 - 0.022	3.97 ± 0.29 3.77 - 4.21
	F	0.96 ± 1.00 0.31 - 2.44	0.01 ± 0.01 <0.01 - 0.01	0.18 ± 0.21 0.07 - 0.50	0.32 ± 0.39 0.09 - 0.91	0.25 ± 0.26 0.08 - 0.64	0.15 ± 0.13 0.04 - 0.32	0.04 ± 0.02 0.02 - 0.06	0.007 ± 0.004 0.004 - 0.012	1.12 ± 1.19 0.34 - 2.88
Retrospective samples[c]	F	0.49	0.04	0.10	0.13	0.13	0.08	0.02	0.001	0.41
	M	0.26	0.03	0.08	0.08	0.06	0.02	<0.01	<0.001	0.17
	M&F	1.47	0.05	0.34	0.43	0.41	0.19	0.05	0.004	1.34
Cumberland Sound	M	4.91 ± 0.25 4.74 - 5.09	0.07 ± 0.03 0.04 - 0.09	1.38 ± 0.01 1.37 - 1.39	1.55 ± 0.08 1.50 - 1.61	1.20 ± 0.20 1.06 - 1.35	0.61 ± 0.01 0.60 - 0.62	0.05 ± 0.02 0.04 - 0.06	<0.001 —	5.26 ± 0.19 5.12 - 5.39
	F	1.15 ± 0.41 0.86 - 1.44	0.07 ± 0.07 0.02 - 0.12	0.29 ± 0.09 0.23 - 0.35	0.25 ± 0.15 0.14 - 0.36	0.26 ± 0.13 0.16 - 0.35	0.18 ± 0.05 0.15 - 0.22	0.04 ± 0.01 0.04 - 0.05	<0.001 —	0.95 ± 0.41 0.65 - 1.24
Beaufort Sea	M	3.33 ± 0.85 2.32 - 4.94	0.06 ± 0.03 0.03 - 0.11	0.69 ± 0.21 0.46 - 1.16	0.97 ± 0.27 0.69 - 1.52	1.05 ± 0.26 0.69 - 1.47	0.46 ± 0.11 0.31 - 0.62	0.08 ± 0.03 0.05 - 0.14	0.006 ± 0.003 0.003 - 0.011	3.85 ± 0.94 2.72 - 5.46
	F[d]	1.23 0.83 - 1.64	0.05 0.05 - 0.05	0.20 0.13 - 0.27	0.32 0.20 - 0.45	0.42 0.30 - 0.53	0.20 0.13 - 0.27	0.04 0.02 - 0.06	0.004 0.002 - 0.006	1.41 0.97 - 1.85

TABLE 3. (continued)

Stock		ΣPCB	Cl_3	Cl_4	Cl_5	Cl_6	Cl_7	Cl_8	Cl_9	Arochlor 1254:1260
Jones Sound	M	2.53 ± 0.57	0.04 ± 0.01	0.67 ± 0.15	0.79 ± 0.20	0.74 ± 0.17	0.26 ± 0.07	0.03 ± 0.01	0.001 ± 0.001	2.66 ± 0.63
		1.88 - 3.74	0.03 - 0.06	0.54 - 1.00	0.60 - 1.25	0.50 - 1.03	0.17 - 0.35	0.02 - 0.06	0.001 - 0.003	1.69 - 3.63
	F	2.46 ± 1.98	0.04 ± 0.02	0.62 ± 0.52	0.75 ± 0.61	0.73 ± 0.59	0.27 ± 0.21	0.04 ± 0.03	0.001 ± 0.001	2.61 ± 2.13
		0.95 - 6.73	0.02 - 0.09	0.24 - 1.74	0.27 - 2.07	0.25 - 2.02	0.09 - 0.71	0.01 - 0.11	0.001 - 0.003	0.89 - 7.19
St. Lawrence estuary	M	75.8 ± 15.3	<0.01	13.9 ± 1.00	8.41 ± 1.45	27.7 ± 6.24	20.4 ± 6.23	4.70 ± 2.40	0.666 ± 0.493	119 ± 25.5
		53.9 - 89.2	—	12.6 - 14.7	6.40 - 9.54	19.0 - 33.7	11.6 - 26.4	1.25 - 6.79	<0.001 - 1.184	83.6 - 144
	F	37.3 ± 22.0	<0.01	5.84 ± 4.55	5.47 ± 2.55	12.7 ± 8.20	10.3 ± 6.29	2.71 ± 1.59	0.289 ± 0.199	54.2 ± 37.6
		14.5 - 68.7	—	1.91 - 13.1	2.67 - 8.58	4.41 - 24.9	3.57 - 19.5	1.20 - 5.02	<0.001 - 0.514	16.4 - 112

[a] Arithmetic mean ± standard deviation and range of concentration.
[b] Dash indicates not determined.
[c] Consisting of 1 adult female, 1 newborn male and a sample of beluga oil (Table 1).
[d] No standard deviation, N=2.

TABLE 4. Ratios of organochlorines in beluga tissues.

Location/tissue	Sex	Ratio				
		ΣPCB/DDE	DDE/ΣDDT	γ/α-HCH	ΣCHLOR/ΣPCB	mirex/ΣPCB
Blubber						
St. Lawrence	M	1.19 ± 0.18	0.66 ± 0.06	0.52 ± 0.15	0.10 ± 0.01	0.012 ± 0.007
	F	4.07 ± 2.76	0.56 ± 0.09	0.43 ± 0.17	0.10 ± 0.02	0.027 ± 0.009
Hudson Bay	M	2.15 ± 0.42	0.57 ± 0.04	0.29 ± 0.04	0.70 ± 0.11	0.009 ± 0.002
	F	2.78 ± 0.56	0.57 ± 0.04	0.18 ± 0.06	0.82 ± 0.19	0.012 ± 0.005
Beaufort Sea	M	5.13 ± 6.89	0.47 ± 0.15	0.34 ± 0.08	0.53 ± 0.04	0.011 ± 0.003
	F	3.78	0.50	0.30	0.54	0.017
Jones Sound	M	2.41 ± 0.62	0.55 ± 0.04	0.32 ± 0.05	0.76 ± 0.22	0.002 ± 0.001
	F	1.98 ± 0.47	0.56 ± 0.05	0.30 ± 0.09	0.84 ± 0.28	0.006 ± 0.002
Retrospective[a]	F	2.07	0.25	0.15	0.29	<0.01
	M&F	0.81	0.48	0.19	0.59	0.0005
Liver[b]	M	2.56	0.72	0.40	0.33	0.002
	F	6.13 ± 1.46	0.65 ± 0.03	0.20 ± 0.05	0.33 ± 0.05	0.004 ± 0.003
Muscle[c]	M	4.76 ± 2.73	0.63 ± 0.11	<0.06	—	—
	F	5.87 ± 7.60	0.48 ± 0.11	<0.08	—	—

[a] Beluga oil samples from 1966/67. See Table 1.
[b] Samples from Cumberland Sound.
[c] Samples from Eastern Hudson Bay. PCBs are Aroclor 1254 equivalents. Mirex and chlordane-related compounds were not determined.

and females in Arctic animals (*t*-test at $P < 0.05$). However, mean levels of ΣHCH in St. Lawrence males were significantly higher than in females. Ratios of the γ- to α- isomers of HCH (Table 4) were significantly higher in St. Lawrence animals than in all Arctic stocks in the case of males and all except Beaufort Sea and Jones Sound animals for females. There were no significant differences in γ/α-HCH ratios for either sex among Arctic stocks.

There were significant effects of location but not of age or length on ΣCBz levels for either sex. Mean ΣCBz concentrations in St. Lawrence males were significantly higher ($P < 0.05$) than means for Jones Sound, E. Hudson Bay and Beaufort Sea stocks but did not differ significantly from Cumberland Sound or W. Hudson Bay stocks. St. Lawrence females had significantly higher mean ΣCBz levels than E. Hudson Bay animals.

Mean levels of mirex in St. Lawrence belugas were 50 to 100-fold higher than in Arctic belugas (Table 2). This was the largest concentration difference between the St. Lawrence and Arctic stocks for any organochlorine studied. Unlike most organochlorines, but similar to α-HCH, mirex levels in males and females were not significantly different (*t*-test at $P < 0.05$). For males, mirex/ΣPCB ratios in St. Lawrence animals were not significantly higher than Hudson Bay or Beaufort sea animals but they were significantly higher ($P < 0.05$) than ratios for the Jones Sound animals. Mirex/ΣPCB ratios in the Hudson Bay and Beaufort Sea stocks were also significantly higher ($P < 0.05$) than the ratio for Jones Sound males.

Dieldrin was present at similar levels to HCB and mirex in both Arctic and St. Lawrence beluga blubber (Table 2). Mean levels of dieldrin in St. Lawrence males were significantly higher than mean levels at any Arctic locations; however, levels in Jones Sound females did not differ significantly from the St. Lawrence animals.

Organochlorine Levels in Other Tissues

Low ng/g (wet wt) levels of PCBs and organochlorine pesticides were found in liver and muscle samples of Arctic belugas (Table 5). In liver, PCBs and PCCs were present at approximately equal concentrations in males (120 ng/g wet wt), unlike blubber in which PCCs were more prominent (Table 2). On a lipid weight basis (liver and muscle averaged 3.4 and 1.3 % extractable lipid, respectively), levels of organochlorines were comparable or higher than those found in blubber. ΣCHLOR/PCB and PCB/DDE ratios (females only) for liver were significantly different (*t*-test at $P < 0.05$) from those calculated for blubber from the same animals (Table 5).

Analysis of Retrospective Samples

Three beluga oil samples collected in 1966/67 contained all of the organochlorines determined in blubber samples from the mid-1980's but concentrations were generally lower. The concentration of ΣDDT in oil from Churchill was higher than the mean concentration in W. Hudson Bay beluga blubber (Table 2). 4,4'-DDD formed a major proportion of ΣDDT, indicating dehydrochlorination of DDT during the preparation of the oil or during storage.

ΣCHLOR and PCC levels were 3- to 6-fold lower in the Churchill beluga oil sample than mean levels of these compounds in male belugas, and 2-fold lower than means in females. The concentration of ΣPCB in the oil of Baffin Island female belugas was within the range seen in present day animals from Hudson Bay and Cumberland Sound (Table 3). DDE/ΣDDT and ΣCHLOR/PCB ratios in the adult female sample from 1966/67 were about 2-fold lower than found in blubber of Arctic animals from the mid-1980's (Table 4).

TABLE 5. Organochlorine concentrations (mean, standard deviation and range, ng/g wet weight) in beluga liver and muscle.

Tissue	Sex	*N*	Lipid (%)	HCB	αHCH	4,4'-DDE	ΣDDT	ΣCHLOR	PCC	Dieldrin	PCB (Aroclor)[a]	Cl_6
Muscle[b]	M	6	1.3 ± 0.7	3.2 ± 1.7	1.7 ± 0.6	18.4 ± 10.2	27.6 ± 12.6	—	—	<0.1	67.2 ± 22.3	8.3 ± 2.3
			0.8 - 2.7	1.8 - 6.3	1.0 - 2.5	3.8 - 33.9	8.9 - 47.0			—	36.9 - 97.0	4.7 - 11.2
	F	6	1.2 ± 0.2	1.7 ± 0.8	1.4 ± 0.5	5.2 ± 5.8	9.9 ± 8.9	—	—	<0.1	26.2 ± 26.0	3.4 ± 2.9
			1.0 - 1.3	0.7 - 3.1	0.6 - 2.0	0.7 - 16.2	1.2 - 26.4			—	<0.1 - 68.2	0.7 - 8.6
Liver[c]	M	2	3.1	22.0	2.4	41.6	57.5	35.0	120	20.1	124	29.2
			2.8 - 3.5	17.1 - 27.0	1.5 - 3.2	33.8 - 49.3	48.4 - 66.5	29.1 - 40.9	86.0 - 153	19.1 - 21.1	89.0 - 160	21.5 - 36.9
	F	3	3.7 ± 1.3	10.9 ± 5.4	4.2 ± 0.7	9.5 ± 3.6	14.4 ± 4.8	19.2 ± 3.0	60.5 ± 5.4	8.5 ± 4.8	70.3 ± 4.2	17.2 ± 0.9
			2.4 - 5.0	7.5 - 17.1	3.6 - 4.9	7.1 - 13.7	11.2 - 20.0	17.3 - 22.7	55.5 - 66	5.5 - 14.1	66.3 - 74.7	16.6 - 18.3

[a] PCB as Aroclor 1254/1260 (1:1) equivalents.
[b] Muscle of Eastern Hudson Bay animals.
[c] Liver from Cumberland Sound animals.

Correlations with Age and Length

Correlations of major organochlorine levels in beluga blubber with age and length were performed on 3 groups (the combined East and West Hudson Bay, Jones Sound and St. Lawrence) (Table 6). Significant negative correlations between ΣPCB, ΣCHLOR, ΣHCH, ΣDDT and ΣCBz concentrations and age and length were observed in females from Hudson Bay (Table 6). For males, only ΣDDT was significantly, positively correlated with age and length. No significant correlations were found for the Jones Sound group except a negative correlation of ΣHCH with length in males. Although only a limited number of males from the St. Lawrence estuary were analysed, there were significant (P <0.01) positive correlations of ΣDDT, ΣPCB and ΣCHLOR with age in this group but not in females from this location.

TABLE 6. Correlations[a] of organochlorine concentrations with age and length in beluga blubber.

Location	Sex	N	Factor	ΣPCB	ΣDDT	ΣCHLOR	ΣHCH	ΣCBz
St. Lawrence estuary	M	4	Age	0.983*	0.997*	0.969*	0.399	0.885
			length	0.972*	0.998*	0.959*	0.447	0.877
	F	5	Age	0.442	0.335	0.301	0.159	0.299
			length	0.022	0.198	0.241	0.446	0.256
Hudson Bay[b]	M	12	Age	0.349	0.587*	0.178	-0.020	-0.146
			length	0.250	0.612*	0.034	-0.281	-0.151
	F	12	Age	-0.774**	-0.747**	-0.860**	0.758**	0.908**
			length	-0.609*	-0.549*	-0.725*	0.850**	0.852**
Jones Sound	M	8	Age	-0.312	-0.424	-0.241	-0.601	-0.511
			length	-0.046	-0.074	-0.557	-0.773*	-0.632
	F	7	Age	-0.191	-0.148	-0.216	0.587	-0.337
			length	-0.221	-0.170	-0.085	-0.481	-0.475

[a] Correlation coefficient significant at P <0.01 (**) or P <0.05 (*).
[b] Combined East and West Hudson Bay data (1984/86 samples).

Discussion

Sources, Pathways, and Transformations of Organochlorine Contaminants

The pattern of PCB congeners and homologs in beluga blubber differed considerably from a mixture of Aroclor standards (Fig. 3 and 4). Levels and relative amounts of homologs were similar in Arctic animals with tetra, penta and hexachloro congeners predominating (Table 3). In the St. Lawrence animals, hexa and heptachloro congeners predominated (Fig. 4) and the homolog pattern resembled a 1:1 mixture of Aroclor 1254:1260 more closely than did the pattern in Arctic animals. The pattern of PCB congeners differed between the Arctic and St. Lawrence males with PCB-153, -138, -187/182 and -180 (all substituted at the 2,4- or the 2,4,5- positions on both phenyl rings) accounting for a higher proportion of ΣPCB in the St. Lawrence group (Fig. 3). This pattern could be indicative of greater metabolic activity in the St. Lawrence animals due to mixed function oxidase enzyme induction by co-planar PCBs such that only the most recalcitrant structures remain. Tanabe et al. (1988) have suggested that small cetaceans lack the capacity to metabolize PCBs with adjacent non-chlorinated meta- and para-carbons (i.e. positions 3,4- or 4,5- on the biphenyl ring). The pattern of PCB congeners seen in both Arctic and St. Lawrence belugas is very similar to that reported for white-beaked dolphins (*Lagenorhynchus albirostris*) and pilot whales (*Globi-*

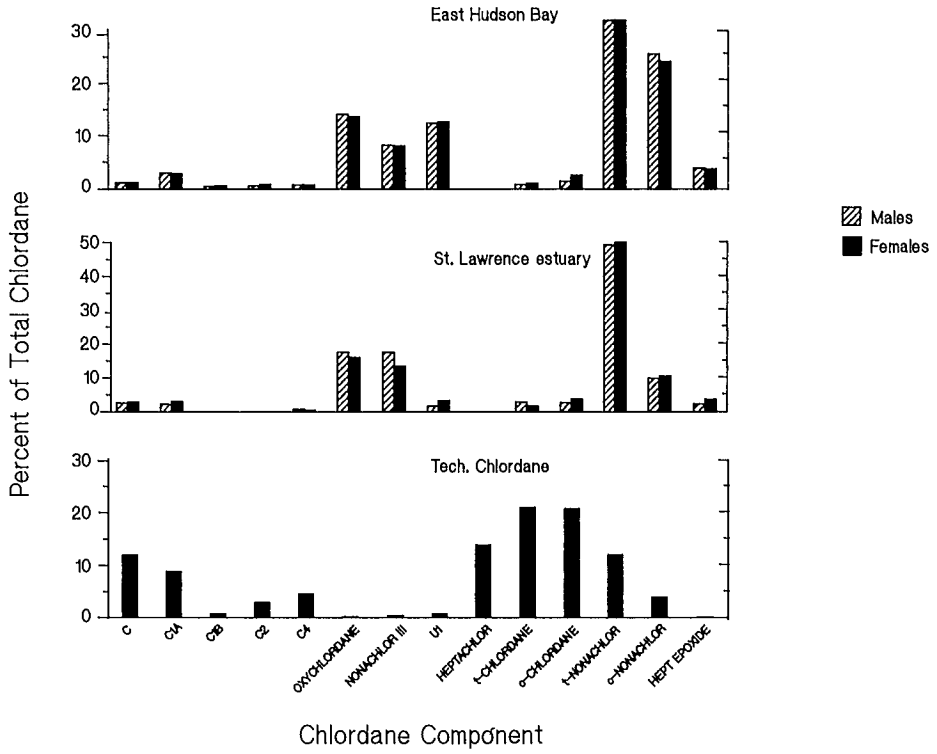

FIG. 4. Comparison of the proportion of PCB homologs in an Aroclor 1242:1254:1260 (1:1:1) standard and in beluga blubber from Hudson Bay and the St. Lawrence estuary.

cephala malaena) from Newfoundland waters (Muir et al. 1988a). Geraci (1989) reported a similar predominance of PCB-153 and -138 in blubber of stranded bottlenose dolphins (*Tursiops truncatus*) from the U.S. central and south Atlantic coast. Tanabe et al. (1984,1988) and Duinker and Hillebrand (1983) have reported similar PCB congeneric patterns for other cetaceans and Japanese waters and in the North Sea, respectively.

The differences in PCB congener and homolog profiles between the St. Lawrence and Arctic stocks may also reflect different sources and pathways of PCB contamination. In the St. Lawrence River, sediments and biota have been contaminated as a result of direct discharge of PCBs to the aquatic environment (Couillard 1982). Atmospheric deposition is also an important pathway for entry of PCBs and other organochlorines into the aquatic environment in the St. Lawrence drainage basin (Eisenreich et al. 1981). In the Arctic marine environment, atmospheric transport, ocean currents, and inputs from north-flowing rivers are the only pathway of introduction of PCBs. There has been some local use of PCBs, for example in transformers in DEW line stations however, there is no evidence of direct contamination of polar bears (Norstrom et al. 1988) or ringed seals (Muir et al. 1990b). Tanabe et al. (1988) noted that tetra and pentachloro-biphenyls formed a greater proportion of total PCB in Dall's porpoise (*Phocoenoides dalli*) from the Bering Sea than in dolphins from temperate and tropical waters. The similar pattern of PCB homologs in Arctic beluga blubber may reflect greater transport and deposition of the volatile tetra- and penta- congeners to the Arctic marine environment. A diffuse atmospheric source is also suggested by the similarity in ΣPCB in all beluga stocks. A latitudinal gradient in PCB homologs might be expected, for example, between the Hudson Bay and Jones Sound animals which are separated by 15 to 20 degrees of latitude. Norstrom et al. (1988) found higher levels of PCBs in polar bears from

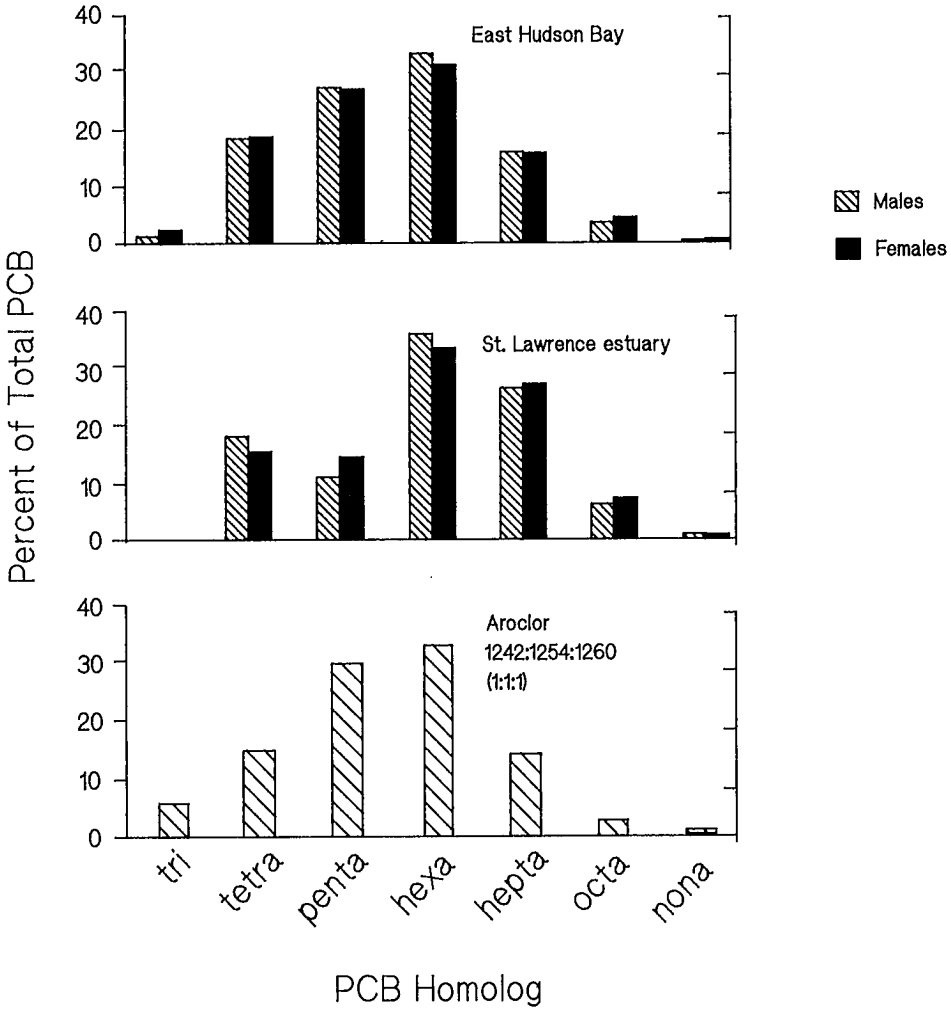

FIG. 5. Chlordane-related compounds as a percent of ΣCHLOR in technical chlordane and and in beluga blubber from Hudson Bay and the St. Lawrence estuary.

West Hudson Bay than in those from the Lancaster Sound area. The lack of a gradient may be due to the different age structure of the Jones Sound animals that were analysed, and to the fact that the Hudson Bay animals are not residents of the Bay for much of the year but are believed to inhabit Hudson Strait during the winter months (Smith and Hammill 1986).

The source of PCCs for both the St. Lawrence and Hudson Bay watersheds may be atmospheric transport and deposition from the southern U.S. where PCCs were used extensively until 1984 (Rapaport and Eisenreich 1988). PCC was an important organochlorine contaminant in sea water sampled during 1986/87 at the ice island located west of Axel Heiberg Island (Bidleman et al. 1989) and is the major organochlorine in marine fish from Canadian Arctic waters (Muir et al. 1987). Little toxaphene was apparently used in the Great Lakes region although PCCs are prominent contaminants in fish in these waters (Schmitt et al. 1983). The higher levels in St. Lawrence belugas may therefore be due to the proximity of the St. Lawrence drainage area to areas of major PCC use, in contrast to the more remote Arctic locations. By the same reasoning, higher levels of PCCs would be expected in Hudson

Bay animals inhabiting waters draining northern Ontario, but this was not observed. Similar PCC levels were observed in all Arctic stocks. Generally higher levels of PCCs were observed in Arctic char (*Salvelinus alpinus*) from the eastern Arctic which was consistent with the northeastern flow of air masses from mid-latitudes in North America to the Arctic (Muir et al. 1990c).

The pattern of PCCs in marine mammals shows extensive transformation in comparison with the standard, making quantitation difficult (Jansson et al. 1979; Muir et al. 1988a). This pattern may also reflect selection of heavier, less water soluble PCCs during atmospheric transport and deposition in sea water and during accumulation by biota (Bidleman et al. 1989). PCCs were a major contaminant in dolphins and pilot whales from Newfoundland waters (Muir et al. 1988a) and in narwhals (*Monodon monoceros*) (Muir et al. 1990a). Andersson et al. (1988) found PCCs were prominent organochlorine contaminants in salmon from the Northwest Atlantic and Greenland, and in harp seals (*Pagophilus groenlandicus*) from the Gulf of St. Lawrence. The PCC/PCB ratio of 0.42 in harp seals (Andersson et al. 1988) was higher to that in St. Lawrence beluga blubber in the present study (0.19) but was lower than ratios in Arctic belugas (mean of 1.5).

The extremely high levels of ΣDDT in St. Lawrence belugas as well as in other cetaceans from the Canadian east coast are indicative of past heavy use of the pesticide for agricultural and forestry uses in Eastern Canada (Gaskin et al. 1983). Deposition of DDT and related compounds to peat bogs in northern and central Ontario and Quebec reached a maximum in the mid-1960's coinciding with the peak production of DDT in North America (Rapaport and Eisenreich 1988). DDE/ΣDDT ratios approaching 0.6, especially in St. Lawrence animals (Table 4), suggest "old" rather than recent DDT inputs (Aguilar 1987; Martineau et al. 1987). DDE/ΣDDT ratios in St. Lawrence males (but not females) were significantly higher than ratios in Arctic animals, which suggests that DDT inputs into the Arctic may be more recent, although the older age of the St. Lawrence animals could also be a factor. ΣDDT levels in St. Lawrence belugas were similar to those in harbour porpoises (*Phocoena phocoena*) from the Bay of Fundy (Gaskin 1982) and about 2-fold higher than found in white-beaked dolphins from the Gulf of St. Lawrence (Muir et al. 1988a). Male bottlenose dolphins from the U.S. east coast had 1.7-fold higher levels of 4,4'-DDE in blubber than St. Lawrence belugas (Geraci 1989) while dolphins from the California coast, collected in the mid-1970's, had about 10-fold higher concentrations (O'Shea et al. 1980).

The prevalence of chlordane-related compounds in Arctic biota is apparent from the higher ΣCHLOR/PCB ratios in Arctic belugas compared with the St. Lawrence stocks. In comparison with other marine mammals in the Canadian Arctic (Muir et al. 1990a) but about 4-fold higher than in ringed seals (Muir et al. 1990c). The St. Lawrence belugas had lower levels of chlordane-related compounds than other east coast cetaceans. White-beaked dolphins had about 1.5- to 2-fold higher levels of ΣCHLOR than did St. Lawrence belugas (Muir et al. 1988a) while bottlenose dolphins from the U.S. east coast had about 5-fold higher levels of t-nonachlor (Geraci 1989). Kawano et al. (1988) found total chlordane concentrations (2.8 μg/g lipid wt) in Dall's porpoise from the northwest Pacific and Bering Sea that were similar to the levels in St. Lawrence belugas.

Like PCCs and DDT, chlordane was used extensively in agriculture until the mid-1970's, particularly in the St. Lawrence river drainage area for insect control in corn production (Von Rumker et al. 1974). Higher levels of ΣCHLOR in St. Lawrence animals may reflect this, as well as possible direct discharge and greater atmospheric deposition compared to Hudson Bay or the Beaufort Sea. As for PCCs, however, there was no trend of declining ΣCHLOR residues with increasing north latitude. There is evidence for atmospheric transport and deposition of chlordane-related compounds to the Canadian Arctic (Gregor 1990; Hoff and Chan 1986) although it is not as prominent in air or seawater as HCH isomers or PCCs (Bidleman et al. 1989).

The lack of differences in α-HCH between St. Lawrence and Arctic belugas is consistent with the ubiquity of this organochlorine. α-HCH was the major form of HCH detected in air and sea water at the ice island (Hargrave et al. 1988). Tanabe et al. (1982) showed that ∑HCH levels over the Pacific Ocean peaked between 30°N and 70°N and concluded that Asia and Southeast Asia were the main sources of HCH isomers. The significantly higher γ-/α-HCH ratios in St. Lawrence belugas may reflect the greater input to the St. Lawrence river of the γ-HCH isomer (lindane) which is still registered for use as an insecticide in Canada and the United States. Transformation of γ-HCH to the more stable α-isomer in the atmosphere (Oehme and Mano 1984) may also contribute to the lower γ-/α-HCH ratios in the Arctic stocks.

∑HCH levels in St. Lawrence belugas were about 2-fold lower than in white-beaked dolphins from Newfoundland waters (Muir et al. 1988a). Mean levels of ∑HCH in blubber of Arctic ringed seals from Northern Baffin Is. and Lancaster Sound were similar to levels in belugas from the Jones Sound and Cumberland Sound stocks (Muir et al. 1988b). Tanabe et al. (1984) and Kawano et al. (1988) have reported much higher proportions of ß-HCH in ∑HCH in small cetaceans from the Northwestern Pacific than observed in belugas in the present study. γ/α-HCH ratios in the N.W. Pacific cetaceans were 0.25 – 0.40, which is a similar range to the ratio in Arctic belugas but lower than in St. Lawrence animals. Greater use of technical BHC, which contains α-, ß- and γ-HCH, in countries bordering the western Pacific may explain the higher proportion of the ß-HCH in cetaceans in that region.

Mirex residues in St. Lawrence beluga blubber clearly distinguish these animals from Arctic belugas and from other Canadian east coast cetaceans. Sources and levels of mirex in St. Lawrence belugas have been discussed by Béland and Martineau (1988). These authors noted that eels migrating down the St. Lawrence River from Lake Ontario, where relatively high levels of mirex are found in sediments and biota, are the most likely source for belugas. Ten- to 100-fold lower levels of mirex in cetaceans not feeding in the St. Lawrence estuary indicate that atmospheric transport and deposition of mirex is a relatively unimportant pathway for the St. Lawrence animals. Although mirex levels were low in Arctic belugas, a distinct gradient was apparent with higher levels in animals feeding in waters influenced by large inputs of freshwater from large rivers (Mackenzie estuary and Western Hudson Bay) than in animals in the High Arctic and Cumberland Sound (Table 2). Mirex was also found in the blubber of white-beaked dolphins from Canadian east coast waters at levels about 10-fold lower than in St. Lawrence animals (Muir et al. 1988a).

HCB and ∑CBz levels in St. Lawrence belugas were very similar to those reported in white-beaked dolphins (Muir et al. 1988a) but about 5- fold higher than reported in blubber of harbour porpoises from the Bay of Fundy. Dieldrin levels in St. Lawrence belugas were similar to those reported in white-beaked dolphins (Muir et al. 1988a) and in pilot whales and white-sided dolphins (*Lagenorhynchus acutus*) from the U.S. east coast in the early 1970's (Taruski et al. 1975) but were about 2-fold lower than those found in harbour porpoises in the Bay of Fundy in the late 1970's (Gaskin 1982).

Age and Sex Differences in Organochlorine Levels

A higher level of PCBs and organochlorine pesticides in male than in female pinnipeds and cetaceans is widely observed and is attributed to loss of pollutants via lactation (Aguilar 1987). Tanabe et al. (1986,1987) found that PCB and DDE residues in female short-finned pilot whale (*Globicephala macrorhynchus*) and in Antarctic minke whales (*Balaenoptera acutorostrata*) were positively correlated with age of immature females and negatively correlated with age of reproductively active females. A similar decline with increasing age was observed for the Hudson Bay female belugas. The average age of the Hudson Bay belugas was 10 ± 4 yr (Table 1). High Arctic females, which averaged 4.6 yr, showed no significant correlations between residues and age and had levels similar to those in males, indicating that

they were too immature to have lactated. By contrast, Martineau et al. (1987) found significant positive correlations between both male and female St. Lawrence belugas and PCB and ΣDDT residues in blubber, and a similar positive correlation (not statistically significant) was seen with the five females from the St. Lawrence that were analysed in the present work. Such a positive trend is unusual in female cetaceans and could be caused by several factors. It may be a reflection of the greater contamination of their diet such that successive lactations do not eliminate a quantity equal to what they are accumulating, whereas in the Arctic females, lactation appears to eliminate greater amounts of PCB and ΣDDT than is contributed via the diet. The positive correlation with age in the females in the St. Lawrence could also be due to a lower frequency of lactation due to a lower reproductive rate or to the older age of the samples which are collected exclusively from dead stranded animals. Tanabe et al. (1986) found evidence for increasing levels in older females which they attributed to reduced numbers of parturitions in this group. A similar relationship, whether it might be age-related or due to reproductive effects of the contaminants, may explain the positive correlation of PCB and ΣDDT levels in female belugas observed by Martineau et al. (1987).

The 4-fold and 2-fold higher levels of ΣDDT and ΣPCB, respectively, found in male than in female St. Lawrence animals in the present study, and by Martineau et al. (1987), are similar to the differences found between the sexes in Hudson Bay and Cumberland Sound animals, and suggest that loss of the most lipophilic organochlorines via lactation is similar in these populations and that, in this respect, the St. Lawrence animals are "normal." Differences in organochlorines between sexes could also be due to diet. However, if this the case, greater differences would be expected for mirex and α-HCH levels. Most of the chlorinated aliphatic compounds (mirex, ΣHCH, cis-chlordane) showed few differences between sexes and, unlike the chlorinated aromatics, do not appear to be preferentially excreted via lactation.

Temporal Trends in Organochlorines

Analysis of beluga oil from 1966/67 indicated that chlordane and PCCs were more prevalent in the 1980's than during the 1960's (Table 2). Beluga oil from the W. Hudson Bay stock had higher levels of ΣDDT and lower levels of PCCs and chlordane than found in the same stock 20 yr later. Because the sex of the animals from which the oil was prepared is unknown, no precise estimate of the increase can be given. These results are consistent with trends between 1969 and 1984 in organochlorines in fat from Hudson Bay and Baffin Bay polar bears (Norstrom et al. 1988), in which ΣCHLOR and ΣPCB levels increased 4.3-fold and 1.9-fold, respectively, and ΣDDT declined slightly. Lower concentrations, especially of chlorinated aliphatic compounds, could also be due to degradation during manufacture and storage of the oil, as was indicated by relatively high 4,4-DDD levels in the sample from Churchill.

The findings in beluga blubber and polar bear fat are not consistent with trends observed in ringed seals in the Canadian Arctic, especially in the case of PCBs. Addison et al. (1986) reported declines of about 60% for PCBs and 40 – 50% for 4,4'-DDE between 1972 and 1981 in blubber of ringed seals from Holman Island. ΣPCB concentrations in Beaufort Sea beluga blubber appear to be higher than observed by Addison and Brodie (1973), who did not detect PCBs in samples collected in 1972, whereas ΣDDT concentrations in adult animals (sex was not specified) in the earlier study were similar to levels that we found in males. However, the absence of detectable PCB in the 1972 samples may reflect lower reliability and reduced sensitivity of PCB analysis using "packed" column gas chromatography, a less elaborate separation technique widely used at that time. Two harbour porpoises collected in 1972 from West Greenland had similar PCB levels (6.7 μg/g) to the Cumberland Sound belugas analysed in this study (Clausen et al. 1974). Mean PCB concentrations for East Hudson Bay animals sampled in 1984/85 and those from 1987 (Table 2 and 3) showed no significant

differences (t-test at $P < 0.05$). ΣDDT levels in 1987 samples were about 2-fold higher than in the earlier samples for both males and females. The greater age of the 1987 group (Table 1) may explain these differences, especially in the case of males where positive correlations of ΣDDT with age were observed.

In conclusion, there are few major differences in organochlorine concentrations among Arctic beluga stocks. This lack of geographical variation is consistent with a diffuse atmospheric source of the contaminants and with wide geographic range of some stocks such as the Hudson Bay animals. The St. Lawrence belugas, in contrast to the Arctic animals, have much higher levels of ΣPCBs, ΣDDT, mirex, and, to a lesser extent PCCs, dieldrin and chlordane-related compounds. The PCB and ΣDDT levels found in the limited number of St. Lawrence animals analysed in this survey were similar to those reported in a larger survey by Martineau et al. (1987). The high levels of PCBs and other organochlorines have been suggested to be the prime cause of the low reproductive rate of the St. Lawrence population (Béland et al. 1988; Sergeant and Hoek 1988) although this has been questioned by Addison (1989). The St. Lawrence population has been reported to have a reproductive rate which is less than half that in Arctic stocks (Sergeant and Hoek 1988). While no cause and effect relationship can be unequivocally established, the comparison with Arctic belugas supports the hypotheses put forward by those authors. The St. Lawrence animals are clearly exposed to much higher levels of organochlorines and other pollutants, such as lead (Wagemann et al. 1990) and polyaromatic hydrocarbons (Martineau et al. 1988), than Arctic animals. Continued study of the St. Lawrence animals is needed because toxicological effects of organochlorines are clearly more likely to be expressed in this stock before becoming apparent in other cetacean populations in Canadian waters.

Acknowledgments

We wish to thank the following individuals for help in sample collection, subsampling and aging of animals: R. Walker and P. Weaver, Fisheries and Oceans, Winnipeg; W. Doidge, Fisheries and Oceans, Ste-Anne-de-Bellevue, R. Plante (Filmar Inc., Bic, P.Q.) and the Hunters and Trappers Associations of Pangnirtung, Eskimo Point and Grise Fiord. We also thank R.J. Norstrom and M. Simon (Canadian Wildlife Service, National Wildlife Research Centre, Hull, P.Q.) for GC-MS confirmation of PCCs and other organochlorines. Collection and analysis of St. Lawrence specimens was supported through a grant from the Wildlife Toxicology Fund.

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Heavy Metals and Selenium in Tissues of Beluga Whales, *Delphinapterus leucas*, from the Canadian Arctic and the St. Lawrence Estuary

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Samples of liver, kidney and muscle tissue from beluga (*Delphinapterus leucas*) from five locations across the Canadian Arctic and the St. Lawrence Estuary were analyzed for copper, zinc, cadmium, mercury, lead and selenium. The St. Lawrence Estuary beluga had significantly higher levels of lead, mercury, and selenium and significantly less cadmium than most Arctic whales. Mercury was positively associated with selenium and age in all animals, and cadmium in kidney was positively associated with selenium and age. Copper concentrations declined with age. Whales from some Arctic sites appeared to have higher levels of cadmium than from other Arctic sites.

Des échantillonages de foie, rein et masse musculaire de marsouins blancs (*Delphinapterus leucas*) provenant de cinq endroits sur l'ensemble de l'Arctique Canadien et de l'estuaire du St-Laurent furent analysés pour le cuivre, le zinc, le cadmium, le mercure, le plomb et le sélénium. Chez le marsouin blanc de l'estuaire du St-Laurent les niveaux de plomb, de mercure et de sélénium étaient d'une manière significative plus élevés et les niveaux de cadmium d'une manière significative moins élevés que dans la majorité des baleines de l'Arctique. Le mercure était positivement associé avec le sélénium et l'âge chez tous les animaux, et le cadmium dans le rein avec le sélénium et l'âge. Les concentrations de cuivre déclinèrent avec l'âge. Les baleines provenant de certains sites arctiques semblaient avoir des niveaux plus élevés de cadmium que ceux provenant d'autres sites arctiques.

Introduction

Marine mammals have been exposed to naturally occurring trace metals throughout their evolutionary history. Some metals are essential for life; others, such as mercury, lead and cadmium, are toxic to biota even at relatively low levels. They have been present in the environment from early times, albeit at much lower concentrations (Patterson 1965; Ericson et al. 1979), but glacial records have shown that global atmospheric fluxes of lead and mercury have increased as a consequence of human activities (Murozumi et al. 1969; Ng and Patterson 1981). The historic increase of lead in the environment has also been revealed by analyses of living and fossil bivalve shells from the eastern Canadian Arctic. Modern shells had approximately five times as much lead as fossil shells (Bourgoin and Risk 1987). Worldwide anthropogenic cadmium emissions have also increased nearly seven-fold since the turn of this century (Boutron and Delmas 1980), and body burdens of cadmium in humans have increased about five-fold during the same time (Drasch 1983).

Marine mammals near polluted coastal areas have been exposed to various contaminants as a result of human activities (Braham 1973; Harms et al. 1978; Viale 1978; Duinker et al. 1979; Hyvärinen and Sipilä 1984). Mercury pollution from the Saguenay River, a tributary of the St. Lawrence Estuary, has been reported (Cossa and Desjardins 1984; Gobeil et al. 1984), and fish in the international section of the St. Lawrence River had high levels of lead, mostly alkyl lead, in 1981 (Wong et al. 1988). The pollution of the St. Lawrence Estuary and the declining beluga (*Delphinapterus leucas*) stocks there (Béland et al. 1988; Martineau et al. 1988) remain concerns among scientists (International Forum 1988) and the public (Boychuck 1988).

Only one beluga from the St. Lawrence was analysed previously for metal contamination (Sergeant 1980) and its mercury level was not considered high. A review of contaminants in marine mammals (Wagemann and Muir 1984) revealed little data on Arctic belugas (Bligh and Armstrong 1971; Beak Consultants 1978; C. T. Hansen, Greenland Environmental Research Institute, Copenhagen, Denmark, personal communication). High metal burdens were reported in other Arctic marine mammals, notably mercury and lead in ringed seals (*Phoca hispida*) (Smith and Armstrong 1975; Wagemann 1989) and cadmium in northern fur seals (*Callorhinus ursinus*) (Goldblatt and Anthony 1983) and narwhal (*Monodon monoceros*) (Wagemann et al. 1983).

Our objective was therefore to collect and analyse samples and test the hypothesis that there are no statistically significant differences in tissue levels of selected metals among belugas from the St. Lawrence Estuary and five Arctic locations.

Methods

Samples of liver, kidney, and muscle were obtained from hunted animals from five locations in the Arctic (Fig. 1) in conjunction with native hunts, and from animals found dead in the St. Lawrence Estuary. The sampling methodology has been described previously (Wagemann et al. 1983). Samples were excised with a clean knife and put into precleaned polyethylene bags. Samples from the Arctic were frozen in the field, shipped on ice and stored at -30°C until analyzed.

Samples were first dried and ground, then analysed for Cu, Zn, Cd, Hg, Pb and Se in Laboratory 1 (R. Wagemann) according to Wagemann et al. (1983). The quality of data on heavy metals in biota from this laboratory has been verified and discussed elsewhere (Wagemann et al. 1983; Wagemann and Armstrong 1988). The St. Lawrence Estuary samples were analysed fresh in Laboratory 2 (C. Desjardins) which was also subject to quality control. Precision and accuracy in both laboratories were monitored by reference to standard samples, by participation in quality check programs (Federal Interdepartmental, International Atomic Energy Commission), and by monthly checks on the recovery of metals. The

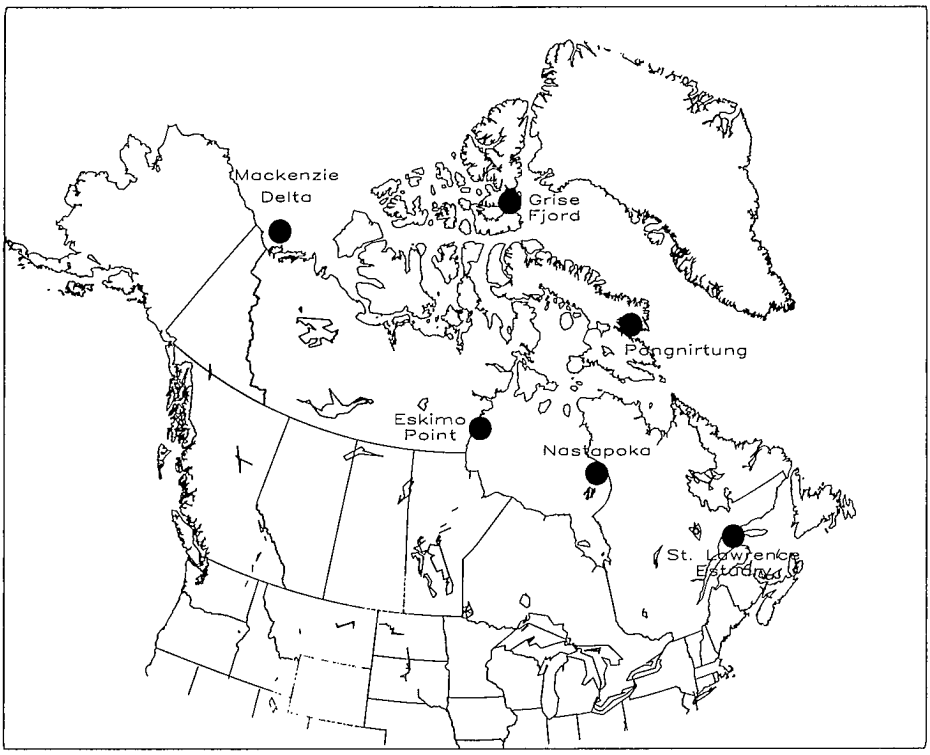

FIG. 1. Capture locations (●) of belugas.

methods used in the two laboratories were similar and were verified by analysing five tissue samples for Hg, Cd, and Pb, in each laboratory. The values obtained agreed within 10% for Hg, 20% for Cd, and 30% for Pb. For St. Lawrence Estuary belugas, results are reported as obtained by Laboratory 2, but converted to a dry weight basis using the average moisture content of the tissues. (Conversion factors were 3.748 for liver; 4.623 for kidney; 3.610 for muscle). Otherwise, moisture was determined on individual samples.

Ages of animals were determined by counts of dentinal annuli in longitudinal thin sections of mandibular teeth, assigning two growth layer groups to a year (Goren et al. 1987). To minimize variations, all sections were examined by the same observer, and were read up to five times each as blind replicates.

Each set of data from the six areas for each metal and each tissue (i.e. 103 sets; Pb-kidney data unavailable from 5 locations) were tested for normality using the Martinez and Iglewicz (1981) test. All groups passed the test except Cu and Pb in muscle of the Mackenzie group. One of these (Cu) passed the normality test when a single high outlier was omitted; the other did not and was omitted from the comparison. Values outside the 99.9 % confidence interval of the mean were considered outliers, but if they did not negate the normality test they were retained in the calculation of the mean. The means were compared using Scheffe's (1959) multiple means test ($\alpha = 0.05$).

Robust (Andrews' sine) multiple linear regression was performed on untransformed data (dry wt) of metals on age and metals on metals. Essentially the same associations between the variables were found with log-transformed as untransformed data in multiple regression of metal concentrations in other marine mammal tissues (Wagemann et al. 1983). All variables were designated sequentially once as the dependent variable and once as the independent variable, and variables were retained when they were significant both ways i.e.

as the dependent and independent variable. A critical probability level of 0.90 was chosen for retention of any variable in the model. The *t*-test ($\alpha = 0.05$) was used to compare two means. Discriminant analysis was performed on all the groups with all metal variables included, using linear discriminant functions for classification.

Some samples differed in their age distributions. No correction was necessary for metal concentrations that were independent of age. For metals that varied with age, age was included as a factor when comparing areas.

Results

Beluga samples were taken from five locations across the Canadian Arctic and from the St. Lawrence Estuary between 1981 and 1987 (Table 1). The relatively small sample size from multiple years precluded an assessment of variation with time and for statistical purposes samples from different years were pooled for each location. The number of animals sampled at each location and their mean age varied among sites. Whales sampled in the St. Lawrence were significantly older than those from Eskimo Point and Grise Fiord, and the latter group was significantly younger than the Mackenzie Delta group.

The concentration of Pb, Cd and Hg varied considerably within each group, as indicated by the relatively large standard deviations of the group mean for each metal (Tables 2–4). Variation in concentration was generally larger for nonessential than essential metals (Table 5). Nevertheless, the mean lead concentration in animals from the St. Lawrence Estuary was significantly higher ($P < 0.05$) in both liver and muscle than in any other group except the Nastapoka group in muscle (Table 6). There were no significant differences in the mean lead concentration among the Arctic locations, although the Nastapoka group had also a relatively high mean lead concentration in both liver and muscle (0.17 and 0.19 µg/g dry wt, respectively). The within-group variations were relatively large (Table 5). In the St. Lawrence Estuary group, the level of lead in the kidney was approximately the same as in the liver. Lead was not measured in the kidney of other groups.

TABLE 1. Mean age, standard deviations and ranges, year of collection and number (*n*) of belugas collected from different locations.

Location	Lat./Long.	Age	Year	*n*
Mackenzie Delta	68° 50′N 136° 15′W	12.3±4.4[a] (2–22)	1981	35
Mackenzie Delta	68° 50′N 136° 15′W	21.1±9.2[a] (12.5–42)	1984	8
Grise Fiord	76° 35′N 83° 14′W	5.6±4.8 (1–21)	1984	17
Pangnirtung	66° 06′N 65° 57′W	11.2±3.7 (6–17)	1984	11
Eskimo Point	61° 06′N 93° 59′W	11.2±6.7 (0–24)	1984	23
Nastapoka (Hudson Bay)	56° 55′N 76° 33′W	13.2±7.7 (1–33)	1984	15
St. Lawrence Estuary	48° 26′N 68° 33′W	17.8±9.9[b] (0–30)	1987	8
St. Lawrence Estuary	48° 26′N 68° 33′W	17.4±8.5[b] (2.5–29)	1982-86	27

[a] Mean age of both groups combined = 13.9±5.5 years.

[b] Mean age of both groups combined = 17.5±8.8 years.

TABLE 2. Mean levels of metals (μg/g, dry wt) and percent moisture (%M), standard deviations (), ranges, and [*n*] in liver of belugas from different Canadian locations.

	Mackenzie Delta	Grise Fiord	Pangnirtung	Eskimo Point	Nastapoka	St.Lawrence
Cu	50.3	39.1	60.7	117.	150.	37.3
	(49.0)	(21.1)	(36.0)	(250.)	(200)	(34.5)
	3.0-220	3.14-96.7	27.4-153	3.68-1241	20.5-699	0.34-162
	[43]	[17]	[11]	[23]	[15]	[30]
Pb	0.038	0.044	0.034	0.082	0.17	0.59
	(0.038)	(0.028)	(0.023)	(0.237)	(0.16)	(0.63)
	0.01-0.17	0.001-0.09	0.003-0.068	<0.001-1.16	0.039-0.60	0.004-2.13
	[39]	[16]	[11]	[23]	[15]	[30]
Cd	8.52	12.2	23.5	25.0	18.9	0.58
	(5.42)	(14.1)	(23.9)	(22.9)	(9.88)	(0.41)
	0.28-23.6	0.64-63.3	2.74-71.2	0.03-97	3.47-39.6	<0.005-1.5
	[43]	[17]	[11]	[23]	[15]	[30]
Hg	44.1	8.27	18.7	24.9	38.4	126.
	(45.5)	(7.71)	(16.8)	(25.2)	(48.0)	(161.)
	0.46-182	1.42-29.4	3.59-58.7	0.04-93	0.60-152	1.42-756
	[42]	[17]	[11]	[23]	[15]	[30]
Se	23.3	9.21	10.3	15.7	16.7	79.2
	(19.7)	(4.74)	(5.57)	(8.78)	(7.97)	(110.)
	0.92-87.4	1.97-14.6	3.94-22.7	1.40-28.4	2.88-28.5	2.72-307
	[43]	[17]	[11]	[23]	[10]	[7]
Zn	92.0	93.6	101.	90.4	93.2	98.4
	(15.5)	(18.8)	(25.9)	(31.4)	(9.99)	(41.8)
	50.4-123	38.3-129	67.5-145	46.8-208	79.6-118	8.62-211
	[43]	[17]	[11]	[23]	[15]	[30]
%M	72.8	74.8	73.0	73.7	72.8	No Data
	(2.29)	(2.53)	(1.86)	(1.90)	(1.88)	
	66.5-78.8	68.4-78.4	69.3-76.1	69.4-78.2	70.5-77.4	
	[43]	[17]	[11]	[23]	[15]	

The mean cadmium concentration was significantly lower in the liver and kidney of the St. Lawrence Estuary group than in all other groups, except the Mackenzie and Grise Fiord groups for liver, and the Grise Fiord group for kidney (Table 6). The Pangnirtung and Eskimo Point groups had the highest cadmium concentrations in both liver and kidney and did not differ significantly from each other. For kidney, the two groups were significantly higher than all other groups except the Nastapoka group, and for liver the Eskimo Point group was also significantly higher than the Mackenzie Delta group. In muscle there were no significant differences in cadmium among any of the groups. The concentration of kidney/liver cadmium was in the range of 3 to 5 in belugas from different Arctic localities and 12 in belugas from the St. Lawrence Estuary.

The St. Lawrence Estuary group had the highest mean mercury concentration in the tissues examined. Mercury levels were 3 to 15 times and 2 to 4 times higher in the liver and muscle respectively than in all other groups, which did not differ significantly from each other. When the values for hepatic mercury in the St. Lawrence Estuary group were compared to the regression of mercury in liver on age for all Arctic groups (Fig. 2), 37% exceeded the upper 95% confidence limit for a single point; less than 4% of the Arctic animals exceeded this limit.

TABLE 3. Mean levels of metals (μg/g, dry wt) and percent moisture (%M), standard deviations (), ranges, and [*n*] in kidney of belugas from different Canadian locations.

	Mackenzie Delta	Grise Fiord	Pangnirtung	Eskimo Point	Nastapoka	St.Lawrence
Cu	10.1 (1.67) 7.3-16.7 [43]	13.1 (3.28) 9.32-24.6 [17]	12.6 (2.86) 9.37-19.4 [11]	11.8 (1.48) 8.82-14.8 [22]	11.9 (1.43) 8.66-14.3 [14]	19.0 (21.9) 7.5-123 [30]
Pb	No Data	No Data	No Data	No Data	No Data	0.69 (0.47) 0.005-1.76 [30]
Cd	44.2 (20.7) 2.9-106 [43]	42.0 (22.3) 5.39-91.2 [17]	106. (75.0) 16.1-277 [11]	96.6 (64.3) 0.052-275 [22]	69.0 (35.1) 17.2-133 [14]	7.01 (4.11) <0.005-17.9 [30]
Hg	13.1 (7.9) 0.90-43.6 [43]	6.81 (4.91) 1.54-19.0 [17]	14.4 (5.98) 2.44-24.5 [11]	11.3 (6.26) 1.01-23.9 [22]	13.4 (9.58) 0.80-32.1 [14]	29.5 (42.4) 1.48-228 [30]
Se	11.3 (3.45) 4.60-25.3 [43]	8.95 (2.12) 5.65-12.5 [17]	11.7 (2.97) 6.76-16.2 [11]	12.7 (4.08) 3.62-19.7 [22]	12.6 (4.21) 5.85-20.9 [14]	13.4 (6.63) 5.22-22.5 [8]
Zn	110. (18.6) 73.2-170 [43]	108. (16.9) 74.8-131 [17]	121. (25.7) 89.7-185 [11]	110. (17.5) 84.1-144 [22]	115. (14.0) 94.6-151 [14]	110. (43.3) 49.9-227 [30]
%M	78.4 (2.99) 72.2-92.4 [43]	78.2 (2.29) 71.8-80.9 [17]	78.2 (1.11) 75.8-79.8 [11]	79.1 (1.19) 77.3-81.1 [22]	77.5 (1.44) 75.5-79.5 [14]	No Data

For mercury in the muscle, the St. Lawrence Estuary group mean, was significantly higher than all other means except the Pangnirtung group mean, and for liver it was also significantly higher than all other groups except the Nastapoka group. The mean mercury concentration in the kidney of the St. Lawrence Estuary group, although also higher than the others (2 to 4 times), was significantly higher only than the Grise Fiord group mean. The other groups did not differ significantly from each other.

The St. Lawrence Estuary group also had a significantly higher mean selenium concentration in the liver compared to all other groups, which did not differ significantly from each other. In kidney and muscle, selenium means did not differ significantly among any of the groups.

Zinc concentration ranged within groups by a factor of two or more and there was no significant difference in mean concentration among the six groups for the three tissues examined. Mean copper concentration in liver and muscle did not differ significantly among any of the groups. Copper in the kidney was highest in the St. Lawrence Estuary group and was lowest in the Mackenzie Delta group, and only these two groups differed significantly.

TABLE 4. Mean levels of metals (µg/g, dry wt) and percent moisture (%M), standard deviations (), ranges, and [*n*] in muscle of belugas from different Canadian locations.

	Mackenzie Delta	Grise Fiord	Pangnirtung	Eskimo Point	Nastapoka	St.Lawrence
Cu	4.58[a]	3.25	3.12	3.92	3.12	5.37
	(5.25)	(0.44)	(0.26)	(2.40)	(0.40)	(4.62)
	2.53-34.0	2.68-3.96	2.70-3.51	2.66-14.1	2.51-4.03	3.03-17.6
	[34]	[16]	[11]	[23]	[14]	[9]
Pb	0.024[b]	0.023	0.028	0.028	0.187	0.37
	(0.025)	(0.046)	(0.012)	(0.016)	(0.338)	(0.45)
	0.01-0.1	<0.001-0.19	0.011-0.050	0.008-0.085	0.021-1.23	0.01-1.37
	[27]	[16]	[11]	[23]	[14]	[9]
Cd	0.43	0.069	0.22	0.65	0.16	0.038
	(0.96)	(0.049)	(0.17)	(2.30)	(0.18)	(0.044)
	0.03-5.35	0.027-0.22	0.026-0.57	0.015-11.2	0.01-0.60	<0.005-0.14
	[35]	[16]	[11]	[23]	[14]	[9]
Hg	3.86	2.39	3.52	3.13	3.00	8.88
	(5.32)	(1.01)	(0.80)	(2.07)	(2.00)	(5.28)
	1.16-33.4	1.13-4.49	1.56-4.64	0.36-8.68	0.43-7.00	3.2-20
	[34]	[16]	[11]	[23]	[14]	[9]
Se	2.20	1.17	1.15	1.77	1.52	2.40
	(5.32)	(0.11)	(0.15)	(1.12)	(0.55)	(1.76)
	0.93-32.8	1.01-1.38	0.83-1.36	1.15-6.44	0.54-2.97	1.25-5.76
	[35]	[16]	[11]	[23]	[14]	[6]
Zn	80.5	68.7	83.4	65.2	74.0	81.9
	(17.9)	(18.0)	(15.5)	(15.2)	(22.5)	(15.3)
	39.3-116	49.3-127	63.7-105	36.4-102	43.6-122	71.5-120
	[35]	[16]	[11]	[23]	[14]	[9]
%M	71.9	71.9	72.0	73.1	72.7	No Data
	(2.32)	(1.11)	(1.53)	(1.87)	(1.37)	
	64.3-75.1	69.7-74.0	70.1-75.3	67.4-75.5	70.2-74.3	
	[35]	[16]	[11]	[23]	[14]	

[a] One high value (241 µg/g) excluded from mean.
[b] One high value (2.02 µg/g) excluded from mean.

Discriminant analysis performed on all the groups with all metal variables included did not reveal any geographic differences. Robust multiple linear regression, performed on all groups combined, revealed a number of associations among metals and between age and metals in the three tissues examined (Table 8). Only lead was not associated significantly with other metals or age in the tissues examined.

Cadmium in the kidney was associated positively with selenium, zinc, and age of animals, and negatively with mercury, and in the liver positively with zinc. In the muscle cadmium was only associated positively with age. Mercury was strongly, positively associated with selenium in all three tissues, and in both liver and kidney was strongly, positively associated with age. Mercury in kidney was negatively associated with zinc and cadmium. Mercury in muscle was not associated with age, but mercury and zinc were positively associated in muscle. Selenium, in addition to the relations already mentioned, was associated positively with zinc and cadmium in the kidney. Copper in all three tissues was strongly negatively associated with age of animals.

Table 5. Coefficient of variation (%) for mean metal concentrations in liver (L), kidney (K) and muscle (M) of belugas from various locations.

		Mackenzie Delta	Grise Fiord	Pangnirtung	Eskimo Point	Nastapoka	St.Lawrence
Cu	L	97.3	54.1	59.3	75.6	133.0	92.4
	K	16.6	25.1	22.8	12.6	12.0	116.0
	M	115.0	13.6	8.2	61.1	12.9	86.0
Pb	L	99.1	63.1	69.1	104. 0	93.9	106.0
	M	103.0	199. 0	41.9	56.6	152.0	121.0
Cd	L	63.6	116.0	101.0	91.9	52.3	70.1
	K	46.8	53.2	71.0	66.5	50.8	58.8
	M	221.0	71.2	79.0	352.0	109.0	117.0
Hg	L	101.0	93.3	90.2	101.0	125.0	128.0
	K	60.3	72.2	41.6	55.2	71.7	144.0
	M	138.0	42.1	22.8	66.3	65.4	59.4
Se	L	84.5	51.5	54.2	55.9	47.6	139.0
	K	30.4	23.6	25.3	32.1	33.3	49.3
	M	242.0	9.0	13.1	63.4	36.5	75.6
Zn	L	16.9	20.1	25.7	34.7	10.7	42.5
	K	16.9	15.7	21.2	15.9	12.1	39.3
	M	22.2	26.2	18.6	23.3	30.4	18.7

Discussion

We tested the hypothesis that metal concentrations in three tissues were the same in belugas from six different putative stocks. This hypothesis was rejected. Belugas from the St. Lawrence Estuary had significantly higher lead and mercury levels in liver and muscle, higher selenium levels in liver, and lower cadmium levels in liver and kidney than most Arctic groups. Belugas from Eskimo Point had significantly more cadmium in their livers than did whales from the Mackenzie Delta. Cadmium levels in kidney of whales from Eskimo Point and Pangnirtung were significantly higher than in whales from the Mackenzie Delta and Grise Fiord.

The sample from the St. Lawrence Estuary may have been biased with respect to contaminant levels. The animals were found dead and the cause of death was not established. If the high lead and mercury concentrations contributed to the whales' deaths, then our sample from this area was biased in favour of high metal levels. If these metals did not contribute to the death of the whales then the reported levels represent the population at large. There are no data to evaluate these potential biases but this does not negate indications of lead and mercury pollution in this aquatic system.

TABLE 6. Significant differences ($\alpha = 0.05$, not underlined) of multiple means of a metal concentration among different locations for three tissues (Scheffe's test).

Metal	Liver	Kidney	Muscle
Cu	6 2 1 3 4 5	1 4 5 3 2 6	1 2 3 4 5 6
Pb	1 2 3 4 5 6	No Data	2 3 4 5 6
Cd	6 1 2 5 3 4	6 2 1 5 4 3	1 2 3 4 5 6
Hg	1 2 3 4 5 6	2 4 1 5 3 6	2 5 4 1 3 6
Se	1 2 3 4 5 6	1 2 3 4 5 6	1 2 3 4 5 6
Zn	1 2 3 4 5 6	1 2 3 4 5 6	1 2 3 4 5 6

1 = Mackenzie Delta
2 = Grise Fiord
3 = Pangnirtung
4 = Eskimo Point
5 = Nastapoka
6 = St. Lawrence Estuary

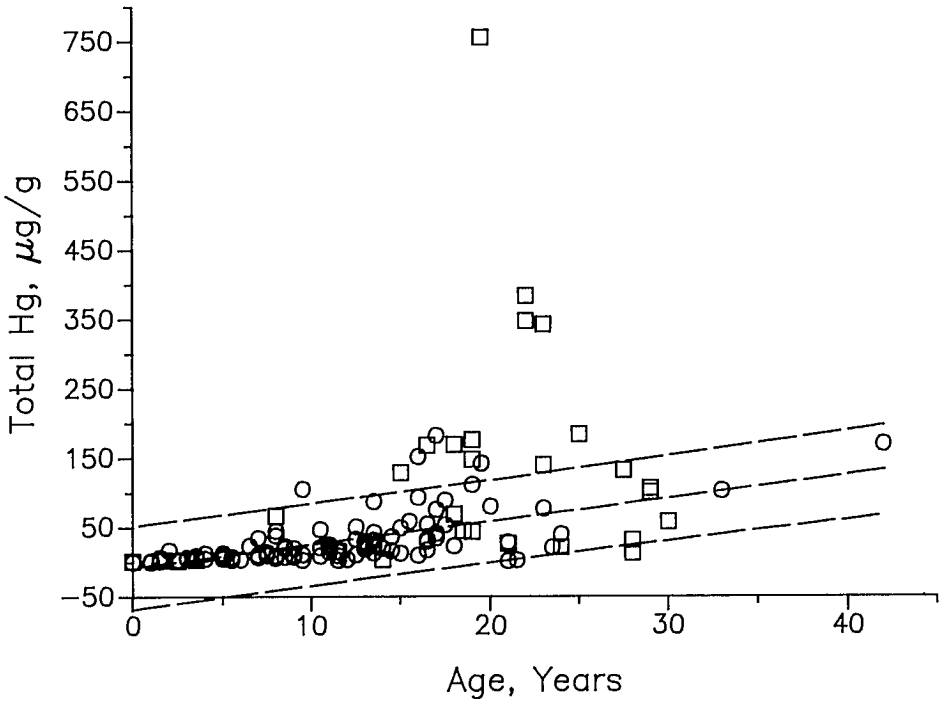

FIG. 2. Regression (Hg = 0.47 + 1.52 Age) using all groups except the St. Lawrence Estuary group, of Hg (μg/g, dry wt) in liver on age (years) of animals with 95% confidence bands, and the St. Lawrence Estuary group superimposed. Each symbol represents one animal. St. Lawrence group (□); all other groups (O).

Belugas from the St. Lawrence Estuary had, on average, about 10 times more lead in liver and muscle than did Arctic belugas (Tables 2,4). This and the presence of lead in fish sampled from the St. Lawrence River in 1981 (Wong et al. 1988) is suggestive of lead pollution in this aquatic system. Regression analysis showed that lead was not correlated with age in any of the soft tissues of the belugas examined, although lead does accumulate with age in hard tissues (Grobler et al. 1985). We found no previous reports on lead in belugas. Compared to narwhal (liver: 0.109 μg/g dry wt; muscle: 0.031 μg/g dry wt, Wagemann et al. 1983), the lead levels in St. Lawrence belugas were higher. In most Arctic belugas the levels were similar to those in narwhal.

The mean mercury concentration in the liver of the St. Lawrence group was significantly higher than in all others except Nastapoka; in muscle it was also higher than in all others except Pangnirtung. Mercury accumulated in liver and kidney with increasing age as it does in other marine mammals (Perttilä et al. 1986; Norstrom et al. 1986; Wagemann et al. 1983). The St. Lawrence Estuary whales had a higher mean age than the Eskimo Point and Grise Fiord whales. The higher age of of the St. Lawrence animals could not account entirely for their high mercury levels. More than a third of the animals in this group exceeded the upper confidence limit (95%) of the hepatic mercury concentration when mercury was regressed on age (Fig. 2). Also, St. Lawrence belugas had a high liver/kidney mercury ratio. Although the liver is the preferred organ for mercury accumulation in mammals generally, and the examined belugas were no exception, mercury accumulated to a greater extent in liver relative to the kidney in St. Lawrence Estuary belugas than in Arctic belugas. In belugas from the St. Lawrence Estuary the liver/kidney ratio of the mean mercury concentration was 4.3, and in Arctic belugas 3.4.

There are only a few previous reports of mercury levels in belugas (Table 7). Sergeant's (1980) determination of mercury in the liver of one beluga from the St. Lawrence (36.9 ppm = 138 μg/g dry wt) is not substantially different from our mean. The levels in St. Lawrence whales were also similar to those found in Mackenzie Delta belugas in 1978 (Table 7). Levels in the Arctic groups were similar to those previously published for western Greenland (Hansen, C. T., personal communication, Greenland Environmental Research Institute, Copenhagen, Denmark) and Hudson Bay (Bligh and Armstrong 1971).

Mercury concentrations in Mackenzie Delta belugas were lowest in 1972 and highest in 1978 (Table 7) and apparently declined thereafter. Drilling for oil and gas and artificial island construction began in the Beaufort Sea in 1973 and peaked toward the end of that decade. It is known that the formation of freshwater impoundments increases the mercury levels in fish in such impoundments (Bodaly et al. 1984; Boucher et al. 1985). Whether or not sediment disturbances in a more open system such as the Beaufort Sea could have a similar effect on upper trophic levels is unknown. Although the pre-activity data (1972) are the lowest, and the highest concentrations coincide with peak activity in the Beaufort Sea, a coincidental correspondence cannot be ruled out in view of the small sample sizes ($n = 7$ for 1972, $n = 8$ for 1978) and the lack of age estimates for these samples.

Comparison with other marine mammals is helpful in obtaining a broader ecological perspective. Mercury levels were higher in the St. Lawrence belugas than previously reported values for northern hemisphere cetaceans except the short- finned pilot whales (*Globicephala macrorhyncha*) from Georgia, USA. (Wagemann and Muir 1984). They were also higher than most published values for northern pinnipeds (Sergeant 1980; Goldblatt and Anthony 1983; Ronald et al. 1984; Wagemann and Muir 1984; Helle 1985). The exceptions were ringed seals from the Baltic ($n = 6$) and Lake Siamma ($n = 3$) (Wagemann and Muir 1984) and from Boothnia Bay ($n = 22$) (Helle 1985); grey seals (*Halichoerus grypus*) from the United Kingdom ($n = 98$) and Sable Island ($n = 7$); harbour seals (*Phoca vitulina*) from New Brunswick ($n = 1$), the Netherlands ($n = 5$), California ($n = 4$) and England ($n = 1$); hooded seals (*Cystophora cristata*) from the Gulf of St. Lawrence ($n = 3$); and bearded seals (*Erignathus barbatus*) from the Canadian Arctic ($n = 6$) (Wagemann and Muir 1984). The

Table 7. Mean heavy metal concentrations (μg/g, dry wt)[a] and sample sizes (*n*) in liver and muscle of belugas from the Arctic.

Cd	Hg	Pb	Zn	Location, Year	Source
		Liver			
No Data	23.5 (7)	No Data	No Data	Mackenzie Delta, 1972	Lutz and Armstrong[c] (1972, unpublished)
11.1	115 (8)	No Data	111 (8)	Mackenzie Delta, 1977	Beak Consultants (1978)
No Data	33.2 (1)	No Data	No Data	Hudson Bay, 1971	Bligh and Armstrong (1971)
5–15[b] (43)	3.82-61.5[b] (43)	No Data	106-112[b] (43)	Western Greenland, 1984-86	Hansen, C. T. 1989 (personal comm.)
		Muscle			
No Data	2.56 (7)	No Data	No Data	Mackenzie Delta, 1972	Lutz and Armstrong[c] (1972, unpublished)
0.41 (11)	7.67 (11)	No Data	92.7 (8)	Mackenzie Delta, 1977	Beak Consultants (1978)
No Data	3.50 (1)	No Data	No Data	Hudson Bay, 1971	Bligh and Armstrong (1971)
No Data	1.91 (43)	No Data	No Data	Hudson Bay, 1971	Bligh and Armstrong (1971)
≤ 0.1[b] (43)	0.03-4.73[b] (43)	No Data	97.5-118[b] (43)	Western Greenland, 1984-86	Hansen, C.T. 1989 (personal comm.)

[a] Converted from a wet to a dry weight basis using factors 3.748 and 3.610 for liver and muscle, respectively.
[b] Median range, converted to dry weight with above-given factors.
[c] Freshwater Institute, Contaminants and Toxicology, Winnipeg, Canada.

small sample sizes of the published data preclude detailed analysis by age, gender and geographic location.

The mean concentration of cadmium was significantly lower in the St. Lawrence Estuary group than in all Arctic groups except the Mackenzie (liver) and Grise Fiord (liver, kidney) whales. Based on the strong, positive correlation of cadmium with age found in most marine mammals (Hamanaka et al. 1982; Honda et al. 1983; Wagemann et al. 1983; Muir et al. 1988), higher cadmium levels were expected in the significantly older St. Lawrence group than were expected to levels in the younger Grise Fiord whales. The cadmium concentration in the St. Lawrence group was also lower than in most other northern hemisphere marine mammals (Goldblatt and Anthony 1983; Wagemann et al. 1983; Ronald et al. 1984; Wagemann and Muir 1984; Helle 1985; Steinhagen-Schneider 1986; Tohyama et al. 1986). The relatively high mercury levels in the St. Lawrence animals may have played a role in the low cadmium levels by competing with cadmium in metallothionein where almost all cadmium is stored (Wagemann et al. 1984). The negative correlation between cadmium and mercury in the kidney, the preferred organ for cadmium accumulation, would tend to support this hypothesized competition.

Belugas from Pangnirtung and Eskimo Point had higher cadmium levels than those from the Mackenzie Delta (liver and kidney) and Grise Fiord (Table 6). There were no significant differences in mean age among the three eastern Arctic groups, although the Grise Fiord mean was low. Levels of cadmium in the Pangnirtung and Eskimo Point groups were also higher than in belugas from western Greenland (Table 7, C.T. Hansen, Greenland Environmental Research Institute, Copenhagen, Denmark, personal communication) and white-beaked dolphins (*Lagenorhynchus albirostris*) from the coast of Newfoundland, but were lower than in long-finned pilot whales (*Globicephala melaena*) from Newfoundland (Muir et al. 1988) and narwhals from northern Baffin Island (Table 7, Wagemann et al. 1983). Whales from Pangnirtung, Eskimo Point, and Nastapoka probably spend part of the year in Hudson Strait (Brodie et al. 1981; Richard and Orr 1986; Smith and Hammill 1986), but whether or not this has a bearing on the higher cadmium levels in their tissues is unknown.

Selenium in liver of the St. Lawrence group was the highest among all the groups. In kidney and muscle it did not differ significantly from any of the other groups, and was significantly, positively correlated with cadmium in kidney in the pooled sample. While selenium may reduce cadmium toxicity (Parízek et al. 1971; Whanger 1979; Ridlington and Whanger, 1981), a positive correlation between selenium and cadmium indicates that it does hot do so by lowering the tissue concentration of cadmium. In the liver, however, there was no such positive correlation and the low cadmium levels in the St. Lawrence Estuary group were accompanied by high selenium levels in that group. The high selenium levels in the liver of St. Lawrence Estuary animals were a direct reflection of the high mercury concentrations in this group. Such a correlation was reported also for other marine mammals (Koeman et al. 1973; Wagemann et al. 1983; Norstrom et al. 1986).

There were no significant differences in the mean copper concentrations in liver and muscle among any of the groups, although four animals from the Nastapoka River had inexplicably high concentrations in liver (200–700 µg/g dry wt) and one animal from Eskimo Point had an even higher concentration (1241 µg/g dry wt). Copper in kidney was significantly higher in the St. Lawrence Estuary group than in the Mackenzie Delta group. The reason for this is unknown. In the pooled sample, copper declined in all tissues with age, indicating either an actual loss of the metal from tissues with age or a dilution of it by tissue growth.

The effects of a changing chemical environment on biota are difficult to measure and assess, and it is particularly difficult to determine sublethal effects of heavy metals on marine mammals in the wild. High levels of nickel were found in the hair of still-born pups of ringed

TABLE 8. Associations between the dependent and independent variables (age, metals, selenium) in beluga whale tissues (all groups combined) at $0.90 \leq P < 0.95$, at $0.95 \leq P < 0.99$ (underlined), and at $0.99 \leq P$ (doubly underlined).

	Liver	Kidney	Muscle
Dependent Variable	Independent Variables		
Cu	-Age	-Age	-Age
Pb	Not Assoc.	No Data	Not Assoc.
Cd	+Zn	+Age, -Hg, +Se, +Zn	+Age
Hg	+Age, +Se	+Age, -Cd, +Se, -Zn	+Se, +Zn
Se	+Hg	+Cd, +Hg, +Zn	+Hg,
Zn	+Cd	+Cd, -Hg, +Se	Not Assoc.

seals from Lake Saimaa in eastern Finland (Hyvärinen and Sipilä 1984). Harp seals fed methyl mercury suffered from a variety of health disorders (Freeman et al. 1975; Ramprashad and Ronald 1977). Common seals (*Phoca vitulina*) fed fish from polluted waters off the coast of the Netherlands showed signs of reproductive failure (Reijnders 1986) and vitamin A and thyroid deficiencies (Brouwer et al. 1989). Only organochlorines were investigated in this study although the waters from which these fish came are polluted also with heavy metals (Reijnders 1980). Less is known about sublethal effects in marine mammals than in terrestrial mammals, in which even low exposures to some toxic metals can affect the nervous system (Maehara et al. 1986; Yamamura et al. 1987), behavior and learning ability, before any overt clinical signs appear.

Our study showed that the anthropogenic pollutants, lead and mercury, have found their way into belugas in the St. Lawrence Estuary. There is therefore reason to speculate that these pollutants together with the high organochlorine levels in these animals (Desjardins et al. 1983a, 1983b; Martineau et al. 1987; Muir et al. 1990) may adversely affect the health of these belugas. Although a definite connection between pollutants of any kind in the St. Lawrence Estuary and death of animals has not been established, Martineau et al. (1985, 1986, 1987, 1988) found the condition of dead, stranded belugas in the St. Lawrence Estuary to be consistent with organochlorine and polycyclic hydrocarbon-induced insults. Findings included a high incidence of tumors, gastric erosions and ulcers, as well as multisystemic diseases and bacterial infections in the more contaminated specimens (Martineau et al. 1988). Any adverse effects would be the result of the combined action of all toxic elements and compounds in the tissues, acting over a relatively long time. The depuration rate of heavy metals in belugas is unknown, but in humans the biological half-life for lead and mercury is about 10 years (Task Group 1973; Friberg et al. 1979) and for cadmium it may be even longer, at 10–30 years (Friberg et al. 1974; Kjellström and Nordberg 1978).

The population of belugas in the St. Lawrence is thought to be declining (Reeves and Mitchell 1984; Béland et al. 1988). In spite of the closure of a chlor-alkali plant on the Saguenay river in 1976 and an alkyl lead production plant closure in 1985 (DuPont, Canada Ltd. at Maitland), the state of pollution of the St. Lawrence and the declining stock of belugas there remain a concern (Boychuk 1988; International Forum 1988).

Acknowledgments

We extend sincere thanks to the Hunters and Trappers Association and hunters of Pangnirtung, Eskimo Point and Grise Fiord for providing most of the animals, to Dr. W. Doidge for providing samples from Nastapoka, to R. Walker and P. Weaver for sampling, subsampling and ageing animals, to R. Plante (Filmar Inc.) for collecting and processing samples and tooth preparations of St. Lawrence Estuary animals, and to G. Boila and D. Savoie in Winnipeg, and R. Maltais, G. Leblanc and P. Arpin in Longueuil for analytical work. We also thank Dr. E. Pelletier, INRS-Océanologie, Rimouski, and three anonymous reviewers for constructive comments on an earlier manuscript, and Dr. C.T. Hansen for providing data on belugas from western Greenland. The enthusiastic assistance with subsampling and analysis by summer students is gratefully acknowledged. Collection and analysis of the St. Lawrence specimens was supported through a grant from the Wildlife Toxicology Fund.

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DUE DATE

25/10/91			
	201-6503		Printed in USA