Meddelelser om Grønland

Studies of white whales *(Delphinapterus leucas)* and narwhals *(Monodon monoceros)* in Greenland and adjacent waters

Compiled and edited by

Born, E. W., Dietz, R. and Reeves, R. R.

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Instructions to authors

See page 3 of cover.

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Contents

Distribution and abundance

Exploitation and status

Habitat use and behaviour

Life History, stock identity and toxicology

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Overview of the special issue "Studies of white whales (*Delphinapterus leucas*) and narwhals (*Monodon monoceros*) in Greenland and adjacent waters"

RANDALL R. REEVES, RUNE DIETZ and ERIK W. BORN

Reeves, R. R., Dietz, R. & Born, E. W. 1994. Overview of the special issue "Studies of white whales (*Delphinapterus leucas*) and narwhals (*Monodon monoceros*) in Greenland and adjacent waters". – Meddr Grønland, Biosci. 39: 3–11. Copenhagen 1994-04-22.

This overview introduces the collection of papers on the Distribution and abundance; Exploitation and status; Habitat use and behaviour; and Life history, stock identity and toxicology of white whales (*Delphinapterus leucas*) and narwhals (*Monodon monoceros*) in Greenland and adjacent waters. It includes brief summaries of the 19 included papers and calls attention to ongoing and future studies on the same or related subjects.

Key Words:
White whale, beluga, *Delphinapterus leucas*, narwhal, *Monodon monoceros*, Greenland, eastern Canadian Arctic, Svalbard.

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Introduction

This special issue of *Meddelelser om Grønland, Bioscience* is devoted exclusively to two arctic species: the narwhal (*Monodon monoceros*) and the white whale or beluga (*Delphinapterus leucas*). Both have a vast range in the Arctic. The narwhal occurs mainly in the arctic regions appended to the North Atlantic Ocean while the white whale's distribution is disjunct circumpolar and extends to subarctic waters in some areas.

The main purpose of this book is to provide a benchmark in our understanding of the populations of white whales and narwhals in waters adjacent to Greenland. The stocks of both species that migrate along the eastern and western fringes of Greenland are believed to move seasonally into international waters or, in some cases, into the coastal waters of other states, particularly Canada and Norway (Svalbard). Contributions have thus been solicited mainly from investigators who study these "shared" stocks of whales in Greenland, eastern Canada and Norway.

The central importance of narwhals and white whales in the traditional Greenlandic culture and economy provides an organizing theme for this compilation of papers. Whale hunting has long contributed to the subsistence of Inuit. Today it provides both food and cash income in the hunting areas. Whales also have symbolic importance to people both inside and outside Greenland. For these reasons we consider it important that hunting be managed to ensure sustainability and that other human activities (*e.g.* marine traffic, pollution, commercial fishing) be managed to minimize their impacts on the stocks of whales. It is the role of scientists to define stock boundaries, assess populations, measure production and recruitment, and identify factors which could affect a whale population's health and productivity. None of these tasks is easy, and there is a continuing need to improve estimates and eliminate uncertainty.

Since Kleinenberg *et al.*'s monograph on the white whale was published in 1964 (English version in 1969), there has been a rapid advance in knowledge about both the white whale and the narwhal. The concise reviews of the white whale by Stewart & Stewart (1989) and Brodie (1989) and of the narwhal by Reeves & Tracey (1980) and Hay & Mansfield (1989) are already "out-of-date" in many respects. Recently Smith *et al.* (1990) provided a collection of papers that demonstrated progress in the systematics, population assessment, behavioural ecology, physiological ecology, age estimation, immunology and health evaluation, and toxicology for the white whales in Alaska and Canada. No similar compilation was available for narwhals or for the white whales in Greenland. We were aware that new literature on both species was appearing every year and that there was a wealth of data in reports ("gray literature") and in the files of government biologists and academics that had not yet been properly analyzed and published. Especially in view of the clear need on the part of managers for better scientific information about white whales and narwhals, we were convinced that a book such as this one, with its geographic emphasis on the waters bordering northeastern Canada, Greenland and Svalbard, should be published. Canada and Greenland established a Joint Commission on the Conservation and Management of Narwhals and Belugas in 1989. Several of the papers published here have already been used (in draft form) by this commission's Scientific Working Group and by the International Whaling Commission's Scientific Committee. We hope that the special issue will become a standard reference for these and other bodies involved in the conservation of arctic whales and their habitat.

Organization and chapter summaries

This collection of papers has been organized into four thematic sections: Distribution and abundance; Exploitation and status; Habitat use and behaviour; Life history, stock identity and toxicology. The matter of placing individual papers into one section or another was not always straightforward. Some contributions contained valuable information relevant to more than one of the sections.

Distribution and abundance

The six papers in this section mainly concern narwhals. Distribution and abundance of the stocks of white whales centered in Baffin Bay and Davis Strait have been reviewed elsewhere recently (Richard *et al.* 1990, Richard 1991a, Heide-Jørgensen *et al.* 1993, Doidge & Finley in press). Richard (1991b) provided a population estimate and a discussion of stock identity for the narwhals in northern Hudson Bay, Foxe Basin and Hudson Strait.

Two papers in the present volume are based on the results of aerial surveys in the eastern Canadian Arctic. Koski & Davis (1994) analyzed data from visual surveys conducted in 1978–1979 and 1981–1982 as part of environmental impact assessments related to oil and gas development. They found considerable variation in the numbers of narwhals entering a given summering ground from one year to the next. They also found narwhals to be widely dispersed in the offshore pack ice in Baffin Bay and Davis Strait during late winter and spring. Their surveys between 12 May and 2 July 1979 resulted in an estimate of somewhat more than 34 000 (SE 8200) narwhals in the Baffin Bay-Davis Strait region. This estimate has very wide 95% confidence limits (approximately 21 600 and 54 600; Burnham *et al.* 1987) and does not include a correction for animals outside the survey area or submerged out of sight as the aircraft flew past. Koski & Davis also estimated the calving and first-year mortality rates of narwhals in this region (0.29 calves/adult female/year and approximately 17%, respectively).

Richard, Weaver, Dueck & Barber (1994) reported on photographic surveys of the major narwhal summering grounds in the Canadian High Arctic. For reasons similar to those mentioned above in relation to the estimate by Koski & Davis (1994), the estimate of 18 000 (90% CI 15 000–21 000) narwhals by Richard *et al.* is probably an underestimate of the true population size. Richard *et al.* identified and discussed various biases that could have affected their results. They also conducted an experiment using life-sized models of adult, juvenile and neonatal narwhals and white whales, placed at different water depths, to evaluate detection probabilities on aerial photographs.

Inglefield Bredning is an important summering area for narwhals. Born, Heide-Jørgensen, Larsen & Martin (1994) conducted a series of census surveys, both from a high-elevation shore site and from airplanes, with the objectives of estimating the size of the summering population and learning about the relative age and sex composition of this population. Their paper presents the results of land-based surveys in 1985 and 1988 and aerial surveys in 1985 and 1986. They concluded that annual differences in the abundance and behaviour of narwhals might be explained at least partly by natural fluctuations in prey populations. The direct count of 4043 narwhals in Inglefield Bredning in August 1984 reported by Born (1986) remains as the highest minimum estimate of this summering population of narwhals.

Relatively little information has been available on narwhals and white whales in East Greenland. Two papers in this volume significantly improve the situation. Dietz, Heide-Jørgensen, Born & Glahder (1994) reviewed historical literature and archival sources for a synthetic appraisal of distribution and relative abundance. Recent catch records and direct observations were also considered. The authors concluded that while narwhals are widespread and common in parts of East Greenland, white whales are largely absent, perhaps due to a lack of suitable habitat. The second paper on East Greenland, by Larsen, Heide-Jørgensen, Martin & Born (1994), gives the results of aerial surveys conducted in Scoresby Sund in September 1983 and 1984. This study, which covered the largest of several fjord systems regularly inhabited by

Fig. 1. White whales were hunted in southwestern Greenland during the 19th and early 20th centuries. This picture was taken in Nuuk around 1915. Photo: Unknown. Copyright Arktisk Institut, Denmark.

narwhals during the open-water season, provided the first quantitative information on narwhals in the Greenland Sea.

The short paper by Gjertz & Wiig (1994) summarizes what is known about white whales in Svalbard. More than 3000 were taken by Norwegian whalers at Spitsbergen between 1945 and 1960, suggesting that there was a fairly large population of white whales at Svalbard in the early 1940s. The white whale is now protected in Norwegian waters, but no population estimates have been made for the Svalbard region. The narwhal's distribution and relative abundance around Svalbard were recently reviewed by Gjertz (1991).

Exploitation and status

This section consists of three papers. Savelle's (1994) examination of archaeological and ethnographic evidence led him to the somewhat unexpected conclusion that prehistoric and early historic Inuit of the eastern Canadian Arctic may not have hunted white whales or narwhals to any great extent. He suggested that the overriding importance of bowhead whales (*Balaena mysticetus*) in the ancient economy of the Thule people may have caused them to pay relatively little attention to the smaller odontocete cetaceans. Hopefully other scholars will accept Savelle's challenge and further explore the interesting questions raised in his paper.

Reeves & Heide-Jørgensen (1994) addressed a problem that brings present-day narwhal hunting and product use into an international context. As narwhal tusks and the craft items made from narwhal ivory are exchanged in a worldwide market system, they become subject to trade agreements and treaty obligations. The character and volume of trade may influence the hunting in various ways. This paper should facilitate two kinds of evaluation – on the one hand how commercial incentives may affect hunt intensity and selectivity, and on the other hand how external trade regulations may affect local economic and cultural development.

The paper by Heide-Jørgensen (1994) provides an overview of recent hunting and population status in West Greenland. According to Heide-Jørgensen the range of white whales in southern and southwestern Greenland has diminished within the present century, presumably due to overexploitation (see Fig. 1). The population that winters off West Greenland has been heavily exploited and appears to have declined substantially since the early 1980s (also see Heide-Jørgensen *et al.* 1993). Among the problems met by the author in trying to evaluate the status of stocks was the lack of complete and reliable catch statistics. He used mattak purchases to document catches in some municipalities, and in the case of Avanersuaq (Thule) this information was used to estimate the landed catch. Simple projections using estimated population sizes in the late 1970s and early 1980s, a range of net rates of annual population increase (0.02–0.04) and known or estimated catches were used to evaluate several different scenarios. According to Heide-Jørgensen the white whale stock off West Greenland would have had to be much larger than 18 600 (the upper limit of the 1981 population estimate – Smith *et al.* 1985) to sustain the catches during the 1980s and early 1990s. The situation for narwhals appears to be less critical. A 1979 population of 34 000 (Koski & Davis 1994) could have sustained the catches; however a 1984 population of 22 000 (Born 1986, Richard *et al.* 1994) could not have.

The population estimates used in the above projections (from Smith *et al.* 1985, Koski & Davis 1994 and Richard *et al.* 1994) are uncorrected to account for whales that were submerged or outside the surveyed areas, but the catch estimates are also uncorrected to account for hunting loss and under-reporting. These countervailing biases are important because their net impact can determine whether catch levels are or are not sustainable. Further information on how the biases have been addressed can be found in Anonymous (1992, 1993) and IWC (1993).

The final paper in this section discusses the interesting question of the extent to which windfall catches made at "sassat", or ice entrapments underneath the dense landfast ice, represent natural mortality vs. hunting mortality (see Fig. 2). The finding of more than 30 dead narwhals in the Uummannaq area in late April 1984 confirms that some entrapped whales are doomed regardless of whether or not they are found and killed by hunters. Siegstad & Heide-Jørgensen (1994) concluded that ice entrapment may have effects on white whale and narwhal populations similar to the effects of mass strandings and epizootics on populations of other marine mammals in tropical and temperate regions. Such "unpredictable catastrophic mortalities" should be considered in stock assessment and management.

Habitat use and behaviour

Although several papers in other sections of the book address similar questions, habitat use and behaviour are central concerns of the two papers in this section. Kingsley, Cleator & Ramsay (1994) studied narwhals in the Eclipse Sound/Milne Inlet/Koluktoo Bay/Tremblay Sound complex, an important summering area in the Canadian High Arctic. Their repeated helicopter surveys between 1987 and 1993 were designed to examine how ice cover, water depth, seafloor relief and shelter from wind might affect narwhal movements and distribution. The whales seemed to remain in the relatively exposed waters of Eclipse Sound only if extensive ice cover was present there. Otherwise they showed an affinity for deep, steep-sided basins. Fortuitously the authors made useful observations of narwhals' responses to forays into these waters by killer whales (*Orcinus orca*).

Smith, Hammill & Martin (1994) reported some of the results of their long-term study of white whale behaviour at Cunningham Inlet in the Canadian High Arctic. Observations were also made of white whales in a small subarctic estuary on the east coast of Hudson Bay (*cf.* Caron & Smith 1990). In both areas the distribution of whales was influenced by tidal processes and to some extent by the date and the volume of river outflow. Adult females, calves and juveniles predominated in the estuaries. The authors argued that the strong philopatry and physiological dependence of white whales on seasonal access to estuaries means that such sites should be carefully protected (see Fig. 3).

Life history, stock identity and toxicology

This section contains a diverse set of papers, all of which are based on analyses done in laboratories using tissue samples collected from whales killed in Greenland or northeastern Canada.

Age estimation is a basic tool for studying animal biology. Although a reliable method for estimating absolute age in narwhals has yet to be developed (*cf.* Hay 1980), a basic method of sectioning white whale teeth and "reading" the growth layers in the dentine and cementum has been available for more than 20 years (Sergeant 1973). Heide-Jørgensen, Jensen, Larsen, Teilmann & Neurohr (1994) sectioned teeth from a large sample of white whales killed by hunters in West Greenland. They found that the lower-jaw teeth of whales from Greenland become significantly worn at a much earlier age than those of white whales from Hudson Bay and the White and Kara seas. Teeth from a captive white whale originally caught in western Hudson Bay exhibited a layering rate of approximately two growth-layer-groups per year, thus reinforcing the conclusions of previous calibration studies (Goren *et al.* 1987, Brodie *et al.* 1990).

Heide-Jørgensen & Teilmann (1994) analyzed tissues from a large sample of white whales from West Greenland to study growth, maturation, reproduction, diet and age structure (see Fig. 4). Their major conclusions were as follows: 1) White whales from West Greenland grow to greater lengths than the whales in all other areas studied. 2) Males reach sexual maturity at 6–7 and females at 4–7 years of age. 3) Mating takes place in May or perhaps later. 4) The gestation period is at least 330 days, and calves are born mainly in April and May. 5) The autumn drive fishery in Upernavik takes mainly

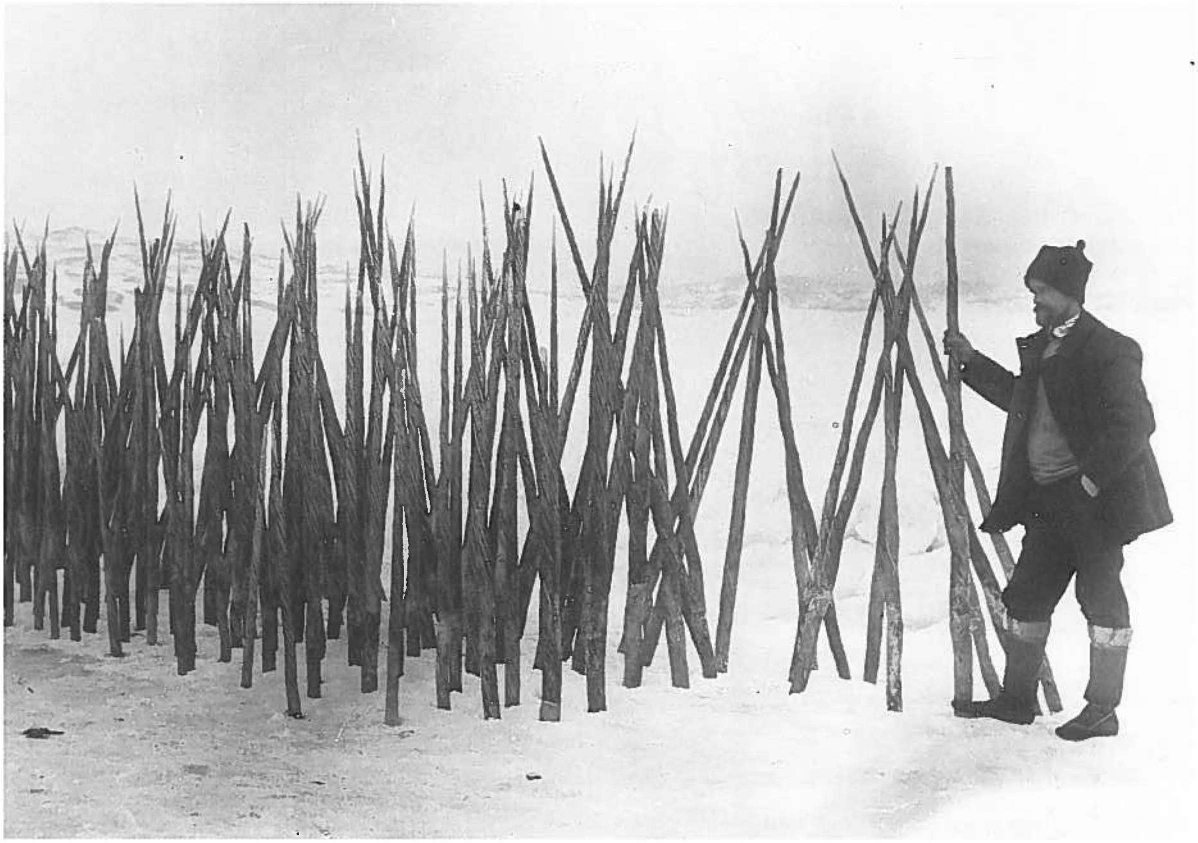

Fig. 2. A display of narwhal tusks obtained from the large ice-entrapment ("sassat") in Disko Bugt, February 1915. Photo: M. Porsild. Copyright Arktisk Institut, Denmark.

juveniles and adult females with calves while the spring hunt in Disko Bugt generally takes a higher proportion of adult whales. 5) The white whales caught today off West Greenland are significantly smaller (in length) than those taken in the drive fishery in southwestern Greenland in the 1910s and 1920s (*cf.* Degerbøl & Nielsen 1930).

The stomach contents of 35 narwhals obtained from the hunt in Inglefield Bredning in the open-water seasons of 1984 and 1985 were sampled and analyzed by Heide-Jørgensen, Dietz & Leatherwood (1994). Arctic cod (*Arctogadus glacialis*), polar cod (*Boreogadus saida*) and other unidentified gadids were found to be the principal prey. The lack of Greenland halibut (*Reinhardtius hippoglossoides*) in this sample of stomach contents was unexpected as both Vibe (1950) and the Inughuit (Thomsen 1993) have reported halibut as important prey of narwhals in northwestern Greenland.

The "stock" is usually regarded as the fundamental unit within a species' total population. However scientists and managers have often had difficulty defining stocks in practical terms. New genetic techniques promise to sharpen our understanding of the stock concept (Dizon *et al.* 1992), but traditional analytical methods can nevertheless provide useful insights. In his paper on size-at-age relationships Stewart (1994a) concluded that white whales from western Hudson Bay were significantly shorter as adults than whales from Cumberland Sound and Jones Sound. This finding is generally consistent with the preliminary results of genetic studies of white whales (Helbig *et al.* 1989, Brown & Clayton 1993, Brennin *et al.* in press). While acknowledging the "waning importance" of morphometric comparisons to questions of stock identity, Stewart pointed out that the variation in body size between populations of white whales remains an interesting biological phenomenon that raises questions related, for example, to differences in marine productivity.

Høier & Heide-Jørgensen (1994) analyzed the steroid hormone and prolactin levels in samples of blood and urine from 131 white whales killed off West Greenland between 1989 and 1992. They confirmed that progesterone levels, measured in either serum or urine, and urine oestrogen levels were reliable indicators of pregnancy in females, and that testosterone levels could be used to judge whether males were or were not sexually mature. Their attempts to use oestrogen content for distinguishing reproductive classes of females (pregnant, nonpregnant, lactating etc.) and to use prolactin for determining lactation were inconclusive. While the authors suggested that

Fig. 3. Large groups of white whales congregate during summer at river outfalls along the coast of Somerset Island, Canadian High Arctic, in this instance near Wadworth Island in Peel Sound, summer 1992. Photo: J. M. Savelle.

the threshold values established in their study could be useful for evaluating the reproductive status of white whales, they also urged caution in applying their results to animals sampled under dissimilar circumstances. The stress from being chased and hunted immediately prior to death could have had a major effect on hormone levels in the white whales used in this study.

Stewart (1994b) measured progesterone levels in the blood serum of 63 female white whales killed in the eastern Canadian Arctic. He concluded that serum progesterone levels of 3 ng/ml or higher provide a reliable indication of pregnancy. He also found that progesterone concentrations were not significantly correlated with ovary, corpus luteum or fetus mass. Female white whales from the three sites sampled by Stewart became sexually mature at 4–7 years of age.

Organochlorines are among the most widespread and dangerous environmental pollutants. Their accumulation in high-order predators, including narwhals and white whales (Muir *et al.* 1988, 1990), has implications both for conservation (Martineau *et al.* 1987, Muir *et al.* 1990) and for human health (Kinloch *et al.* 1992). Although body burdens of heavy metals in cetaceans from West Greenland were given by Hansen *et al.* (1990), organochlorine levels have not been reported previously for white whales from Greenland. The paper by Stern, Muir, Segstro, Dietz & Heide-Jørgensen (1994) documents organochlorine levels in blubber from 138 white whales and skin and kidney samples from 20 individuals taken in western Greenland. As is true in other mammals, substantial quantities of organochlorines are transferred from the mother white whale to her calf via the milk. Ontogenetic changes in contaminant levels led the authors to infer that lactation in white whales lasts for less than one year and that most females bear their first calf at 5–6 years of age. Organochlorine levels in narwhals from Greenland have not been studied.

Remaining gaps and continuing studies

We have no illusions that this volume is either comprehensive or definitive. It advances our knowledge of the monodontids but does not close the books on any aspect of their history, biology, behaviour or ecology. Much remains to be learned.

Of particular and immediate relevance to management is the need for better information on stock relations and diving behaviour. Uncertainty surrounding these two sub-

Fig. 4. Biological samples are obtained from the hunt at Upernavik in October darkness. Photo: M.P. Heide-Jørgensen.

jects has seriously impeded stock assessment. The attachment of satellite-monitored radio transmitters to whales has become feasible only recently. Yet it has already begun to transform our understanding of the animals' behaviour and physiology. This research "tool", along with genetic studies, is expected to clarify many of the discussions about stock identity during the coming years. It may also improve our ability to "correct" population estimates from visual or photographic surveys to account for whales that are present within the sampled area but are not detected because they are submerged when the aircraft passes overhead.

It is disappointing not to have something in the volume that compares the narwhal and the white whale, in terms of their ecological roles and biological characteristics. Qualitative comparisons by earlier workers (Sergeant 1978, Mitchell 1984) began the development of a theoretical framework, and Finley *et al.* (1990) and Doidge (1990) used field data to compare aspects of behaviour and anatomy, respectively, in the two species. Although white whales and narwhals are closely related, eat similar prey and are sympatric in a broad sense, their habitat preferences are clearly different. During the open-water season many white whales move into shallow estuaries while narwhals congregate in deep fjords. During the winter narwhals tend to be widely dispersed in heavy pack ice while white whales are more typically found in wide leads and expanses of open water. These are only central tendencies rather than strict rules, and a closer examination of the differences and similarities between the two species is needed. Hopefully the material in this volume will help stimulate and provide background for more comparative work.

We would also like to have had more coverage of Inuit perspectives in the volume. The recent studies by Remnant & Thomas (1992) in Canada and by Thomsen (1993) in Greenland are welcome additions which recognize the value of knowledge gained by the people who observe, hunt, dissect and consume narwhals and white whales as a regular part of their lives. Too often in the past this accumulated wisdom has been ignored. Thomsen's report from Greenland became available very late in the process of preparing this collection of papers, so it was impossible to ensure that its contents were consistently addressed and appropriately incorporated in all cases.

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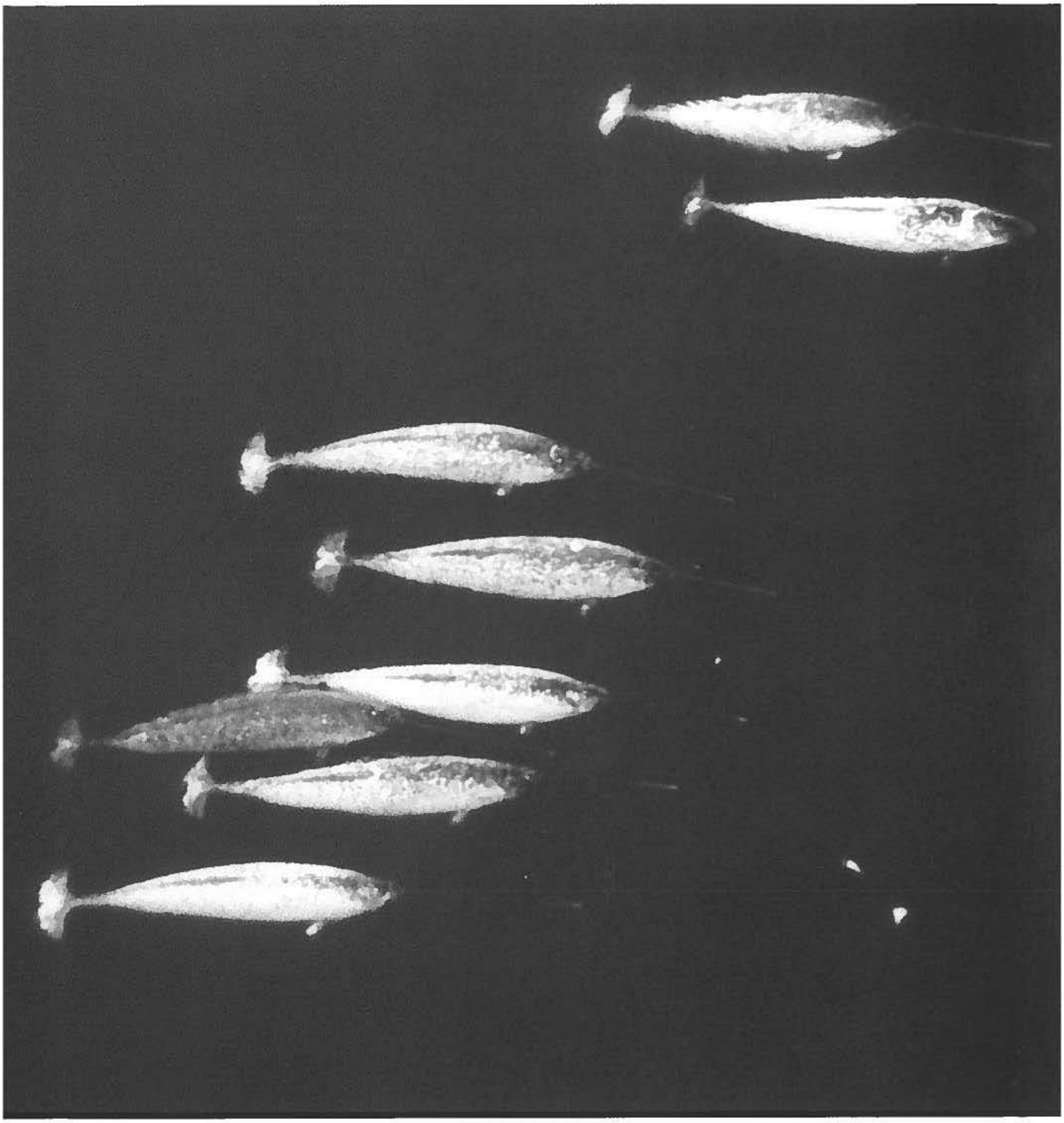
Distribution and abundance



Narwhals in Scoresby Sund, Central East Greenland. Photo: A. R. Martin.

Distribution and numbers of narwhals (*Monodon monoceros*) in Baffin Bay and Davis Strait

WILLIAM R. KOSKI and ROLPH A. DAVIS

Koski, W. R. & Davis, R. A. 1994. Distribution and numbers of narwhals (*Monodon monoceros*) in Baffin Bay and Davis Strait. – Meddr Grønland, Biosci. 39: 15–40. Copenhagen 1994-04-22.

Aerial surveys were conducted over Baffin Bay during May-October 1978–79 and off West Greenland and over southern Baffin Bay, Davis Strait and Hudson Strait during March 1981–82. Narwhals (*Monodon monoceros*) were dispersed throughout the pack ice in northern Davis Strait and Baffin Bay during late winter and spring and moved into nearshore areas in and adjacent to Lancaster Sound during late June and July. Important summering areas were identified in Buchan Gulf, Eclipse Sound, Admiralty Inlet, Prince Regent Inlet and Peel Sound, and possibly in Smith Sound and Home Bay, but there was considerable variation in the numbers of narwhals entering these areas each year. Narwhals remained in nearshore areas until late September or early October when they moved south in advance of and with the newly-forming pack ice. During autumn narwhals tended to migrate in large herds, moving both along the coast of Baffin Island and through offshore waters.

Our best estimates of the size of the narwhal population have come from surveys conducted in late spring when the whales are widely dispersed among the offshore pack ice. An estimated 34 363 (± SE 8282) narwhals were present in offshore areas of Baffin Bay that were surveyed four times in May-July 1979. This late spring estimate included narwhals that later summered on both the east and west sides of Baffin Bay and Davis Strait, but excluded animals that summered in northern Hudson Bay. It does not include animals outside the survey area nor is it corrected to account for animals below the surface.

Our aerial survey data indicate that 7.8–9.0% of narwhals in summering areas were calves. An estimate of calving rate is 0.29 calves/adult female/year based on sightings of 1-month-old calves without considering mortality between birth and the survey date. The mortality rate of calves from 1 month to 13 months of age is estimated as approximately 17%.

Key Words:
Narwhal, *Monodon monoceros*, distribution, movements, numbers, age, sex, reproduction, calf mortality.

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Introduction

The narwhal (*Monodon monoceros*) is an ice-associated cetacean that frequents dense offshore pack ice for 8–10 months of the year. Because the narwhal is essentially inaccessible to humans for much of the year, most information on the species has come from coastal observations during the summer open-water period. This has led to a fairly biased understanding of the distribution, movements and biology of the species. During the late 1970s and early 1980s, we conducted large-scale aerial survey programs in the Canadian High Arctic, Baffin Bay, and Davis Strait in conjunction with proposed offshore oil and gas exploration, production, and transportation proposals. These surveys provided coverage of the offshore pack ice frequented by narwhals during the winter and during spring migration. The surveys also included the open-water season and the onset of the fall migration of narwhals. The results of these surveys are presented here to provide an understanding of the distribution, annual movements, size, age and sex composition, and life history of the Baffin Bay narwhal population. This population includes all narwhals that summer in or adjacent to Baffin Bay and Lancaster Sound. It excludes whales that

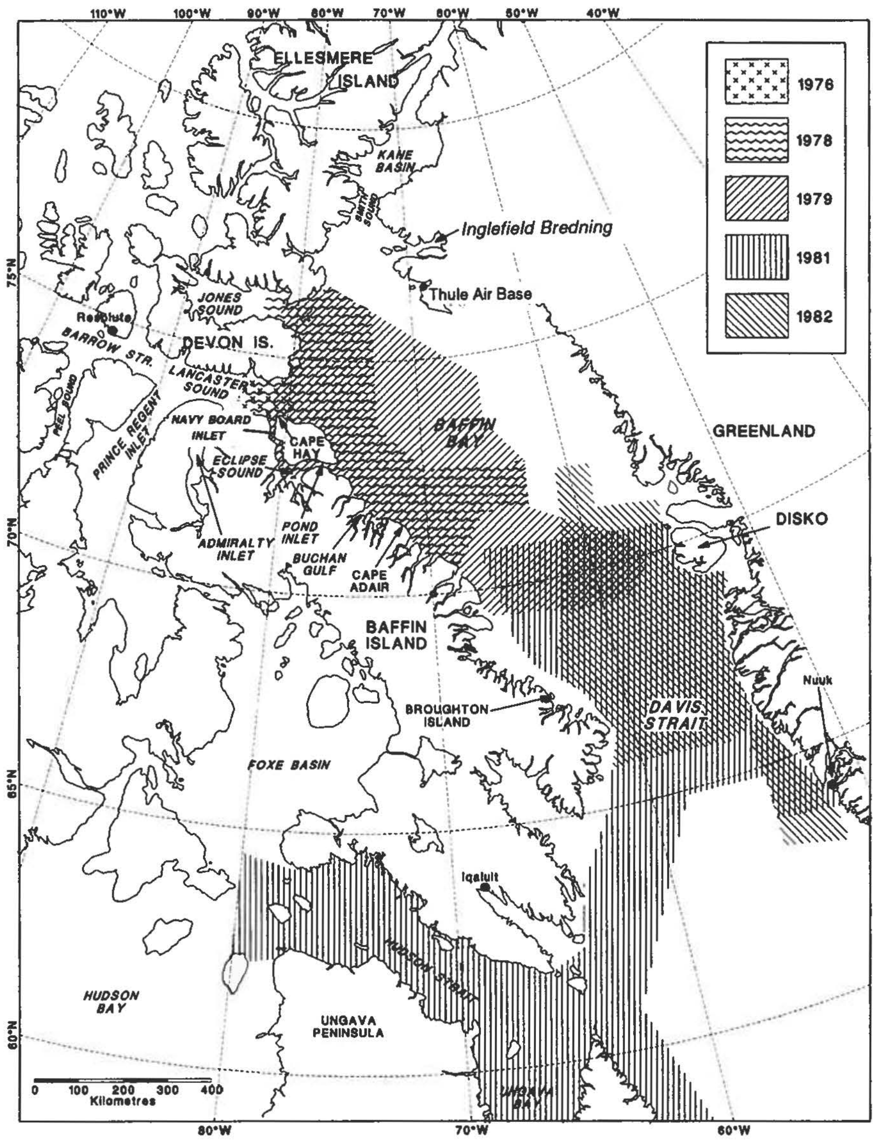


Fig. 1. Map of Baffin Bay, Davis Strait and surrounding areas showing the areas covered during systematic aerial surveys, 1976–1982. See text for other areas that were surveyed on one to a few occasions, 1975–1979.

summer in northern Hudson Bay and that probably winter in eastern Hudson Strait (Richard 1991).

The results from three major, and several smaller, aerial survey projects are reported in this paper. The first was a 5-month (May-September) study of the eastern half of Lancaster Sound conducted in 1976 for Norlands Petroleums Limited, Calgary, as part of an assessment of the potential effects of offshore hydrocarbon exploration in the area (Fig. 1). The second major project was the Eastern Arctic Marine Environmental Studies (EAMES) program conducted in Lancaster Sound and adjacent channels, Jones Sound and Baffin Bay in the May to early October periods of 1978 and 1979. EAMES was a multi- and inter-disciplinary study initiated by the Canada Department of Indian Affairs and Northern Development, Ottawa, and managed and funded by Petro-Canada Explorations, Inc., Calgary (see Sutterlin & Snow 1982 for a description). The third major survey project was conducted in March 1981 and 1982 to document the winter distribution of marine mammals in Davis Strait and southern Baffin Bay to facilitate selection of routes for year-round icebreaking liquid natural gas (LNG) carriers proposed by the Arctic Pilot Project, Calgary. Ancillary winter studies in March 1981 were conducted in southwestern Davis Strait and the northern Labrador Sea (funded by Petro-Canada Explorations, Inc.) and in Hudson Strait and northern Hudson Bay (funded by Canada Department of Fisheries and Oceans). Additional open-water surveys of channels in the central Canadian Arctic were conducted in 1976–77 for the Polar Gas Project.

Table 1. Survey effort and number of narwhals recorded on-transect[a] in Lancaster Sound, Baffin Bay and Davis Strait, 1978–1982.

	All coastal and ice-edge areas			All nearshore areas			Offshore Lancaster Sound			Offshore Baffin Bay and Davis Strait		
Survey period	Area surveyed (km^2)	On-transect[a] narwhals	Density (no./km^2)	Area surveyed (km^2)	On-transect narwhals	Density (no./km^2)	Area surveyed (km^2)	On-transect narwhals	Density (no./km^2)	Area surveyed (km^2)	On-transect narwhals	Density (no./km^2)
1978												
May and Jun	3638	2115	0.58	2050	312	0.15	3767	251	0.07	3903	231	0.06
Jul to mid-Aug	2169	4348	2.00	1047	353	0.34	1619	198	0.12	2120	116	0.05
mid-Aug to mid-Sep	2005	81	0.04	1054	3	0.00	808	0	0.00	1277	0	0.00
mid-Sep to Oct	1817	1159	0.64	1196	419	0.35	685	110	0.16	1187	105	0.09
1979												
May and Jun	2604	1279	0.49	54	6	0.11	2846	143	0.05	4900	561	0.11
end Jun to end Jul	1189	1355	1.14	208	146	0.70	1032	170	0.16	1377	104	0.08
Sep to Oct	9127	7969	0.87	1025	647	0.96	2231	257	0.12	1580	11	0.01
1981												
Mar – heavy pack ice										10416	246	0.024
Mar – open pack ice										3604	38	0.011
1982												
Mar – heavy pack ice										4858	144	0.030
Mar – open pack ice										11024	168	0.015

[a] Excludes narwhals seen outside the transect strip.

Materials and methods

The data presented here came primarily from the extensive aerial survey programs conducted in 1978–79 and 1981–82. These data were supplemented with observations from coastal vantage points in summer and autumn. We also conducted surveys of Lancaster Sound in 1976; results of these surveys are summarized in Davis *et al.* (1978) but some previously unpublished 1976 data are included here.

Survey coverage

Fig. 1 shows the area included in systematic surveys each year and Table 1 gives the survey coverage (km^2) in coastal/ice-edge, nearshore and offshore waters each year. Coastal/ice-edge transects were flown parallel to and centred 200 or 400–600 m seaward of the coast/ice edge when the survey altitude was 45 or 90 m above sea level (a.s.l), respectively. Nearshore transects were flown parallel to and centered 1400 or 1600 m seaward of the coast/ice edge. Offshore transects were flown along lines of latitude or longitude without regard for the presence or absence of open-water leads. The survey effort is summarized for periods when narwhals were present in the offshore pack ice (March to June), moving into summering areas (July to mid-August), present in summering areas (mid-August to mid-September), and moving out of summering areas (mid-September to October).

In 1978 and 1979 the transects were repeatedly surveyed at 7–10 day intervals from May to October; the systematic coverage of offshore areas was more extensive during May-June than during July-October. In addition to the systematic coverage of areas indicated in Fig. 1, we surveyed the coasts of Ellesmere Island and Greenland from 76°30' N latitude to southern Kane Basin on 31 May, 1 June and 5 July 1978 (see Figs 6 and 7, later); narwhal summering areas in Prince Regent Inlet, Admiralty Inlet, Eclipse Sound, Jones Sound and Lancaster Sound during July-September of 1978 and 1979; and the coast of eastern Baffin Island from Pond Inlet to Broughton Island on 13 and 18 September 1979. Most areas surveyed in 1981 and 1982 were surveyed once, but the open pack ice south of Disko was surveyed twice in 1982.

Aerial survey procedures

All surveys were conducted from a DeHavilland Twin Otter equipped with standard windows, a VLF navigation system, radar altimeter, and (during most surveys) a colour radar. The VLF navigation system determined aircraft position and was essential for surveys in offshore locations. The radar altimeter helped to maintain a constant altitude; this was important to estimate the distances of narwhal sightings from the aircraft. The radar helped to maintain the position of the aircraft relative to ice edges or coastlines.

Either two or three observers were present during each survey; one observer sat in the co-pilot's seat (right front) and the second observer sat in the second seat behind the pilot on the left. A third observer was occasionally present in the second seat behind the co-pilot's seat. Observers dictated information for each sighting into portable tape recorders. For each sighting, the species, total number of individuals, number of individuals in each group, behaviour, direction of movement, general and specific habitat, relative age, sex, distance from the centre of the transect, and any other relevant comments were recorded.

All transects were divided into two-minute intervals using a timing device that was audible to observers. Data were recorded, mapped and summarized by two-minute intervals (5.3–9.3 km segments, depending on the speed of the aircraft).

1978–79

The majority of surveys conducted during 1978–79 were designed to document distributions of both marine birds and marine mammals. Because many birds could not be seen or identified from altitudes >50 m a.s.l., most coastal and some offshore surveys were flown at 45 m a.s.l. and ground speeds of 160–185 km/h. However, surveys that were primarily for marine mammals were conducted at 90 m a.s.l. and 220–260 km/h (pack-ice surveys) or 150 m a.s.l. and 200–280 km/h. The primary search area (transect width) was 200, 400 or 800 m on either side of the aircraft during surveys conducted at 45, 90 or 150 m a.s.l., respectively. A line directly below the aircraft was the inner boundary of the transect. The front observer recorded animals that were directly below the aircraft and therefore in a blind spot for the rear observer. Sightings beyond the transect width were recorded when possible.

During low-level surveys conducted in the springs of 1978 and 1979, particularly along the Lancaster Sound ice edge during late June to mid-July, extremely large numbers of marine birds and mammals of many species were encountered. Counts of narwhals along coasts and ice edges during these periods may underestimate considerably the actual numbers present; counts in nearshore and offshore areas better reflect the actual numbers present because observers were not inundated by observations of other species.

1981–82

All 1981–82 surveys were conducted at 150 m a.s.l. and 200–240 km/h; the primary search area included strips 800 m wide on either side of the aircraft, for a transect width of 1.6 km.

In 1981, at the same time as the above surveys were being conducted, part of northern Hudson Bay, Hudson Strait and the northeast coast of Labrador were surveyed. The survey methods were identical to those described for Davis Strait and Baffin Bay and the coverage is shown in Fig. 1. The data on white whales (*Delphinapterus leucas*) in Hudson Strait were reported by Finley *et al.* (1982). Data for white whales in Davis Strait are reported in Heide-Jørgensen *et al.* (1993). Results for narwhals for the entire area are reported here.

Shore-based observations

Observations of migrating marine mammals were made from a 209 m a.s.l. observation post located at Cape Adair, NE Baffin Island (Fig. 1). Observations were made from 13 September to 7 October 1978 (260 h) and from 20 September to 16 October 1979 (277 h). Observations were continuous during daylight hours, except during periods of poor visibility. Binoculars, spotting telescopes and (1979 only) a surveyor's theodolite were used to facilitate spotting, identification and counting of marine mammals.

We conducted observations of spring-migrating narwhals from a cliff 9 km west of Cape Hay on northern Bylot Island (Fig. 1) from 28 July to 9 August 1978 and Greendale & Kerr (1979) attempted observations from the same location from 25 June to 2 August 1979. However, in 1979 persistent fog from 14 July to 2 August prevented observations during the main migration of narwhals.

Relative age and sex composition

Relative age and sex were recorded for some narwhals sighted during aerial surveys. Relative age was estimated based on size and colour of the animal: large light-coloured animals with mottling or spots were called adults and small dark-coloured animals with faint spots were called subadults (*cf.* Mansfield *et al.* 1975). Experienced observers can distinguish calves and yearlings from other subadult narwhals. Newly-born calves (neonates) appear white or light gray because of the presence of the neonatal skin; after it is sloughed, they appear to be slate gray (Reeves & Tracey 1980) and can be distinguished from other subadults by their small size (approx. 40% of mother's length). Yearlings are noticeably larger than calves (50–60% of mother's length), appear more rotund, and are much darker (neonatal skin present on calf) or lighter coloured (neonatal skin sloughed by calf). During our surveys of summering areas in August and early September the neonatal skin was present on calves and they were readily distinguishable from yearlings by experienced observers.

Our surveys were conducted by observers with varying experience and ability to estimate the relative age of narwhals. As a result, we have not used age-classification data from bird surveys (45 m a.s.l.) unless they were recorded by the senior author. We used all data from mammal surveys (>50 m a.s.l.) because most were obtained by experienced marine mammal observers.

Narwhals with tusks were assumed to be males and those without tusks were assumed to be females, although a small proportion of tusked animals are females (Mansfield *et al.* 1975) and an occasional adult male may not have a tusk (Reeves & Tracey 1980).

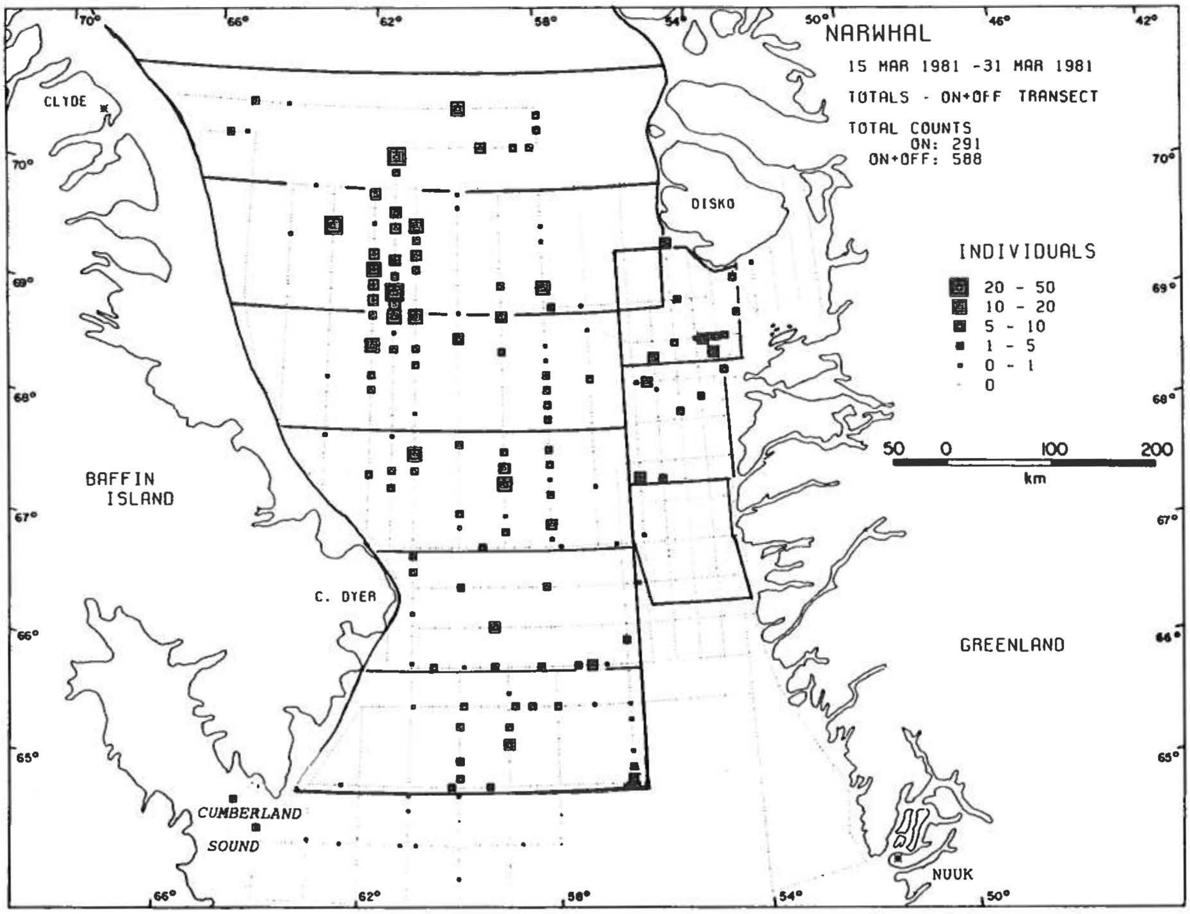


Fig. 2. Survey routes and narwhal sightings in southern Baffin Bay and northern Davis Strait, 15–31 March 1981. On this and subsequent figures individual symbols indicate the number or density of narwhals in a 2-minute transect segment. Each symbol may include sightings of several groups.

Group size

Narwhals that were within one body length of each other were defined as comprising a pod; activities (such as turns or dives) of animals in pods tended to be synchronous. Aggregations of pods were called herds; within herds, pods of narwhals were separated by 5–10, or more, whale lengths. Different pods within a herd frequently behaved differently.

Estimates of numbers in survey areas

Ideally, surveys to estimate numbers of animals should be conducted using randomly chosen transect lines (Cochran 1977, Caughley 1977, Eberhardt 1978). However, the major objective of our surveys was to determine the distributions of the different marine mammal species in the surveyed areas. In such situations, systematic survey patterns are desirable (Caughley 1977, Eberhardt 1978) provided that transects are designed to cross, rather than follow linear features of the habitat that affect animal abundance, *e.g.* coasts, ice edges, leads in sea ice or depth contours. We excluded surveys of coastal/ice-edge and nearshore transects from our estimates of numbers because these transects followed physical features that strongly influenced narwhal distribution. Because transect lengths varied, the ratio estimation procedure (Cochran 1977, Eberhardt *et al.* 1979) was used to estimate densities and numbers of narwhals present in offshore areas. Because densities varied among strata, we used the separate ratio method for sampling without replacement to estimate the total number of narwhals present during selected periods. Caughley & Grigg (1981) describe the method and calculations as applied to a sampling design similar to ours. Our estimates do not include coastal and ice-edge areas or offshore areas outside of our survey

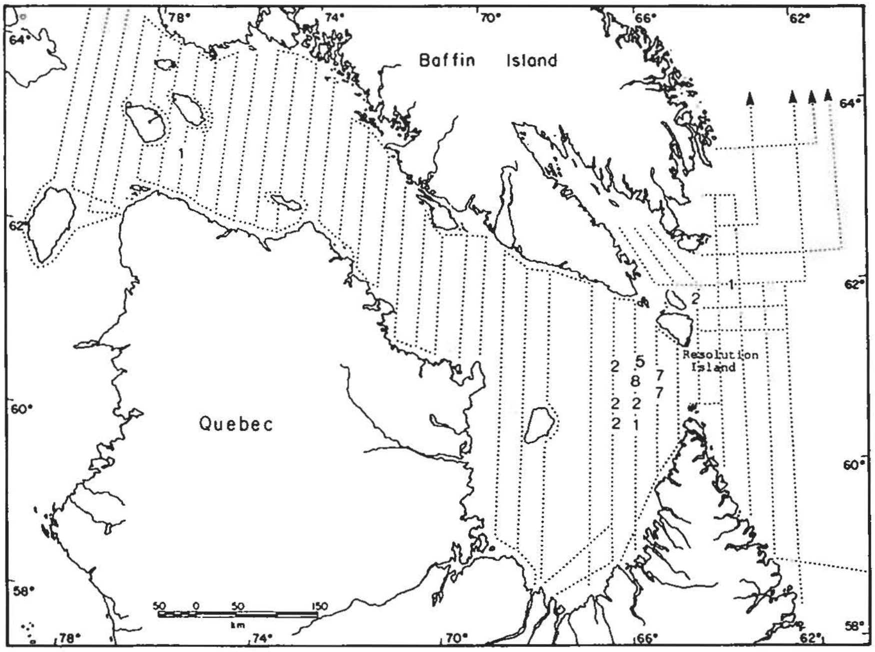


Fig. 3. Survey routes and narwhal sightings in southwestern Davis Strait and Hudson Strait, 14–30 March 1981. Numbers indicate individuals sighted in 2-minute intervals.

strata (see Fig. 11, later), nor do they account for animals that were below the surface at the time of the survey.

Results

Distribution and movements

Late winter 1981

Narwhals were widely dispersed in small groups throughout the pack-ice areas surveyed during the late winter of 1981 (Fig. 2). The average pod size was 2.08 (N=289), including a few groups recorded south of the areas that were included in extrapolations (Fig. 2). Narwhals were found in highest densities in areas where ice cover was 90–99% and only one narwhal was seen in an open-water area. Although narwhals were found among the loose pack ice south of Disko, they were found in highest densities among the heavy pack ice farther west in southern Baffin Bay.

Our surveys in 1981 also included the pack ice along SE Baffin Island, in Hudson Strait and along the NE Labrador coast. Small numbers of narwhals were recorded among the pack ice east of Cumberland Sound (Fig. 2) and in eastern Hudson Strait southwest of Resolution Island, but they were rare or absent in other areas south of 65°N (Fig. 3).

Late winter 1982

Although the overall study area was similar in March of 1981 and 1982, survey effort in 1982 was concentrated in the area along the coast of Greenland from Nuuk to Disko. Less coverage of the offshore pack ice in southern Baffin Bay was obtained. The distribution of narwhals appears to have been similar in 1981 and 1982 (Figs 2 and 4). Densities of narwhals were lower in the open pack ice along the coast of Greenland (0.015/km^2) than in the close pack ice farther north and west (0.030/km^2). The only area where significant numbers of narwhals were found in the open pack ice was south and southwest of Disko, where they occurred in both years. Within each of the two main categories of ice, the mean pod size was similar in 1981 and 1982: 2.42 and 2.44, respectively, in open pack ice and 2.04 and 2.08 in close pack ice. The difference in the distribution of pod sizes between open and close pack ice was not significant ($\chi^2 = 7.85$, df = 5, $P>0.05$).

Spring 1978

The surveys in 1978 were concentrated along the coasts and ice edges and in nearshore areas. Narwhals were not recorded during the first low-altitude aerial survey of coastal and ice-edge areas conducted 4–7 May 1978 and only 70, including sightings outside of the survey strip, were recorded during the second survey of the same route on 8–14 May. However, large numbers of narwhals were present among the offshore pack ice in Baffin Bay by mid-May; 0.12 narwhals/km^2 were recorded during sur-

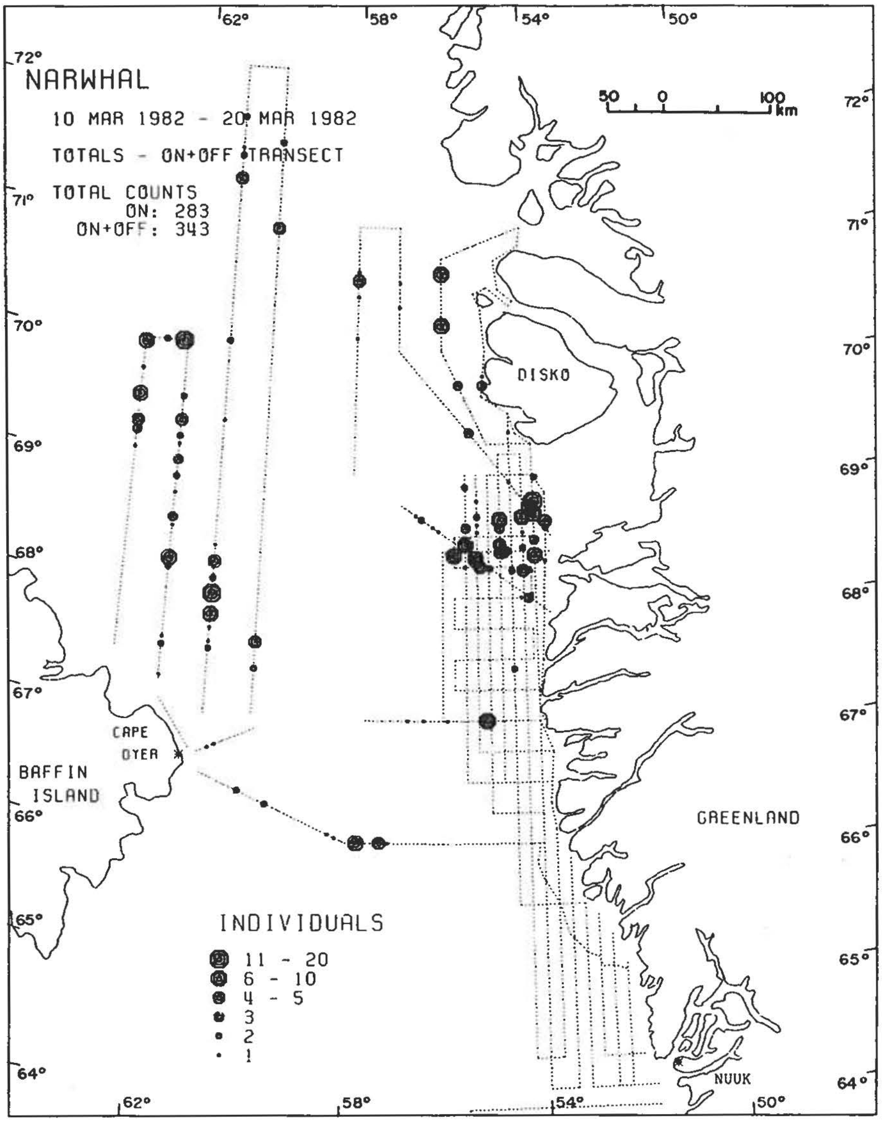


Fig. 4. Survey routes and narwhal sightings in southern Baffin Bay and northern Davis Strait, 10–20 March 1982. Legend: see Fig. 2.

veys of the offshore pack ice conducted at 90 m a.s.l. on 12–14 May. Our low-altitude surveys documented a gradual movement of narwhals into coastal and ice-edge areas in and adjacent to Lancaster Sound from early May until late July (Table 2). Distributional evidence and headings of animals sighted suggested that most of these narwhals came from the offshore pack ice at latitudes between 73°30'N and 74°30'N (Fig. 5, see also 1979 data in Figs 8–12). Few were seen in offshore waters north of 74°30'N.

Some of the narwhals that arrived in Lancaster Sound from the offshore pack ice appeared to move north along the east coast of Devon Island, the ice edge across Jones Sound and SE Ellesmere Island to Smith Sound. Surveys conducted in northern Baffin Bay on 31 May-1 June and 5 July 1978 detected 282 and 325 narwhals, respectively, along the east coast of Ellesmere Island but none along the coast of Greenland except at the Hvalsund ice edge (2 and 573, respectively, Figs 6 and 7). In addition, most narwhals sighted in offshore waters of Baffin Bay west of 75°W were swimming west; few were seen moving north. Along the Smith Sound ice edge, we saw 120 narwhals on 31 May-1 June and 1216 on 5 July 1978.

The weekly surveys in the spring of 1978 sampled only a small part of the total area of offshore pack ice; however, densities of narwhals recorded in the pack ice did not decrease as the numbers increased in coastal and fast-ice areas. Densities recorded in the pack ice were 0.03–0.05/km^2 during each of five surveys from 18 May to 21 June, and increased to 0.17/km^2 on 1 July. After 1 July few narwhals were seen in the pack ice in Baffin Bay. However, they must have been present in areas that

Table 2. Numbers and densities of narwhals on coastal and ice-edge transects, 4 May-2 August 1978.

	Coastal and ice-edge transects		
Survey period	Area surveyed (km^2)	On-transect narwhals	Density (no./km^2)
4– 7 May	372	0	0.00
8–14 May	431	42	0.10
15–18 May	372	35	0.09
22–26 May	384	106	0.28
29 May-2 Jun	356	90	0.25
8–11 Jun	409	49	0.12
12–16 Jun	440	268	0.61
19–23 Jun	438	936	2.14
26–30 Jun	436	589	1.35
3– 8 Jul	457	857	1.88
10–17 Jul	374[a]	1322[a]	3.53[a]
21–26 Jul	308[a]	696[a]	2.26[a]
28 Jul-2 Aug	537	1425	2.65

[a] These surveys were not completed because of low ceilings and fog.

were not surveyed because movements into Lancaster Sound from the offshore pack ice continued until late July or early August (see *Summer* sections, below).

A fast-ice edge remained intact across eastern Lancaster Sound until after 8 July in 1978. Until then, numbers of narwhals recorded along coastal and ice-edge transects tended to increase over time because narwhals arriving from the offshore pack ice could not move westward into Lancaster Sound (Table 2). The decline in numbers between the 19–23 and 26–30 June survey periods was probably due to the northward movements of narwhals from the Jones Sound ice edge to Smith Sound (*i.e.* north of our regular survey area). When cracks developed in the Lancaster Sound fast ice during the 9–18 July period, we saw narwhals moving west of the survey area through these cracks.

Spring 1979

By 9 May, when surveys were initiated, most of the narwhal population was probably present in the pack ice in Baffin Bay in or adjacent to our offshore survey area (Figs 8 and 9; see **Numbers of narwhals** – *Spring surveys*). The distribution of heavy pack ice (>75% ice cover) in June of 1979 as determined from satellite imagery is shown in Fig. 11; it was slightly more extensive in May when imagery was not available. Few narwhals were recorded on coastal and ice-edge transects on 12–15 and 17–22 May. Numbers of narwhals in coastal and ice-edge areas increased gradually during the spring period in 1979 (Table 3), similar to the pattern in 1978. However, extreme cold in combination with calm winds on 22 and 23 May froze most leads and cracks in the heavy pack ice and probably caused most narwhals to retreat into areas of lighter ice cover to the east and south (Fig. 10 vs Fig. 9). Many narwhals appear to have remained in the eastern part of our survey area, and possibly to the east of it, during the last two surveys of the Baffin Bay pack ice conducted on 19–23 June and 28 June-2 July (Figs 11 and 12). However, most narwhals had apparently moved into northern and central Baffin Bay because few narwhals were present along the most southerly offshore transect during either of these last two offshore surveys.

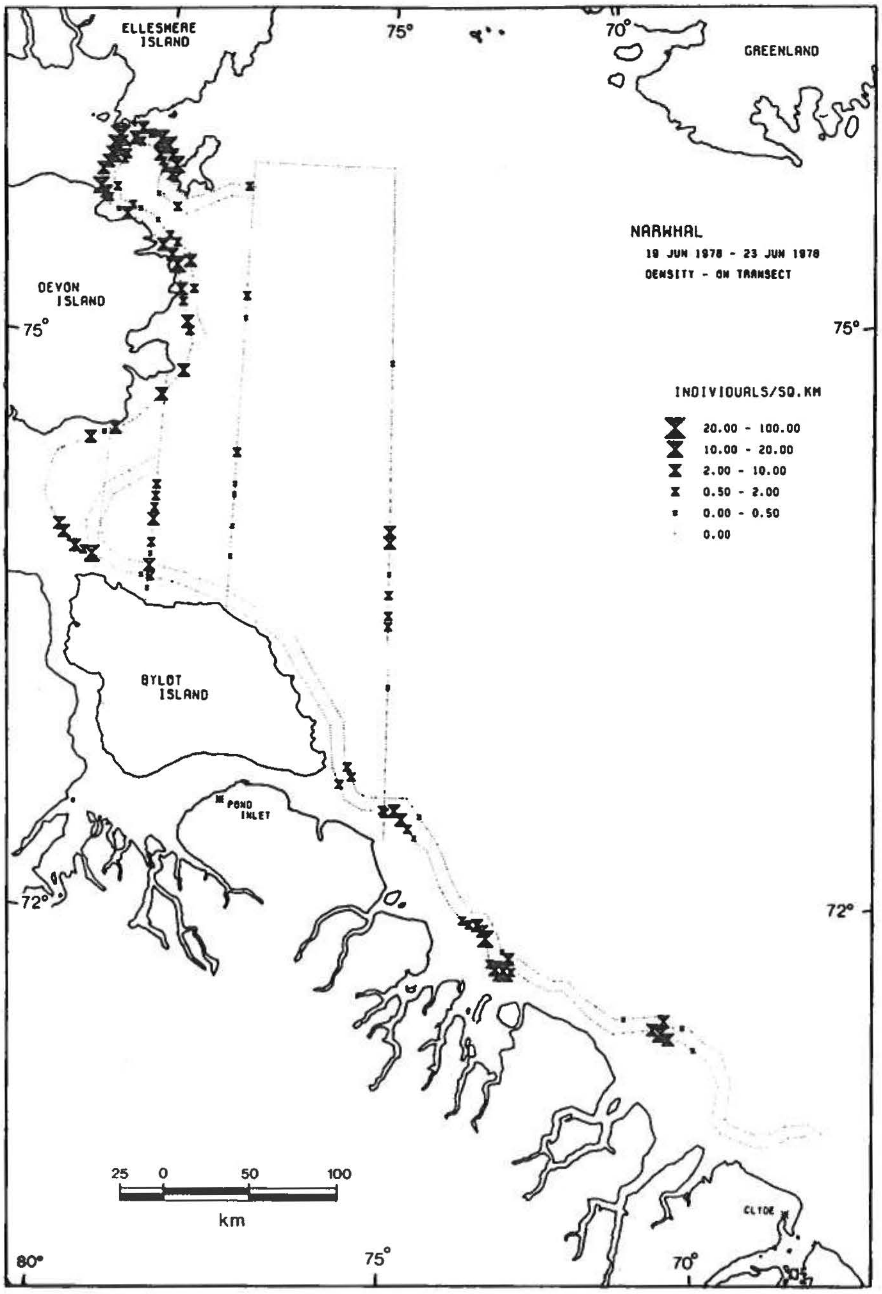
In 1979, the mean pod sizes of narwhals were significantly smaller in offshore Lancaster Sound (1.65, N =113) and Baffin Bay (2.02, N = 390) than in coastal and ice-edge areas both in (2.52, N = 522) and outside of Lancaster Sound (2.91, N = 538, $P<0.01$; Kruskal-Wallis ANOVA and Dunn's Multiple Comparison, Hollander & Wolfe 1973). Most of the large symbols on Figs 8–12 represent several sightings of small groups of narwhals

Table 3. Numbers and densities of narwhals along coastal/ice-edge and offshore transects in Baffin Bay and Lancaster Sound, 9 May-15 July 1979.

	Coastal and ice-edge transects			Offshore transects		
Survey period	Area surveyed (km^2)	Number of narwhals	Density (no./km^2)	Area surveyed (km^2)	Number of narwhals	Density (no./km^2)
9 May	136	3[a] (10)[b]	0.02	56	6 (6)	–
12–15 May	445	34 (64)	0.08	1133	154 (266)	0.14
17–22 May	562	72 (78)	0.13	1521	179 (273)	0.12
24–26 May	53	0 (0)	–	1321	68 (121)	0.05
1 Jun	261	143 (143)	0.55	101	0 (0)	0.00
10–14 Jun	573	431 (439)	0.75	2439	170 (219)	0.07
19–23 Jun	574	596 (646)	1.04	1173	116 (200)	0.10
28 Jun-2 Jul	589	722 (741)	1.23	1665	167 (305)	0.10
8–15 Jul	549	519 (578)	0.95	744	107 (138)	0.14

[a] Number on transect.
[b] Number on+off transect.

Fig. 5. Survey routes and narwhal densities in NW Baffin Bay, 19–23 June 1978. Nearshore transects, which were parallel to and 1.4 km from the landfast ice edge, are plotted seaward of their actual position to enhance legibility.



within a 5–9 km segment of transect rather than one or a few sightings of large groups.

Summers 1974–76

Our surveys in 1974–76 indicated that movements of narwhals into Lancaster Sound started in late May to mid-June. Surveys were not frequent enough to determine the periods of peak movements in 1974 and 1975; however, peak movements were in late June to mid-July in 1976 (Davis *et al.* 1978).

Summer 1978

In 1978, the major movements of narwhals into Lancaster Sound appear to have occurred from mid-July to early August, when poor weather prevented us from completing our surveys. Break-up of the fast ice in Lancaster

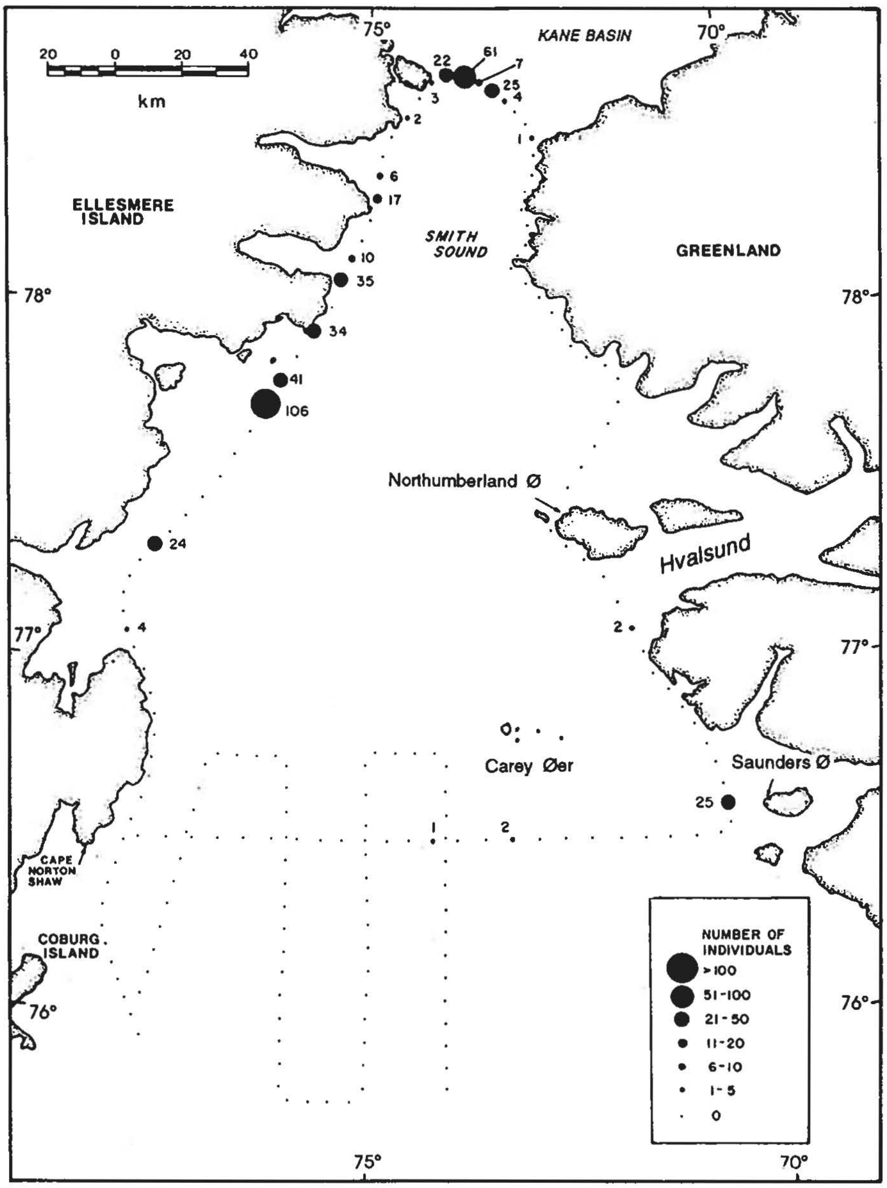


Fig. 6. Survey routes and narwhal sightings in northern Baffin Bay, 31 May-1 June 1978.

Sound occurred between 9 and 18 July. Small numbers of narwhals were recorded moving west through offshore Lancaster Sound during incomplete surveys on 21–26 July. Although none were recorded in offshore areas during surveys on 28 July-2 August, 651 narwhals were counted on coastal and nearshore transects along northern and northeastern Bylot Island. During periods of good visibility from 28 July to 9 August, 2709 narwhals were counted passing within view of our land-based observation site west of Cape Hay on northern Bylot Island. If similar rates of passage occurred during periods of observations and during periods when observations were not conducted due to poor visibility, 4844 narwhals passed the observation site from 28 July to 9 August.

Most of the narwhals that summer in Eclipse Sound enter that area through Pond Inlet rather than Navy Board Inlet. During a 30 July 1978 survey of the fast-ice edge across Pond Inlet and of cracks west of there, we counted 622 narwhals. Most of them were moving west through newly-formed cracks. During the same survey period no narwhals were seen in Navy Board Inlet or Eclipse Sound where ice cover was 80–90%.

Summer 1979

Fog and low cloud cover prevented aerial surveys or shore-based observations from mid-July to mid-August in 1979. The land-fast ice edge remained intact across Lan-

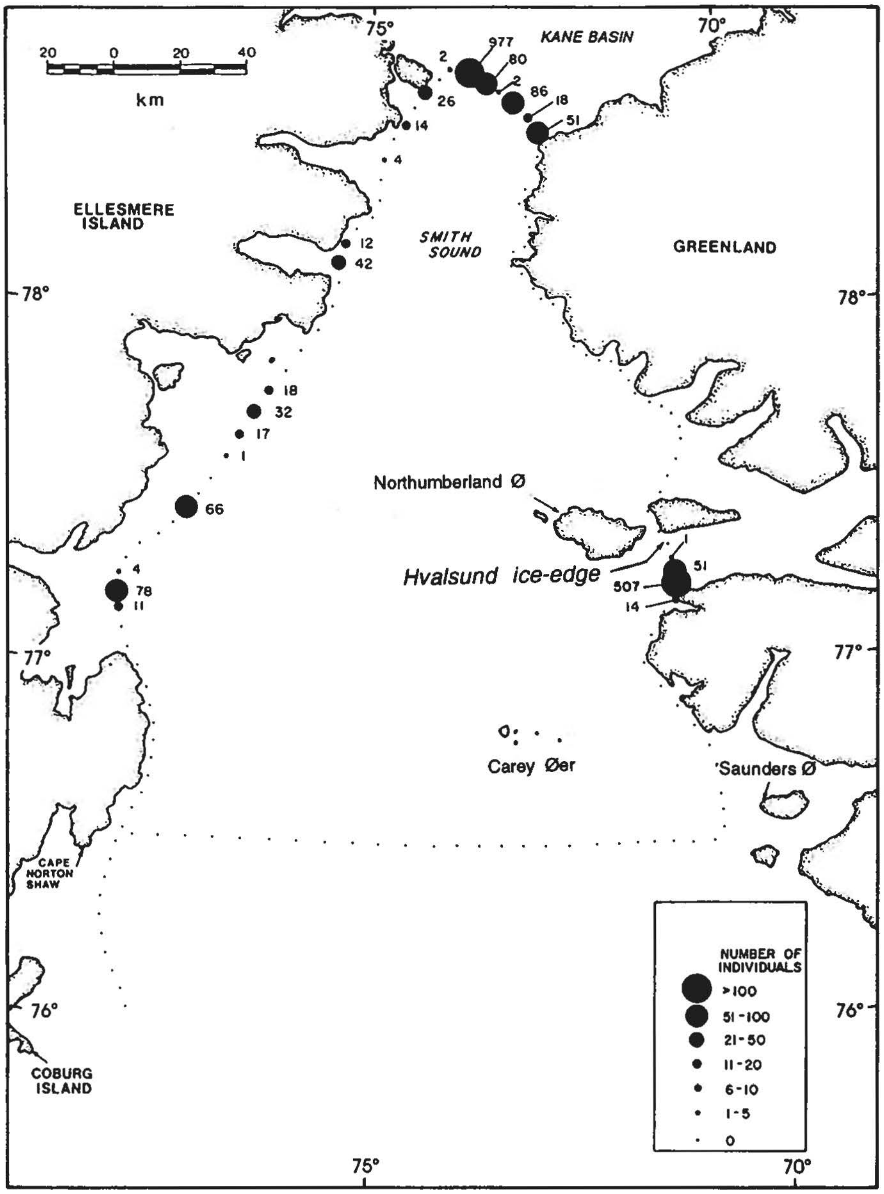


Fig. 7. Survey routes and narwhal sightings in northern Baffin Bay, 5 July 1978.

caster Sound until 2 August when cracks started to form. The majority of narwhals are suspected to have entered Lancaster Sound during early to mid-August in 1979.

Our systematic and opportunistic surveys identified several summering areas of narwhals, some of which had not been documented previously (Fig. 13). Unlike white whales, which frequently use shallow estuaries during summer, narwhals remain in deeper waters during summer (Mansfield *et al.*. 1975, Born 1986, Born *et al.* 1994). They sometimes enter deep fiords such as Tay Sound or Buchan Gulf but are most often found in larger water bodies such as Eclipse Sound, Milne Inlet, Admiralty Inlet and others listed in Table 4 (later). Our surveys were not designed to estimate the numbers of narwhals present in most of these areas. However, Table 4 gives maximum counts obtained during this study and estimates, where available, for numbers of narwhals summering in these areas.

Our data suggest that narwhals do not usually summer in Jones Sound. When fast ice blocked access to summering areas in 1978 and 1979, large numbers of narwhals were recorded along ice edges blocking access to Lancaster Sound, Pond Inlet, Buchan Gulf and Inglefield Bredning but numbers of narwhals along the Jones Sound ice edge were low: only 8 on 24 July 1978 and 36 on 9 July 1979. This occurred even though several hundred had been recorded there earlier in the year, and even though the ice edge was intact. In addition, opportunistic surveys

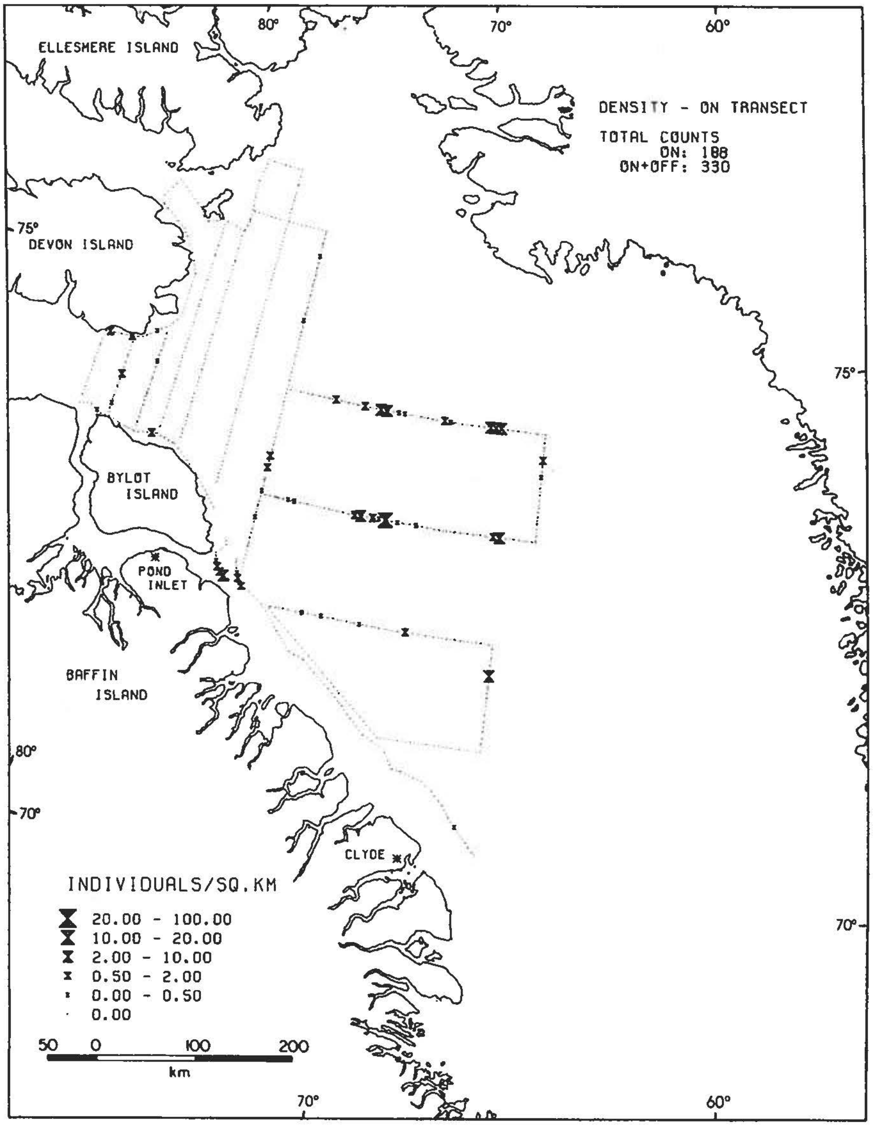


Fig. 8. Survey routes and narwhal densities in NW Baffin Bay, 12–15 May 1979.

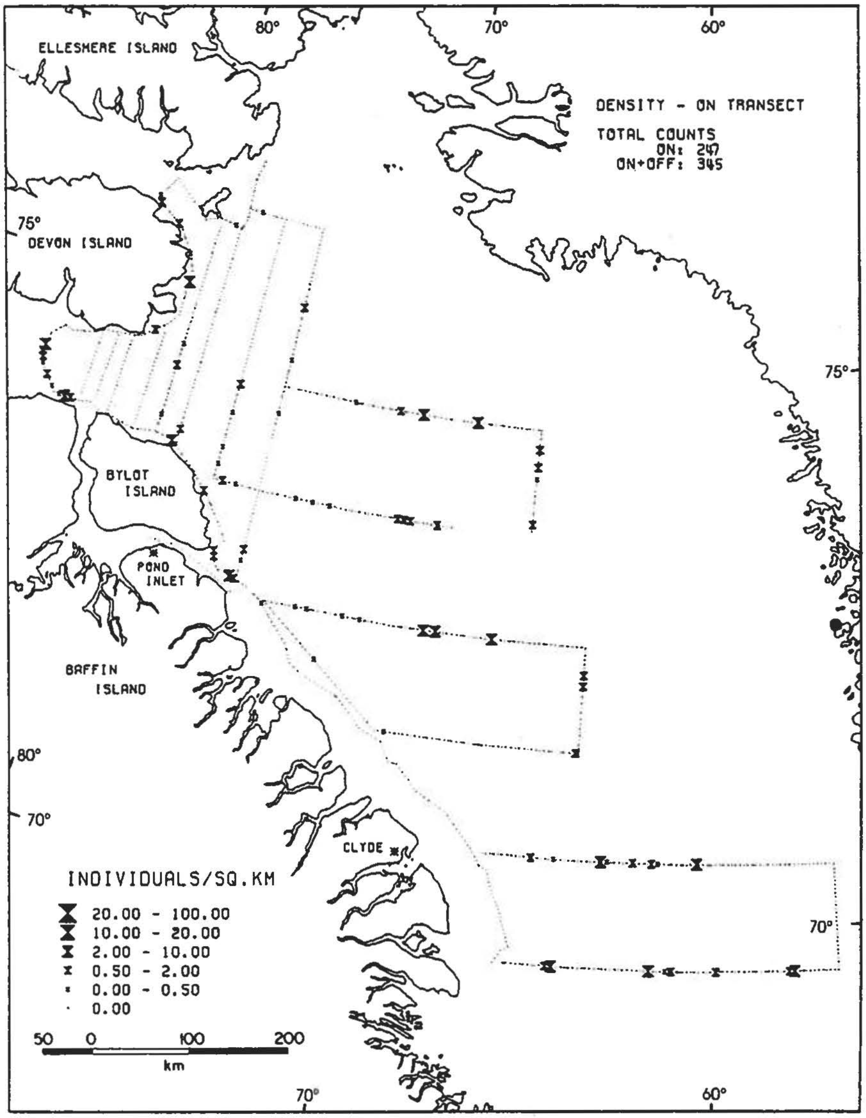
of Jones Sound during the summer and early autumn of 1977–79 detected no narwhals on 22 August 1977 and 21 August 1979 and only 11 and 22 on 15 September 1978 and 14 September 1979, respectively.

Autumn 1978

In 1978, narwhals started to move out of summering areas during the 23–27 September period. During late September and early October, before the offshore areas started to freeze, most narwhals followed either the north or south coast of Lancaster Sound eastward into Baffin Bay. Many then followed the coast of Baffin Island southeastward. Some continued east and offshore from SE Devon Island into Baffin Bay; for example, on 29 September 60–90 narwhals were seen moving east into Baffin Bay from the southeast corner of Devon Island even though no ice was present. Few narwhals were recorded swimming north along the east coast of Devon Island during autumn, even though narwhals were common along the south coast of Devon Island during late September and early October. This suggests that few if any narwhals migrated north along eastern Devon Island in autumn. During the 7–10 October survey, after new ice had started to form in offshore Lancaster Sound and along NE Baffin Island, narwhal movements were dispersed throughout the offshore pack ice and no longer followed the coast of Baffin Island.

Shore-based observers recorded narwhals moving south past Cape Adair on northeast Baffin Island during a four-day period from 29 September to 2 October in 1978. During this period, 4963 narwhals were recorded; all but

Fig. 9. Survey routes and narwhal densities in NW Baffin Bay, 17–22 May 1979.



21 were recorded as part of four major pulses. About 97% of the narwhals seen were within 700 m of shore, 3% were 700–1500 m from shore and only 18 (0.4%) were farther than 1500 m from shore. Some narwhals may have moved past Cape Adair at night and therefore would not have been counted. Also, aerial surveys indicated that many narwhals moved past Cape Adair after the shore-based observations were terminated on 7 October.

Autumn 1979

In 1979, narwhals were first observed leaving summering areas in Lancaster Sound during the 18–21 September survey when 572 narwhals were recorded along the south coast of Devon Island. On 24–26 September a major movement from Admiralty Inlet across Lancaster Sound to the south coast of Devon Island was documented (Fig. 14). A total of 672 narwhals was recorded along the south coast of Devon Island; 91% of these were moving strongly eastward. In addition, substantial numbers were recorded moving northeast through Lancaster Sound between Admiralty Inlet and the south coast of Devon Island. Extrapolation of numbers recorded on offshore transects to areas between those transects yields an estimate of approximately 1200 narwhals in offshore areas. This does not include numbers that were probably south and west of the survey area based on the observed distribution of sightings (Fig. 14, later). Some of the narwhals from Admiralty Inlet did not cross Lancaster Sound to the north side but appeared to follow the coasts of Baffin and Bylot islands to the east and south (Fig. 14).

By 28–29 September, pan ice had started to form

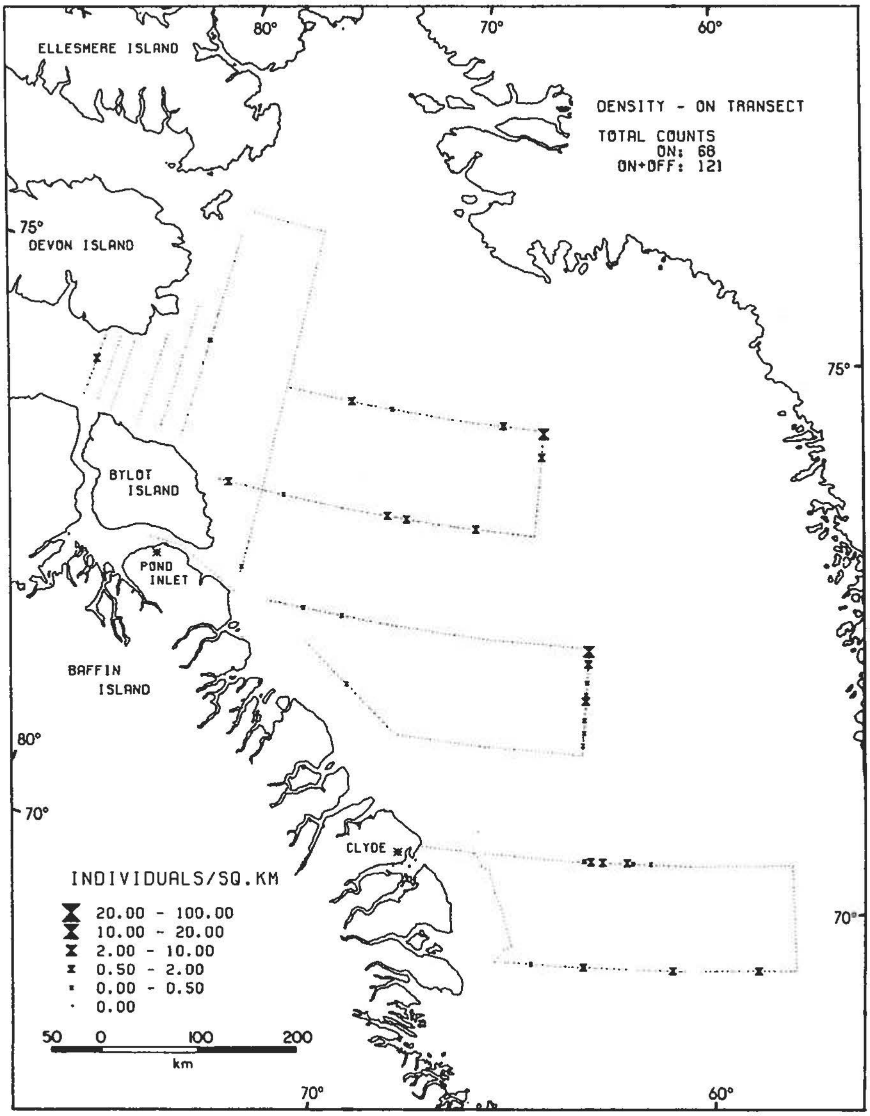


Fig. 10. Survey routes and narwhal densities in NW Baffin Bay, 24–26 May 1979.

offshore in Lancaster Sound. From this time on, few narwhals were sighted along either coast of Lancaster Sound. They were dispersed among the offshore ice. Narwhals that summered in Buchan Gulf apparently started to leave their summering area on these dates as 154 narwhals were seen just outside of Buchan Gulf.

A total of 4491 narwhals (including on- and off-transect sightings) was counted in Pond Inlet and an additional 900 were counted along NE Baffin Island between Navy Board Inlet and Cape Adair during an aerial survey on 1 October 1979. The number present in Pond Inlet was higher than the actual count. The survey covered all coastal areas but only 12% of the offshore waters where large numbers were present.

A large group of narwhals was observed moving north along the east coast of Bylot Island on 2 October; 2893 were counted during a single pass over the group but a complete count was not attempted. The 2 October group was probably the same, or part of the same, group seen in Pond Inlet the previous day.

Narwhals were recorded moving southeast along the Baffin Island coast from 27 September to 17 October 1979; most of the animals were in a few large groups. Observers at Cape Adair recorded 9 narwhals on 27 September, 1415 on 30 September, 185 on 2 October, groups of 283 and 117 on 10 October, and 800 on 13 October. All except the ones seen on 2 October were moving southeast along the coast. Poor weather prevented observations for most of 9 and 11–13 October, when many narwhals appear to have migrated southeast along the coast of Baffin Island. Aerial surveys detected groups of 350 and 550 narwhals that were 115 and 80 km

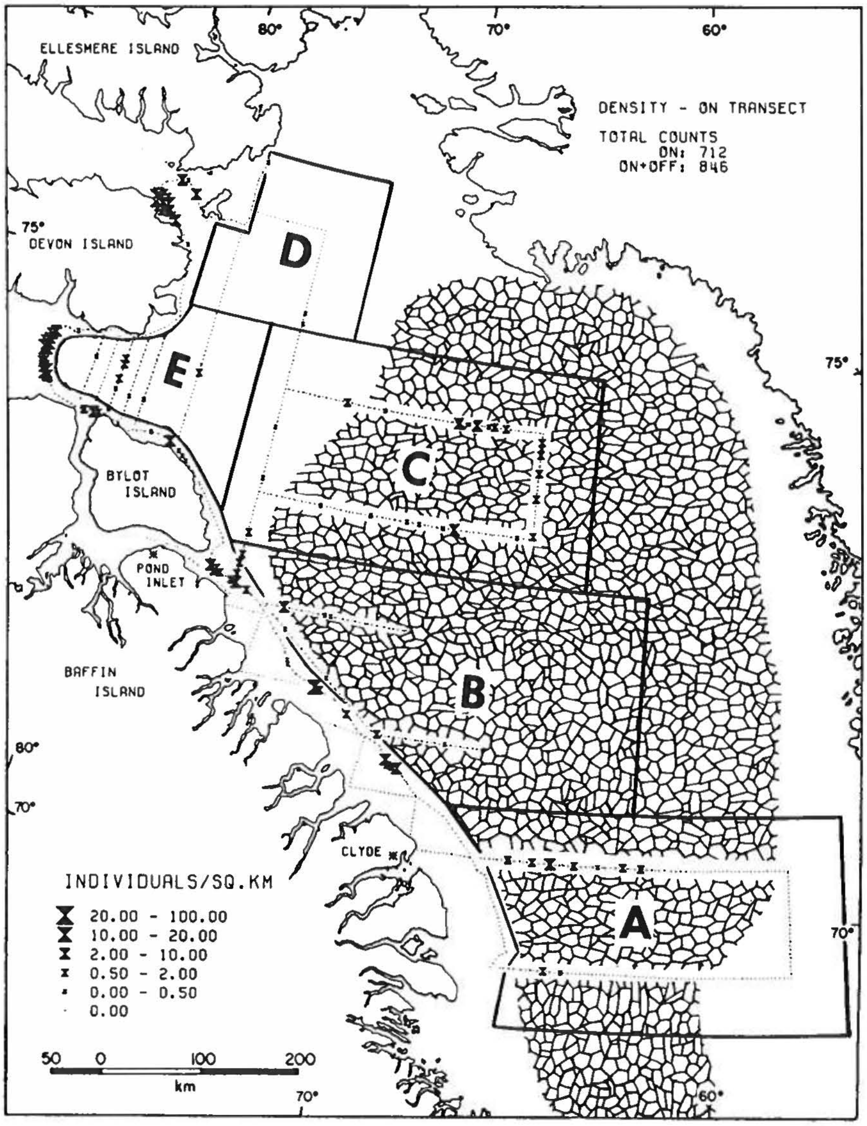


Fig. 11. Survey routes and narwhal densities in NW Baffin Bay, 19–23 June 1979. The outlined areas are the blocks to which extrapolations were made (see Table 8) and the shaded area indicates the extent of 75% pack ice in late June 1979 as determined from NOAA satellite imagery.

northwest of Cape Adair on 4 and 10 October, respectively; these groups were not detected by observers at Cape Adair. The 10 October survey also detected a group of 400 narwhals south of Cape Adair; only 117 of these were recorded from Cape Adair. Based on the combined aerial and shore-based observations narwhals appear to have continued to move at night and during periods of fog. Thus, the net southward movement of 2439 narwhals that was observed from Cape Adair in 1979 seriously underestimated the numbers of narwhals using this coastal route.

Narwhal movements during the autumn were more directed and appeared to be faster than those during other times of year. We do not have rates of movement for other times of year but we determined the minimum speeds of several large groups of narwhals that were resighted during the autumn migration. We have reliable estimates for two groups of narwhals that moved at ~12 km/h over a period of 3–4 h and for two groups that moved at 7 km/h over periods of 2–4 h (Table 5). In addition, the large group sighted in Pond Inlet on 1 October must have moved at a net speed of 7 km/h (based on the position of the centre of the group on each date) to reach the position where it was assumed to have been resighted on 2 October. However, the group had reversed course between sightings and its average speed was probably considerably greater.

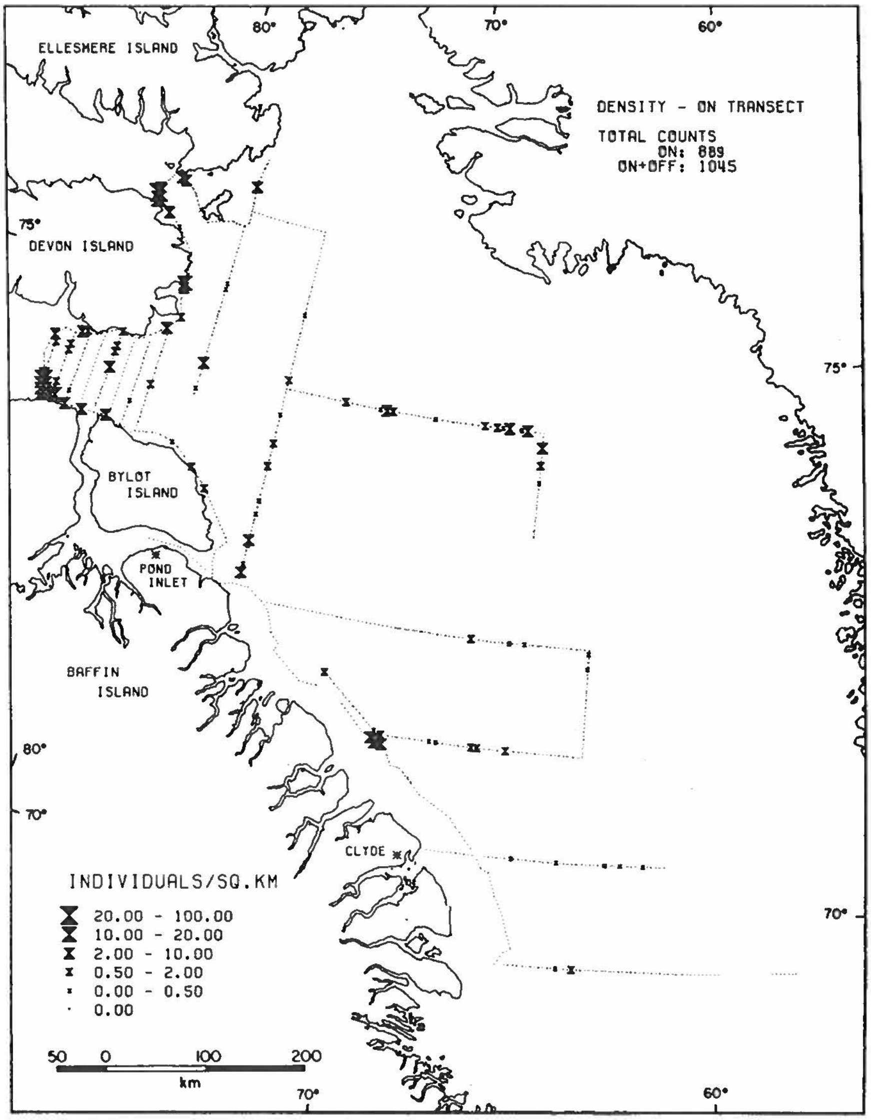


Fig. 12. Survey routes and narwhal densities in NW Baffin Bay, 28 June-2 July 1979.

Relative age and sex composition

The relative age and the sex of narwhals were recorded whenever possible. The data on sex ratios are biased toward males. If we were not certain of the sex we did not classify an animal to sex. When an animal was seen briefly, the presence of a large conspicuous tusk identified the animal as a mature adult male. Many animals without large tusks could not be sexed when seen briefly because they could have been either females or males with short tusks.

Offshore winter

In 1981 and 1982, 70 and 79%, respectively, of narwhals that were aged were adults and 68 and 61%, respectively, of the animals sexed were females (Table 6). These proportions were similar in the two types of habitat surveyed; 72 and 76% of narwhals were classified as adults and 68 and 60% as females in close and open pack ice, respectively. However, females with 7- to 8-month-old calves tended to avoid the open pack ice in favour of the close pack ice ($\chi^2 = 4.92$, $P<0.05$); calves formed 2.5 and 10.5% of all narwhals classified to an age category (N=80 and 209, respectively) in the open and close pack ice, respectively. The low number of males among the narwhals that were sexed in winter suggests that large num-

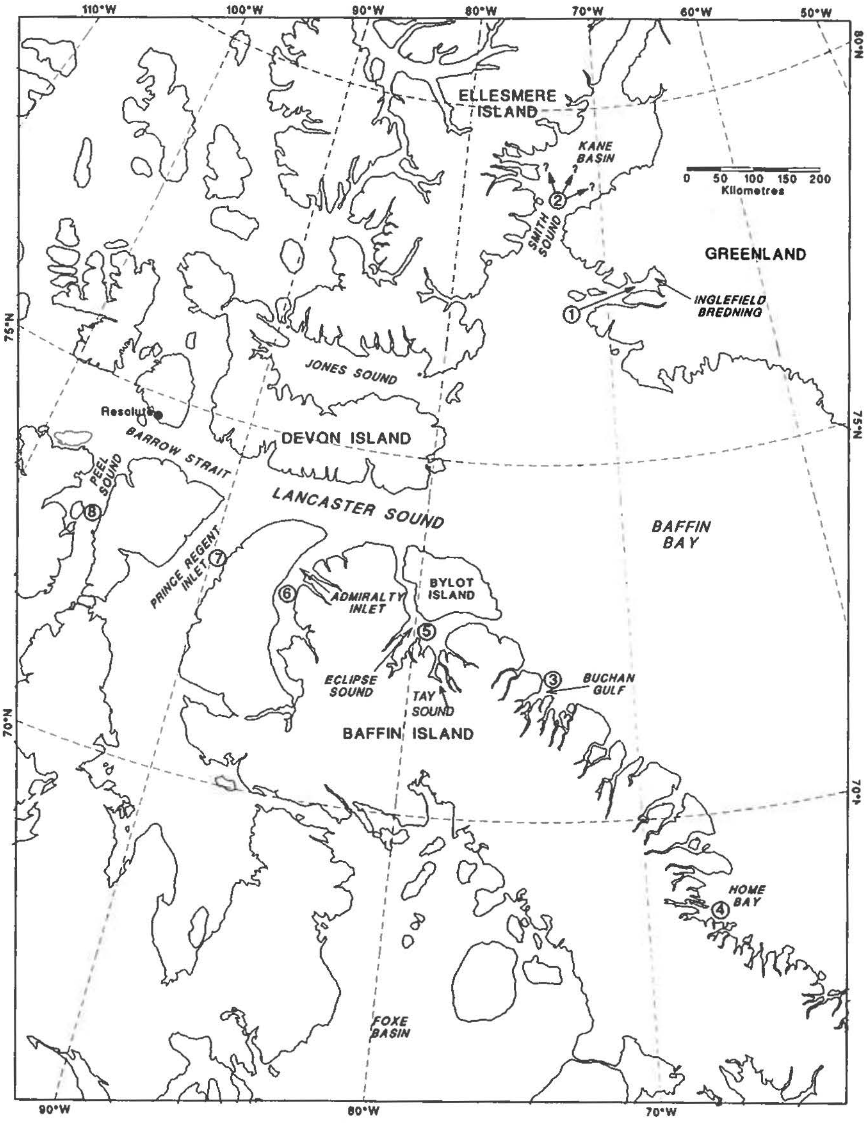


Fig. 13. Summering areas used by narwhals in 1976–1979. See Table 4 for information concerning surveys of each area.

bers of narwhals were present somewhere outside of the area surveyed.

Offshore spring

Adults comprised 74% of narwhals aged during offshore surveys of the pack ice in spring and the ratio of males: females was 48:52 (Table 6); the sex ratio was not significantly different from unity (χ^2 = 0.38, P>0.50). The areas covered by these surveys appear to have included all age and sex categories, and therefore were not biased by the absence of a particular age or sex group. Data presented below indicate that adult males began moving into summering areas from the pack ice before females with young and subadults; therefore, fewer males may have been present in offshore areas during surveys conducted from 19 June to 2 July.

Migration to summering areas

Data from our surveys indicate that adult male narwhals entered Lancaster Sound before females with young and subadults. Furthermore, when entering Lancaster Sound adult males tended to move into coastal and ice-edge areas, whereas females with young and subadults tended to move through offshore waters (Table 6).

Few neonates were born before narwhals started to move into summering areas even though these movements were later in 1978 and 1979 than in most years. Only three neonates (<1% of all sightings) were recorded

Table 4. Estimates of numbers of narwhals present in summering areas surveyed during 1978 and 1979. Estimates and counts do not include correction factors to account for animals at the surface but not seen by observers or for animals below the surface at the time of the survey.

Location[a]	Date	No. Counted	Estimate of no. present	Comments	Other estimates (rounded to the nearest 100)
1. Inglefield Bredning (Greenland)	5 July 1979	573	>573[b]		4000 in 1984 (Born 1986) 800–1400 in 1985 (Born *et al.* 1994: aerial surveys) 1500 in 1985 (Born *et al.* 1994: ground counts) 2700–4400 in 1986 (Born *et al.* 1994) 500 in 1988 (Born *et al.* 1994: ground counts)
2. Smith Sound	5 July 1979	1216	>1500[b]	Includes 325 along Ellesmere Isl.	None
3. Buchan Gulf	11–15 Aug 1978	302	300		None
4. Home Bay	18 Sep 1979	95	>95	Widely dispersed; partial count	None
5. Eclipse Sound	24 Aug 1978	519	622	Good conditions	1200 in 1984 (Richard *et al.* 1994)
	8–9 Sep 1979	887	>3100	Poor conditions during part of survey, estimate low.	
6. Admiralty Inlet	24 Aug 1978	1362	7000		9700 in 1975 (Fallis *et al.* 1983)
	3 Sep 1979	231	>>1473	Partial survey and poor conditions	5600 in 1984 (Richard *et al.* 1994)
7. Prince Regent Inlet	17–18 Aug 1979	26	>569	Partial survey and poor conditions	9800 in 1984 (Richard *et al.* 1994)
	30 Aug–4 Sep 1979	85	>1614	Partial survey and poor conditions	10,800 in 1981 (Smith *et al.* 1985)[c]
8. Peel Sound	4 Sep 1976	378	900	Excellent conditions	1700 in 1984 (Richard *et al.* 1994)

[a] See Fig. 12 for locations.
[b] These counts were early in the season before major movements into summering areas had occurred (see Born 1986).
[c] This estimate is believed to be high (see text).

before mid-July in the two years. The earliest neonate and its presumed mother were recorded along the Pond Inlet ice edge on 19 June 1979. Other early records of presumed mothers with neonates were amidst the pack ice east of Pond Inlet on 28 June 1979 and amidst the pack ice along our most southerly offshore transect on 2 July 1979.

Summering areas

During surveys of summering areas of narwhals in 1978 and 1979, 67% (range = 63–74%, Table 6) of the 1230 animals aged were classified as adults, 19% (12–22%) as large subadults, 6.5% (3.7–7.7) as yearlings and 7.8% (5.9–10.2) as newborn calves. Females comprised 40% and males 60% of the animals that were sexed. This sex ratio is significantly different than unity ($\chi^2 = 34.1$, $P<0.001$). However, we believe that the observed ratio is biased by the ease of identifying adult males that was mentioned above. The surveys were conducted in late August and early September so that virtually all calves of the year should have been included. Based on the combined summer data from 1978 and 1979 (Table 6), the Gross Annual Recruitment Rate (GARR) was 0.085 calves/non calf/year. An estimate of the birth or calving rate, which considers only the ratio of calves to adult females for a species that calves seasonally, is 0.29 calves/adult female/year. However, this probably underestimates the true birth or calving rate because some calf mortality undoubtedly occurred after birth but before our surveys.

Autumn migration

Movements of narwhals during autumn migration were more rapid than at all other times of year. This made estimation of the relative age and sex of subadult animals difficult; as a result, we have not included age and sex data from autumn surveys in Table 6. The large herds of narwhals that were encountered seemed to consist of all age and sex categories, but the animals within pods seemed to be segregated by age and sex.

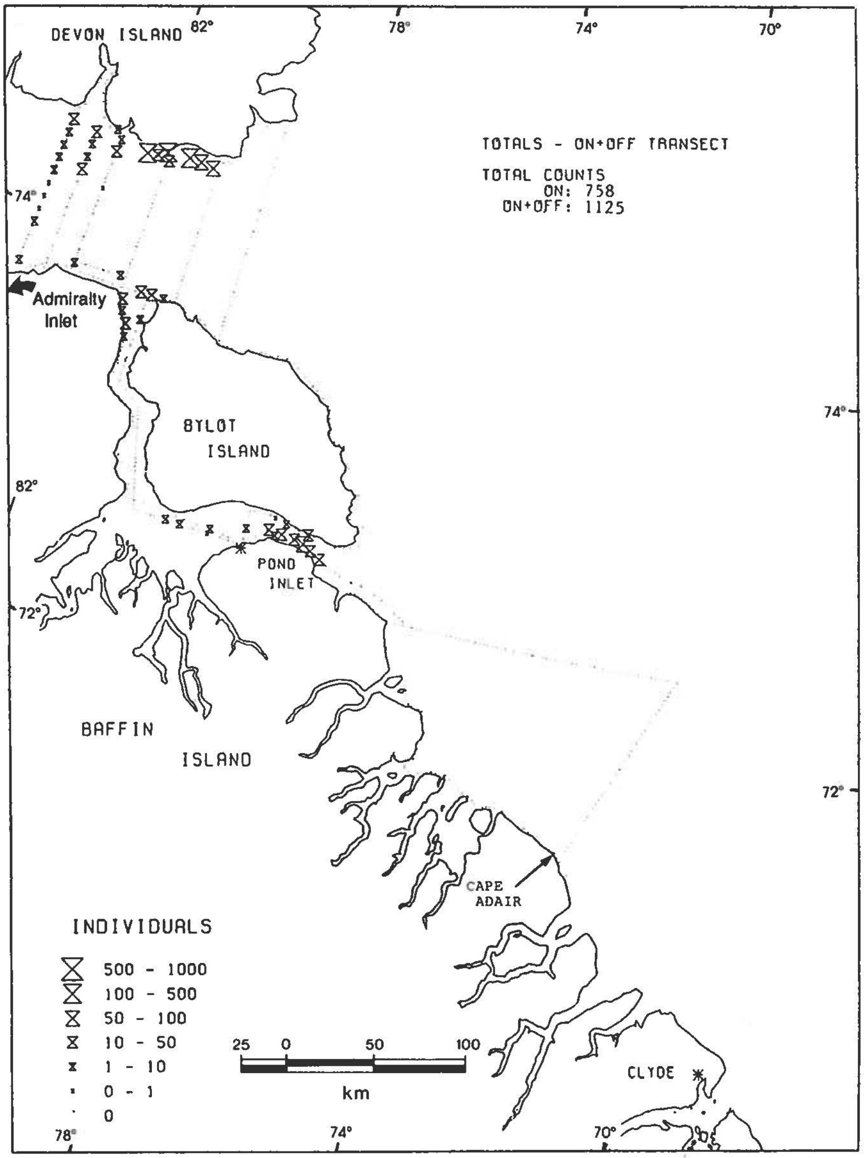


Fig. 14. Survey routes and narwhal sightings in NW Baffin Bay, 24–26 September 1979.

Table 5. Speeds of movement of narwhals sighted along NE Baffin Island, 30 September-10 October 1979.

Date of Sighting	Method of sighting initial/final	Elapsed time between sightings (h:min)	Distance travelled (km)	Speed (km/h)
30 Sep (group of 12)	G/A[a]	1:51	12.5	6.7
30 Sep (large group)	G/A	2:36–4:18	17.5–32.0	6.8–7.4
1–2 Oct	A/A	17:00	>>115[b]	>>6.8[b]
2 Oct	A/G	2:50	>32	>11.3
4 Oct	A/A	0:45	3.6	4.8
10 Oct	G/A	3:35–4:09	44–50	12.0–12.3

[a] A:sighted from the Twin Otter; G:sighted by observers at Cape Adair.

[b] This group had reversed course when it was resighted 2 October. The actual distance travelled and speed are probably much greater than those given (see text).

Table 6. Percent of narwhals in different age and sex categories recorded during surveys of Davis Strait, Baffin Bay and Lancaster Sound and vicinity, March-October 1978–1982.

	Age					Sex		
	Adults	Large subadults	Yearlings	Calves	Number aged	Males	Females	Number sexed
Winter								
Baffin Bay – Davis Strait (1981)	69.9	19.4	ND[a]	10.8[a]	186	32.5	67.5	117
Baffin Bay – Davis Strait (1982)	78.6	17.5	ND	3.9	103	38.6	61.4	57
Spring and early summer								
Baffin Bay (1979)	73.8	20.4	5.8[b]	NA[b]	80[c]	48.3	51.7	319
Lancaster Sound offshore (1979)	54.2	45.8	0.0	NA	36[c]	21.1	78.9	57
Lancaster Sound coastal (1979)	89.0	5.5	5.5	NA	82[c]	80.8	19.2	276
Summer								
Eclipse Sound (1978)	74.2	12.0	3.7	10.1	89	67.2	32.8	67
Admiralty Inlet (1978)	62.8	21.8	6.9	8.5	578	60.8	39.2	403
Central Arctic (1979)	73.1	11.8	6.7	8.3	108	51.9	48.1	79
Eclipse Sound (1979)	69.7	18.0	6.4	5.9	406	59.8	40.2	301
Admiralty Inlet (1979)	69.4	12.8	7.7	10.2	49	52.6	47.4	38
Total Summer Surveys	67.1	18.6	6.5	7.8	1230	59.8	40.2	888

[a] ND – in March, calves are approximately 7–8 months old, and yearlings (19–20 months old) are difficult to distinguish from other subadults.

[b] NA – calves are 10–12 months old and are called yearlings; most calves-of-the-year are born in late July-early August, although some are born as early as late June.

[c] Only age data collected by the senior author were used during these periods; see methods.

Numbers of narwhals

Winter surveys

The two major strata surveyed during the winters of 1981 and 1982 were open pack ice (<90%) and close pack ice (≥90%); these strata were further subdivided by latitude. The 1982 surveys extended farther north into central Baffin Bay than the 1981 surveys (Figs 2 and 4). Totals of 6027 and 8045 narwhals were estimated to have been present in the surveyed areas during 14–31 March 1981 and 10–20 March 1982, respectively. Large areas with suitable pack ice were present in Baffin Bay, north of our study area (see Fig. 1). The presence of this available habitat and the observed distribution of narwhals, suggests that substantial numbers wintered north of the survey areas in both years. In addition, some narwhals were probably present south of the survey area in 1982. A total of 450 (± SE 89) was estimated to have been present in the pack ice between 65 and 66°N during our 1981 surveys. An additional 650 were present south of 65°N based on extrapolations from scattered sightings, primarily in Hudson Strait and Davis Strait, south of Cumberland Sound (Fig. 3). These latter animals may be part of the Hudson Bay population (Richard 1991).

Spring surveys

Totals of 29 931 (± SE 7008) to 38 988 (± SE 6629) narwhals were estimated to have been present in surveyed areas of Baffin Bay during four surveys from 12 May to 2 July 1979 (Table 8). Estimates from surveys conducted 24–26 May and 10–14 June are not included because many narwhals apparently had moved east of the survey area when leads froze due to extremely cold weather. The combined estimate for the four surveys was 34 363 (± SE 8282).

Discussion

Distribution and movements

Late winter

Little was known about the distribution and movements of narwhals during the winter, spring and early summer previous to our surveys. Vibe (1967) and Kapel (1975, 1977) considered that narwhal wintering areas extended from Disko Bugt south to about 65°N. Turl (1987) found large numbers of narwhals in the close pack ice in west and central Davis Strait between 66°30' and 68°15'N in February-March 1976. Our surveys suggest that narwhals probably winter throughout the close pack ice in Davis

Table 7. Estimates of numbers of narwhals present in areas surveyed in northern Davis Strait and southern Baffin Bay, March 1981 and 1982.

Survey block[a]	Area in block (km^2)	Area surveyed (km^2)	No. transects	No. narwhals on-transect	Density[b] (no./km^2) ± SE	Estimated[b,c] number ± SE
Close pack ice, 15–31 March 1981						
70°N-71°N	49,354	1005.3	8	32	0.0318±0.0126	1571±623.7
69°N-70°N	47,464	2257.6	16	66	0.0292±0.0117	1388±553.3
68°N-69°N	40,641	2058.5	13	50	0.0243±0.0067	988±271.8
67°N-68°N	33,005	1661.4	10	53	0.0319±0.0104	1052±343.9
66°N-67°N	26,064	1492.2	12	18	0.0121±0.0043	314±112.7
65°N-66°N	32,392	1941.8	11	27	0.0139±0.0028	450± 88.9
Totals	228,920	10,416.8	70	246		5763±952.8
Open pack ice, 17–24 March 1981						
68°30'N-69°30'N	8044	1175.2	13	35	0.0298±0.0127	240±101.8
67°30'N-68°30'N	10,000	1212.9	13	1	0.0008±0.0008	8± 7.8
66°30'N-67°30'N	9605	1215.5	12	2	0.0016±0.0016	16± 15.0
Totals	27,649	3603.6	38	38		264±102.1
Close pack ice, 10–20 March 1982						
71°N-72°15'N	72,670	560.3	6	9	0.0161±0.0089	1167± 643.5
70°N-71°N	49,354	971.7	6	37	0.0381±0.0167	1879± 825.0
69°N-70°N	47,464	1144.8	7	20	0.1747±0.0062	829± 294.9
68°N-69°N	40,641	830.4	5	25	0.0301±0.0165	1224± 670.9
67°N-68°N	33,005	765.0	5	34	0.0444±0.0285	1467± 942.0
66°N-67°N	26,064	586.1	4	19	0.0324±0.0192	845± 500.1
Totals	269,198	4858.2	33	144		7411±1664.4
Open pack ice, 10–17 March 1982						
68°30'N-69°30'N	7211	1380.2	15	56	0.0406±0.0120	293± 86.7
67°30'N-68°30'N	10,000	2372.6	26	69	0.0291±0.0074	291± 74.7
66°30'N-67°30'N	9605	1916.2	22	10	0.0052±0.0036	50± 35.4
Totals	26,816	5669.0	63	135		634±119.8

[a] See Fig. 2 for location of survey blocks.

[b] Densities, estimated numbers and their standard errors are based on the ratio method.

[c] Estimates do not account for animals at the surface that were not seen or for submerged animals.

Strait and southern Baffin Bay, with relatively small numbers (<750) among the open pack ice south of Disko Bugt as far south as 68°N. The latter animals are predominantly females without young and subadults. We saw few narwhals south of 68°N along the Greenland coast even in 1982 when the pack ice extended farther south along the coast than normal. Heide-Jørgensen *et al.* (1993) found similar distributions and numbers of narwhals among the pack ice south of Disko during their surveys in 1990 and 1991. However they did not record narwhals south of 68°20'N where we had a few scattered sightings.

Finley & Renaud (1980) conducted three surveys of the North Water Polynia at the north end of Baffin Bay during March and April of 1978 and 1979 and found only one group of 12 narwhals. Their data are consistent with our results that indicate that narwhals avoid open water and ice-edge areas during the winter in preference to areas of 90–99% close pack ice. Hence, narwhals would not be expected in the polynia surveyed by Finley & Renaud (1980).

Spring

Narwhals were dispersed in small groups throughout the offshore pack ice in Baffin Bay and northern Davis Strait during spring. This distribution was unknown previous to our surveys.

Table 8. Estimated numbers of narwhals present in areas surveyed in offshore Baffin Bay and Lancaster Sound, 12 May-2 July 1979.

Survey block[a]	Area in block (km²)	Area surveyed (km²)	No. transects	No. narwhals on-transect	Density (no./km²) ± SE	Estimated number ± SE
12–15 May						
A	80,797	0	0	–	–	–
B	73,276	278	7	14	0.050±0.027	3692± 1944
C	80,119	355	11	135	0.380±0.148	30,451±11,873
D	24,699	223	12	2	0.009±0.006	221± 143
E	26,900	276	12	3	0.011±0.007	292± 194
Totals	285,791	1133	42	154		34,655±12,034
17–22 May						
A	80,797	338	9	65	0.192±0.056	15,543±4547
B	73,276	363	9	39	0.107±0.038	7876±2811
C	80,119	336	11	58	0.172±0.048	13,820±3856
D	24,699	182	10	5	0.027±0.022	679± 535
E	26,900	302	13	12	0.040±0.017	1,069± 452
Totals	285,791	1521	52	179		38,988±6629
19–23 June						
A	80,797	293	7	22	0.075±0.040	6057±3266
B	73,276	192	5	27	0.141±0.063	10,325±4633
C	80,119	355	11	50	0.141±0.049	11,278±3949
D	24,699	112	6	2	0.018±0.017	442± 426
E	26,900	221	8	15	0.068±0.041	1829±1099
Totals	285,791	1173	37	116		29,931±7008
28 June-2 July						
A	80,797	411	5	15	0.037±0.013	2951±1089
B	73,276	624	8	53	0.085±0.034	6224±2470
C	80,119	241	8	63	0.261±0.065	20,916±5236
D	24,699	117	6	3	0.026±0.017	635± 408
E	26,900	282	10	33	0.117±0.048	3152±1283
Totals	285,791	1674	37	167		33,879±6042

[a] See Fig. 11 for area included.

Movements into summering areas

Small numbers of narwhals (primarily males) move into coastal and ice-edge areas during May and early June. Larger numbers arrive in Lancaster Sound and adjacent coasts through offshore waters between 73°30' and 74°30'N from mid-June to early August. Some of those that arrive in June followed the east coast of Devon Island north to the Jones Sound ice edge, and from there, continue north to Smith Sound.

During 1978 and 1979 most narwhals moved west into Lancaster Sound during July to mid-August with peak numbers entering in late July and early August. The movements into Lancaster Sound appear to have been later than normal in 1978 and 1979. In 1976, Greendale & Brousseau-Greendale (1976) and Davis *et al.* (1978) documented peak movements of narwhals during early July with the main period of migration occurring from late June to mid-July. The delayed migration in 1978 and 1979 was probably due to the persistent fast-ice edge that remained across Lancaster Sound until 9–18 July in 1978 and 2 August in 1979.

Summer

Some of the summering areas of narwhals that were identified during our surveys have been surveyed comprehensively by others to estimate the numbers of narwhals present (Fallis *et al.* 1983, Smith *et al.* 1985, Born 1986, Born *et al.* 1994, Richard *et al.* 1994). Substantial year-to-year variation is evident both from our data alone and from comparisons among studies (Table 4). The largest summering populations are found in Admiralty Inlet, Prince Regent Inlet, Eclipse Sound, Inglefield Bredning and possibly Smith Sound-Kane Basin.

Three possible summering areas that we identified have not been systematically surveyed: Home Bay and Buchan Gulf along eastern Baffin Island and Smith Sound-Kane Basin. Of these areas, Kane Basin probably contains the largest number of narwhals; we counted

1226 narwhals along the Smith Sound ice edge and 325 along the east coast of Ellesmere Island south of there on 5 July 1979. In 1979, narwhals continued to move into Lancaster Sound until early August, so movements into Kane Basin may have continued after our last survey there, on 5 July. The presence and size of the group summering in Smith Sound-Kane Basin need to be confirmed by surveys conducted in mid-August to early September. It is possible that there is interchange between narwhals summering in Kane Basin and in Inglefield Bredning. Born (1986) estimated that at least 4000 narwhals summered in Inglefield Bredning in 1984, and Born *et al.* (1994) estimated that numbers in Inglefield Bredning were between 847 and 1366 in 1985 and between 2683 and 4369 in 1986. Although their surveys did not include Hvalsund, where some narwhals may summer, the large inter-year variation suggests that some whales that summered in Inglefield Bredning in 1984 and 1986 summered elsewhere in 1985.

Riewe (1977) suggested that Jones Sound is a summering area for narwhals in some but not all years. We saw few narwhals along the Jones Sound ice edge during the 3–4 weeks previous to break-up or during four surveys in late summer and early autumn. We suspect that narwhals may concentrate along the Jones Sound ice edge to feed during their spring migration north into Smith Sound and Kane Basin, but that only a few tens of narwhals normally summer in Jones Sound.

Autumn

Autumn migration from summering areas begins in late September just before summering areas begin to freeze. During autumn, narwhals tend to migrate in large herds ranging in size from a few hundred to several thousand animals. Narwhals that summer west of, or in the vicinity of, Lancaster Sound follow both coasts of Lancaster Sound eastward. A large proportion of the narwhals from Admiralty Inlet cross to the north side of Lancaster Sound and follow the south coast of Devon Island eastward into offshore Baffin Bay. Narwhals that follow the south coast of Lancaster Sound continue southeastward along the coast of Baffin Island. Observations from Cape Adair along NE Baffin Island suggest that a substantial proportion of the population follows the coast southward in some years; however, poor weather and darkness have prevented accurate estimation of the proportions of the population that use coastal and offshore routes. After freeze-up begins, narwhals disperse among the offshore pack ice where southward movements continue.

Swimming speed

We estimated the swimming speed of migrating narwhals as 5–12 km/h over periods varying from 0.8 to 17 h. We did not obtain estimates for other times of year but our impression was that movements during autumn were faster and more directed. Our estimated speeds are faster than those for narwhals in summering areas (Fallis *et al.* 1983) but are slower than those for rapidly-migrating (Koski & Davis 1979: 14 km/h) or fleeing white whales (Vladykov 1944: 14–18 km/h).

Relative age and sex composition

Our data indicate that narwhals are segregated by age and sex during some times of the year. During late winter, females are found farther south than males. In addition, females with 7- to 8-mo-old calves are found in areas of heavier ice conditions than are other females. During late spring, male narwhals precede females during movements toward summering areas; this temporal segregation was also recorded by Greendale & Brousseau-Greendale (1976). When moving into summering areas, adult males follow coasts and ice edges, whereas females and young move through offshore waters.

Silverman (1979) observed that although herds of narwhals in summering areas were not segregated by age or sex, pods or groups within the herds were segregated. We observed the same segregation within herds both during summer and during fall migration.

Based on our overall data from surveys of summering areas, which may be biased by overestimates of numbers of adult males, 67% of narwhals are estimated to be adults. Other surveys of summering areas have yielded similar proportions of adults and subadults (for a review see Born *et al.* 1994: Table 5).

Calf production

Data from summering areas suggest that the birth rate was 0.29 calves/adult female/year based on sightings of 1-mo-old calves. With an allowance for some early mortality and aborted fetuses, our data agree with those of Hay (1984) who found a range of pregnancy rates of 0.30–0.38/adult female. For the summering area of Scoresby Sund in eastern Greenland Larsen *et al.* (1994) reported a ratio of neonates to total number of females of 0.38. Kingsley *et al.* (1994) estimated 9.6% calves among 1395 narwhals that they classified and Born *et al.* (1994) estimated 14.9% among 228 animals. Silverman (1979) estimated that neonates made up 10.3% of the narwhals in Tremblay Sound during 1977 and 1978; males and females were 44% and 56% of her adult sample so that the sex bias in her sample was opposite to ours. Her data may slightly overestimate the proportion of calves in the total population. Our direct observations suggest that 1-mo-old calves form 7.8% of the sampled population but males may be over-sampled during our surveys. If the sex ratio of males:females is equal, and we equalize the sex ratio in our sample, calves make up 9.0% of all narwhals in late August to early September. With an allowance for the potentially biased sampling in Silverman's (1979) study, her data are similar to ours but still have a higher proportion of calves. Based on a review of the narwhal literature, Strong (1988) suggested an annual population birth rate of 0.07 (*i.e.* calves would make up 6.5% (7/(100+7)) of all narwhals). Our data, which are from only two years, and the data of Silverman (1979), Born *et al.* (1994) and Kingsley *et al.* (1994) suggest that this estimate may be low. Collection of data on the age and sex ratios of narwhals from different summering areas should be a high priority of future surveys. Surveys should be either low-level photographic surveys (150 m a.s.l. with a 200–300 mm lens) or aerial count surveys by experienced observers; we have found that many observers can not reliably distinguish the various age classes that we used during this study.

Other life history data

Timing of calving

Our data suggest that most narwhals calve after mid-July when they normally would be in summering areas. Although the relative ages of few narwhals were estimated during our surveys in coastal/ice-edge areas, we would have recorded many neonates had they been common. Only three neonates (<1% of sightings) were recorded before mid-July during two years of intensive surveys yet 5.9 to 10.2% of animals in summering areas surveyed in late August to early September were neonatal calves. These data are consistent with those of Best & Fisher (1974). They listed dates and sizes of narwhal fetuses and neonates from the literature and found only one record of a neonate before July (28 June 1936, in Eales 1950). Best & Fisher (1974) found three records of near-term fetuses in early July but no other records of neonates until 12 July. Analyses conducted by Hay (1984) agree with our observations and those of Best & Fisher (1974). Using data on fetal sizes and growth rate, Hay (1984) estimated that narwhals calve from 30 June to 29 August. Data presented by Cosens & Dueck (1990) appear to suggest that neonatal calves are common in May and June at the mouth of Admiralty Inlet. They reported 22 narwhal neonates from 27 May to 25 June 1986; this was approximately 6% of the animals observed in groups that contained neonates (Cosens & Dueck 1990). However neonates were only 2% of all narwhals that they sighted during their surveys (Sue Cosens, Depart. of Fish. and Oceans, Winnipeg, pers. comm.). Their surveys were conducted over the same general area on most days, so that it is possible that some were sighted repeatedly. The sightings reported by Cosens & Dueck (1990) may represent a few mothers with neonates that moved toward summering areas in Admiralty Inlet earlier than other whales. It is also possible that a few of their sightings were narwhal yearlings that were mistaken for neonates (Sue Cosens, pers. comm.).

Calf mortality

Our data from the summering areas permit estimation of mortality during the first year of life. One-mo-old calves made up 7.8% of our 1978–79 sample and 13-mo-old yearlings made up 6.5%. Therefore, first year mortality is estimated at 17% ((7.8–6.5)/7.8). A second estimate of mortality can be made using the same data. Neonates were 8.7% of all narwhals recorded in summering areas in 1978 and yearlings were 6.6% of all narwhals recorded in summering areas in 1979. If neonates born in 1979 are excluded from the 1979 sample, yearlings were 7.2%. Again the mortality from age 1 mo to 13 mo is estimated to be 17% ((8.7–7.2)/8.7). These estimates of mortality are not independent since the second uses a subset of the data used for the first. They must be treated cautiously because mortality rates may vary among years and small changes in the proportion of calves or yearlings in either 1978 or 1979 would cause large changes in estimated mortality rates.

Numbers of narwhals

Narwhals were widely dispersed among the pack ice in Baffin Bay during May and June. Our best estimates of the size of the narwhal population come from surveys conducted at this time of year. These estimates include narwhals that later summer in both Canadian and Greenland waters. In 1979, we estimated that 29 931 (± SE 7008) to 38 988 (± SE 6629) narwhals were present in offshore waters of our study area during four different surveys (Table 8). The four individual estimates were remarkably similar given the low overall coverage. The mean number present was 34 363 (± SE 8282). In addition to the offshore animals, some narwhals were present along coasts and ice edges in and north of the study area and others may have been present in the offshore pack ice east of the surveyed area. Throughout the offshore surveys in all years and all seasons, narwhals strongly preferred ice cover of 90–99%, and less strongly, ice cover of 80–89%. The only suitable narwhal habitat that was not directly covered by our estimates during the late spring of 1979 was in eastern Baffin Bay, to the east of block B, and to the east and northeast of block C (Fig. 11). These areas are not large in comparison to the area included in the estimates. However, some additional narwhals were undoubtedly present in the unsurveyed areas, particularly during the 19–23 June survey when many were recorded in the eastern part of block C (Fig. 11).

The estimates for offshore waters have not been corrected (1) for animals that were present near the water surface but were not seen by observers or (2) for animals that were below the surface and not recorded. They do include animals that were seen swimming below the surface, whether or not they surfaced in view of the observers. We believe that few animals near the surface were missed during these surveys. Most of the survey area was covered with extensive ice pans, enabling observers to search the few cracks and leads, both ahead of and behind the aircraft. The prolonged search of these restricted open-water areas made it less likely that observers would miss an animal that was present on the surface; it also permitted detection of animals that were below the surface when the aircraft was perpendicular to them but that surfaced up to one minute before or after the normal viewing period.

Dueck (1989) studied the behaviour of narwhals during the open-water period in Admiralty Inlet and found that narwhals were visible at the surface only 38% (95% CI 29–52%) of the time. Born *et al.* (1994) found that narwhals were present at the surface for a similar (36%) proportion of the time while travelling. Thus, to correct instantaneous counts for the probability that a narwhal is below the surface, counts should be multiplied by 2.63–2.77 (1.00/0.38 or 0.36). Their data could be used to calculate a correction factor for submerged animals that allows for the extended search period during our surveys (see Eberhardt 1978). However, narwhal behaviour is likely different in offshore pack ice in spring than in open water in Admiralty Inlet and Inglefield Bredning in summer and any such calculation is of dubious validity.

Previous studies have not attempted to estimate the size of the entire narwhal population but several studies have estimated the numbers in various summering areas (Table 4; see also below) and the numbers of narwhals entering Lancaster Sound. Narwhals that enter Lancaster Sound summer primarily in Admiralty Inlet, Prince Regent Inlet and Peel Sound. Davis *et al.* (1978) used a combination of aerial surveys and ground-based observations to estimate the number of narwhals that entered Lancaster Sound in 1976. Their estimate of 20 000–30 000 animals was based on several conservative decisions and the actual number may have been higher.

Smith *et al.* (1985) attempted to estimate the number of narwhals in the Canadian High Arctic. They estimated that 11 142 (95% CL 9035–13 891) narwhals were present within their survey area in Lancaster Sound, Barrow Strait and Prince Regent Inlet and that an additional 2000 and 2117 were present in Peel Sound and Admiralty Inlet, respectively. Thus their total estimate was 13 200–18 000. Although Admiralty Inlet is a major summering area for narwhals entering Lancaster Sound (see below and Table 4), Smith *et al.* (1985) did not include Admiralty Inlet in their survey area and their allowance of 2117 for this area is likely low. In addition, for Prince Regent Inlet in early August, Smith *et al.* (1985) extrapolated densities recorded in northern Prince Regent Inlet to unsurveyed areas in central Prince Regent Inlet even though higher densities occurred on transects in the northern half of the area that was surveyed. Therefore, the Smith *et al.* (1985) estimate of 10 807 for Prince Regent Inlet may be an overestimate.

Richard *et al.* (1994) conducted photographic surveys of Peel Sound, Prince Regent Inlet, Admiralty Inlet and Eclipse Sound during 1984. Their combined estimate was 18 000 (90% CL 15 000–21 000) for the areas that they surveyed. The areas surveyed by Richard *et al.* likely contained most of the narwhals that entered Lancaster Sound in 1984. There was little ice in Barrow Strait and Lancaster Sound at the time of their survey, and their maps of narwhal distribution suggest that most narwhals had entered summering areas. They concluded that most of the biases in their estimates were negative and agreed with Davis *et al.* (1978) that the Canadian High Arctic narwhal population was probably 20 000–30 000 animals.

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Distribution and numbers of Canadian High Arctic narwhals *(Monodon monoceros)* in August 1984

PIERRE RICHARD, PATT WEAVER, LARRY DUECK and DAVID BARBER

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Aerial photographic surveys of the numbers and distribution of narwhals (*Monodon monoceros*) in fjords and inlets south of Parry Channel, N.W.T., Canada, were conducted between 17 and 29 August 1984. Narwhals were concentrated in waters 350 m or more in depth and were most abundant in Prince Regent Inlet and Admiralty Inlet. An estimate of 18 000 narwhals (90% CI 15 000–21 000) was obtained by combining estimates for the Eclipse Sound area, Admiralty Inlet, Prince Regent Inlet and Peel Sound. We evaluated the visibility of narwhal and white whale *(Delphinapterus leucas)* models submerged to different depths. Models of adult narwhals could be seen when submerged to 10 m but could only be clearly distinguished from white whales at depths of 2 m. Such results indicate a limit to counting submerged narwhals. This problem, along with other factors, constrains the estimation of population size.

Key words:
Narwhal, *Monodon monoceros*, distribution, photographic survey, Canadian High Arctic.

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Introduction

In the Canadian High Arctic, narwhals *(Monodon monoceros)* summer in deep fjords and channels south of Parry Channel (Lancaster Sound and Barrow Strait) from mid-July to September or October (Mansfield *et al.* 1975, Finley & Johnston 1977, Davis *et al.* 1980, Finley *et al.* 1980, Finley & Miller, 1982). A first approximation of the size of this population was obtained by extrapolation from counts of narwhals migrating through Lancaster Sound in 1976 (Davis *et al.* 1978) but more precise estimates are needed for management of the subsistence hunt practiced by local Inuit. Smith *et al.* (1985) flew surveys in Lancaster Sound and Prince Regent Inlet in August 1981 but did not cover the Eclipse Sound area, Admiralty Inlet and Peel Sound (Figs 1–2) which also have large summer narwhal concentrations (Davis *et al.* 1980, Fallis *et al.* 1983, Finley & Johnston 1977, Mansfield *et al.* 1975).

Between 17 and 29 August 1984 we flew a series of surveys in all four areas (Fig. 2). Counts of narwhals were also made at Inglefield Bredning, NW Greenland, during that period (Born 1986). The combination of these efforts provided the first extensive coverage of the Baffin Bay narwhal stock. Preliminary estimates for the Canadian part of these surveys were given by Strong (1988) and Barber (1989) analyzed the observed distribution of narwhals in relation to sea-surface temperature features occurring during these surveys.

In this paper we present details of the distribution of narwhals and estimates of numbers for the August 1984 Canadian surveys. The distribution is discussed and compared to other studies. Methods used to estimate numbers are discussed in the light of the bias demonstrated by a model experiment and of other known or potential counting and sampling biases.

White whales *(Delphinapterus leucas)* and narwhals are sympatric in Peel Sound and Prince Regent Inlet. Narwhals may be confused with white whales or missed entirely when they are submerged. A model experiment was conducted in July 1984 to study the visibility and ease of recognition on aerial photographs of narwhals submerged to varying depths. We present the results of this experiment here because they are important to the understanding of counting error in aerial surveys.

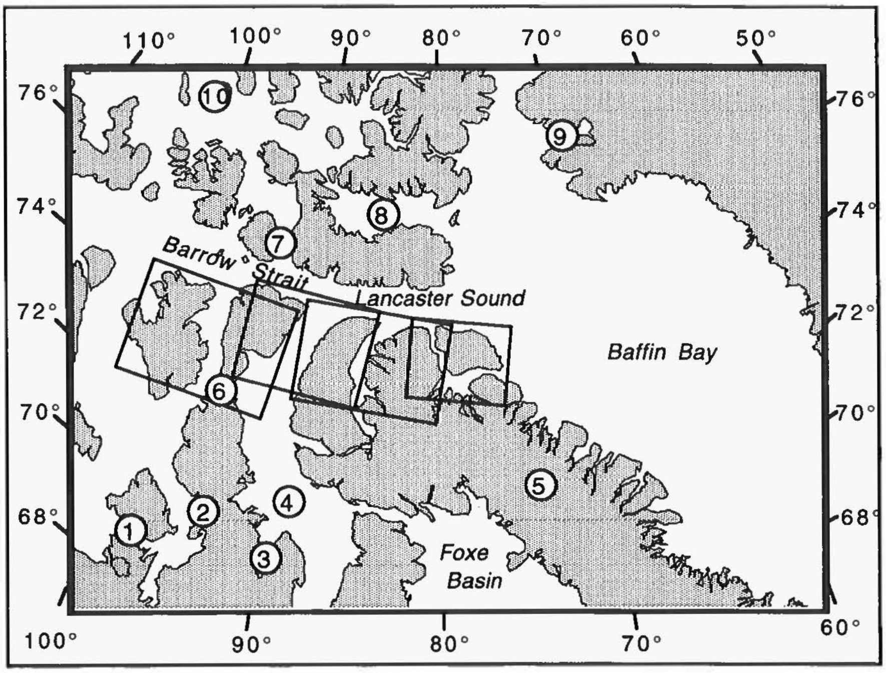

Fig. 1: Canadian High Arctic. Numbered locations are: 1- Gjoa Haven, 2- Spence Bay, 3- Pelly Bay, 4- Gulf of Boothia, 5- Baffin Island, 6- Bellot Strait, 7- Wellington Channel, 8- Jones Sound, 9- Inglefield Bredning (Greenland), 10– Maclean Strait. Insets delimit the survey areas shown in Fig. 2.

Materials and methods

Study area

Surveys were flown between 17 and 29 August 1984 in the Eclipse Sound area, Admiralty Inlet, Prince Regent Inlet and Peel Sound (Fig. 2). These four areas are bays or channels with zones of deep water that exceed 350 m in depth. At the end of August the Eclipse Sound area and Admiralty Inlet are normally ice-free, and Prince Regent Inlet and Peel Sound have ice in low concentrations (Markham 1981).

Aerial surveys

Surveys were flown in a DeHavilland Twin Otter (DHC6) equipped with a gyrostabilized 230.8 mm by 230.8 mm format camera (Wild-Leitz RC8) with a 153.8 mm lens mounted vertically at the rear camera port of the aircraft. The navigator used an Omega navigation system to locate transects and maintain headings; landmarks were used to confirm positions and update the navigation system. The pilot maintained a constant ground speed of 187 km/h and an altitude of 923 m throughout the transects. The camera was triggered by an intervalometer at 29 sec intervals to obtain a stream of photographs separated by a slight gap, each covering an area of 1385 m by 1385 m. Kodak Aerocolor 2445 colour negative film was used for all the

Table 1. Details of survey strata and narwhal population estimates, 17–29 August 1984.

Date (Aug.)	Stratum (see Fig. 2)	Transects	Census area (km²)	Coverage	Transects	Count	Density	Estimate	CV	Confidence limits lower 90%	upper 90%
17	Eclipse I	1W-13W	1502	19.34%	13	0	0	0	–	–	–
17	Eclipse II	14E-18E	2048	20.43%	5	111	0.26522	543	59%	166	1784
18	Eclipse III	19W	493	15.10%	1	102	1.37087	675	–	–	–
23	Admiralty	all	6319	8.44%	13	469	0.87925	5556	22%	3759	8213
25	Peel Sound I	1E-9E	7998	7.67%	11	65	0.10591	847	26%	531	1352
26	Peel Sound II	10W-15E	2252	7.96%	4	68	0.37922	854	23%	498	1464
27	Prince Regent I	1E-7E	8623	8.19%	7	447	0.65617	5461	29%	3139	9500
29	Prince Regent II	8E-11W	5742	9.18%	4	394	0.7476	4293	17%	2918	6316
	All blocks combined							17991	10%	14724	21258

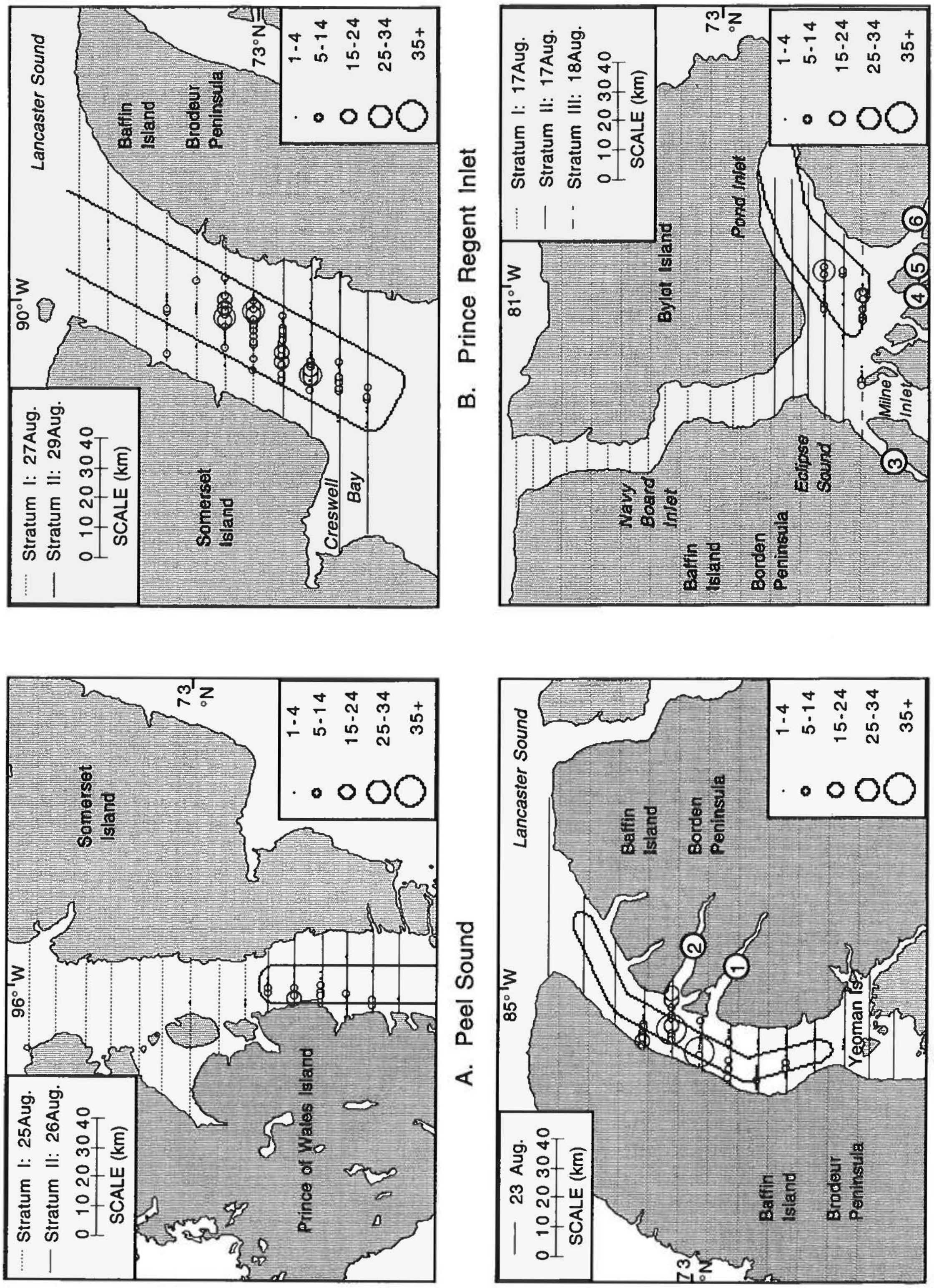

Fig. 2: Distribution of narwhal counts in survey areas. Note: circles represent categories of narwhals counted per photograph. Count categories are given in the legends. Numbered locations are: 1- Adams Sound, 2- Strathcona Sound, 3- Tremblay Sound, 4- Tay Sound, 5- Paquet Sound, 6- Oliver Sound. The line contours delimit the approximate locations of waters with depths greater than 350 m.

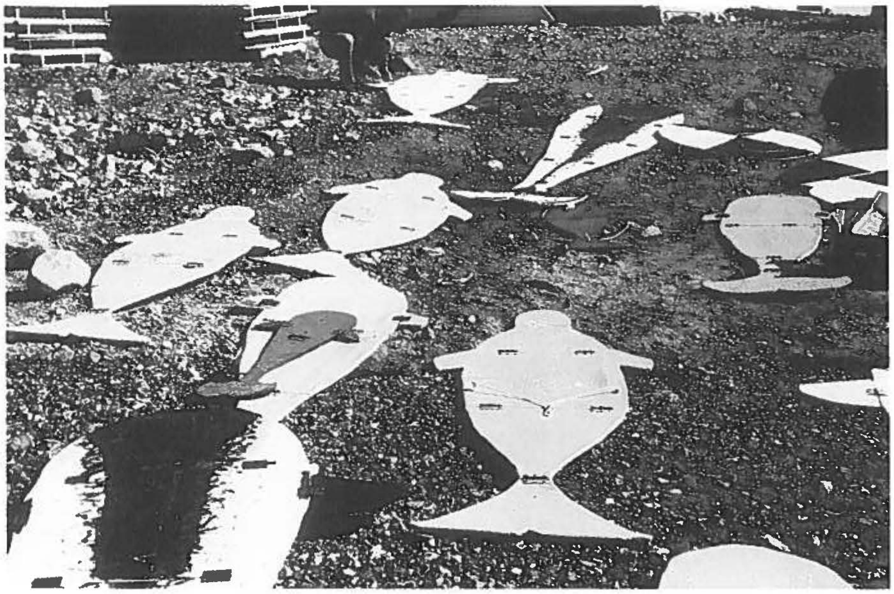

Fig. 3: Narwhal and white whale models used in the model experiment.

surveys. Surveys were flown during periods surrounding solar noon to maximize available light and minimize surface glare.

Systematic east-west transects were flown in daily strata, as described in Fig. 2a-d and Table 1. The first two strata in the Eclipse Sound area were flown on the same date (17 August 1984) but were kept separate to group transects of similar lengths and to minimize the effect of uneven transect areas on the variance of the estimate. Surveys were flown only when sea state for the stratum averaged 2 or less and did not exceed 3 on the Beaufort scale (wavelets, little or no whitecaps).

Photographic coverage consisted of transects spaced every 8' of latitude except in the Eclipse Sound area, where transects were spaced every 4' of latitude, yielding coverage of about 8% and 20% respectively (Table 1). The Eclipse Sound area was flown at a higher coverage to study the distribution of narwhals in more detail. In all areas but Admiralty Inlet, it took two or three days to complete the surveys.

Photographs were scanned for narwhals at a magnification of 10x using a Nikon SMZ-1 stereoscopic microscope mounted on a Richards GFL-940MC light table, and following a grid that divided the frame into nine equal-sized blocks. In addition to narwhal counts, the readers noted environmental conditions such as sea state (Beaufort index), ice concentration or the presence of fog. The heading of each whale relative to true north was also noted. For areas requiring two or more days to complete, we calculated the frequency of narwhal headings by survey stratum to determine if there was any directional trend in the orientation of narwhals when an area was covered in two or more days.

Methods described by Kingsley *et al.* (1985) and Smith *et al.* (1985) were used to obtain estimates of variance and confidence limits. We used methods suggested by Gasaway *et al.* (1986) to calculate an estimate of population size and one of population variance for all areas combined. These methods are described in detail in Appendix I.

Ninety-percent confidence limits are reported. Ninety-five percent confidence limits are traditionally given for population estimates but setting $\alpha = 0.10$ gives added power to test for population change (Peterman 1990). This is an important tool since in resource management the consequences of a Type II error (*i.e.*: accepting the null hypothesis of no decline in population size when it is wrong) are more serious than those of a Type I error (*i.e.*: rejecting the null hypothesis of no decline when it is true). The former may lead to over-exploitation and long-term harm to the resource.

Model experiment

Experiments were conducted at Repulse Bay (66°50'N, 86°30'W) on 30 July 1984 with life-sized models of narwhal and white whale adults, juveniles and calves to evaluate the visibility and ease of identification of the models of age classes of each species submerged to different depths.

The models were made by stretching white canvas on plywood forms cut in the shape and size of adult, juvenile and neonatal animals. Gray and black colour was added to imitate the natural colour of narwhals and white whales. The shape and colour of each model were made to approximate the dorsal aspect of each age class (Fig.3) and were based on aerial photographs of narwhals and white whales and on photographs of animals landed by

Table 2. Frequency of narwhals with North (330°–30°) and South (150°–210°) headings in each stratum.

Date (August)	Stratum	North Frequency	North Proportion	South Frequency	South Proportion	Total Frequency	Chi-Square Goodn.-of-Fit
17	Eclipse Sound II	7	7%	48	46%	105	$p < 0.005$
18	Eclipse Sound III	5	5%	37	39%	96	$p < 0.005$
25	Peel Sound I	2	33%	0	0%	6	$p > 0.100$
26	Peel Sound II	15	12%	38	31%	122	$p < 0.005$
27	Prince Regent Inlet I	81	20%	48	12%	413	$p < 0.005$
29	Prince Regent Inlet II	67	18%	66	18%	365	$p < 0.005$

local hunters in various localities in the N.W.T. Model lengths (Table 3) were based on data from Hay (1984) for narwhals and from Sergeant & Brodie (1969) for white whales.

Models were submerged and stabilized on a horizontal plane at predetermined depths using floats and anchors. A set of randomly assorted white whale and narwhal models of various age classes (2 adults, 2 juveniles and 2 neonates of each species) were anchored along a cable and submerged to 2 m, 5 m and 10 m. Vertical aerial photographs were taken from four altitudes (Table 3). The photographs were read by an experienced reader who did not know the depths or age classes of the models. The reader noted all visible whale models and determined their species and age class where possible.

Results

Aerial surveys

All surveys were flown on days with low surface winds (Beaufort index <4) and good visibility conditions. Ice cover was lower than expected for that time of year (Markham 1981). In all but one survey area, the water surface was free of ice except for a few occasional patches of loose pack (<10%). Peel Sound had ice scattered along its entire length in low concentration (<10%). On 18 August in the Eclipse Sound area only one transect was partially surveyed owing to dense fog which covered the middle section of that transect and all transects to the south. High winds (Beaufort index ≥4) over the stratum in the following days caused the cancellation of the survey.

In Peel Sound (Fig. 2a) narwhals were found to be concentrated in the south part of the channel, from the center to the coast of Prince of Wales Island. Of the four areas, Prince Regent Inlet (Fig. 2b) had the largest number of narwhals. Their distribution followed the longitudinal axis of the inlet and the largest numbers were found in the center. Few narwhals were counted near the coasts of Baffin Island and Somerset Island

In Admiralty Inlet visual reconnaissance flights were conducted in Adams and Strathcona sounds on 22 August, but no narwhals were seen. During systematic photographic surveys on 23 August narwhals were distributed throughout Admiralty Inlet, north of the mouth of Strathcona Sound to Yeoman Island (Fig. 2c). The largest numbers were counted near Strathcona and Adams sounds.

Table 3. Narwhal and beluga models visible and identifiable on aerial photographs taken at four different altitudes.

Altitude of camera	360 m			370 m			680 m			990 m		
Depth of models	2 m	5 m	10 m	2 m	5 m	10 m	2 m	5 m	10 m	2 m	5 m	10 m
Model type												
420 cm adult beluga	*	*		*	*		*	*		*	*	
460 cm adult narwhal	*			*			*			*		
Adult unknown species			*			*			*			*
250 cm juvenile beluga	*			*			*			*		
250 cm juvenile narwhal	*			*			*			*		
Juvenile unknown species					*			*			*	
160 cm neonate beluga												
160 cm neonate narwhal												
Neonate unknown species				*	*							
Unknown species/class	*	*										

Note: an asterisk indicates that the model type was visible on film.

In the Eclipse Sound area visual reconnaissance flights were flown in Tay Sound, Paquet Bay and Oliver Sound on 15 August but no narwhals were seen. In systematic surveys flown on 17 August narwhals were not found in stratum I or in the northern three transects of stratum II (Fig. 2d). Narwhals were in relatively large groups in the southern two transects of stratum II on 17 August and in the single transect flown in stratum III on 18 August (Fig.2d).

The 90% confidence limits for all strata combined suggest a total visible (*i.e.* not corrected for whales that were submerged out of sight) population of between 15 000 and 21 000 narwhals (Table 1), of which about half were in Prince Regent and a third in Admiralty Inlet.

The frequency of south orientation (12%) of narwhals in Prince Regent Inlet's survey stratum I is less than expected from random orientation (Table 2). This is opposite to what one would expect if large numbers of narwhals were moving toward stratum II during the survey. Stratum II of the Eclipse Sound area (Table 2) had a higher than expected proportion of narwhals pointing south (46%). This indicates that movement to stratum III, which was flown the next day, could have taken place.

Model experiment

Irrespective of photograph altitude, adult models of both species were visible at a depth of 10 m (Table 3) but adult models of narwhals and white whales could only be distinguished to species at depths of 2 m and 5 m, respectively. Juvenile models of both species were only seen and recognized at 2 m from all altitudes. Neonate models submerged at 2 m and 5 m were seen only on low-altitude photographs (370 m) and could not be identified to species.

Discussion

Distribution

In all four survey areas (Fig. 2) narwhals were aggregated in a portion of the area and these aggregations appear related to bathymetry. In southern Peel Sound narwhals were concentrated along the western edge of a zone of water about 380 m deep (Fig. 2a). Narwhals were also concentrated over the deep central waters of Prince Regent Inlet, where depths average 400 m (Fig. 2b). In Admiralty Inlet most narwhals were also near the deepest waters of the inlet, zones where depth averages about 500 m (Fig. 2c). The largest numbers were counted near the mouths of Adams Sound and Strathcona Sound where depth increases to 600 m. In the Eclipse Sound area narwhals were most concentrated over the deep waters of Pond Inlet which average about 400 m (Fig. 2d).

Other authors have reported a similar distribution of narwhals in late summer. During surveys of southern Peel Sound on 28 August and 4 September 1976 Finley & Johnson (1977) observed narwhals in the same zone of deep water. From 172 narwhals observed on six transects on 4 September 1976 they estimated the density of narwhals to be about 0.54 narwhal/km^2, a density greater than that estimated for our 26 August 1984 survey (0.38 narwhal/km^2; Table 1: Peel Sound II). Most of the narwhals observed during Smith *et al.*'s (1985) August 1981 systematic surveys were also in the deep waters of Prince Regent Inlet. Dueck (1989) reported densities of between 0.4 and 1.29 narwhals/km^2 from systematic surveys of Admiralty Inlet on 17 August 1983, 21 August 1984 and 14 August 1985. In all three surveys most narwhals were in or near the deep waters, but in 1984 and 1985, they were most concentrated south of the mouths of Adams Sound and Strathcona Sound. Dueck's (1989) counts indicate some variation in the distribution of narwhals in Admiralty Inlet. There are no other systematic surveys with which to compare our results but Kingsley *et al.* (1994) observed relatively fewer narwhals in Eclipse Sound than in fjords and bays to the south of it.

Our results combined with the above-mentioned studies indicate a preference for deep water. The choice of deep water by narwhals may be related to bottom-feeding activity. Vibe (1950) reported that the summer diet of narwhals in northwestern Greenland consists partly of Greenland halibut *(Reinhardtius hippoglossoides)*, a deepwater fish. Finley & Gibb (1982) sampled narwhals in Eclipse Sound during the open-water period and reported that four of 11 narwhal stomachs had remains of polar cod *(Arctogadus glacialis)*, another deep-water fish (*A. glacialis* is usually called arctic cod in Europe). They concluded that narwhals did not feed very much during the open-water period. However the narwhals that they sampled were taken on the west side of Eclipse Sound, at least 30 km from Pond Inlet. If narwhals had been feeding in Pond Inlet, they could have fully digested their prey by the time they reached the west side of Eclipse Sound. Finley & Gibb (1982) did find remains of Greenland halibut and redfish *(Sebastes marinus)* in stomachs of narwhals captured in the deep waters of Pond Inlet earlier in the season. Heide-Jørgensen *et al.* (1994) found *Arctogadus glacialis* to be the dominant food item of the narwhals in Inglefield Bredning (NW Greenland) during summer.

Population size

Our estimates provide an index of the population size of Canadian High Arctic narwhals. An estimate of true population size is constrained by several factors.

First and foremost is the fact that narwhals spend considerable time at depths where they cannot be detected or identified on vertical photographs. The model experiment shows that at standard photographic survey altitudes (>680 m), models of narwhal and white whale adults and juveniles can be detected at depths of 10 m and 5 m, respectively, but species identification of both adults and juveniles is only possible at depths within 2 m of the surface. Neonate models of both species can not even be detected at 2 m depths. There is a clear bias due to under-counting of juveniles and neonates that are not near the surface. In areas where narwhals and white whales are sympatric, such as Prince Regent Inlet and Peel Sound, species identification of submerged animals can be a problem.

The dive durations of adult narwhals likely also contribute to the underestimation of their numbers, even though they comprise the largest portion of the population. Depth profiles obtained from an adult female narwhal equipped with a satellite transmitter revealed that, during a 10-day period in August 1991, 44% of its time was spent at depths greater than 6 m (Martin *et al.* 1994). From cliff and helicopter observations Dueck (1989) estimated the probability of narwhals being visible to an observer during a visual survey. His sighting probability (0.38, 95% CI 0.29–0.52) was derived from observations made at oblique angles, and as such is probably lower than if it had been derived from vertical observations, owing to poorer water penetration at oblique angles.

Second, bias occurs when photographs are read because readers miss some narwhals that are visible on the film. Double-count experiments using white whale photographic survey data showed that, on photographs taken in clear offshore waters of the Beaufort Sea, the probability of a reader's counting a white whale when it is visible on the film was 0.84 (Richard, unpubl. data). For visual surveys conducted in the same area Norton & Harwood (1985) reported a probability of 0.4 that a white whale would be counted when it was visible in a strip-census survey. A similar bias may exist in our narwhal photographic counts but we have not made double-counts of these survey photographs.

Third, counting biases may be caused by narwhals' movement out of a survey stratum during the survey or from one stratum to the next between flights. Such biases could cause either under- or over-estimates. Our analysis of narwhal orientation shows no indication of mass movement between strata in Prince Regent Inlet, but it is possible that some movement took place. There is indication of movement from stratum II to stratum III of the Eclipse Sound area. Although a high frequency of common headings does not necessarily mean that narwhals did move to the next survey stratum, it is cause for caution in the interpretation of our estimates. If such a movement did occur, it could have caused double-counting and biased the total estimate for the Eclipse Sound area. In this case the number of narwhals involved is relatively small and therefore the potential bias on the overall population estimate is relatively small.

Movement out of survey strata is also possible during surveys. Narwhals have been observed to make mass movements in response to weather, ice distribution or the presence of killer whales (*Orcinus orca*) but, in contrast, narwhals fitted with telemetry instruments have also been observed to spend several weeks in the same area during summer (Kingsley *et al.* 1994). The extent to which movement has affected our surveys is unknown. However it may be balanced by a simultaneous immigration to the surveyed areas.

Fourth, the southern part of Eclipse Sound, Milne Inlet and adjacent bays and fjords were not surveyed. Some of these areas are known to be preferred by narwhals in summer but the total numbers occurring in these areas are not large (Kingsley *et al.* 1994).

Finally, we only covered areas known to have relatively high densities of narwhals in August. Narwhals have a wide distribution in the Canadian Arctic archipelago in late summer (Fig.1). They have been observed in low numbers north of our study area, in Barrow Strait, Maclean Strait, Wellington Strait and Jones Sound (Mansfield *et al.* 1975, Roe & Stephen 1977, Davis *et al.* 1978, Koski 1980, Sergeant & Williams 1983) and south of it, in Bellot Strait, the Gulf of Boothia and northern Foxe Basin (Anders 1965, Finley & Johnston 1977, Sergeant & Williams 1983). Narwhals are also hunted in some years in Gjoa Haven, Spence Bay and Pelly Bay (Mansfield *et al.* 1975, Smith & Taylor 1977, Strong 1989). The unpredictable occurrence and low numbers of narwhals in a given year do not justify the allocation of survey effort to these areas. For example, Koski (1980) reported narwhal observations in Barrow Strait between 17 and 20 August 1979 but Smith *et al.* (1985) did not observe any narwhals on their 6 and 14 August 1981 transects through Barrow Strait.

Most of the above sources of error will cause an underestimation of true population size. Consequently our overall estimate of 18 000 narwhals is only an index of the population size. If biases are relatively constant from year to year, indices derived from annual surveys could be used to track narwhal population changes. Studies of narwhal movement and diving behaviour are badly needed to understand the extent to which some of these biases vary and affect the index.

The ability to detect changes also hinges on the precision of the estimates and our survey estimates have low precision (high variance) owing to the low density and clumped distribution of narwhals (Fig. 2) and the low sampling fraction. It is not clear whether we could reduce the sampling variance in future surveys by stratifying the survey areas into sub-areas of high and low density. Even though narwhals often concentrate near the deepest parts of their summering areas, their distribution is dynamic and unpredictable (Finley & Johnston 1977, Dueck 1989, Kingsley *et al.* 1994). Reconnaissance surveys to find high-density sub-areas just prior to the census flights might enhance the chance of effective stratification.

An alternative to stratification is to repeat surveys several times to reduce the sampling variance (Gerrodette 1987). However if movements occur into or out of survey areas between successive flights, then the numbers estimated are not the same and combined estimates are not valid. A second and preferred alternative suggested by Kingsley *et al.* (1994) is to use several planes simultaneously to survey each area at high coverage. Neither of these alternatives comes without a substantial increase in cost, but unless population estimates can be made more reliable, they will only detect large changes in population size.

Our results lead us to conclude that the size of the Canadian High Arctic narwhal population is most likely greater than or equal to 20 000 animals since the 90% lower confidence limit is 15 000 and most sources of error probably result in an under-estimate. Born (1986) counted a maximum of about 4 000 narwhals on 18 August 1984 in Inglefield Bredning, which is only a part of the summer range of narwhals in northwestern Greenland (Vibe 1950, Meldgaard & Kapel 1981). This suggests that the total Baffin Bay narwhal population is at least 19 000 narwhals and may well exceed 22 000 narwhals.

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Appendix I : Formulas used to calculate estimates of population size.

Except where indicated, the following formulas and notation were taken from Kingsley *et al.* (1985). Average density within strata was calculated as:

$$\hat{R} = \frac{\sum_{1}^{I}\sum_{1}^{J} t_{ij}}{\sum_{1}^{I}\sum_{1}^{J} a_{ij}} \tag{1}$$

where $\hat{R}$ = average density of the survey area,
t_{ij} = whale count in photograph j on transect i,
a_{ij} = area of photograph j on transect i.

Transect counts were not weighted for meridian convergence since our transects were oriented east-west.

The variance of $\hat{R}$ is calculated by:

$$V_S = \left(1 - \frac{n}{N}\right)\left(\frac{I\sum_{1}^{I-1}(d_i - d_{i-1})^2}{2(I-1)\left(\sum_{1}^{I}\sum_{1}^{J} a_{ij}\right)^2}\right) \tag{2}$$

where $d_i = Y_j - \hat{R}X_i$,
n = number of transects flown (I),
N = total number of transects possible across the survey area.

The term (1 – n/N) is the finite population correction and is effectively equal to (1 – survey fraction).

V_s is an estimate of variance based on serial differences between neighbouring transects (S_2^2 in Kingsley *et al.* 1985). V_s is less biased than Cochran's (1977) variance estimator when neighbouring transects are positively correlated, a situation likely to occur when animal distribution is clumped (Kingsley & Smith 1981), as was the case in our study (Fig. 2).

Error coefficients of variation (CV; E in Kingsley *et al.* 1985) were calculated as follows:

$$CV = \frac{\sqrt{V}}{R} \tag{3}$$

To obtain confidence limits of mean density, we assumed that true mean density and sampling variance were proportional, and that this proportion (P) could be estimated from the ratio of sampling variance to sampling estimate of density (Cochran 1977, Smith *et al.* 1985):

If $$P = \frac{V}{\hat{R}} \tag{4}$$

then $$\hat{R} = R_L - t\sqrt{PR_L} \tag{5}$$

and $$R_L - t\sqrt{\frac{V}{\hat{R}}}\sqrt{R_L} - \hat{R} = 0 \tag{6}$$

where R_L = confidence limit of the density estimate,
t = critical point of Student's t distribution.

Equation 6 is a quadratic with two solutions, the upper and lower confidence limits:

$$R_L = \left(\frac{\frac{-t\sqrt{V}}{\sqrt{\hat{R}}} \pm \sqrt{\frac{t^2V}{\hat{R}} + 4\hat{R}}}{2}\right)^2 \tag{7}$$

For each survey stratum the population estimate T and confidence limits were calculated as follows:

$$\hat{T} = \hat{R}\,A \tag{8}$$

and

$$T_L = R_L\,A \tag{9}$$

where A = survey stratum area.

Population estimates $\hat{T}_n$ and variance estimates $V(\hat{T}_n)$ for each stratum were summed to obtain estimates of the total population $\hat{T}_t$ and its variance $V(\hat{T}_t)$ (Gasaway *et al.* 1986):

$$\hat{T}_t = \hat{T}_1 + \hat{T}_2 + \ldots + \hat{T}_n \tag{10}$$

and

$$V(\hat{T}_t) = V(\hat{T}_1) + V(\hat{T}_2) + \ldots + V(\hat{T}_n) \tag{11}$$

The degrees of freedom associated with the summed estimate (Satterthwaite 1946) were calculated as follows:

$$\upsilon_t = \frac{[V(\hat{T}_1) + V(\hat{T}_2) + \ldots + V(\hat{T}_n)]^2}{\dfrac{V(\hat{T}_1)^2}{\upsilon_1} + \dfrac{V(\hat{T}_2)^2}{\upsilon_2} + \ldots + \dfrac{V(\hat{T}_n)^2}{\upsilon_n}} \tag{12}$$

Confidence limits were calculated by:

$$CL = \hat{T}_t \pm t\sqrt{V(\hat{T}_t)} \tag{13}$$

Abundance and stock composition of narwhals *(Monodon monoceros)* in Inglefield Bredning (NW Greenland)

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Born, E.W., Heide-Jørgensen, M.P., Larsen, F. & Martin, A.R. 1994. Abundance and stock composition of narwhals *(Monodon monoceros)* in Inglefield Bredning (NW Greenland). Meddr Grønland, Biosci. 39: 51–68. Copenhagen 1994-04-22.

The abundance of narwhals *(Monodon monoceros)* was estimated in Inglefield Bredning (NW Greenland) during the open-water season. Land-based observations were made in August 1985 and 1988 and aerial surveys using line-transect methodology were flown during late August 1985 and early August 1986. Group sizes based on both land-based and aerial surveys are given in relation to behavior and the age and sex composition of groups. The aerial surveys in 1986 indicated that adults comprised about 68%, non-adults (including neonates) 32%, and neonates about 15% of the population present in Inglefield Bredning. On 20 August 1985 a direct land-based count of 1548 whales was obtained in the eastern part of Inglefield Bredning. The aerial surveys in August 1985 resulted in estimates of between 847 (95% CI 344–2085) and 1366 (95% CI 854–2276), uncorrected to account for those out of sight underwater. The aerial surveys in 1986 resulted in uncorrected estimates of between 2683 (95% CI 1029–6998) and 4369 (95% CI 2037–9341). Between late July and mid-August 1988, remarkably fewer narwhals were observed from land in the eastern parts of Inglefield Bredning. The maximum number of narwhals that could be accounted for during this period was 473 narwhals.

Key words:
Narwhal, *Monodon monoceros*, NW Greenland, line transect, aerial survey.

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Introduction

Narwhals (*Monodon monoceros*) occur in waters bordering northwestern Greenland during summer. Their presence in the Smith Sound area in July, prior to break-up of the fjord ice in Inglefield Bredning (Kangerlussuaq) in the Avanersuaq (Thule) area, was reported by Koski & Davis (1979, 1994) and Born & Knutsen (1990). Meldgaard & Kapel (1981) and Born (1987a) reported observations of narwhals in Melville Bugt during August. Although narwhals have been observed in large numbers along eastern Ellesmere Island (Canada) close to the Thule area, Inglefield Bredning is the major narwhal summering area in northwestern Greenland (Vibe 1950, Born 1986). Prior to ice break-up, which usually occurs about mid-July, the narwhals use lead systems in Hvalsund (Fig. 1) to penetrate the summering areas at the head of Inglefield Bredning. Although some narwhals migrate via Murchison Sund which is relatively shallow, the main migration usually occurs in the southern parts of the deeper Hvalsund. By the time of the formation of solid new ice, usually between late September and early October, the narwhals have left Inglefield Bredning (Born 1986). Observations of narwhals in Inglefield Bredning, with estimates of numbers, were reported by Vibe (1950), Bruemmer (1971), Durham (1979), Born (1986, 1987a), Heide-Jørgensen & Leatherwood (1987) and Born & Knutsen (1988). In Inglefield Bredning, hunting of narwhals is an important element of the maritime subsistence hunting by Inuit (Vibe 1950, Bruemmer 1971, Durham 1979, Born 1987b).

Information on group size and the sex and age composition of narwhal populations has implications for the evaluation of survey results and hence for the determination of population status. Such information has been

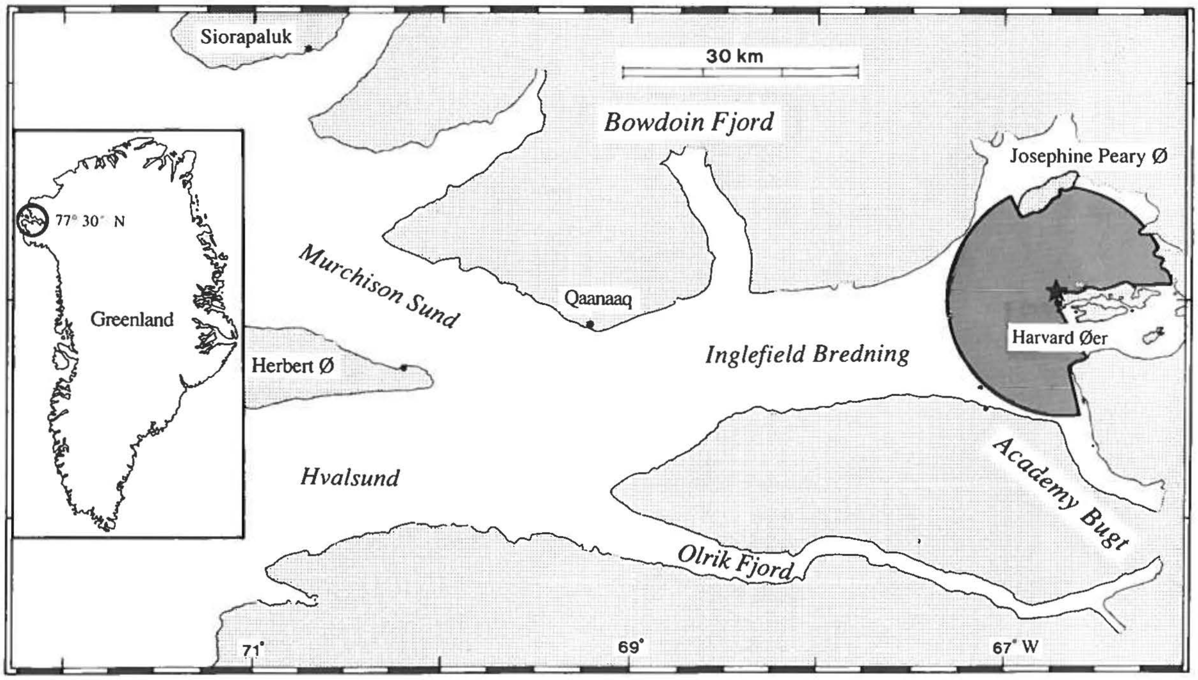


Fig 1. A: Inglefield Bredning study area with the observation site (⋆) on Harvard Øer (Qeqertat) used for land-based observations in 1984, 1985 and 1988. The perimeter of the observation area is shown.

presented from inshore narwhal summering areas in Canada (*e.g.* Silverman 1979, Fallis *et al.* 1983, Koski & Davis 1994, Kingsley *et al.* 1994) but not from Greenland. For comparative reasons such information collected in Inglefield Bredning in 1984, 1985 and 1988 is presented in this paper. We also present results of land-based surveys in August 1985 and 1988 and of aerial surveys in August 1985 and 1986, with the primary objective of estimating the number of narwhals in Inglefield Bredning.

Materials and methods

Land-based surveys

In 1985 and 1988 a continuous watch for narwhals was maintained from the 78-m high promontory of Nuussuaq, situated on the northwestern tip of Harvard Øer (Qeqertat) in Inglefield Bredning (Fig. 1; photo). This same site had been used for narwhal studies in August 1984 (Born 1986). Although much of the 1984 data was published by Born (1986), the estimates of group size were not; they are included here for comparative purposes. In 1985 observations were made for a total of 403 hours (59% of available time during the period) between 2 and 30 August. In 1988 a total of 105 hours (49% of available time) was used for observations between 30 July and 1 August, and from 6 to 11 August. In 1985, and during the first segment of the 1988 study, the team consisted of three observers. During the second segment in 1988 only two observers participated. In 1985 a Svarowski binocular telescope (30 × and 75 × magnification) and 7 × 50 Zeiss binoculars were used. In 1988 a Kowa SN-1 monocular zoom telescope (20 × - 60 ×) and Zeiss binoculars (7 × 42) were used.

A narwhal group (pod) was defined (after Silverman 1979) as one or more narwhals swimming in close proximity (no more than a few meters, and usually less than one meter, apart). An aggregation of two or more narwhal groups is called a herd.

We attempted to maintain watch round the clock in continuous light conditions. Observation was usually suspended when the sea state exceeded Beaufort 1, because it was no longer considered possible to detect and observe narwhals reliably at any distance. The entire observation area was searched carefully through the telescope at least once every hour. Depending on observation conditions (for example sea state or haze) and the number of observations, the scanning lasted between half an hour and one hour. Between the scannings the area was studied regularly by use of hand-held binoculars. For all observations of narwhals the following was recorded: time, position (compass direction to observation and estimated distance in km), direction of movement, behavior and herd and group size. Wind force (m/sec at observation level), sea state and cloud cover (in octas) were also noted. It was possible during good conditions (*i.e.* calm and clear with no haze or mirage) to detect and count narwhals out to a distance of 14–15 km from the observation site. Crude distances to observations were obtained by comparison with known distances to points on the surrounding coasts. However the relatively low angle and great distance involved in the majority of observations made it impossible to collect data on sex and age of the narwhals consistently.

During directed movement narwhals spend proportionally more time at the surface than they do when milling or remaining in the same area (Silverman 1979, Cosens & Dueck 1988). In 1985 we used methods described in Born (1986) to count narwhals in herds when the animals showed fast "directed movement". In 1988, when fewer narwhals were present within the study area, we also attempted to count narwhals in stationary herds. Whenever possible, numbers of animals in groups were counted. In cases where the behavior of a herd did not allow counting of individuals, we estimated the herd size by multiplying the total number of groups by the mean group size obtained for that particular behavior (see Results. Group size etc.).

Replicate counts of herds under similar observation conditions were made in 13 cases in 1985. These herds remained within the study area between the counting sessions, and no immigration to, or emigration from, the herds during the short period of time between the counts was observed.

Dive times for groups were recorded under circumstances where the group in question could not be mistaken with other groups. Time spent at the surface and submerged was noted with distance travelled at the surface and submerged, respectively. Crude estimates of distance were obtained by comparing the length of the group's track with lengths of individuals. Similar data on dive times obtained in 1984 and 1989 are included.

Aerial surveys

Survey coverage and procedures

Between 27 August and 3 September 1985 four systematic aerial surveys were flown in Inglefield Bredning and adjacent fjords (Figs 2 a & b; Table 1). On 25 August 1985 a reconnaissance survey was flown over Inglefield

A view to the west from the 78-m high observation site on Harvard Øer (Inglefield Bredning) used for observation of narwhals in 1984, 1985, 1987 and 1988. Photo: E. W. Born.

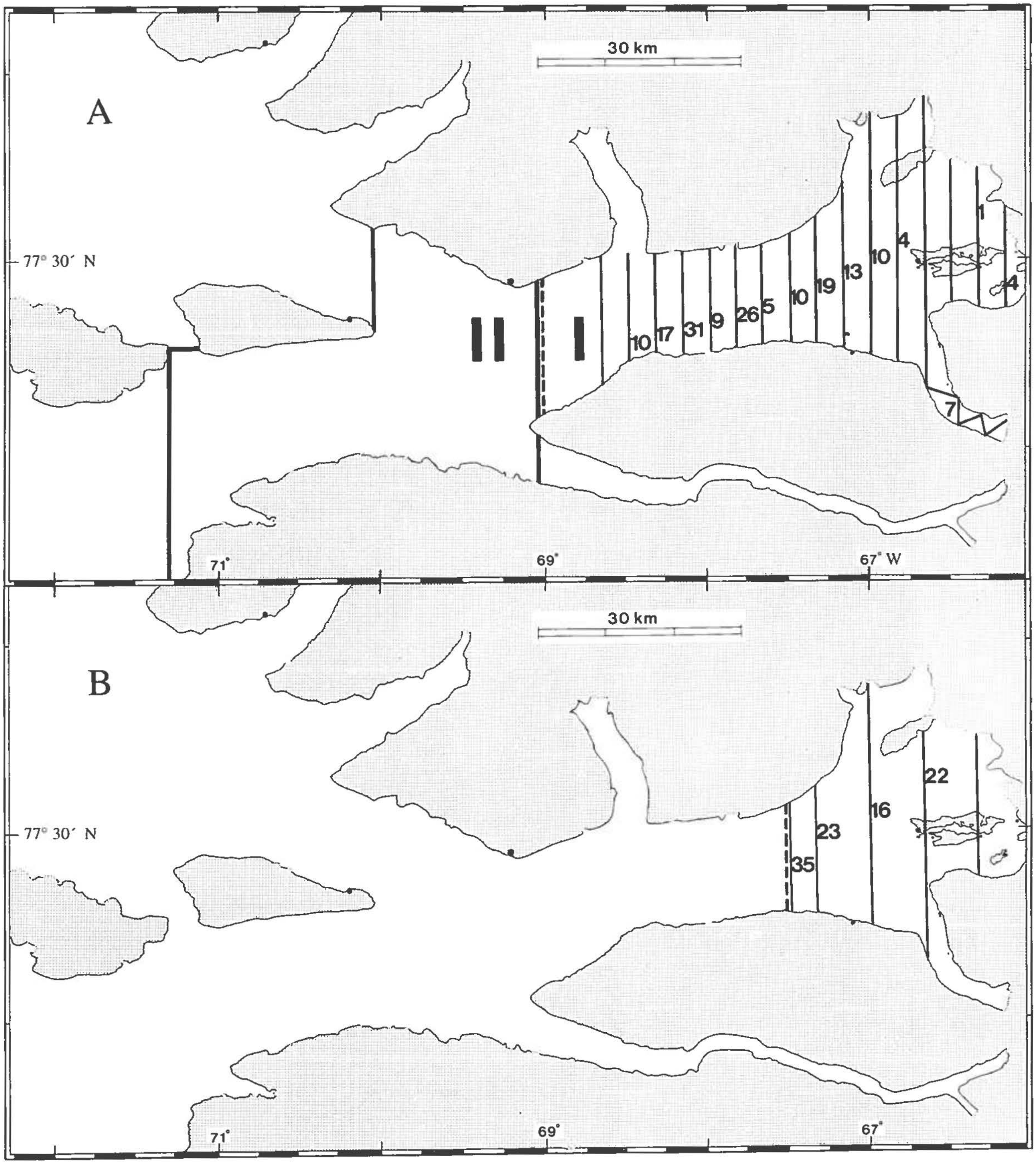


Fig. 2a. A: Inglefield Bredning with Strata I and II used for aerial surveys of narwhals in August 1985 and 1986. Figures at the transect lines refer to total number of narwhal groups observed on 27 August 1985. B: Survey lines flown on 28 August 1985. Legend: Solid lines = transects with sea state 0 and 1 (used for calculation of abundance of narwhals). Broken lines = borders of sample area (A) used for calculation of abundance of whales.

Bredning with the purpose of collecting data on narwhal group size. In 1986 five aerial surveys were conducted in the same areas between 6 and 10 August. Olrik Fjord and Murchison Fjord were not surveyed in either year because narwhals are known to be rare in these relatively shallow fjords.

In 1985 the fast fjord ice had disappeared from the study area before the surveys. Thus the ice coverage was

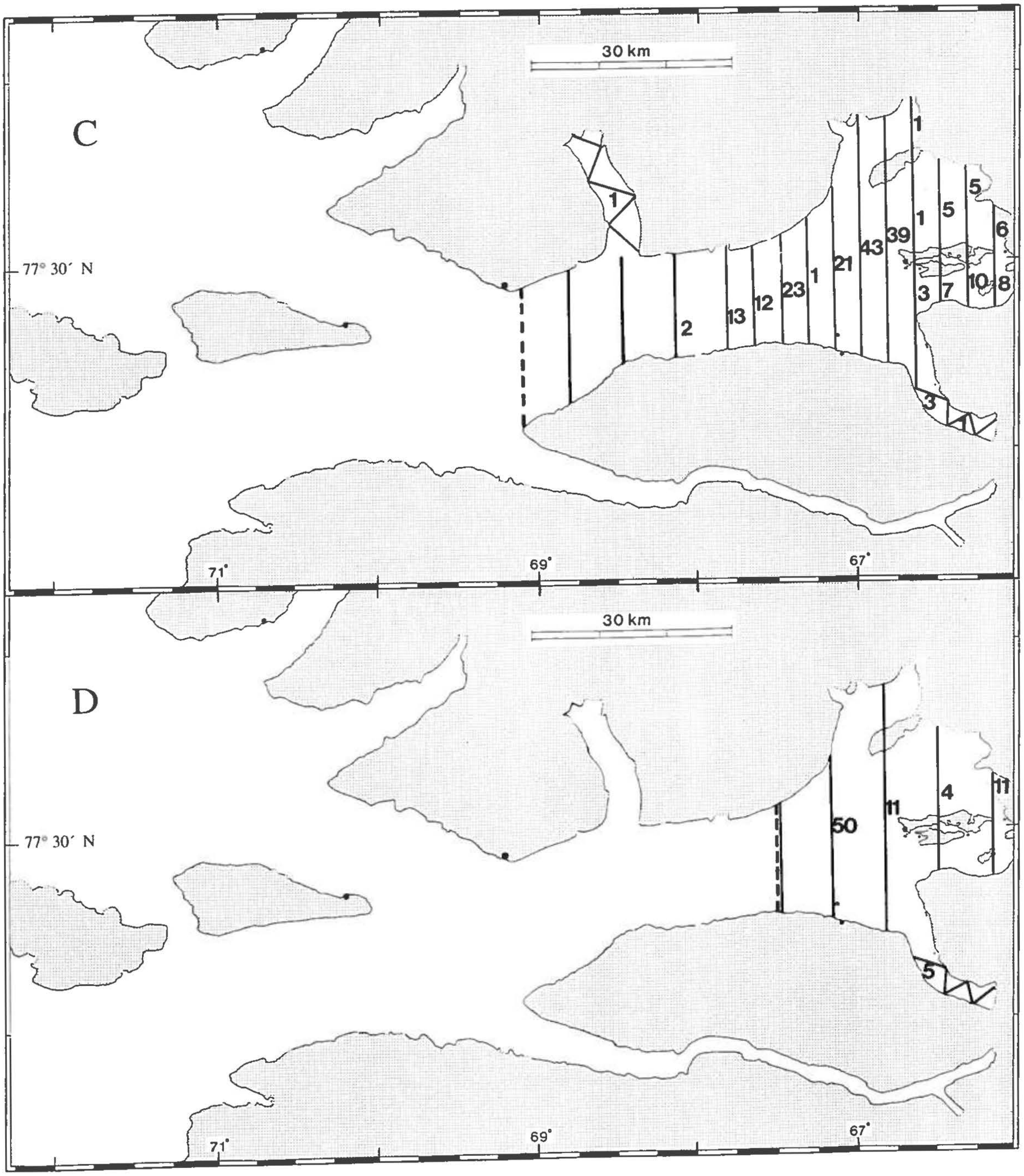


Fig. 2b. C: Inglefield Bredning with transect lines flown on 29 August 1985 with observations of groups of narwhals. D: Transect lines flown on 3 September 1985 and observations of groups of narwhals.
Legend: Solid lines = transects with sea state 0 and 1 (used for calculation of abundance of narwhals). Broken lines = borders of sample area (A) used for calculation of abundance of whales.

less than 10% and consisted entirely of ice bergs. Adverse weather prevented us from surveying the entire study area (which included Hvalsund) systematically, so we concentrated our effort on areas where high densities of narwhals were known to occur (Born 1986): Inglefield Bredning, Bowdoin Fjord and Academy Bugt (Figs 2 a & b). In August 1986 parts of Inglefield Bredning were still covered by fjord ice during the surveys (Figs 3 a & b).

Table 1. Aerial surveys flown over Inglefield Bredning (Thule area, NW Greenland) and adjacent fjords in 1985 and 1986 (see also Figs 2 a–b, and 3 a–b).

Year	Month	Day	Target altitude (m)				
1985	Aug.	25	264	Survey to obtain group size data			
				Area surveyed			
				Stratum (transect number)		Academy Bugt	Bowdoin Fjord
				I	II		
1985	Aug.	27	183	1–16	–	+	–
	Aug.	28	183	2–9	–	–	–
	Aug.	29	183	1–17	–	+	+
	Sep.	3	183	1–9	19–23, 25–29	+	–
1986	Aug.	6	305	1–18	–	+	+
	Aug.	6	305	–	19–32	–	–
	Aug.	8	305	7–14	–	–	+
	Aug.	9	305	1–18	–	+	+
	Aug.	9	305	1–18	–	+	+
	Aug.	10	915	6–18	–	+	+

In both years the survey lines were placed systematically with intervals of 10° longitude (distance between transects = 4.13 km) in Inglefield Bredning and Hvalsund. Inglefield Bredning was denoted stratum I and Hvalsund stratum II. When time allowed, Bowdoin Fjord and Academy Bugt were surveyed in a "zigzag" manner which was operationally convenient. However, due to time constraints the flight track followed the coast in these fjords in some cases in 1986.

In both years the surveys were carried out in a Partenavia P68 Observer, a high-wing, twin-engine aircraft with a plexiglass nose. In 1986 bubble windows were installed on each side at the rear observers' seats, thus allowing for the detection of narwhals on or close to the track line. Navigation was by a Litton 3000 Omega navigation system corrected by observations of recognizable land marks. All surveys were flown at an airspeed of 167 km/h (90 knots). In 1985 the systematic surveys were flown at a target altitude of 183 m (Table 1). The 1986 surveys were flown at a minimum of 305 m. A survey was also conducted at 915 m on 10 August 1986 when weather conditions were excellent (Table 1).

In 1985 there were two observers, both sitting in rear seats. In 1986 a different crew of three observers participated. The third observer sat in the co-pilot's seat and his effort was dedicated to recording ice cover, sea surface conditions and the size and composition of narwhal groups. The observers sitting in the rear seats recorded sightings of narwhal groups. By using inclinometers the rear observers measured the angle between the horizon and each narwhal group when the sighting was abeam the aircraft. If time allowed (depending on the concentration of groups) the observers also recorded direction of movement of the groups, reactions to the aircraft and other behavior, group size and group composition. When possible, narwhals were classified by their sex and relative age, based on size and coloration. Size categories used were: adults (3.5–5+ m; light mottled appearance); subadults (2–3.5 m; uniformly dark); neonates – young of the year (about 1.6 m, grayish brown). Animals with a tusk were regarded as males, all other adults as females. This information was collected in a consistent manner in 1986, but more sporadically in 1985. In 1985 all data collected by the two observers were recorded by one of the observers on a tape recorder. In 1986 data were recorded individually by the observers on cassette tape recorders.

Treatment of data from the aerial surveys

Line transect estimates of group density were made using the theory and techniques described in Burnham *et al.* (1980). For calculating probability density functions, f(x), sighting rates, N/L, and their associated empirical variances, we used the computer package "Distance" developed by Laake *et al.* (1991).

The distribution of perpendicular distances was fitted to the half-normal model, the negative exponential model, the hazard-rate model and a Fourier series. Adding of up to three adjustment terms was allowed. The model with the least adjustment terms, lowest coefficient of variation (CV) of f(0) and best goodness of fit determined by the chi-square distance between observed and expected distances was chosen. The chosen model was scaled to integrate to 1 to derive the f(x) which was evaluated at f(0) to obtain the Effective Search half-Width (ESW).

The stratum density of narwhals, D, was estimated as:

$$D = \frac{N \cdot f(0) \cdot C}{2 \cdot L} \qquad (1)$$

where N is the number of sightings of groups, C is the mean group size and L is the linear distance (in km) that was searched.

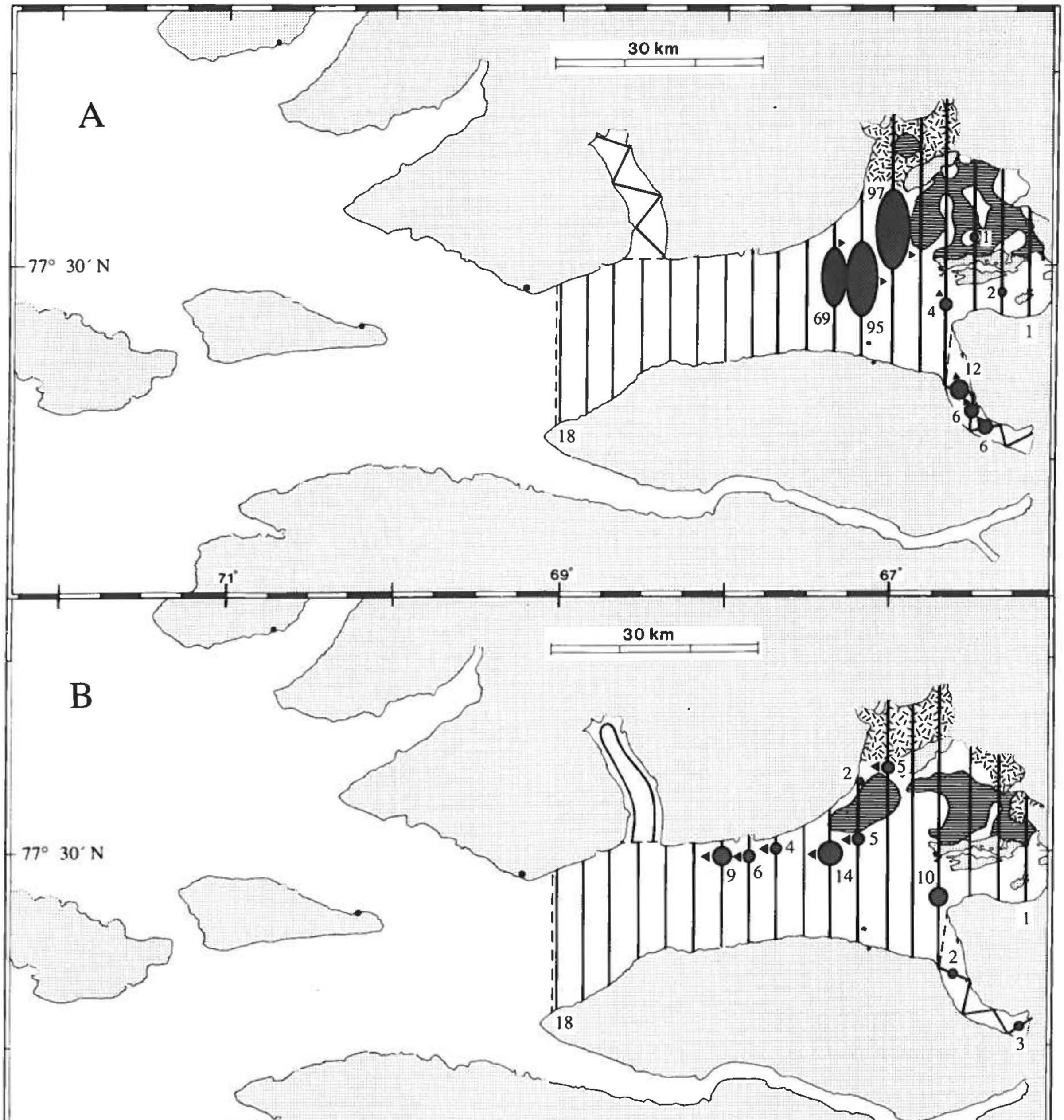


Fig. 3a. A: Transect lines flown during first aerial survey on 9 August 1986 with total number of groups of narwhals recorded by the rear observers. B: Transect lines flown during second aerial survey on 9 August 1986.
Legend: Arrows indicate main direction of movement of groups. Broken lines = borders of sample area (A) used for calculation of abundance of whales. ⊠ = 4–6/10 ice cover, ▦ = solid fjord ice ● = narwhal herd

Stratum variance of narwhal density and abundance was estimated according to Burnham *et al.* (1980):

$$\mathrm{var}(D) = D^2(CV(f(0))^2 + CV(N/L)^2 + CV(C)^2) \quad (2)$$

where CV is the coefficient of variation calculated as the standard error in proportion to the mean.

We assumed that D has a log normal distribution, and we constructed the 95% confidence interval using the method developed by Burnham *et al.* (1987) where the

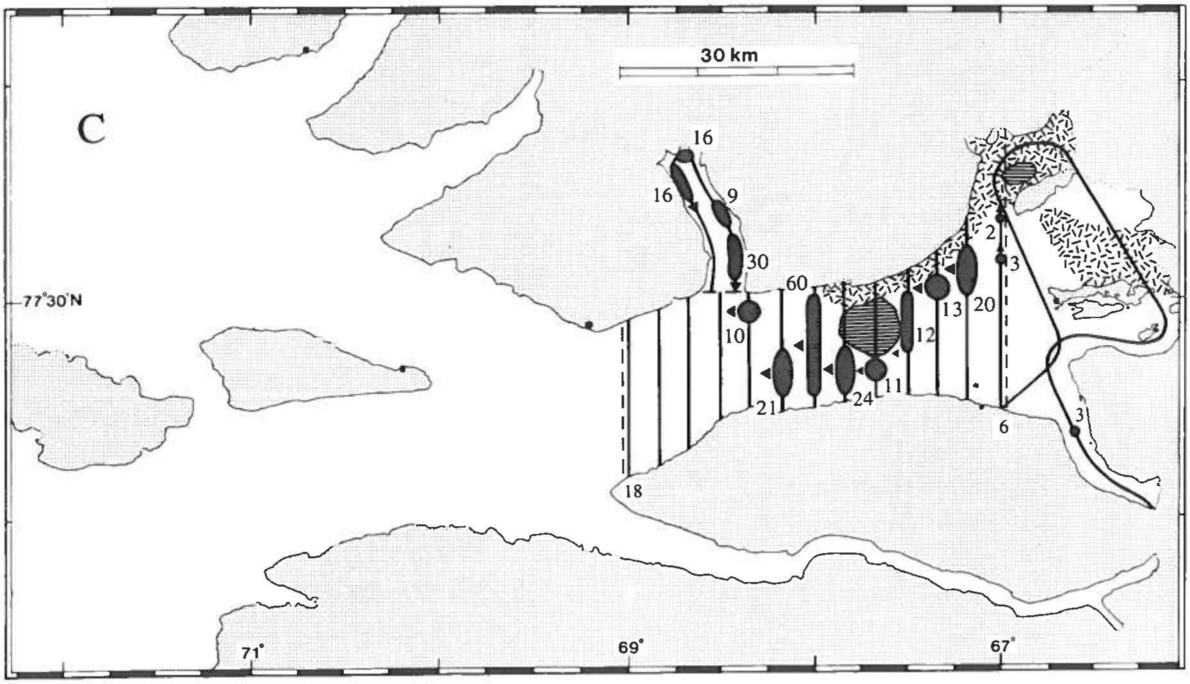


Fig. 3b. C: Transect lines flown during the aerial survey on 10 August 1986. Calculations of abundance of narwhals on this date (Table 9) refer to the area between transects 6 and 18. See also legend to Fig. 3 a.

lower and upper confidence limits are D/V and D · V, respectively, and:

$$V = \exp[1.96 \cdot \sqrt{\{\mathrm{var}(\ln D)\}}] \qquad (3)$$

where

$$\mathrm{var}(\ln D) = \ln[1+\mathrm{var}(D)/D^2] \qquad (4)$$

For the data collected in 1985 we made an inside truncation at 150 m and an outside truncation at 1200 m from the track line. For the 1986 data an outside truncation was made at 2000 m from the track line.

Because the transects were short, a weighting factor was not applied to the counts for meridian convergence. For calculation of total number of narwhals, densities were extrapolated only to those parts of the fjord system (total sample area A) that were surveyed systematically during that particular survey (Figs 2a–b & 3a-b). Areas covered with solid fjord ice were subtracted from the total sample area (A) and the transect area (a).

A correction factor to compensate for submerged animals that were missed during the flights was *not* applied in any of the calculations, which thus apply only to the visible portion of the population.

Table 2. Narwhal group sizes from land-based counts in Inglefield Bredning, August 1984, 1985 and 1988. In 1988 group sizes were counted both during directed movement and when the groups were stationary (see text). * = counted when the group formed a feeding aggregation.

Year	Median	Mean	SD	Range	N	Remarks
1984	4.8	7.2	6.2	1–35	72	Directed movement
1985	6.8	8.9	8.2	1–63*	65	Directed movement
1988	4.8	5.7	2.8	1–15	122	Directed movement
1988	2.5	3.6	2.7	1–16	129	Stationary

Results

Group size, sex and age composition and dive times

Group sizes recorded during land-based surveys

Estimates of group size obtained during the land-based observations are presented in Table 2. In 1985 the frequency distribution of group size was significantly different from that in 1984, and also from the comparatively large male-female groups reported by Silverman (1979: fig. 8c) for the openwater season in Lancaster Sound (Kolmogorov-Smirnov (K-S) two-sample tests; $P < 0.05$). The frequency distribution of group sizes observed by us in 1984 did not differ significantly from that reported by Silverman (1979) for Lancaster Sound (K-S; $P > 0.05$).

Table 3. Narwhal group sizes from aerial surveys in Inglefield Bredning on 25 August 1985 and between 6 and 10 August 1986.

Year	Day (Aug.)	Median	Mean	SD	Range	N
1985	25	2.0	2.2	1.6	1–9	80
1986	6	2.7	4.1	3.4	1–12	15
	8	1.8	2.9	2.3	1–13	158
	9 (1st)	1.7	2.9	2.4	1–23	267
	9 (2nd)	5.1	6.5	4.4	1–32	85
	10	2.2	4.0	3.3	1–18	325

In 1988 group sizes were also recorded when groups within a herd were scattered widely over a large area. This behavior, where the herd is "stationary" and many of the groups are "circling" ("milling"), is thought to be associated with feeding and social activity (Silverman 1979). The narwhals often remained almost stationary, infrequently exposing a small portion of their back; such behavior was described as "hanging" and "back exposed" by Silverman (1979) and Cosens & Dueck (1991). In 1988 the frequency distribution of group sizes obtained during fast directed movement differed significantly from that when the herd was stationary (K-S, $P < 0.01$). Furthermore, noticeably more narwhals occurred singly during the stationary situation than during directed travel in all years. The frequency distribution of travelling group size in 1988 did not differ significantly from that in 1984 (K-S; $P > 0.05$) but did differ significantly from that in 1985 (K-S; $P < 0.05$).

Group sizes recorded during aerial surveys

Group sizes observed during the aerial surveys are given in Table 3. The mean group sizes in 1986 were somewhat larger than those in 1985, but the difference was not significant (Mann-Whitney U-tests, $P > 0.05$). The frequency distributions of group sizes obtained by the front observer and by the rear observers in 1986 did not differ significantly (K-S, $P > 0.05$). In none of the surveys were there statistically significant differences between group sizes observed in different sea states (K-S; sea states 0,1,2, 3 and 5; $P > 0.05$). Group sizes observed during the second survey on 9 August 1986 differed significantly from those observed during the other surveys (Mann-Whitney U-test, $P<0.05$). The somewhat smaller group sizes from the surveys in 1985 and on 6, 8, 9 (1st) and 10 August 1986 did not differ significantly from group sizes observed during the land-based surveys in 1988, when narwhals were counted in essentially stationary herds. Neither was there a significant difference between the relatively large group sizes observed during the second survey on 9 August and the group sizes obtained in 1988 when groups were counted during fast directed movement (Mann-Whitney U-tests, $P > 0.05$).

Table 4. Percentages of narwhals classified as adult, subadult and neonate by the front and the rear observers (only for classified animals) during aerial surveys in Inglefield Bredning in August 1986.

	Adults %	Subadults %	Neonates %	N=identified
Front observer	68.0	17.1	14.9	228
Rear right observer	74.0	2.9	23.1	238
Rear left observer	64.2	9.4	26.4	261

Sex and age composition of narwhals in 1986

Of all groups observed by the front observer 39% (31% of the narwhals) were classified by sex and relative age. The rear observers classified 24% of all groups and 21% of all narwhals. Neonates comprised 14.9% and 23–26 % of all narwhals that were categorized by sex and age class by the front observer and the rear observers, respectively (Table 4). Due to a difference in proportions of neonates and subadults, the age composition of the narwhals identified by the front and the rear observers differed significantly ($\chi^2 = 19.025$; $P < 0.01$; Table 4). As the collection of data on sex and age was a primary task of the front observer but was only a secondary task of the rear observers, the front observer's data are probably more reliable. During different surveys the percentage of neonates classified by the front observer varied between 1.9 ($N_{\text{total narwhals}} = 58$) and 36.7 ($N = 30$). Sixty-eight per cent of the narwhals categorized by the front observer were classified as adults, 32% as subadults. The proportions of adult males and adult females were comparable with those obtained during aerial surveys in the Canadian High Arctic during the inshore summering period (Table 5).

As also reported by Silverman (1979) for narwhals summering inshore in Tremblay Sound (Canada), all-male groups (mean = 5.6 narwhals/group) and mixed groups consisting of males and females (mean = 4.4) were the largest types of group in Inglefield Bredning.

Dive times

During directed movement narwhals in a group surfaced and dived synchronously, or at least within a few seconds of one another. On a few occasions it was possible to record dive times of groups under conditions where there was no risk of mistaking one group in the area from another. During directed movement groups were at the surface for an average of 151 seconds (SD = 148.9; range: 46–481; N = 8) and submerged for an average of 264 seconds (SD = 170.1; range: 40–540 sec.; N = 16). Thus the average surface time:subsurface time ratio for travelling groups was 1:1.7 (about 64% of the time was spent submerged).

Table 5. Percentages of narwhals classified as adult, subadult and neonate during aerial and land- based surveys in various areas and seasons. * = land-based surveys; others are aerial surveys.

Area	Month	Adult (%)	Subadults (%)	Neonates (%)	Adult males (%)	Adult females (%)	Source
Off Central West Greenland	March	67	33	–	22	68	McLaren & Davis 1981
Off Central West Grenland	March	79	21	–	39	61	McLaren & Davis 1983
Offshore Baffin Bay	May-July	74–88	26–12	–	48–51	49–52	Koski 1980
Offshore Lancaster Sound	May-July	59	31	–	–	–	Koski 1980
S. coast Lancaster Sound*	June-July	82	18	3.8	68	32	Greendale & Brousseau-Greendale 1976
Inglefield Bredning, NW Greenland	August	68	32	14.9	57	43	This study
Tremblay Sound, NE Canada*	August	54.5	45.5	10.3	57	43	Silverman 1979
Lancaster Sound, NE Canada*	August	–	–	2.7	63	37	Silverman 1979
Milne Inlet, NE Canada	August	74	26	10.0	67	33	Koski & Davis 1979
Admiralty Inlet, NE Canada	August	67.5	32.5	9.1	61	39	Koski & Davis 1979
Eclipse S., Admiralty Inlet, Central Canadian Arctic	Mid.Aug. Mid.-Sep.	67.1	32.9	7.8	59.8	40.2	Koski & Davis 1994
Scoresby Sund	September	–	–	23.5	–	–	Larsen *et al.* 1994
Scoresby Sund	September	–	–	10.9	–	–	Larsen *et al.* 1994

Estimates of numbers of narwhals

Land-based surveys in 1985 and 1988

Sea and weather conditions are important factors affecting the sightability of narwhals. In 1985 weather conditions generally were more moist and windy than experienced in 1984 and during the relatively short observation period in 1988. In 1985 the sea state was 0 and 1 for 47% and 40% of the observation time, respectively. In 1988 the sea state was 0 and 1 for 73% and 27% of the time, respectively. The difference between years was significant ($\chi^2 = 21.16$; DF = 2; $P < 0.01$).

Narwhals rarely occurred close to the observation site on the Harvard Øer. In 74% of the 65 cases when herds could be counted in 1985 they were between 5 and 11 km from the observation site. In 1988, 83% of the 41 herds were between 4 and 8 km away when they were counted.

As also experienced in 1984 (Born 1986), the number of narwhals occurring within the observation area varied from day to day. However on many days during August 1985 more than 1000 narwhals were counted, and on 20 August 1985 a single herd with 1548 whales was observed (Fig. 4). On several occasions replicate counts of the same herd were achieved. In such cases the minimal counts averaged 85% of maximal counts (SD = 15.6, range: 54–98%, N = 13). In cases when the same herd was counted twice during fast directed movement, the minimal count was on average 92% of the maximal count (SD = 8.6, range: 75–98 %, N = 8). On six occasions when a herd was counted during both fast directed movement and other behavior (stationary or slow directed movement), the count during fast directed movement was higher. The difference between minimal and maximal counts of a herd in 1985 was not significantly different ($P > 0.05$; $t = 1.924$; DF: 11) from the difference between replicate counts reported in Born (1986).

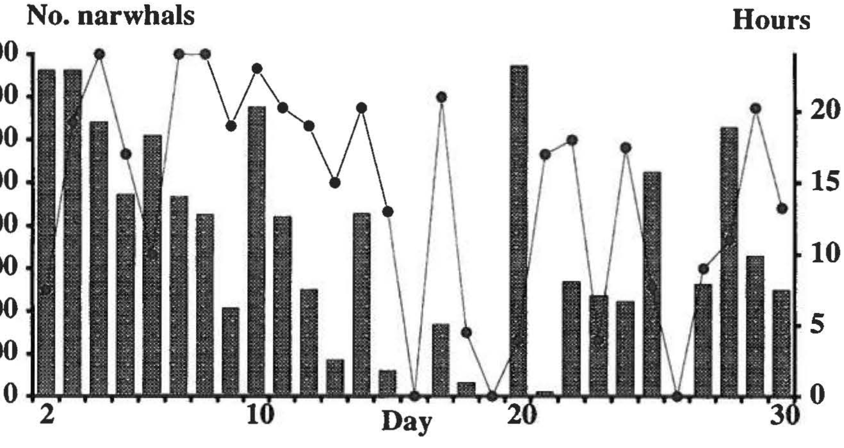
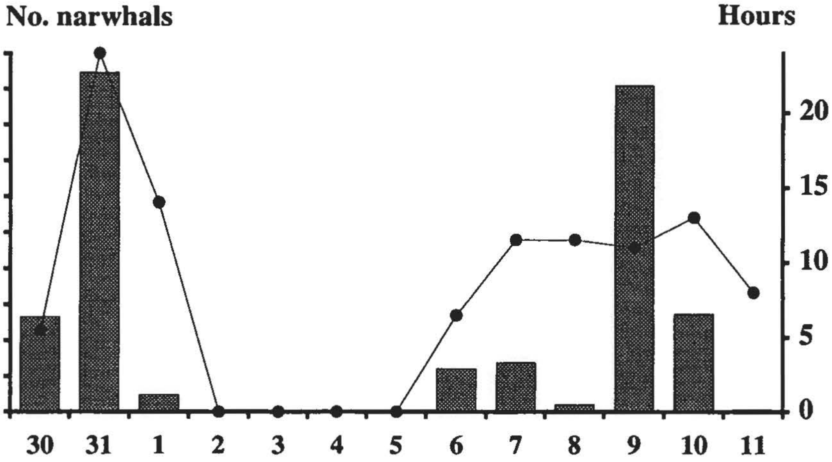


Fig. 4. Number of narwhals counted (bars) in the head of Inglefield Bredning in the period 2 to 30 August 1985, with cumulative observation time per 24 hours (dots).

Fig. 5. Number of narwhals counted (bars) in the head of Inglefield Bredning in the period 31 July to 11 August 1988, with cumulative observation time per 24 hours (dots).



In 1988 the daily counts of narwhals within the study area fluctuated widely (Fig. 5). However the daily total number of narwhals was lower compared with the same period in 1984 (Born 1986) and in 1985 (Fig. 4). On 31 July 1988 a total of 353 narwhals in three herds consisting of a total of 55 groups were counted. At the same time another stationary herd consisting of 33 groups was observed. Multiplying by an average group size of 3.6 animals (Table 2), an estimated 120 whales were in this herd. Hence the highest number that could be accounted for at any time between 30 July and 11 August 1988 was about 473 narwhals on 31 July (Fig. 5).

Estimates of abundance based on aerial surveys in 1985 and 1986

The half-normal model was found to adequately estimate ESW for most of the stratifications of the sighting distances and hence it is used in the following. In both years detectability of narwhals decreased with increasing sea states. Both the medians of the frequencies of distance to observations of narwhals and the ESWs decreased from sea state 0 to 5 (Table 6).

In 1985 the data were not recorded in a manner that allowed tests of possible inter-observer differences. Hence the observers are assumed to have been equally efficient. However during the surveys in 1986 for which estimates of abundance of narwhals were achieved, the rear left observer detected about twice as many narwhal groups per linear km flown as the rear right observer (Table 7). Estimates of group size did not differ significantly among the three observers (K-S; P > 0.05).

For all three survey altitudes the sighting-distance data showed a deficiency of sightings close to the track line (Fig. 6). In calm seas narwhals were observed up to 3500 m and in some cases even up to about 10 km away. However as transects were placed 4.1 km apart, no observation beyond 2000 m from the flight track is included in the analyses. For the surveys at 183 m a bimodal distribution of sighting distances with peaks at 200–300 m and

Table 6. Sea-state specific Effective Search half-Widths (ESW) and medians of frequencies of distance to sightings of narwhals during aerial surveys in Inglefield Bredning and adjacent fjords in 1985 and 1986, respectively.

Sea state	1985					1986				
	ESW Altitude: 183 m*	CV	N	Median	N	ESW Alt.=305 m	CV	N	Median	N
0	375	0.30	98	476	119	1298	0.21	20	838	20
1	443	0.22	226	411	267	542	0.12	45	281	46
2	146	0.35	16	324	24	529	0.08	199	348	204
3	324	0.48	13	293	15	423	0.15	101	327	102
4	247	0.66	9	248	12	–	–	–	–	–
5	–	–	–	–	–	392	0.12	44	275	37
						Alt.=915 m				
1						1194	0.13	141	641	141
2						1039	0.14	31	884	31

Legend: *= ESWs were fitted to the half-normal model.
1985: Observation distances were truncated at 1200 m.
1986: Observation disatances were truncated at 2000 m.

Table 7: Observer-specific sighting rate, Effective Search half-Widths (ESW) and medians of frequencies of distance to observation of narwhals during aerial surveys in Inglefield Bredning and adjacent fjords in 1986.

Day (August)	Altitude (m)	Sighting rate (SD) (Groups/lin. km)*		ESW (CV) and Median (N)**			
		Right observer	Left observer	Right observer		Left observer	
9 (1st)	305	0.196 (0.350)	0.392 (0.257)	420 (0.07)	270 (90)	508 (0.11)	405 (192)
9 (2nd)	305			617 (0.53)	230 (13)	505 (0.15)	351 (45)
10	915	0.509 (0.607)	0.839 (0.625)	1244 (0.05)	839 (68)	935 (0.12)	518 (104)

Legend: *= Groups observed per linear km flown; transects without narwhals are excluded.
**= Groups observed. Observation distances truncated at 2000 m.

1200 m is indicated. Therefore, to obtain a probability density function that decreased monotonically, it was decided to truncate the 183 m survey at 1200 m.

During the aerial surveys conducted at 183 m in 1985 good sea-state conditions (0 and 1) generally prevailed. Because ESWs obtained for sea states 0 and 1 did not differ (Table 6) a common ESW for sea states 0 and 1 was derived and used to calculate abundance of narwhals on the respective dates (Table 8; Fig. 6).

The uncorrected point estimates in Inglefield Bredning and tributary fjords (Figs 2 a–b) between 27 August and 3 September 1985 range between 847 and 1366 narwhals (Table 8).

Although the 1985 estimates did not differ significantly (Table 8), the two surveys that covered only the eastern part of stratum I (Fig. 2a:B & 2b:D) revealed higher densities of narwhals than those covering the entire stratum I. This reflects the fact that narwhals occasionally concentrated in the eastern parts of Inglefield Bredning, as also was found to be true during the land-based observations.

Sea states were generally worse during surveys in 1986 than in 1985, and only about 4.7% and 29.9% of the effort was flown at sea states 0 and 1, respectively. Only a few narwhals were observed in areas with sea state 0. Calculations of ESWs include observations of narwhals in sea states 0 to 3.

During the surveys in 1986 the ESWs of the right observer varied inconsistently between surveys, whereas those of the left observer did not (Table 7). Because of this variability and because the right observer also missed a considerable proportion of the narwhals (Table 7), abundance calculations were made for these three surveys using only data recorded by the rear left observer.

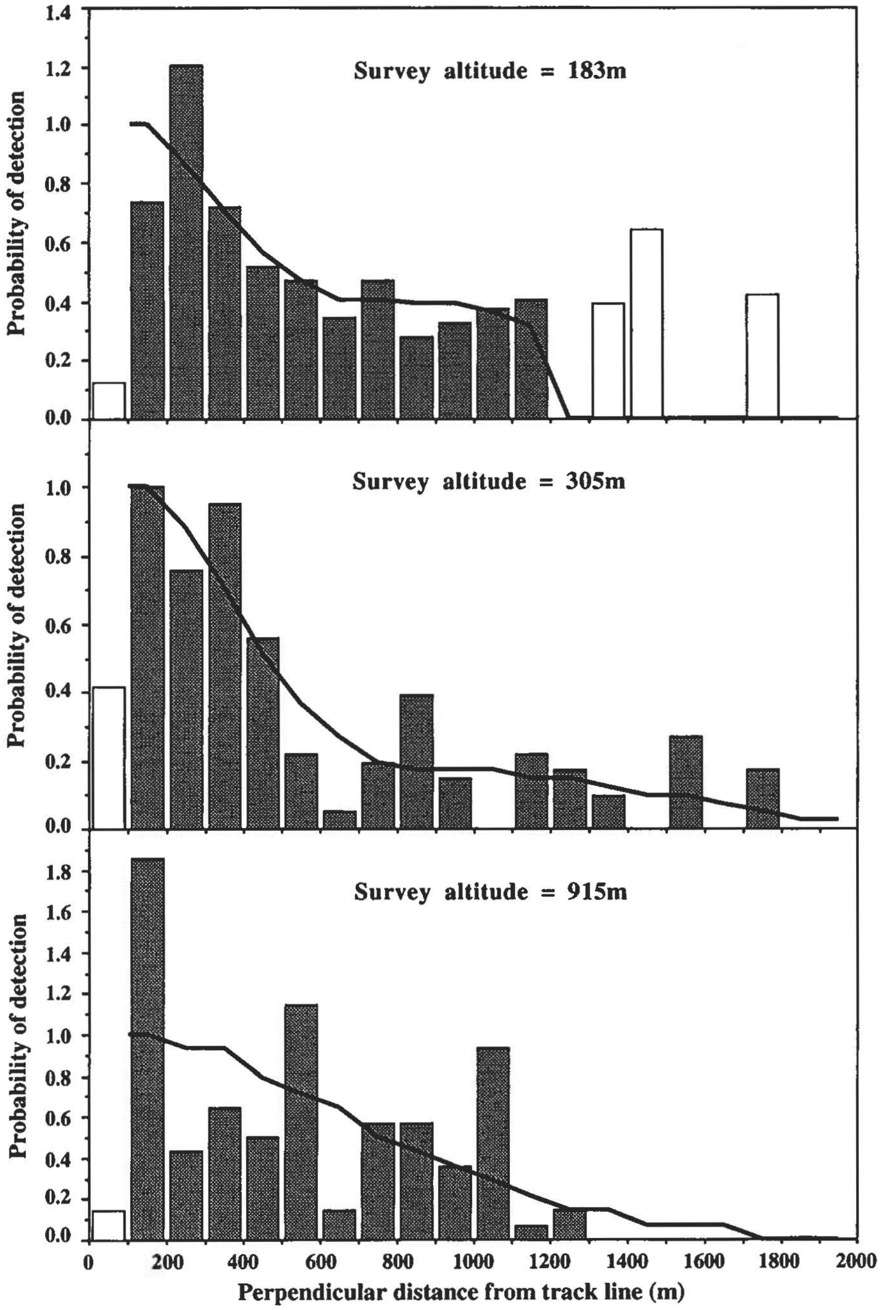
The two surveys conducted at 305 m and the one at 915 m in 1986 gave almost identical estimates of narwhal density (Table 9). However due to differences in the areas surveyed, the 915 m survey provided a slightly lower estimate of abundance. Despite the inclusion in 1986 of data obtained in less favourable weather conditions, all the estimates of abundance from 1986 are larger, and some significantly so, compared with the 1985 survey results. Both at 183 m and 305 m altitudes a similar sampling effort at all distances from the track line was found, and therefore the increase in mean sighting rate (N/L) from 0.44 groups/km (95% CI 0.32–0.63) in 1985 to 0.63 (95% CI 0.40–1.01) in 1986 is a reliable estimator of an increased number of narwhals present in Inglefield Bredning in 1986 compared with 1985.

The two uncorrected point estimates of narwhals in Stratum I and tributary fjords on 9 August 1986 were 4369 and 2683 whales. These do not differ significantly and the combined estimate for the two surveys was 3539 narwhals (95% CI 1869–6722). The estimates of the visible population in the western part of Stratum I on 10 August was 1894 narwhals (95% CI 929–3752; Table 9).

On a single occasion it was possible to compare estimates of herd size obtained from the aerial surveys and the land-based surveys. On 28 August 1985, 1262 narwhals were counted in one herd at 7.5 hours from the observation site on land. This herd was observed continuously until it was covered by the aerial survey on the same day, at 13.2–13.9 hours (Fig. 2 a:B). The aerial survey resulted in an uncorrected estimate of 932 narwhals (95% CI 382–2012) in this herd (Table 8).

After the 1985 surveys some hunters in the area indicated that the engine noise of the survey aircraft had scared narwhals, causing them to dive and thereby interfering with the hunting of narwhals from kayaks. Hence, to reduce the risk of scaring the narwhals the surveys in 1986 were conducted at higher altitudes. However, even during the surveys at 305 m altitude in 1986, the narwhals often dived at distances of 500 to 1000 m in front of the aircraft, and we suspected that this was a reaction to the aircraft. When the aircraft passed over the narwhals, groups were observed approximately two to five meters under the sea surface, frequently descending. On some occasions newborn narwhals were observed alone at the surface while the mother had apparently dived, and this was interpreted by us as indicating an escape response. Of 161 groups observed by the front observer, about 18% were noted as diving in front of the

Fig. 6. Frequency distribution of narwhal sightings with distance from track line. At 183 m (1985) and 305 m (1986) altitude, sightings beyond 1200 m from the track line were excluded from the estimation of abundance. At 915 m (1986) sightings beyond 2000 m from the track line were excluded. At all altitudes sightings at the first 150 m from the track line were eliminated for calculations of abundance. Data have been fitted to the half-normal model: $g(x) = \exp[-y^2 / (2 \cdot A_1^2)]$. The fitted curves show the expected number of sightings and the histograms the actual observations. Also see Tables 8 and 9.



aircraft during the surveys at 305 m. Of a total of 518 groups observed by the rear observers, about 18% were submerged when the aircraft passed over them. During the survey at 915 m, 18% of 80 groups dived in front of the aircraft, whereas about 39% of 252 groups observed by the rear observers were diving, or underwater.

Discussion

Group size

Land- and ship-based observations indicate that narwhals usually occur in groups of 3 to 10 (*e.g.* Vibe 1950, Bruemmer 1971, Tomilin 1967, Meldgaard & Kapel 1981). Narwhals in Admiralty Inlet (Canada) moved in

Table 8. Estimates of abundance of narwhals based on aerial surveys over Inglefield Bredning and tributary fjords in late August and early September 1985. Sighting-distance data truncated at 150 and 1200 m from the track line were pooled for all four days and used to derive a common Effective Search half-Width (ESW) by fitting the half-normal model. Only effort and sightings from sea states 0 and 1 were included. The estimate of mean group size was obtained on 25 August during a survey mounted specifically for information on group size.

Month Day	August 27	August 28	August 29	September 3
Survey altitude (m)	183	183	183	183
A: Total sample area (km^2)[1]	1435	825	1435	825
Effort (L,km)	233	104	306	94
No. of sightings (N)	66	57	141	54
Sighting rate (N/L)	0.28	0.55	0.46	0.57
Coefficient of variation	0.47	0.39	0.21	0.61
Mean group size (C,N = 80)	2.21	2.21	2.21	2.21
Coefficient of variation	0.08	0.08	0.08	0.08
ESW-pooled (1/f(0),m,N = 374)	535	535	535	535
Coefficient of variation	0.09	0.09	0.09	0.09
Density (groups/km^2)	0.26	0.51	0.43	0.54
Density (narwhals/km^2)	0.59	1.13	0.95	1.19
Coefficient of variation	0.49	0.41	0.24	0.62
Abundance estimate	847	932	1366	979
Confidence interval	344–2085	382–2012	854–2276	320–3011

[1] For areas surveyed, see Figs 2 a–b.

tight groups of 5 to 8 animals with distinct spaces between groups (Fallis *et al.* 1983). According to Greendale & Brousseau-Greendale (1976) group size varied from single animals to 21, but was usually 3 to 8, as narwhals migrated past Cape Hay (Bylot Island, Canada). The estimates of group size in our study are consistent with those obtained during land-based observations in Canada during the break-up and open-water periods. However we cannot explain why average group size was larger in 1985 than in any of the other years.

Table 9. Estimates of abundance of narwhals based on aerial surveys over Inglefield Bredning and tributary fjords in early August 1986. Sighting distance data were truncated at 150 and 2000 m from the track line. A common Effective Search half-Width (ESW; N= 227) was derived by fitting the half-normal model to the data from the two surveys on 9 August. ESW for the survey on 10 August was obtained by fitting the half-normal model to the data (N=77). Effort and sightings from sea states 0 to 3 were included.

Day	9(I)[1]	9(II)	*(I+II)	10
Survey altitude (m)	305	305	305	915
A: Total sample area (km^2)[2]	1435	1435	1435	902
Effort (L,km)	179	167	346	114
No. of sightings (N)	178	47	225	103
Sighting rate (N/L)	0.99	0.28	0.65	0.91
Coefficient of variation	0.38	0.34	0.31	0.35
Mean group size (C) (N)[3]	2.89 (63)	6.28 (18)	3.58 (81)	3.23 (77)
Coefficient of variation	0.11	0.15	0.10	0.08
ESW-pooled (1/f(0),m)	472	472	472	713
Coefficient of variation	0.08	0.08	0.08	0.08
Density (groups/km^2)	1.05	0.30	0.69	0.64
Density (narwhals/km^2)	3.04	1.87	2.47	2.07
Coefficient of variation	0.40	0.38	0.34	0.37
Abundance estimate	4369	2683	3539	1894
Confidence interval	2037–9341	1029–6998	1869–6722	929–3752

[1] I = 1st survey on 9 August 1986; II = 2nd survey; *I+II = 1st and 2nd survey on 9 August combined.
[2] For areas surveyed, see Figs 3 a–b.
[3] Independent estimates of group size obtained by the front observer.

Estimates of group size obtained in Inglefield Bredning in 1988 are similar to those reported by Silverman (1979) for Tremblay Sound (NE Baffin Island) where average group size was 5.1 narwhals/group during "directed movement" and 3.5 narwhals/group during "localized movements". An average group size for all observations in 1988 in Inglefield Bredning of 4.6 narwhals/group (SD = 2.9; range: 1–16; N = 251) is similar to that given by Silverman (1979) of 4.1 narwhals/group (N = 635) for groups with both sexes and all ages.

During aerial surveys of narwhals in inshore summering areas, average group sizes varying between 2 and 3 animals/group, but often around 2, have been reported (*e.g.* Koski & Davis 1979, 1994, Cosens & Dueck 1991, Kingsley *et al.* 1994, Larsen *et al.* 1994). However under certain conditions narwhal group size estimated from aerial surveys is larger. In Lancaster Sound between 13 June and 10 August 1976, Johnson *et al.* (1976) observed that narwhal groups that occurred along coasts without fast ice tended to be larger (average group size 7.1- 9.0) than groups occurring in nearby areas with more ice. During a mass movement of narwhals on 29 August in Maud Bight average group size was 4.05 (Koski & Davis 1979). Group size also varies according to sex and age composition. As also seen in our study, Koski (1980) observed that groups containing only males tended to be larger (average 3.4) than male-female groups (2.8) or groups of females (2.4). Cosens & Dueck (1988) found that group size was larger (mean = 3.3) during disturbance by an ice-breaking vessel at the Lancaster Sound ice edge than during the non-disturbance situation (mean = 2.2). Average group size observed during our second survey over Inglefield Bredning on 9 August 1986 was significantly larger than that obtained during the other surveys (Table 3). The comparatively large group sizes are believed to reflect that during this particular survey a herd of narwhals was observed during a fast "mass movement", whereas during the other surveys the whales were either stationary or moving slowly.

The discrepancy between narwhal group sizes obtained from land-based surveys and those from aerial surveys might be explained by 1) the difference in angle of view and 2) the difference in time allowed for observations. During our land-based observations the low angle of view, in combination with the foreshortening from using powerful telescopes, presumably sometimes caused us to judge that whales which were more than "one whale length" apart belonged to the same group. Nevertheless we found no correlation between group size and distance to observation. During land-based observations in Canada (*e.g.* Silverman 1979) where observations were made from a higher platform and the narwhals occurred closer to the observation site, estimated group sizes also were larger than those reported for aerial surveys. Almost certainly, the difference between estimates of group size relates to the fact that from a fast-moving aircraft a momentary "static" view of the groups is obtained, whereas from land the maximum number of whales which surface together during the observation period is recorded.

Sex and age composition

The estimated sex and age composition of the narwhal population found during the aerial surveys in Inglefield Bredning in 1986 was similar to that reported for inshore summering areas in Canada (*cf.* Table 5). During our study 15% of the narwhals observed were classified as neonates by the front observer. Aerial surveys conducted in August and September in inshore areas resulted in estimates of percentage of neonates of total narwhals observed between 9.6 (Kingsley *et al.* 1994) and 23.5 (Larsen *et al.* 1984). In our study significantly more neonates were recorded by the rear observers. These observers concentrated on recording numbers of groups and narwhals and measuring angles to observations; they only recorded information on sex and age if time allowed. Most of the narwhals occurred in dense herds and generally little time was left for recording sex and age. It is therefore very likely that the rear observers unintentionally paid special attention to conspicuous animals such as adult males and neonates, so that these categories are over-represented in our data and the resulting estimates of sex and age composition are biased accordingly. Silverman (1979) found that segregation by sex does not usually occur between entire narwhal herds but rather occurs within a given herd. However, cow-calf groups comprised 27% of narwhals in Koluktoo Bay and 24% in Milne Inlet whereas this proportion was only 4% in Eclipse Sound. These observations indicate that females and young are a smaller proportion of narwhals in exposed waters than in more sheltered waters (Kingsley *et al.* 1994). Similarly, Vibe (1950) found indications that females with young showed special preference for the head of Inglefield Bredning while males tended to occur further west in less sheltered waters. Our aerial surveys covered primarily the more sheltered parts of the Inglefield Bredning and Hvalsund fjord complex. It cannot be excluded that during the 1986 aerial surveys, which were conducted during a very brief period, females with young predominated in Inglefield Bredning, resulting in an overestimate of the fraction of neonates in this summering stock.

Dive times

Our land-based observations indicate that travelling narwhals are at the surface for about 36% of the time. Depth profiles obtained from an adult female narwhal equipped with a satellite transmitter revealed that, during a 10-day period in August 1991, about 45% of its time was spent between 0 and 1 m from the surface (Martin *et al.* 1994).

Effects of aircraft engine noise

Narwhals react to underwater and airborne ship engine noise by "freezing" (*i.e.* they sink quietly beneath the surface with little audible respiratory sound; Finley *et al.* 1990). In Inglefield Bredning narwhals are hunted only from kayaks. There is, however, considerable boating activity during the hunting season because the hunting teams travel to and from the hunting grounds in motorized vessels, and hunters report that motor noise scares the narwhals. The lower estimate of mean group size obtained during the 1985 aerial surveys compared with 1986 can partially be explained by a greater number of animals diving as a reaction to the noise of the aircraft which flew at a lower altitude in 1985. Kingsley *et al.* (1994) noted that their survey aircraft (Bell 206 helicopter), even at 305 m altitude, disturbed narwhal groups and caused some whales to dive before the helicopter passed over them. Narwhals that are far below the water surface cannot be detected (see Richard *et al.* 1994) and consequently aerial surveys tend to underestimate the number of whales and their group size. If the narwhals really dived in response to our survey aircraft it would imply that the estimates of abundance of narwhals in Inglefield Bredning are negatively biased.

Other factors affecting the aerial-survey results

The lack of observations close to the track line during the surveys at 183 m in 1985 is easily explained by the flat windows used in the aircraft; these windows prevented observations within the first 100–150 m from the track line. However surveys in 1986 showed that narwhals were still missed in the areas close to the track line even though bubble windows had been installed. This could have been caused by inattention to the area near or under the aircraft, by avoidance reaction of narwhals close to the track line or by a combination of both.

Aerial surveys in Inglefield Bredning showed that under good sighting conditions narwhals could be seen at long distances. In other aerial surveys of narwhals using strip-census methods, half-strip widths of 400 m (Smith *et al.* 1985) and 800 m (Richard 1991) have been used. However our study indicates that the assumption in strip censusing that the probability of detection is constant across the half strip width is violated. Theoretically some of the potential bias caused by the narwhals' avoidance of the aircraft can be reduced in line-transect surveys where sightings close to the track line are omitted and distant sightings are included.

Because narwhals often occurred in one or a few large herds, the sightings were sometimes concentrated on relatively few transects (Fig 3 a:A). The major source of variation in the abundance estimates was the sighting rate, which usually contributed more than 50% of the variation. Furthermore it was suspected that some groups were missed as we flew over high-concentration areas because observers could not simultaneously measure angles to sightings and continue searching. Under such circumstances high-altitude photographic surveys (Richard 1991, Richard *et al.* 1994) may seem to have advantages in terms of counting the number of groups and in estimating group sizes. However this method also has limitations and tends to underestimate true numbers because when the photos are read the readers miss some narwhals on the film (for discussion see Richard *et al.* 1994).

Although our surveys were relatively imprecise, they still indicate an increase from 1985 to 1986 in the density of groups and the sighting rate, which are unaffected by the various group-size estimates.

Our surveys showed that surveys of narwhals at high altitudes (> 300 m) are preferable to surveys at lower altitudes. Narwhals apparently showed avoidance response to the low-flying survey aircraft, presumably causing underestimates of group size and narwhal densities. Furthermore, from a low-flying aircraft the field of view is relatively narrow; this reduces sighting time and increases the likelihood that narwhals will be missed.

Fluctuations in numbers of narwhals in Inglefield Bredning

The results of the surveys in Inglefield Bredning in the various years (Born 1986, this study) are influenced to an unknown degree by differences in survey methods and effort, but also by annual and seasonal fluctuations in the number of narwhals present in the fjord system. The land-based surveys covered only a limited part of the narwhal's range in Inglefield Bredning and tributary fjords, and narwhals were present outside the observation area during the observation sessions. During August narwhals are also observed in Hvalsund, and during this same month some animals apparently move from Inglefield Bredning into Smith Sund. An influx to Inglefield Bredning may also occur during August (Born 1986), so the geographical distribution of the stock during the short summer is fluid and variable both within and between years, as has also been observed in Canada (*e.g.* Fallis *et al.* 1983).

When narwhals were present in the observation area in 1985 the groups were more widely distributed and scattered in comparison with the situation in 1984. In 1984 the large herds showed a greater tendency to travel rapidly from one section of the observation area to another (Born 1986). Furthermore in 1985 they spent comparatively less time in the northern parts of the observation area between the Harvard Øer and Josephine Peary Ø. The reason for this apparent change in distribution and behavior is not clear. In contrast to the situation in August 1984, when the whales spent comparatively more time within the observation area at the head of Inglefield Bredning, frequently in large herds (Born 1986), they were more widely scattered and therefore less easy to count in 1985 and 1988.

It is likely that natural fluctuations in narwhal prey in Inglefield Bredning affect the number of whales summering in the area and also influence the whales' behavior and distribution. In Inglefield Bredning narwhals feed on polar cod (*Boreogadus saida*; Vibe 1950, Born 1986, Heide Jørgensen *et al.* 1994), arctic cod (*Arctogadus glacialis*; Heide-Jørgensen *et al.* 1994), Greenland halibut (*Reinhardtius hippoglossoides*; Vibe 1950), other fish, cephalopods and crustaceans (Heide-Jørgensen *et al.* 1994). During August they are often observed feeding on schools of polar cod or arctic cod (Born 1986, Born & Knutsen 1988). They often form "feeding frenzies" together with harp seals (*Phoca groenlandica*) and sea birds. There is, however, no quantifiable evidence that would allow us to determine the relationship and annual variation in number of narwhals and prey biomass in the Inglefield Bredning area.

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Occurrence of narwhals (*Monodon monoceros*) and white whales (*Delphinapterus leucas*) in East Greenland

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Dietz, R., Heide-Jørgensen, M. P., Born E. W. & Glahder C. M. 1994. Occurrence of narwhals (*Monodon monoceros*) and white whales (*Delphinapterus leucas*) in East Greenland. – Meddr Grønland, Biosci. 39: 69–86. Copenhagen 1994-04-22.

Narwhals (*Monodon monoceros*) have been observed along the east coast of Greenland from Umiiviip Kangertiva (64°10'N, 41°W) to Kilen (81°N, 13°W). The fjord complexes of Sermilik, Kangerlussuaq and Scoresby Sund are important inshore summering areas. Narwhals occur in these fjords from ice breakup in May-July until new ice forms in September–November. Narwhals also occur at the entrances to these fjords during winter. Historical information from whalers indicates that narwhals are present in the pack ice of the Greenland Sea between May and September. Narwhals are believed to be widely scattered in the pack ice between eastern Greenland and Svalbard during winter, and the narwhals in this area may comprise a single population. During the period 1981 to 1990 the catch of narwhals in eastern Greenland has averaged at least about 80 animals per year. White whales *(Delphinapterus leucas)* are rare and only occasionally caught in eastern Greenland. The general absence of white whales in this area is probably due to a combination of severe ice conditions along the East Greenland coast and a general lack of suitable shallow-water habitat.

Key words:
Narwhal, *Monodon monoceros*, white whale, beluga, *Delphinapterus leucas*, distribution, migrations, food, gestation period, catch, East Greenland.

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Introduction

Huge masses of heavy polar pack ice are transported year-round south along the east coast of Greenland by the East Greenland Current. This ice makes living conditions in this area harsh for both humans and wildlife. Access to the coast is difficult, and as a result there are vast unpopulated areas in eastern Greenland. Nowadays small groups of Inuit live only in the Ammassalik (66°N) and Scoresby Sund (Kangertiitivaq, 70°30'N) areas of southeastern and eastern Greenland. North of Scoresby Sund the coast is unpopulated except for a few people who live year-round at the weather stations at Daneborg (74°20'N) and Danmarkshavn (77°N). Few observations of wildlife have been recorded in eastern Greenland outside the populated areas. Most of the available information has come from English and Scottish whalers navigating the Greenland Sea in search of bowhead whales (*Balaena mysticetus*), early European explorers, Danish and Norwegian trappers living in northeastern Greenland during the first half of the 20th Century, and some recent expeditions which have operated primarily during summer.

Observations of narwhals (*Monodon monoceros*) and white whales (*Delphinapterus leucas*) in the East Greenland area have been reviewed by Winge (1902) and Dietz *et al.* (1985). In a summary of observations of narwhals in the "Norwegian High Arctic" Gjertz (1991) included information on narwhals in the Greenland Sea east of 5°W.

Based on a variety of sources, we summarize the occurrence of narwhals along the coast of eastern Greenland by region from south to north. Offshore observations of narwhals in the Greenland Sea and Fram Strait (between eastern Greenland and Svalbard) are presented separately. We also describe a few observations of feeding and the birth period of narwhals in eastern Greenland, and we summarize the available data on narwhal catches. Finally we review the few records of occurrence and catch of white whales in eastern Greenland.

Materials and methods

Titles of publications dealing with narwhals and other marine mammals in eastern Greenland and in the Greenland Sea area were compiled from the libraries at the Scott Polar Research Institute (Cambridge, UK), Museum of Tromsø and Library of Tromsø, Norwegian Polar Research Institute (Oslo), Arctic Institute (Copenhagen) and Greenland Fisheries Research Institute (Copenhagen). Published works containing information on marine mammals were selected based on the title or on our knowledge of the merits of the author(s). These publications were obtained from the libraries of the University of Copenhagen, the Royal Danish Veterinary Agricultural University, the Royal Danish Library and the Danish National Archives.

Information was extracted from unpublished Ittoqqortoormiit (the settlement of Scoresbysund) journals for the period 1925–1940 held at the National Archives. Recent information concerning narwhals was obtained from interviews with the residents of Scoresby Sund municipality carried out in August 1983 (Born 1983), and hunters in the same area in August 1990 (Mosbech 1990). An extensive series of interviews to obtain information on wildlife was conducted in Kangerlussuaq in summer 1991 (Glahder 1992). During August-September 1991 narwhals were observed opportunistically from r/v *Thetis* and a helicopter operating in the Greenland Sea between 70°N and 80°N and from 10°W to 25°W (Søder 1991). During the cruise of r/v *Polarstern* extensive helicopter surveys were conducted between 27 May and 18 June 1993 over the pack ice between 79°00'N (Norske Øen) and 81°58'N (Kap Ringkøbing) and between 10°30'W and 21°20'W. Observations of narwhals made during these surveys are included here (Born unpubl. data). Sporadic observations of narwhals and white whales made by various expeditions visiting East Greenland have also been included in this study.

Results

Coastal observations of narwhals

Coastal observations of narwhals are presented in Tables 1 and 2 a,b,c and Figs 1–3. Areas with numerous observations are cross-hatched in the figures.

The southernmost record of narwhals in East Greenland is from Umiiviip Kangertiva (Gyldenløves Fjord; 64°11'N, 41°W) in early July 1982 (Table 1, Fig. 1). Although narwhals occur along the entire coast between Ammassalik and Scoresby Sund, they are particularly abundant in Sermilik, Kangertitsivaq and Kangerlussuaq fjords (Fig. 1).

Narwhals occur frequently in the Tasiilaq (Ammassalik) area, where they are caught between February and December (Fig. 8; Winge 1902, Holm & Petersen 1921, Chapman 1932). Historically they were caught primarily in Sermilik Fjord (Mikkelsen & Sveistrup 1944) and further north in Kangertiitivatsiaq (Holm & Petersen 1921, Chapman 1934). According to Holm (1887) narwhals were taken in all seasons at Kialineq, Ammassalik municipality.

Narwhals reportedly occur at Kangerlussuaq year-round (Holm & Garde 1889, Pedersen 1931), and Kangerlussuaq has been cited as an important summering area (Amdrup 1902, Mikkelsen 1933, Degerbøl 1935, Iversen 1936, Mikkelsen & Sveistrup 1944). Narwhals certainly occur in this fjord complex from the time when the fjord ice breaks up in May until the newly forming ice forces them offshore into Denmark Strait in October–

Table 1. Observations of narwhals south of Scoresby Sund presented from south to north. Numbers refer to Fig. 1.

Obs.	Locality	Day	Month	Year	Remarks	Reference
1	Umiiviip kangertiva	Primo	July	1982	2–3 seen in leads in the fast ice	Sivertsen pers. comm.
2	Kangertiitivatsiaq	Primo	July	1933	1 "white" female with a calf and two dark animals seen	Chapman 1934
		Primo	Aug.	1933	17 seen in the fjord	*Ibid.*
3	Langø	18	Aug.	1980	5–6 observed	Andersen 1982
4	Aggas Ø	15	Aug.	1980	3–4 observed	*Ibid.*
5	Denmark Strait	21	Oct.	1923	1 seen	Bistrup 1924
6	Mikis Fjord			1991	Present in open-water season	Glahder 1992
7	J. C. Jacobsens Fjord			1991	Present in open-water season	*Ibid.*
		6–8	Aug.	1980	Two pods of 3–5 seen	Andersen 1982
8	Rybjerg Fjord			1991	Present in open-water season	Glahder 1992
9	Søkongen Ø			1991	Present in open-water season	*Ibid.*
10	Kap Beaupré	23–24	July	1980	5–8 narwhals seen	Andersen 1982
11	Turner Sund	27	July	1900	Some seen	Jensen 1909
		Ultimo	July	1990	About 30 shot	Mosbech 1990
		2–7	Aug.	1990	About 20 shot	*Ibid.*
12	Steward Ø	14	July	1974	2 observed	Meltofte 1974
13	South of Kap Brewster	5	Oct.	1922	1 shot	Isachsen 1925

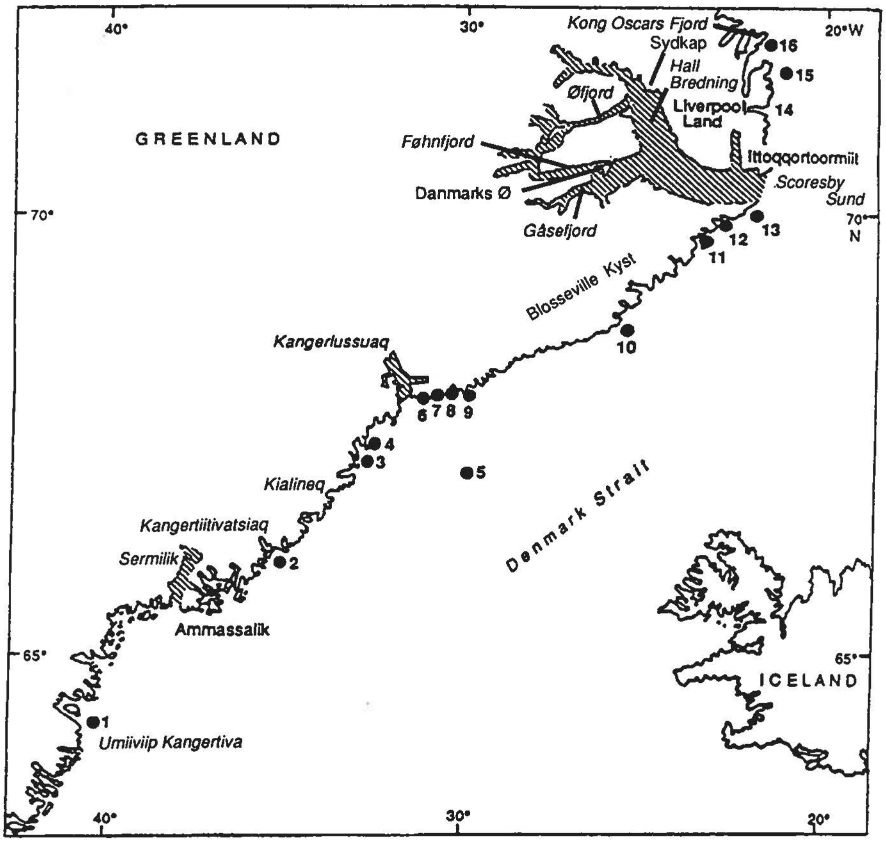


Fig. 1. Coastal observations of narwhals between Umiiviip Kangertiva and Kong Oscars Fjord. The numbers refer to sightings presented in Tables 1 and 2a. Cross-hatched areas indicate fjords where narwhals occur regularly during the open-water season.

Table 2a. Observations of narwhals north of Scoresby Sund presented from south to north. Numbers refer to Figs. 1 and 2.

Obs.	Locality	Day	Month	Year	Remarks	Reference
14	Storfjorden	20	Sep.	1985	Several seen inside and off this fjord	Born unpubl.
15	Northern Liverpool Land	Ultimo	July	1899	Some seen	Nathorst 1900
		Ultimo	Aug.	–	6–8 seen. A 4 m long female shot	Giæver 1944
16	Entrance to Carlsberg Fjord	1	Sep.	1900	2 dark and 1 very light one seen	Jensen 1909
17	In Alpefjord			1931	Many present during summer	Boyd 1935
18	Segelsällskapets Fjord			1931	Many present during summer	*Ibid.*
19	Narhvalsundet	22	Aug.	1899	One pod seen	Nathorst 1900
20	Ella Ø			1934	Single animal killed by Inuit	Pedersen 1942
		10	Aug.	1984	2 seen	Born unpubl.
21	In Kjerulf Fjord			1933	Many seen	Boyd 1935
22	Entrance to Kjerulf Fjord		Summer	1931	Many seen	*Ibid.*
23	Franz Joseph Fjord		Summer	1931	Many seen	*Ibid.*
24	Nordfjord		Sep.	1950	A deal whale found	Johnsen 1953
25	Kap Giesecke	20	July	1899	Some seen	Nathorst 1900
26	Eastern part of Franz Joseph Fjord			1931–1939	A few observed regularly	Pedersen 1942
27	Foster Bugt	13	Aug.	1922	Some seen	Isachsen 1922
28	Mackenzie Bugt	27	July	1891	Some seen	Giæver 1937
29	Myggbukta	2	Oct.	1936	A pod seen in a lead, 3 shot	Røstad 1960
30	Godthåbsgolfen	Ultimo	July	1889	Some pods. One animal with a 10 ft tusk	Knudsen 1890
31	In the river estuary in Dødemandsbugten	Primo	July	1932	About 25 observed	Larsen 1934
32	Dødemandsbugten				1 shot	Malmquist 1955
33	Eastern part of Dødemandsbugten	23	Aug.	1984	5 seen	Andersen 1984
34	Gael Hamkes Bugt			1933	A young narwhal observed	Pedersen 1942

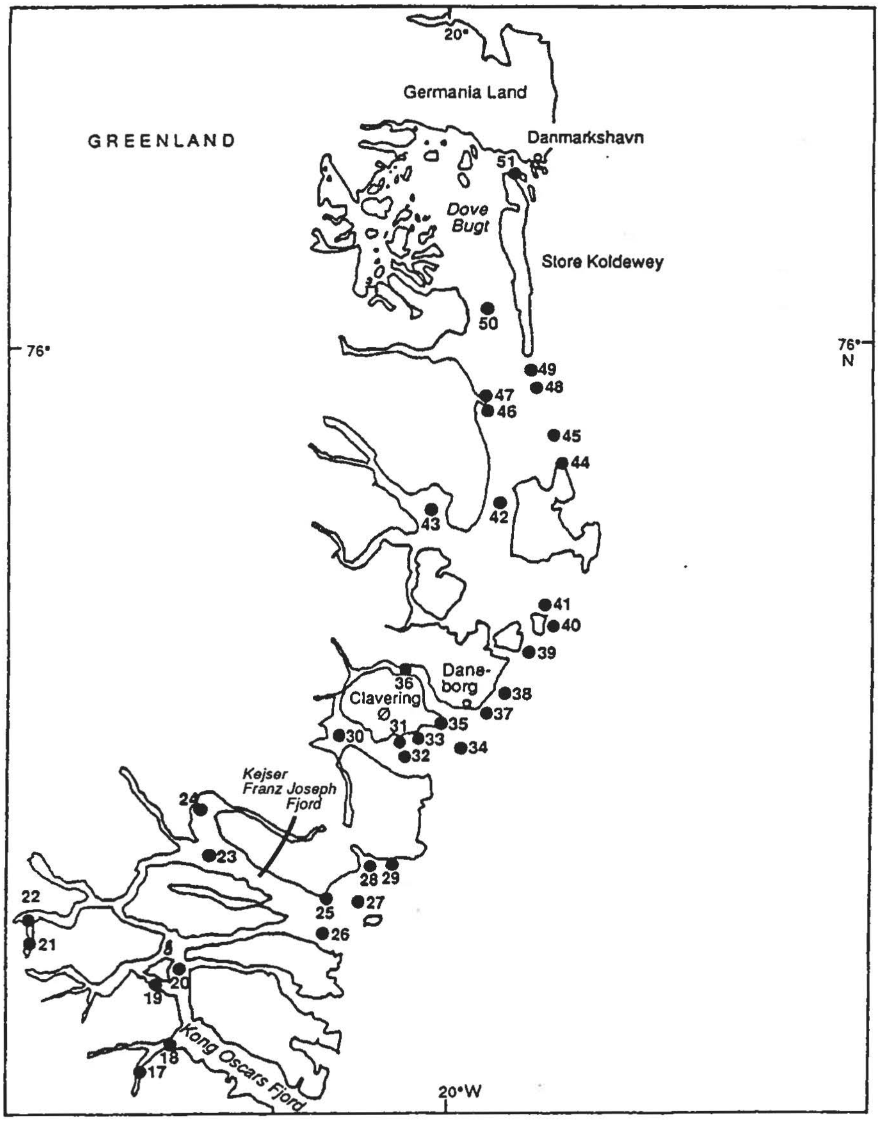


Fig. 2. Coastal observations of narwhals between Kong Oscars Fjord and Germania Land. The numbers refer to sightings presented in Table 2a and 2b.

November. During summer narwhals also occur in Mikis Fjord, J. C. Jacobsen Fjord and Ryberg Fjord, and further north at Søkongen Ø (Glahder 1992, Fig.1, Table 1).

Narwhals were observed in Scoresby Sund by Scoresby (1823) in August 1822, and Bay (1896) found that they occurred regularly in the fjord. Narwhals migrated into the fjord complex during summer and left in September (Ryder 1895). When the "Ryder Expedition" wintered at Danmarks Ø the first narwhals were observed on 21 July 1893, two days after the ice broke up (*ibid.*). In July narwhals migrated into Scoresby Sund in groups consisting of 15–20 animals (Mikkelsen & Sveistrup 1944). Reports of narwhals became more regular after 1925, when the settlement of Ittoqqortoormiit was established at the entrance of Scoresby Sund. Many narwhals were observed in the entrance to Scoresby Sund during the mild winter of 1925–26, especially in December, January, February and May (Petersen 1926). In late February 1928 and 1929 large herds were observed along the ice edge at the entrance to Scoresby Sund and near Liverpool Land. They remained there until they were able to penetrate Scoresby Sund after the ice broke up in mid-July. Narwhals remained at the entrance to the fjord until new ice formed in October (Pedersen 1931).

Narwhals are still observed in Scoresby Sund from February until the formation of new ice, usually between mid-September and mid-October (Sølberg 1980, Born 1983, Dietz *et al.* 1985, Sandell & Sandell 1991, Larsen *et al.* 1994). They can be observed at the mouth of Scoresby Sund until December (*e.g.* Dietz *et al.* 1985). Based on systematic aerial surveys conducted in September, Larsen *et al.* (1994) made point estimates of 300 and

Table 2b. Observations of narwhals north of Scoresby Sund presented from south to north. Numbers refer to Fig. 2.

Obs.	Locality	Day	Month	Year	Remarks	Reference
35	Kap Breusing	20	Aug.	1984	3 seen	Andersen 1984
36	Zachenberg Bugt			1947	A pod seen	Johnsen 1953
				1948	One taken in salmon net	*Ibid.*
37	Kap Borlace Warren				Some seen	Giæver 1930, 1937
38	Wollaston Forland	14	Aug.	1975	30–40 observed	Meltofte 1975
39	Sabine Ø				Some seen	Peters 1874
40	Pendulum Ø	6	July	1899	1 seen	Nathorst 1900
41	Hochstetter Bugt, south	17	Aug.	1984	16 seen	Andersen 1984
42	Shannon Sund	28	Aug.	1991	Female with young	Søder 1991
		28	Aug.	1991	Female with young	*Ibid.*
		28	Aug.	1991	4 seen	*Ibid.*
43	Peters Bugt			1933	Some seen	Pedersen 1942
		31	Aug.	1991	13 seen	Søder 1991
44	Kap Børgen, Shannon	12	Aug.	1984	6 seen	Andersen 1984
		28	Aug.	1991	Two pods of five seen	Søder 1991
45	Between Shannon and Store Koldewey	1	Oct.	1909	Many observed	Mikkelsen 1914
		11	Aug.	1984	36–40 seen	Andersen 1984
		10	Aug.	1984	75–80 seen	*Ibid.*
46	Roseneath Bugt	12	Aug.	1938	A subadult seen	Pedersen 1942
47	Off Haystack	16	Sep.	1991	2 seen	Søder 1991
48	South of Store Koldewey	15	Aug.	1938	2 adult seen	Pedersen 1942
49	Kap Alf Trolle	16	Sep.	1991	A total of 10 seen. 3 with tusks	Søder 1991
50	Southern part of Dove Bugt		Aug.	1938	Some seen	Pedersen 1942
		31	Aug.	1991	Three pods with a total of 21 seen	Søder 1991
51	Between Store and Lille Koldewey	10	July	1984	20–25 seen. Some with tusks	Knud Fischer, pers. comm.

Table 2c. Observations of narwhals north of Scoresby Sund presented from south to north. Numbers refer to Fig. 3.

Obs.	Locality	Day	Month	Year	Remarks	Reference
52	Skærfjorden		July	1925	Many seen	Isachsen & Isachsen 1932
53	SW of Kap St. Jacques, Ile de France	27	July	1989	30–50 seen in pods of 2–10 along ice edge	Andreasen 1988
		12	Aug.	1989	80 seen in pods of 4–8 animals heading south along ice edge	Peter Brandt. pers. comm.
54	Northeast of Ile de France	23	Aug.	1991	Several observed with tusks	Søder 1991
55	About 75 km east of Norske Øer	24	July	1984	13 seen	Andersen 1984
56	79°09'N 15°24'W	18	Jun.	1993	A total of 37 narwhals (both sexes and all age groups except neonates) seen heading south. Observed in a 500 m wide lead between fast ice and pack ice	Born, unpubl.
57	50 km east of 79-fjorden	23	July	1984	Pods, with a total of 19 animals seen	Andersen 1984
58	79°32'N 15°57'W	9	Jun.	1993	About 150 seen	Axel Bochert, pers. comm.
	79°32'N 15°57'W	9	Jun.	1993	7 adult males seen heading N about 10 m from fast ice edge	Born, unpubl.
59	5 km E of Kap H. N. Andersen	11	Jun.	1993	1 adult (no tusk) seen heading north	*Ibid.*
60	Kap H. N. Andersen	11	Jun.	1993	60 observed (both sexes and all age groups except neonates). Within 100–200 m from fast-ice edge. All heading south	*Ibid.*
61	Ice edge at Dijmphna Sund	17	Jun.	1993	About 40 seen along fast-ice edge	Jette Østergaard, pers. comm.
62	Mallemukfjeldet	21	July	1984	14 seen	Born, unpubl.
63	80°20'N 14°55'W	15	Jun.	1993	1 adult (no tusk) seen in 9/10 ice	*Ibid.*
64	10 km E of Eskimonæsset	30	May	1993	1 adult male seen in 9/10 pack ice	*Ibid.*
65	5 km E of Eskimonæsset	30	May	1993	5+3 adult males seen heading S in lead in 9/10 pack ice	Born, unpubl.
66	Few km N of Eskimonæsset	29	May	1993	5+4 seen (3 with tusks) along ice edge	René Ramseier, pers. comm.
67	Henrik Krøyers Holme	22	July	1992	2 seen	Reinhardt Møbjerg pers. comm.
68	Kilen, south	16	July	1984	2 seen	Andersen 1984

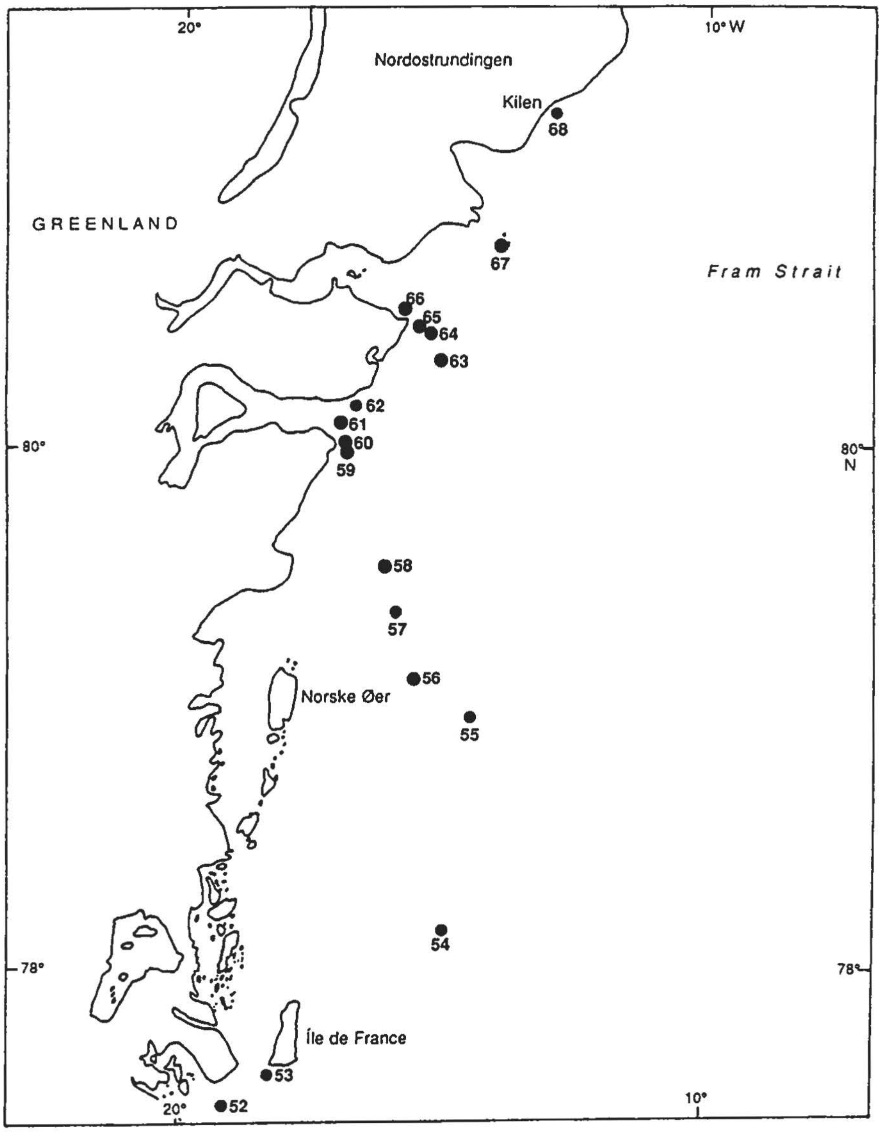


Fig. 3. Coastal observations of narwhals between Germania Land and Nordostrundingen. The numbers refer to sightings presented in Table 2c.

102 narwhals in 1983 and 1984, respectively. The estimates covered the visible part (*i.e.* they were not corrected for submerged animals) of the population of narwhals in the entire fjord complex including Hall Bredning, Øfjord, Føhnfjord and Gåsefjord. The difference was ascribed to either low survey precision, due to the clumped distribution of narwhals in this fjord or the fact that new ice prevailed in the inner regions of Scoresby Sund in 1984, causing a substantial proportion of the whales to leave the fjord by the time of the survey (*ibid.*). In February 1991 numerous narwhals were seen along the ice edge in Scoresby Sund (Knudsen *in litt.*).

North of Scoresby Sund narwhals have been observed at the entrances to most of the fjords between Kong Oscars Fjord and Germania Land (Fig. 2 and Tables 2a-c). They have been observed in the heads of the fjords between Kong Oscars Fjord and Kejser Franz Joseph Fjord, and also in the fjords around Clavering Ø (Fig. 2). The first recorded sighting of narwhals at the Danmarkshavn Station was in 1984, when narwhals were observed in a lead between the mainland and the northern coast of Store Koldewey (Knud Fisher pers. comm.). During a kayak expedition from Nordostrundingen south to Scoresby Sund in 1984 (7 July-6 September) a total of 146 narwhals were observed by Andersen (1984) along the coast between Danmarkshavn and Scoresby Sund (Figs 2–3, Tables 2a-c). No narwhals were observed by the "Danmarks-Expedition" in Dove Bugt (Johansen 1910), and our survey indicates that narwhals rarely, if ever, occur in this relatively shallow bay. There are few

Table 3. Offshore observations of narwhals in the Greenland Sea and Fram Strait. The numbers refer to Fig. 4.

Obs. no.	Positions		Day	Month	Year	Remarks	Reference
	N (degr./ min.)	W/E (degr./ min.)					
1	73°30'	12°00'W			1875	Many seen on Southern Whaling Ground	Gray 1929
2	79°00'	02°00'W	25	May	1877	Many seen heading NNW	Gray 1931
3	74°00'	14°00'W	28	June	1885	Many seen (1 with two tusks)	Gray 1933
4	75°01'	00°42'W	2	May	1886	One seen	Gray 1887
5	79°57'	04°20'E	18	May	1886	Many seen	*Ibid.*
6	79°24'	02°02'E	28	May	1886	Hundreds seen	*Ibid.*
7	78°50'	01°16'E	8	June	1886	Mothers with young commonly seen	*Ibid.*
8	79°29'	04°12'E	13	June	1886	Several seen	*Ibid.*
9	78°50'	00°00'E	19	June	1886	Several seen	*Ibid.*
10	78°28'	00°52'E	21	June	1886	Hundred seen. Abundance of *Calanus finmarchius*	*Ibid.*
11	73°26'	15°16'W	4	July	1886	Many seen	*Ibid.*
12	73°21'	14°59'W	5	July	1886	Several with young seen	*Ibid.*
13	75°05'	05°15'W	26	July	1886	Some seen	*Ibid.*
14	80°00'	05°00'E	27	May	1887	Many seen heading NE	Gray 1931
15	79°50'	05°15'E	15	May	1888	Many seen	Gray 1889
16	80°00'	05°00'E	19	May	1888	Many seen heading NE	Gray 1931
17	75°14'	09°28'W	28	May	1888	Many seen	Gray 1889
18	74°37'	11°00'W	1	July	1888	Many seen, one caught with a foetus	*Ibid.*
19	74°40'	12°00'W	5	July	1888	Narwhal caught with a foetus	*Ibid.*
20	74°49'	10°30'W	22	July	1888	One shot	*Ibid.*
21	74°43'	11°30'W	24	July	1888	Many poods observed including females with newborn	*Ibid.*
22	78°34'	00°10'W	6	Aug.	1888	Many seen heading NW	*Ibid.*
23	73°41'	15°00'W	12	Aug.	1888	Many males seen	*Ibid.*
24	72°00'	19°00'W	6	Aug.	1895	Some seen	Gray 1931
25	73°40'	15°00'W	25	July	1869	Several observed	Payer 1877
26	76°30'	05°00'W	24	June	1909	1 seen	Kmunke 1910
27	71°50'	21°00'W	31	Aug.	1907	A female with total length of 412 cm caught	Leverkus 1909
28	73°30'	18°00'W	15	Aug.	1907	1 seen	*Ibid.*
29	80°45'	05°45'E	20	Apr.	1979	Narwhals and bowhead whale seen	Christian Vibe pers. comm.
30	82°00'	00°24'W	23	Apr.	1979	4 seen	Christian Vibe pers. comm.
31	82°41'	16°14'E	17	Apr.	1982	20–30 seen in a lead	Kristoffersen 1982
32	83°00'	12°00'E	17	May	1896	Some seen	*Fram* obs. cited in Gray 1931
33	78°30'	01°34'W	5	May	1874	Great numbers seen migrating north	*Eclipse* & *Hope* obs. cited in Gray 1931
34	72°00'	17°00'W	20	July	1898	Some seen going northeast	*Active* obs. cited in Gray 1931
35	74°00'	15°00'W	16	June	1899	Some seen going northeast	*Ibid.*
36	74°00'	12°00'W	27	July	1873	Some seen going northeast	*Mazinthien* obs. cited in Gray 1931

records of narwhals occurring north of Danmarkshavn. However the waters along the entire coastal stretch are seldom navigated. In August 1984 Andersen (1984) observed a total of 48 narwhals between Nordostrundingen and Norske Øer (Fig. 3, Table 2c). In July and August 1989 an estimated 50–80 narwhals were observed twice along the southwestern coast of Île de France (Andreasen 1989, Peter Brandt pers. comm.). Between 29 May and 17 June 1993 groups of narwhals were observed several times between Norske Øer and Eskimonæsset (Fig. 3, Table 2c). On 9 June 1993 an estimated 150 narwhals were seen (no. 58; Table 2c). The majority of the whales occurred along the edge of the land-fastice (Born unpubl. data).

Narwhal bones uncovered in Eskimo ruins in Independence Fjord, Peary Land (north of Nordostrundingen), show that narwhals have occurred along this coast, but do not indicate their current presence (Knuth 1952).

Offshore observations of narwhals

Narwhals were observed by bowhead whalers in the Greenland Sea and Fram Strait. Narwhals and bowhead whales occurred in the same regions of the Greenland Sea (Scoresby 1980, Gray 1931). In fact the observation of narwhals was regarded as an indication of the presence of bowheads in an area (Gray 1931). The bowhead whalers most often initiated their hunting west of Svalbard at about 80°N or even further north in April-May. During June they followed the edge of the pack ice in a southwesterly direction until the hunt was terminated in August at about 70°N, off the coast of Liverpool Land in East Greenland (*ibid.*).

Observations of narwhals in the Greenland Sea and Fram Strait made from whaling and expedition ships, whose routes are not known in detail, are plotted on Fig. 4

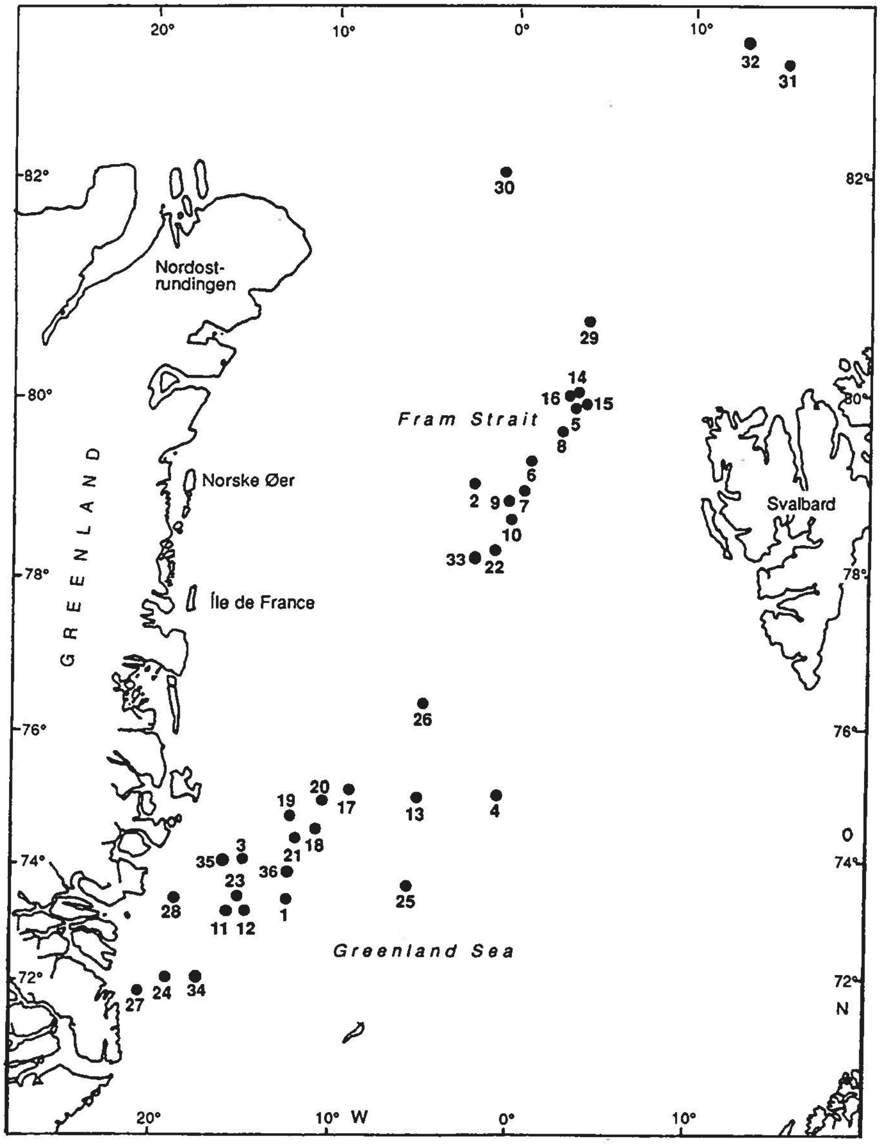


Fig. 4. Offshore observations of narwhals in the Greenland Sea and Fram Strait. The numbers refer to sightings presented in Table 3.

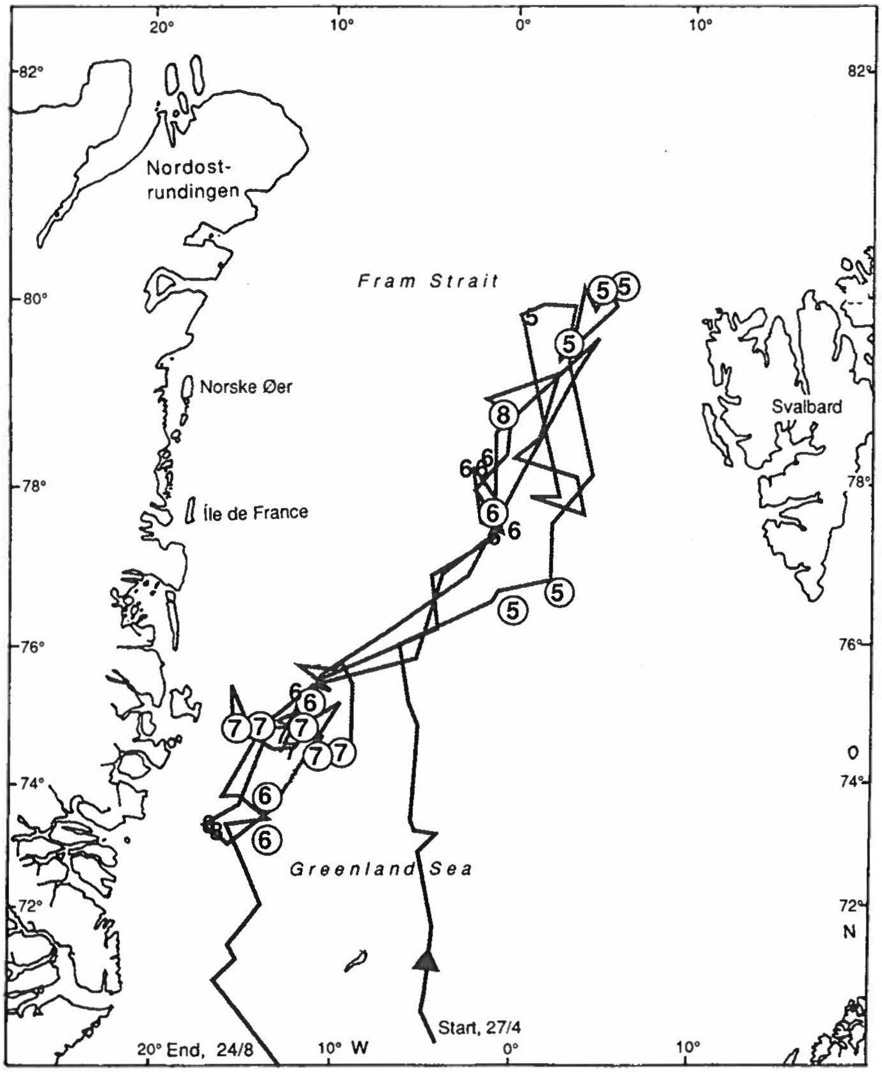
and listed in Table 3. The observations made on 17 April at 82°41'N, 16°14'E (no. 31; Table 3) and on 21 October at 67°N, 67°W (no. 5; Table 1) represent the earliest and the latest offshore observations of narwhals in this area. Two whaling logbooks in particular (Livingstone-Learmonth 1888, Kinnear 1907) give precise information on narwhals in the Greenland Sea (Figs. 5 and 6). Narwhals were usually encountered in groups of 5–6 at the "Northern Whaling Ground", between 78°N and 80°N west of Svalbard (Kinnear 1907).

The miscellaneous observations in Figs. 4–6 confirm the findings of Gray (1931), that the narwhals concentrated in two areas: the "Northern Whaling Ground", where they were found in May-June, and the "Southern Whaling Ground" (off the coast of eastern Greenland between 71°N and 75°N), where they were observed in July-August (see Fig. 6).

Migrations

Narwhals and bowheads were thought to migrate together. Whalers observed that narwhals arrived from southwest in spring from their presumed wintering grounds between Iceland and Kap Farvel (Nunap Issua) on the southern tip of Greenland. In May-June narwhals migrated in a northeasterly direction into dense pack ice (Gray 1931). Observations of narwhals at several local-

Fig. 5. Offshore observations of narwhals in the Greenland Sea and Fram Strait. The observations were made from S.S. *Eclipse* from 27 April to 24 August 1888 (Livingstone-Learmonth 1888). Numbers indicate the month of observation. Circles indicate "groups"; no circles indicate solitaries. Lines indicate the sailing route.



ities in the Polar Basin suggest a continuous distribution north of 80°N (Nansen 1897, Rutilevskii 1958, Vibe 1981, Belikov *et al.* 1984, Belikov 1988). From the observations reported in this study the observations of narwhals migrating northwest at the "Northern Whaling Ground" (Gray 1931), and findings of remains of narwhals in Eskimo ruins, it appears that narwhals also summer along the coast of Northeast Greenland. However a survey of wildlife observations in North Greenland revealed no sightings of narwhals along the nothern coast of Greenland between Nordostrundingen and Humboldt Gletscher (Northwestern Greenland; Dietz & Andersen 1984). The possibility of a connection between narwhals in East and West Greenland, and dispersal farther north across the Polar Basin, is indicated by several observations of narwhals north of 84°N which are shown in Table 4 and Fig. 7 (*e.g.* Nansen 1897, Rutilevskii 1958, Belikov *et al.* 1984, Belikov 1988). Narwhals that were observed on the "Southern Whaling Ground" were thought to have migrated southwest from the "Northern Whaling Ground" (Gray 1931).

Food

The information obtained during the interview survey in 1991 indicates that the main food of narwhals in Kangerlussuaq is cephalopods and Greenland halibut (*Reinhardtius hippoglossoides*). Redfish (*Sebastes* sp.) and crustaceans are eaten to a lesser extent (Glahder 1992).

The narwhals in Scoresby Sund in August-October feed on polar cod (*Boreogadus saida*), Greenland halibut, crustaceans (Pedersen 1930, Born 1983) and cephalopods (Isachsen 1925).

Gray (1887, 1889, 1929) found cephalopods (*Gonatus*

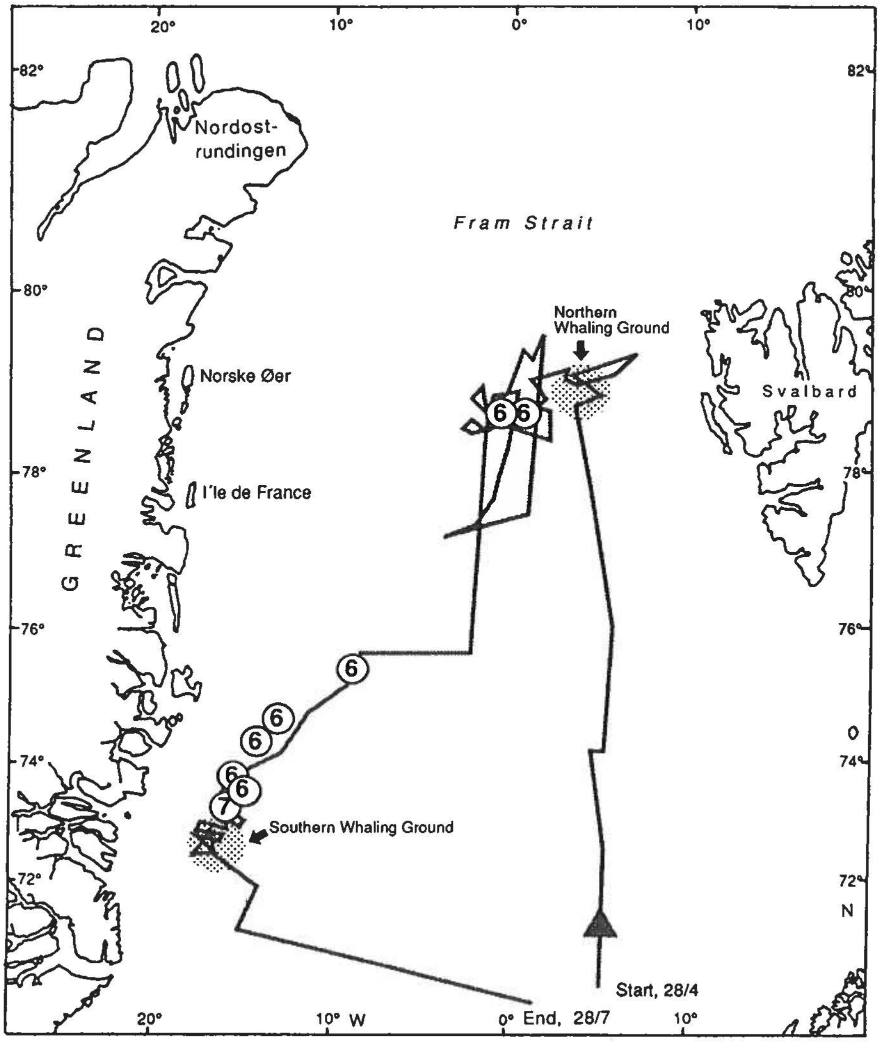


Fig. 6. Offshore observations of narwhals in the Greenland Sea and Fram Strait. The observations were made from S.Y. *Scotia* from 28 April to 28 July 1907 (Kinnear 1907). Numbers indicate the month of observation. Circles indicate "groups"; no circles indicate solitaries. The stippled areas indicate large concentrations. Lines indicate the sailing route.

fabricii) and decapods *(Pasiphaea tarda, Hymenodora glacialis)* in the stomachs of six narwhals caught at the Southern Whaling Ground in July-August. According to Gray (1931), the narwhals feed mainly on cephalopods. Manby (1822) reported finding cephalopods and crustaceans in narwhal stomachs. One narwhal caught in the Greenland Sea had flatfish (Heterosomata), cod (Gadidae) and rays *(Raia batis)* in its stomach (Scoresby 1823).

Gestation period

Eales (1950) presented length data on three narwhal foetuses from the Courtauld Expedition to Kangerlussuaq in 1935–36. A female foetus from 29 May was 13.7 cm long, a foetus from 28 June measured 15.0 cm and a male foetus from 28 July was 28.0 cm. Glahder (1992) interviewed hunters in Kangerlussuaq, who had observed both foetuses (small and large) and calves from May to August. In this area a full-term foetus had been observed in June, and on 18 July a 150 cm foetus was recorded, but small foetuses could also be seen in July. In August, near-term foetuses as well as a 30–40 cm long foetus have been observed in Kangerlussuaq (Glahder 1992).

The earliest observations of narwhals with calves were on 8 June and 5 July on the "Northern and Southern Whaling Grounds", respectively (Gray 1887). On the "Southern Whaling Ground", Kinnear (1907) observed a narwhal with a newborn on 15 July. In this area, Gray (1931) observed many pods of narwhals with newborn, one narwhal had a 19 cm long foetus. In the same area narwhals were caught with 150 and 155 cm long foetuses on 1 and 5 July, respectively (Gray 1889). Manby (1822) observed a narwhal with a suckling calf on 20 July, but he

Table 4. Observations of narwhals in the Polar Basin. The numbers refer to Fig. 7.

Obs. no.	Positions		Day	Month	Year	Remarks	Reference
	N (degr./ min.)	W/E (degr./ min.)					
1	82°00'	00°24'W	23	Apr.	1979	4 seen	Christian Vibe pers. comm.
2	82°41'	16°14'E	17	Apr.	1982	20–30 seen in a lead	Kristoffersen 1982
3	83°00'	12°00'E	17	May	1896	Some seen	Nansen 1897
4	81°00'	20°00'E	?	Apr.	1980	1 seen in 1/10 ice cover	Belikov *et al.* 1984
5	84°25'	73°00'W	30	July	1956	A single one stayed for 5 days	Ice drift station Northpole-5, cited in Rutilevskii 1958
6	84°40'	69°08'E	19	Sep.	1956	Snoring heard, presumably from narwhals	Ice drift station Northpole-5, cited in Rutilevskii 1958
7	84°42'	72°22'W	26	June	1956	A single one stayed here for 5 days	Ice drift station Northpole-5, cited in Rutilevskii 1958
8	79°13'	169°08'W	7	Aug.	1950	3 seen	Ice drift station Northpole-5, cited in Rutilevskii 1958
9	80°55'	45°40'E	?	Apr.	1971	4 seen in shore ice polynia	Belikow *et al.* 1984
10	81°00'*	52°00'E	?	?	1970s	6 seen in open water of British Canal Strait	Belikow 1988
11	81°00'	55°00'E*	?	?	1950s	10 seen open water near Franz Josef Land	Belikow 1988
12	81°30'*	50°00'E*	?	Apr.	1980	2 seen in opening between ice	Belikov *et al.* 1984
13	82°00'*	59°00'E*	?	?	1983	6 seen 25 km north of Rudolf Island	Belikov 1988
14	83°49'	13°20'E	17	May	1896	5 seen	Nansen 1897
15	83°23'	64°09'E	18	May	1895	Snoring heard	Nansen 1897
16	83°28'	64°07'E	17	May	1895	2 seen, snoring heard, probably many in the area	Nansen 1897
17	82°24'	66°10'E	30	May	1895	Pod observed	Nansen 1897
18	82°20'	65°53'E	5	June	1895	Some heard	Nansen 1897
19	84°32'	80°20'E	22	June	1895	7–8 observed	Nansen 1897
20	84°40'	74°19'E	2	July	1895	The polynia was swarming with narwhals	Nansen 1897
21	84°53'	78°42'E	6	Sep.	1895	Playing narwhals were seen	Nansen 1897
22	82°28'	136°26'E	17	Aug.	1938	Some observed	*G Sedov* observation, cited in Rutilevskii 1958
23	82°10'	136°18'E	13	Aug.	1938	3 observed, one was light-coloured	*G Sedov* observation, cited in Rutilevskii 1958
24	82°04'	136°50'E	11	Aug.	1938	4 seen	*G Sedov* observation, cited in Rutilevskii 1958
25	82°00'	137°03'E	8	Aug.	1938	Some observed	*G Sedov* observation, cited in Rutilevskii 1958
26	82°01'	136°52'E	7	Aug.	1938	3 seen	*G Sedov* observation, cited in Rutilevskii 1958
27	81°51'	136°38'E	29	July	1938	3 seen	*G Sedov* observation, cited in Rutilevskii 1958
28	81°19'	137°20'E	4	July	1938	A big animal seen swimming in the polynia	*G Sedov* observation, cited in Rutilevskii 1958
29	81°17'	138°07'E	30	June	1938	7 seen	*Malygin* observation, cited in Rutilevskii 1958
30	76°00'*	165°00'E*	?	?	1970s	8 seen in 20–30 m wide lead	Belikov *et al.* 1984

*Approximate position representing observations in an area.

did not mention the location. These scattered observations suggest that the gestation period lasts between May and July the following year. The peak of births probably occurs in late July.

Catch of narwhals in eastern Greenland

Narwhal hunting was important for the survival of early Inuit in eastern Greenland (Sandell & Sandell 1991) The catch of narwhals appears to have less importance for the modern Inuit communities in East Greenland. The narwhal catch in the Tasiilaq (Ammassalik) municipality between 1954 and 1990 is based on the Hunters' Lists of Game (HLG 1955–1990) and other sources (Table 5a). During the last decade (1981–1990), the catch in this area has averaged about 50 narwhals per year (Table 5a). The hunting period, which extends from February until December, peaks in July-September (Fig. 8). Kangerlussuaq is the most important narwhal hunting area in southeastern Greenland. Interviews with hunters in the Kangerlussuaq area in 1991 indicated that during the period 1951–1991 the average annual catch in this area was 20–30 narwhals (Glahder 1992). In the period 1986–1991, when the information was particularly precise, an average of 24

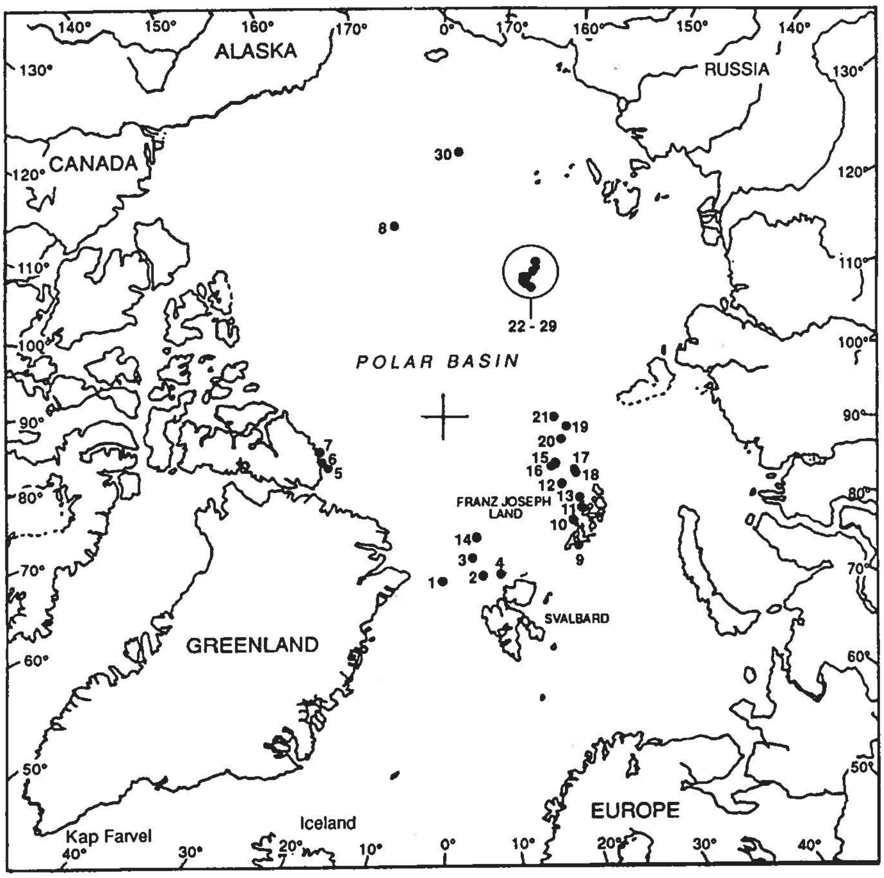


Fig. 7. Observations of narwhals in the Polar Basin. The numbers refer to sightings presented in Table 4.

narwhals (range: 11–44) were caught annually. In Kangerlussuaq narwhals are hunted between May and November with a peak in July (Fig. 9). The whales are either harpooned from kayaks, or shot from skiffs with outboard engines. Sometimes the narwhals are chased into shallow waters where they are shot. After they have sunk they are retrieved with a hook. In some cases the whales are shot from land or taken in nets. Of 81 narwhals caught in Kangerlussuaq for which sex was stated, about 56% were males and 44% females (Glahder 1992).

Narwhals are caught at the entrance to Scoresby Sund between April and July. They are shot either from the ice edge or from skiffs. Between August and October some have been shot inshore as far west as Sydkap (Born 1983; Fig. 1). This area, which was one of the best hunting grounds, has not been used for many years (Sandell & Sandell 1991). During their emigration in fall, narwhals are driven into shallow water and shot. Kayaks and harpoons have not been used to hunt narwhals in Scoresby Sund since the early 1970's (Born 1983). Some hunters have resumed the use of harpoons to catch narwhals in particular at Steward Ø (Sandell & Sandell 1991). Since 1984, narwhals were also caught in nets (Sandell & Sandell 1991). This method of hunting ceased, however, because many narwhals were believed to leave the area once a few animals had been netted (Mosbech 1990). Based on interviews with the hunters in this region in 1983, Born (1983) estimated that the annual narwhal catch in the Scoresby Sund area was 10–20 animals, and the mean reported catch during 1981–1990 was 27 (HLG). According to information obtained from hunters in 1990, narwhals are no longer hunted far west in Scoresby Sund, at Sydkap and Danmarks Ø during the open-water season. Instead, they are caught primarily at Turner Ø and Steward Ø on the Blosseville Kyst in July–August (Fig. 1, nos. 11–12; Table 1). In 1989 and 1990, an estimated 70–80 narwhals were caught in these areas (Jonas Brønlund pers. comm., Mosbech 1990). The reason for this apparent change in the distribution of narwhals and in hunting practice is unclear. The seasonal distribution of the catch in Scoresby Sund, according to HLG, is shown in Fig. 10.

This somewhat heterogeneous information shows that between 1955 and 1990 the total catch of narwhals in eastern Greenland has averaged 41 animals per year, ranging from 0 to 158 animals in one year (see Tables 5a,b). The data show a significant increasing trend in the catch, but this trend is mainly explained by large catches in 1981, 1982, 1989 and 1990 and the increased figures from interviews during later years. Glahder (1992) de-

Table 5a. Hunting statistics on narwhals (N) and white whales (W) from Tasiilaq (Ammassalik) municipality (HLG 1954–1990).

Year	Skjold-ungen	Kanger-lussuaq	Imarsi-vik	Isor-toq	Tinite-qilaq	Umig-tuars-suit	Ikka-teq	Akor-miaq	Kulu-suk	Kuu-miut	Sermi-liaq	Kap Dan	Am-massa-lik	Tasiilaq Estimate	Tasiilaq Total
	N/W	N/W	N/W	N/W	N/W	N/W	N/W	N/W	N/W	N/W	N/W	N/W	N/W	N/W	N/W
1955		1/–			5/–										6/–
1956	–/1		–/1												–/2
1957							1/–				4/–				5/–
1958					1/–										1/–
1959					4/1	2/2					3/–				9/3
1960					1/–						1/–	–/1			2/1
1961					3/–						1/–				4/–
1962					3/–							–/1			3/1
1963					12/–					1/–	5/–	1/–	2/–		21/1
1964															
1965															
1966		42 (66*)/–									1/–				43(67*)/–
1967		20/–													20/–
1968		29/–									1/–				30/–
1969		16/–			1/–										17/–
1970		6 (23**)/1			9/–						15/–				30(47**)/1
1971		(11–12**)/–								3/1	7/–			11/1	21(33**)/1
1972		(4–5**)/–			8/–					1/9	1/–			10/9	20(25**)/18
1973		(9–12**)/–			4/–					2/2					6(18**)/2
1974		(7**)/–			13/1					6/4	4/–			10/2	33(40**)/7
1975					1/–					1/–					2/–
1976									1/–	3/1	4/–				8/1
1977					3/–					10/1	4/–				14/1
1978													1/–		1/–
1979		(13**)/–		4/–	1/–					1/–				1/–	7(20**)/–
1980				4/–	24/–				5/–	16/–					49/–
1981				2/–	9/–		1/–		2/–	4/–			4/–	106/–	128/–
1982				36/–	8/–					2/–			2/–	36/–	84/–
1983					8/–						3/–			1/–	12/–
1984															
1985														21/–	21/–
1986		(22**)/–		1/3	2/–				2/–	3/–				132/12	42(63**)/15
1987		(21**)/–		1/75	7/–				–/1	3/–	1/–		30/–		19/–
1988		(11**)/–													(11**)/–
1989					13/–					6/–					19/–
1990		(44**)/–			3/–					26/–	15/–				44(88**)/–

*Interviews in 1988 (Siegstad 1989). **Interviews in 1991 (Glahder 1992).

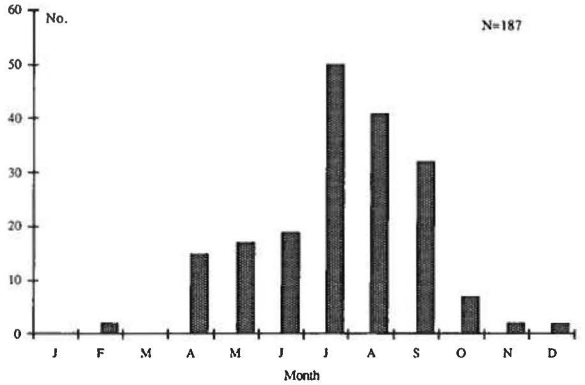


Fig. 8. Seasonal distribution of the narwhal catch in Tasiilaq municipality (excluding the Kangerlussuaq area, Fig. 9) between 1974 and 1983 (Source: Hunters' Lists of Game).

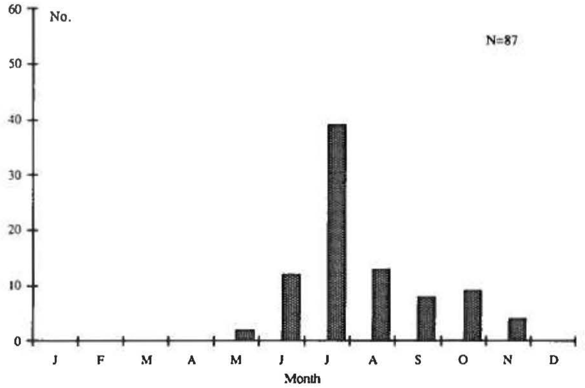


Fig. 9. Seasonal distribution of the narwhal catch in the Kangerlussuaq area (municipality of Tasiilaq) between 1967 and 1991 (Source: Glahder 1992)

Table 5b. Hunting statistics on narwhals (N) and white whales (W) from Scoresbysund and total East Greenland (HLG 1954–1990).

Year	Ittoqqortoormiit Scoresbysund N/W	Pikiullit N/W	Kap Brewster N/W	Sydkap N/W	Itaijivi Kap Hope N/W	Unarteq Kap Tobin N/W	Scoresbysund Estimate N/W	Scoresbysund Total N/W	East Greenland Total N/W
1955	8/–			8/–		2/–		18/–	24/–
1956	3/–		3/–		4/1			10/1	10/3
1957	4/–		3/–		1/–	1/–		9/–	14/–
1958	7/–			16/–	1/–	4/–		28/–	29/–
1959	13/–				–/2	4/–		17/2	26/5
1960					50/–	4/–		54/–	56/1
1961	7/–				1/–	4/–		12/–	16/1
1962									3/1
1963							8/–	8/–	29/1
1964							8/–	8/–	8/–
1965	–/5							–/5	–/5
1966	2/1							2/1	45(69*)/1
1967									20/–
1968									30/–
1969					6/–			6/–	23/–
1970	6/2							6/2	36(53**)/3
1971		1/–			4/–			5/–	26(38**)/1
1972	1/–							1/–	21(26**)/18
1973					4/–			4/1	10(22**)/3
1974	2/–					–/1		2/1	35(42**)/8
1975	1/–					1/–		2/–	4/–
1976	1/–							1/–	9/1
1977	4/–				1/–			5/–	19/1
1978	1/–							1/–	2/–
1979							10/–	10/–	17(30**)/–
1980							10/–	10/–	59/5
1981							15/–	15/–	143/–
1982					10/–		15/–	25/–	109/–
1983	2/–					12/–	29/–	43/–	55/–
1984	50/15							50/15	50/15
1985	28/–							28/–	49/–
1986									42(63**)/15
1987									19/–
1988	(ca. 40 #)/–							(ca. 40#)/–	(ca. 51**#)/–
1989	1 (ca. 70 #)/–							1 (ca. 70 #)/–	20 (ca. 89 #)/–
1990	(ca. 70 #)/–							(ca. 70 #)/–	44 (ca. 158**#)/–

*Interviews in 1988 (Siegstad 1989). **Interviews in 1991 (Glahder 1992). #=caught at Steward Ø and Turner Ø (Mosbech 1990).

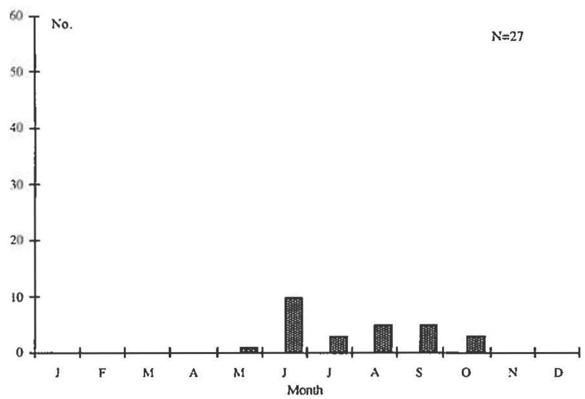


Fig. 10. Seasonal distribution of the narwhal catch in Ittoqqortoormiit (Scoresbysund) municipality between 1974 and 1983 (Source: Hunters' Lists of Game).

scribed the narwhal catch as ranging between 40 and 60 animals per year, based upon nearly the same data. We conclude that during the period 1981 to 1990 the total catch of narwhals in eastern Greenland has averaged at least about 80 animals per year. The number of whales killed but lost is not well documented. However, during the open-water hunts, losses are substantial in some cases (Glahder 1992).

The narwhal's skin (mattak) is traded to the Greenland Trade Department (KNI) for 50 Dkr per kg (approximately 8 US dollars, Heide-Jørgensen 1994). A substantial proportion of the mattak is given to family. Most of the meat is dried for human consumption. Some meat is also used for feeding sled dogs (Born 1983, Sandell & Sandell 1991, Glahder 1992). The tusks are traded to KNI for approximately 725 Dkr per kg (Ca. 121 US dollars, Reeves & Heide-Jørgensen 1994). Some ivory is used for handicrafts and for making tools such as harpoons (Glahder 1992). In 1990, a total of 19 narwhal tusks were traded to KNI in Scoresbysund (R.v.d. Pedersen pers.

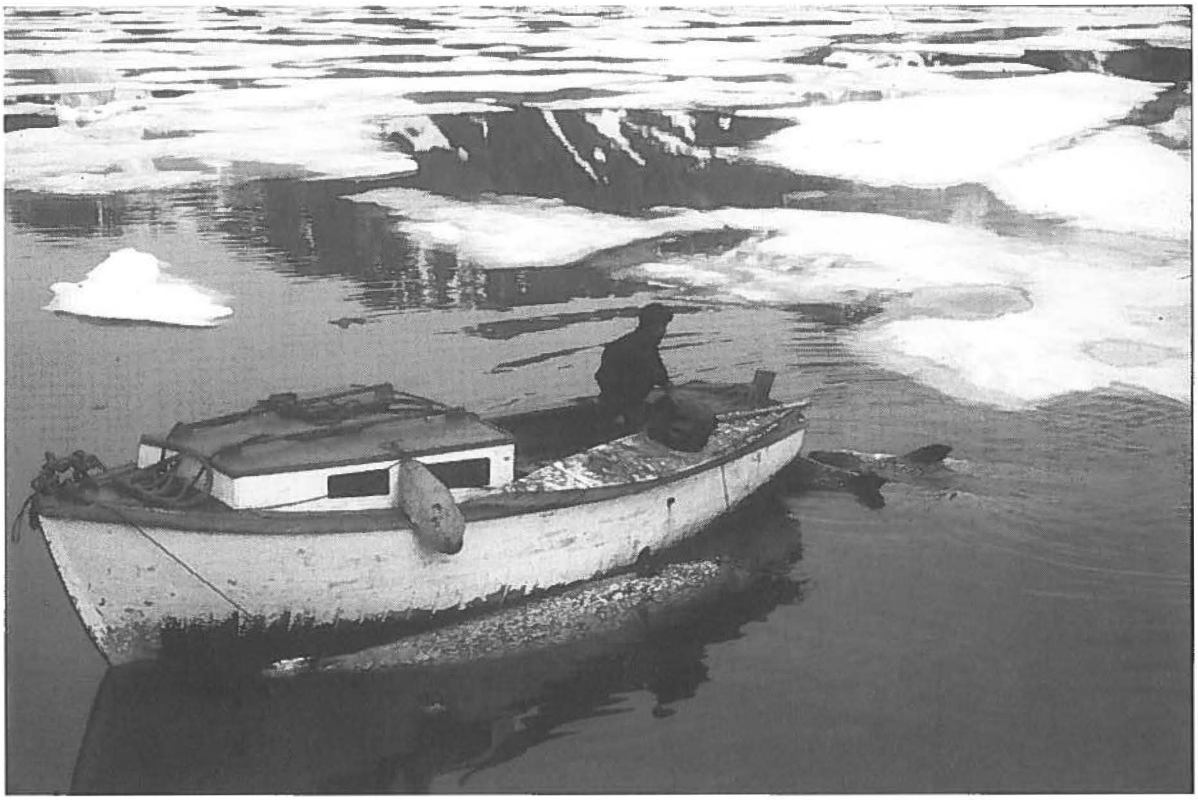


Fig. 11. Four narwhals taken from kayak being towed by a small fishing vessel in Kangerlussuaq, late July 1991. Photo: C.M. Glahder.

comm.). In 1989 and 1990, KNI in Scoresbysund bought 1884 kg of mattak.

Occurrence and catch of white whales in eastern Greenland

In eastern Greenland white whales occur far less frequently than narwhals. Few observations of white whales have been reported in eastern Greenland in the May-August period. Holm and Petersen (1921) wrote that white whales were seen and caught occasionally in the Ammassalik area, whereas Mikkelsen and Sveistrup (1944) mentioned that they were seldom taken and had no significance in the hunting economy. A few white whales are listed in the catch statistics from this municipality (see Table 5a), but all recent reports are believed to be erroneous (Jakob Sivertsen pers. comm.). Iversen (1936) saw white whales in August 1932 in Kangerlussuaq.

In Scoresby Sund scattered observations of white whales have been recorded (*e.g.* Nathorst 1900, Mikkelsen 1925, Meltofte 1974). Sølberg (1980) stated that herds of 5–10 animals were seen in some years. In the hunting statistics (Table 5b) between 4 and 15 animals are listed within decades (HLG 1954–1990). Born (1983) presented similar figures from the 1960s and 1970s, but Sandell & Sandell (1991) could not verify these statistics. North of Scoresby Sund only a single observation of a small pod was made in the middle of August 1900 in Kejser Franz Joseph Fjord (Kolthoff 1901, 1903). White whales have been observed in late June in the Greenland Sea between eastern Greenland and Svalbard (Kolthoff 1903, Kinnear 1907).

Discussion

Our assessment of the narwhal's occurrence off East Greenland is based on observations made over a long period of time. Moreover the sources that we reviewed vary greatly in detail and precision. Although we merely summarize where and when narwhals have occurred in the past, we believe that this summary provides a good general idea of their present-day occurrence. As Gjertz (1991) concluded for the Svalbard area, there is no evidence of changes in narwhal distribution and abundance in the Greenland Sea and Fram Strait.

In the western part of their range narwhals occur primarily in deep-water areas (*e.g.* McLaren & Davis 1983, Koski & Davis 1994). They spend the winter in Davis Strait and Baffin Bay, widely distributed in the closed pack ice in deep water. They summer in deep fjords of the Canadian and West Greenland High Arctic (*e.g.* Born *et al.* 1994, Richard *et al.* 1994).

Any account of narwhal distribution in East Greenland waters reflects the nature of the observation platform, particularly in the days when vessels were limited to sail power for penetrating the pack ice in the Greenland Sea. It is thus not surprising that the majority of observations of narwhals during the 19th and early 20th centuries are from the eastern fringes of the pack ice in the Greenland Sea. Only a few narwhals have been observed during expeditions with ice-breaking research vessels navigating the pack ice in the East Greenland and Svalbard areas during summer (Ugland & Ree 1983, Søder 1991, this study). Even these observations were not made from the ships but from accompanying helicopters.

Narwhals have been observed in the pack ice as early as April, but otherwise there are few observations in the pack ice during winter months. By analogy with the situation in Davis Strait and Baffin Bay, it seems likely that narwhals move far into the pack ice of the Greenland Sea during winter. This inference is supported by several observations at the entrance to Scoresby Sund, where narwhals have been seen in February, and by a catch of 16 narwhals in Sermilik Fjord in April 1992 (Jakob Sivertsen pers. comm.). Narwhals probably occur throughout the year in the pack ice of the Greenland Sea and Fram Strait. During summer some narwhals migrate into the East Greenland fjords, particularly Sermilik, Kangerlussuaq and Scoresby Sund. Other narwhals migrate to areas northeast of the Svalbard archipelago. In East Greenland narwhals are frequently seen as far south as 66°N during summer, whereas in West Greenland they are rarely seen south of 70°N between June and October. Generally, the distribution of narwhals and white whales is mutually exclusive at all seasons. The summering and wintering areas differ in time and space, suggesting that competition for a common food supply is avoided by spatial segregation (Sergeant 1979). Where narwhals and white whales occur sympatrically they apparently reduce competition by feeding at different water depths (Mitchell 1983). Narwhals probably feed at a great range of depths (*e.g.* Hay & Mansfield 1989) and occur during winter (*e.g.* Koski & Davis 1994) and summer (*e.g.* Born *et al.* 1994) in areas with deep waters. White whales to a greater extent feed bathypelagically and prefer areas with less deep waters (*e.g.* Sergeant 1979, Kingsley *et al.* 1994, Smith *et al.* 1994). The striking scarcity of narwhals in the Svalbard area is puzzling. Although a substantial part of the surrounding water is less than 100 m deep several fjords are between 200 and 400 m deep, and the major food items of narwhals are available in Svalbard waters (Ian Gjertz pers. comm.). It therefore remains unclear why narwhals do not summer around Svalbard.

In offshore areas of the Greenland Sea, narwhals feed mainly on squid (*Gonatus sp.*) and decapods, which occur primarily in areas with deep waters. After break-up of the fjord ice, narwhals penetrate the deep fjords of eastern Greenland, where the main food is cephalopods, Greenland halibut, redfish, polar cod and crustaceans (Isachsen 1925, Pedersen 1930, Born 1983, Glahder 1992). This summer diet is generally consistent with that of narwhals in Canadian and West Greenland waters (Vibe 1950, Finley & Gibb 1982, Hay & Mansfield 1989, Heide-Jørgensen *et al.* 1994). The scattered observations from East Greenland suggesting that gestation lasts from May to July are in agreement with published results cited by Hay & Mansfield (1989), who gave 15.3 months as an estimate for narwhals off northern Baffin Island. Best & Fisher (1974) estimated the gestation period to be only 14 months for western Greenland and eastern Canada. The peak of births seems to occur in late July in East Greenland, which again is consistent with the Canadian findings (Hay & Mansfield 1989, Koski & Davis 1994).

Observations of white whales in the Greenland Sea between eastern Greenland and Svalbard in June suggest that whales from the two areas belong to a single population. Few white whales have been observed during recent times south of 65°N in West Greenland, and it is therefore unlikely that the few white whales seen in East Greenland come from West Greenland. The white whales appearing in East Greenland from time to time are probably stragglers from the Svalbard population. In Davis Strait and Baffin Bay white whales tend to winter in coastal areas with less dense ice cover than those areas inhabited by narwhals (*e.g.* Heide-Jørgensen *et al.* 1993, Koski & Davis 1994) . We therefore hypothesize that white whales are rare in eastern Greenland because of the limited availability of suitable habitat. This is in contrast to the situation at Svalbard where white whales are relatively common (Gjertz & Wiig 1994) and narwhals are quite rare (Gjertz 1991). White whales are presumably deterred from dispersing westward from Svalbard because to do so they would need to cross areas with deep water and penetrate dense pack ice.

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Line-transect estimation of abundance of narwhals (*Monodon monoceros*) in Scoresby Sund and adjacent waters

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Larsen, F., Heide-Jørgensen, M.P., Martin, A.R. & Born, E.W. 1994. Line-transect estimation of abundance of narwhal (*Monodon monoceros*) in Scoresby Sund and adjacent waters. – Meddr Grønland, Biosci. 39: 87–91. Copenhagen 1994-04-22.

An aerial line transect survey of narwhal (*Monodon monoceros*) abundance in Scoresby Sund and adjacent fjords in East Greenland was conducted in September 1983 and 1984. An effort of 1747 and 1973 linear kilometers resulted in 66 and 19 primary sightings of narwhal pods in 1983 and 1984, respectively. The mean pod size increased slightly but not significantly from 1.99 to 2.56 between the two years. The resulting estimates of abundance of narwhals (not corrected for submerged animals) were 300 (95% CI 165–533) and 102 (95% CI 36–276) in 1983 and 1984, respectively. These two estimates are not significantly different. The difference between the two estimates is most likely due to annual variation, perhaps in combination with the formation of new ice in 1984, which could have forced the narwhals out of the study area.

Key words:
Narwhal, *Monodon monoceros*, Greenland, aerial survey, line transect.

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Introduction

Little information on the occurrence and distribution of whales exists from East Greenland. Despite exploitation of narwhals (*Monodon monoceros*) by hunting communities in this region (Sandell & Sandell 1991, Dietz *et al.* 1994), the population size of this species in East Greenland has so far not been estimated.

Several accounts indicate that the Scoresby Sund fjord system is one of the major summering areas for narwhals (Scoresby 1823, Bay 1896, Winge 1902, Pedersen 1930, Sølberg 1980), but give very little detailed information on distribution and abundance within the fjord system. The need for such information became apparent in relation to planned industrial activities in adjacent Jameson Land in the mid-1980's. As a consequence, aerial surveys were flown in 1983 and 1984 with the purpose of assessing the distribution and abundance of narwhals in Scoresby Sund and adjacent fjords. This paper describes the methods used and presents results of these surveys.

Materials and methods

Aerial surveys were flown from 9 to 21 September 1983 and from 18 to 24 September 1984. The surveys were designed as line-transect surveys covering Scoresby Sund, Hall Bredning and adjacent fjords, Kong Oscars Fjord and the coastal waters off Liverpool Land. Hall Bredning, Scoresby Sund and Kong Oscars Fjord were surveyed using transect lines separated by one nautical mile going east-west in Hall Bredning and north-south in Scoresby Sund and Kong Oscars Fjord. Lines to be flown were chosen at random without replacement from the total number of lines. In the narrower fjords it was considered impractical to fly randomly chosen transect lines and instead zig zag lines were used with transect legs incident to the coast line at about 45°. This procedure was also adopted along the coast of Liverpool Land. The zig zag lines were treated as one line for the estimation of sighting rates. The blocks NN, N, S and SE (Fig. 1) were surveyed twice in each year; all other areas were surveyed only once.

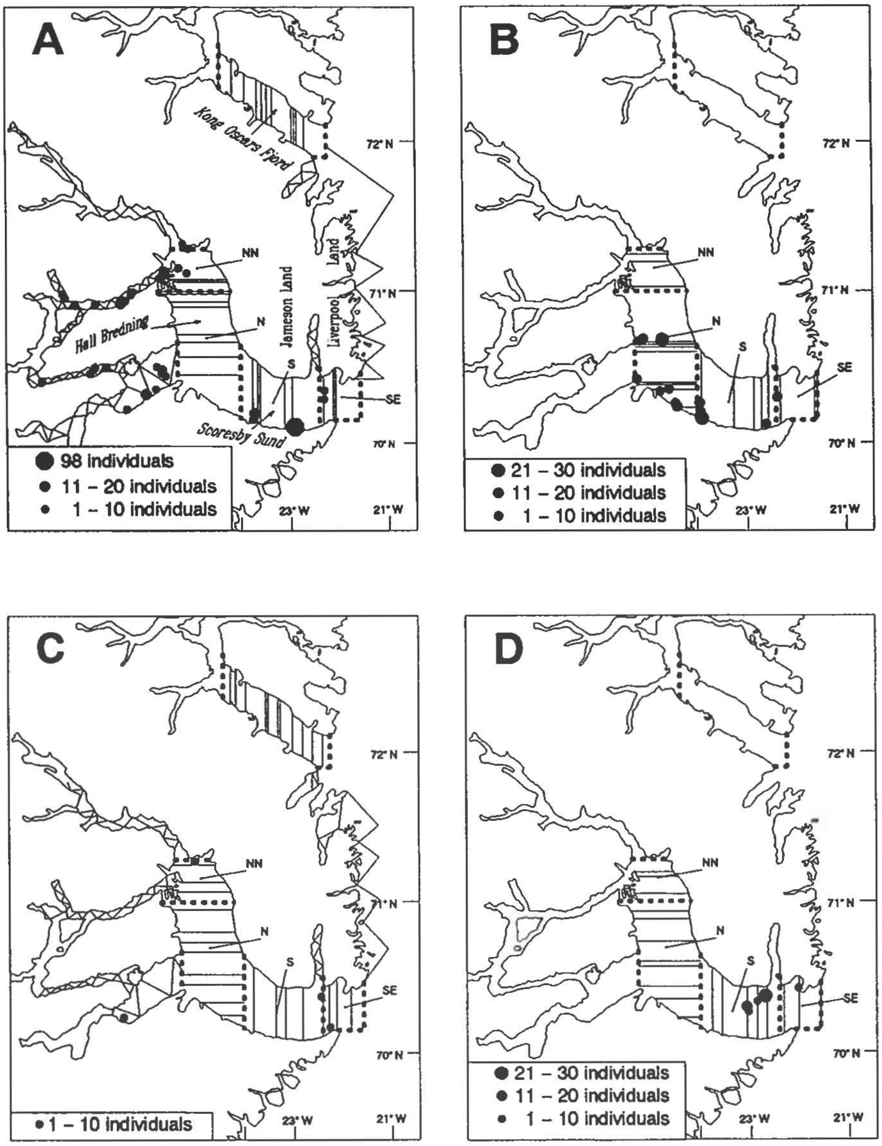

Fig. 1. Map of the study area with transect lines flown and positions of sightings of narwhals in Scoresby Sund and Kong Oscars Fjord and off Liverpool Land, September 1983 and 1984. NN, N, S and SE are main survey blocks. A) First coverage in 1983. B) Second coverage in 1983. C) First coverage in 1984. D) Second coverage in 1984.

The surveys were flown in a twin engine, high winged Partenavia P 68 Victor Observer (OY-CAG) equipped with a Collins VLF/OMEGA navigation system. The aircraft had standard flat windows at the observers' seats, resulting in poor coverage from the track line out to around 150 m perpendicular distance. Surveys were conducted at a target altitude of 183 m and an approximate ground speed of 167 km/h. The crew consisted of a pilot, two observers and one recorder. The observers were in the right front (copilot's) seat and in the left rear seat. The person recording was in the right rear seat. This person recorded information on all sightings of marine mammals into a portable tape recorder. The information included species, numbers, group and age structure, direction of movement, comments on behaviour and associated remarks about position and time of sighting, declination angle to the sighting when abeam, sea and ice conditions and visibility. The declination angle was measured by means of an inclinometer (Silva type 65) and used together with information on the altitude for calculating the perpendicular distance to all sightings of pods. A pod was defined as one or more whales moving together closely, usually less than a few meters from each other, and usually diving synchronously. Adult animals with a tusk were considered to be males, all other adults were considered to be females (see Fig. 3, below).

Estimation of abundance of narwhals was based on line-transect sampling theory as described by Burnham *et al.* (1980) and Buckland *et al.* (1993). For estimation of the effective search half-width (ESW) and its associated

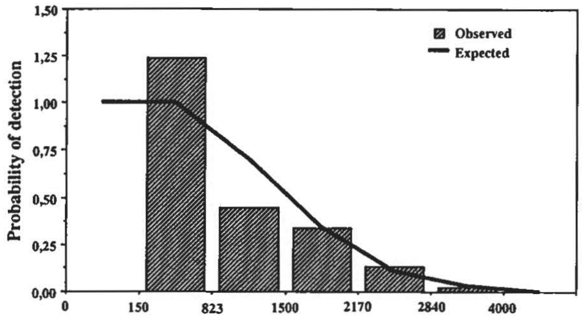

Fig. 2. Frequency distribution of narwhals at various distances from the trackline. Sightings from 0 to 150 m from the trackline and sightings more than 4000 m from the trackline were excluded. Data has been fitted with a Fourier series model with two cosine adjustment parameters and the fitted curve shows the expected number of sightings.

empirical variance we used the computer package "Distance" developed by Laake *et al.* (1993). Estimation of the ESW was based on all sightings with an associated distance, whereas estimation of densities was based on only primary sightings, *i.e.* sightings made from the transect line while on effort. The coefficients of variation (CV) were estimated as the standard error divided by the mean.

We assumed that the density estimates were log normally distributed and we applied 95% confidence intervals developed by Burnham *et al.* (1987, p. 212). Data to allow the estimation of the probability of sighting a pod on the transect line were not collected so the estimates of abundance of narwhals have not been adjusted to account for whales submerged during the surveys.

Results

During the survey in 1983 most areas in Scoresby Sund were covered by less than 3/10 ice and only the inner parts of the fjords had more than 7/10 ice. In 1984 new ice was found throughout most of Scoresby Sund with grey new ice in the inner parts of fjords.

An effort of 1747 linear km surveyed resulted in a total of 164 pods of narwhals with 311 animals observed in the study area in September 1983 (Fig. 1A-B). Because of the clumped distribution of the pods, only 66 of the 164 pods were primary sightings. All sightings were made in Scoresby Sund, Hall Bredning and adjacent fjords.

Of the 95 animals observed in narrow fjords in 1983 for which information on direction of movement is available, 79 (83%) were moving outwards, and of the 256 animals observed in Hall Bredning and Scoresby Sund 169 (66%) were moving outwards.

Of 164 pods for which information on pod composition is available, 21 were comprised of single males and 57 of single females. Of 63 pods with two or more adults only 7 (11%) were mixed male-female pods. A total of 73 neonates, corresponding to 23.5% of the total number of animals sighted, were seen during the surveys. Thirty of these were found in mother-calf pairs. The ratio of neonates to total number of adult females was estimated at 0.38. Average pod size was estimated at 1.99 (95% CI 1.72–2.08).

An effort of 1973 linear km surveyed resulted in the observation of a total of 25 pods of narwhals (64 whales including 7 neonates) in September 1984 (Fig. 1C-D). Nineteen of these pods were primary sightings. Except for four sightings, all pods were seen in the eastern part of Scoresby Sund. Only one of the four pods (25%) was moving outwards, and only 7 of the 19 pods (37%) found in the eastern part of Scoresby Sund were heading outwards. Neonates constituted 10.9% of the total number of animals sighted. Average pod size was estimated at 2.56 (95% CI 1.30–3.82).

The mean pod size did not differ significantly between years and the pooled mean pod size estimate was 2.03 animals (range: 1–14).

The nineteen primary sightings from 1984 are too small a sample for estimating ESW for that particular year. Instead all sightings from 1983 and 1984 were pooled to derive a common detection function. This was justified by the use of identical survey techniques in the two surveys. Based on the chi-square value for the observed frequency distribution of sightings compared to the predicted (χ^2=0.92) a Fourier series model with two cosine adjustment parameters was chosen (Fig. 2).

Because the flat windows prevented observations directly below or very near the aircraft, the first 150 m from the trackline was omitted from the analysis of densities. Sightings more than 4000 m from the trackline (1% of the

Table 1. Line transect estimation of narwhal abundance in Scoresby Sund, Hall Bredning and adjacent fjords in 1983 and 1984. The Effective Search half-Width (ESW) was estimated by fitting a Fourier series model with two cosine adjustment parameters (see text and Fig. 2) to the frequencies of sighting distances (Fig. 2). The estimates of mean pod size include secondary sightings. CV is the coefficient of variation calculated as the standard error in proportion to the mean.

	1983	1984
Area (km^2)	10993	10993
Effort (L, km)	1747	1973
No. of primary sightings (N)	64	19
Sighting rate (N/L)	0.037	0.010
CV	0.29	0.50
Mean pod size	1.99	2.56
CV	0.05	0.24
ESW (1/f(0), m)	1355	1355
CV	0.08	0.08
Density of narwhals	0.027	0.009
CV	0.31	0.56
Abundance estimate	300	102
Confidence interval	165–533	36–276

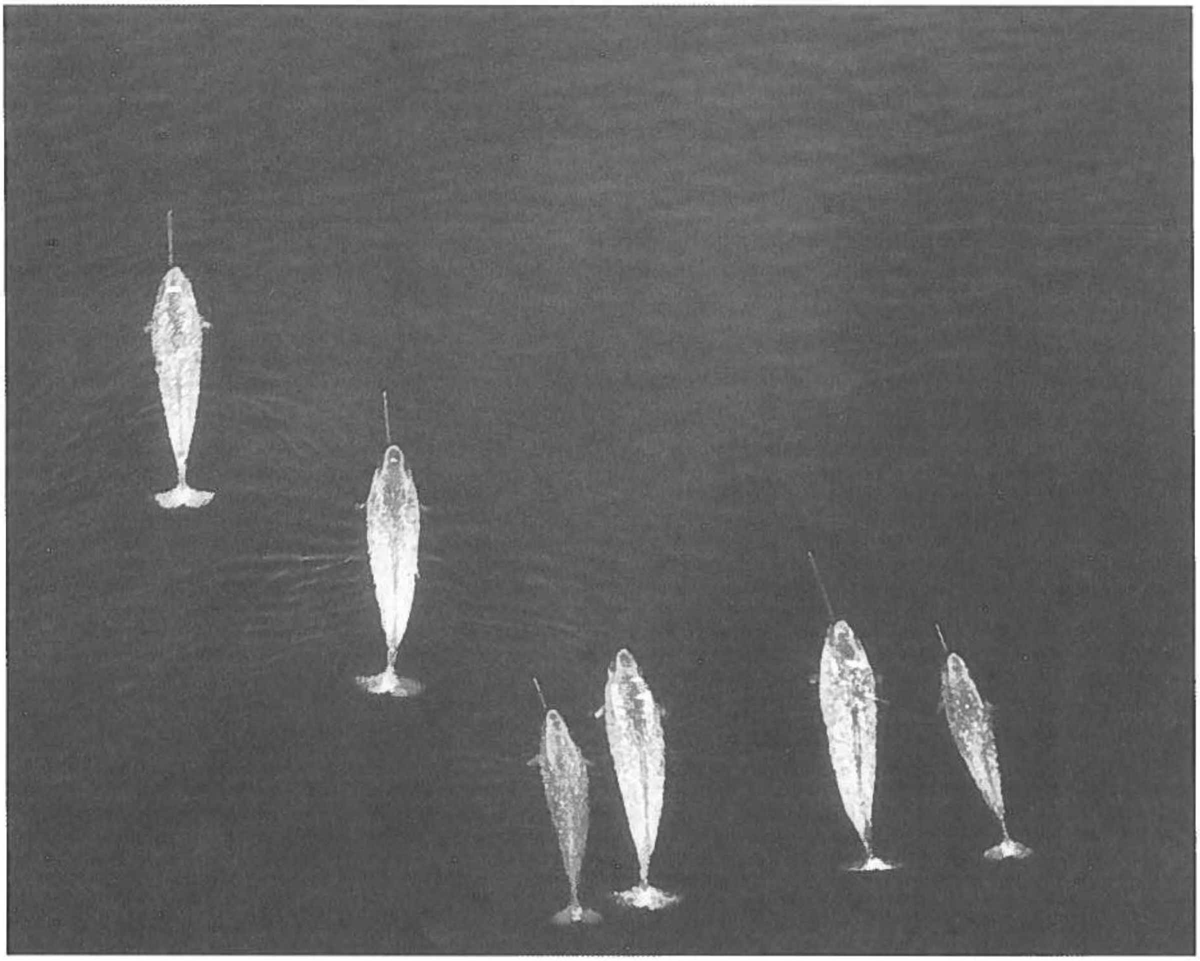

Fig. 3. A group of adult narwhal males in Scoresby Sund. Photo: A. R. Martin

total number of primary sightings) were also excluded to ensure a monotonically decreasing detection function.

The resulting estimates of relative abundance indicate that three times as many narwhals were present in Scoresby Sund in 1983 compared to 1984 (Table 1). However, the two estimates are not significantly different.

Discussion

The survey results from both 1983 and 1984 both indicate a great lack of survey precision which must be attributed primarily to the clumped distribution of the narwhals in Scoresby Sund (Fig. 1), which led to highly variable sighting rates.

The lower number of narwhals found in 1984 could be explained by this lack of precision or by annual variability in the presence of narwhals within Scoreby Sund. A contributing factor could be the widespread formation of new ice in the fjords in 1984. Narwhals leave Scoresby Sund in the autumn and are assumed to winter offshore in open water areas in the Greenland Sea. The formation of new ice in the inner parts of Scoresby Sund probably determines the timing of the departure of narwhals from these areas in the early autumn. More new ice was present during the survey in 1984 than in 1983, and this probably explains why so few narwhals were present in the inner parts of Scoresby Sund in 1984.

The information on the direction of movement of the narwhals observed in the different parts of the fjords in the two years does not obviously support this hypothesis. However, results from behavioural studies of narwhals in eastern Canada (Silverman 1979) suggest that tidal effects may be more important in determining the direction of movement at any given time.

It is evident that a relatively large number of narwhals can be found during the late summer in Scoresby Sund. None of the estimates are corrected for submerged whales and hence they must be considered to be biassed downwards in this respect. No correction factors are at present available for this type of survey, but an analysis of diving behaviour of narwhals in a similar habitat in eastern Canada indicates that multiplying by 1.5–1.8 may be appropriate (Martin *et al.* 1994). Another factor that could contribute to a downward bias is the left-truncation of the frequency distribution of primary sightings. The magnitude of this bias will depend on the actual shape of the distribution in the interval from the track line out to the truncation point.

The high number of neonates found in this study suggests that Scoresby Sund is an important calving or nursery area for narwhals. The proportions of neonates found in this study are high compared to results from other areas (*e.g.* Born *et al.* 1994). The observation on a number of occasions during the surveys of single neonates or neonates accompanied by only males suggest that the females may leave their calves at the surface when diving, so that these proportions may be biassed upwards. Segregation of the population, with mainly the adult females and calves summering in Scoresby Sund and adjacent fjords as indicated for other areas, *e.g.* Vibe (1950), may also contribute to the relatively high values of these proportions.

Acknowledgements

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Distribution and catch of white whales (*Delphinapterus leucas*) at Svalbard

IAN GJERTZ and ØYSTEIN WIIG

Gjertz, I. & Wiig, Ø. 1994. Distribution and catch of white whales (*Delphinapterus leucas*) at Svalbard. – Meddr Grønland, Bioscience 39: 93–97. Copenhagen 1994-04-22.

The distribution and catch of white whales at Svalbard are discussed based on literature, interviews with local residents, trappers and pilots, opportunistic observations recorded in the Norwegian Polar Institute fauna-data-base, and personal observations by the authors. The total number of white whales killed in Svalbard from the 18th century to the early 1960s was considerably higher than 15 000 animals. Today white whales are protected in Norwegian waters. Most white whales seem to appear at Svalbard in the spring and to leave again when the western fjords freeze in the autumn. However it is not known whether they come from and return to the eastern Greenland Sea or the Barents Sea. The number of white whales using the Svalbard area is not known, but since they have been protected for the last 30 years the population is assumed to be secure.

Key words:
White whales, beluga, *Delphinapterus leucas*, Svalbard, catch, distribution.

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Introduction

Since the white whale fishery at Svalbard ended in the 1960s white whales (*Delphinapterus leucas*) have, in effect, been totally protected and may only be hunted under permit in Norwegian waters (Anonymous 1939, 1978, 1983, Wiig & Gjertz 1992). Little attention has been paid to the species in Norway and little new information is available on its biology and distribution. The recent data consist mostly of opportunistic observations. In the last few years, however, the Norwegian Polar Institute (NP) has started mapping the distribution of white whales and other species in Svalbard based on data from aerial surveys and interviews with local residents.

Svalbard is largely uninhabited. Most of the human population is confined to the inner fjord areas along the west coast of Spitsbergen (Fig. 1). Large migrations of whales in the archipelago may therefore go undetected. However in three different periods there has been a significant hunt of white whales at Svalbard. Information from hunters and from recent opportunistic interviews permit some conclusions as to the migrations of white whales to Svalbard and their distribution within the archipelago.

Materials and methods

Much of our information on white whales at Svalbard comes from interviews with local residents, trappers and pilots, opportunistic observations recorded in the NP-fauna-data-base, and our personal observations. In addition, information on biology and possible migrations was obtained from the literature.

In the summer of 1990 large parts of Svalbard were photographed from the air, mostly in colour, and 870 of these photographs which covered coastlines at a scale of 1:15 000 were scrutinised for white whales. These photographs covered the southern part of Isfjorden and Van Mijenfjorden (Fig. 1).

In 1992 NP undertook one aerial survey for walruses (*Odobenus rosmarus*) on 30 May and two aerial surveys for white whales on 31 May and 30 June. The first covered the lead from south of Nordaustlandet northeastwards to Kvitøya, parts of the north coast of Nordaustlandet and part of Hinlopenstretet. The second survey covered the west coast of Spitsbergen from Sørkapp to Isfjorden, and the last covered Isfjorden, Van Mijenfjorden and Bellsund (Fig. 1).

From 1 to 11 September 1992 all of Svalbard's coast-

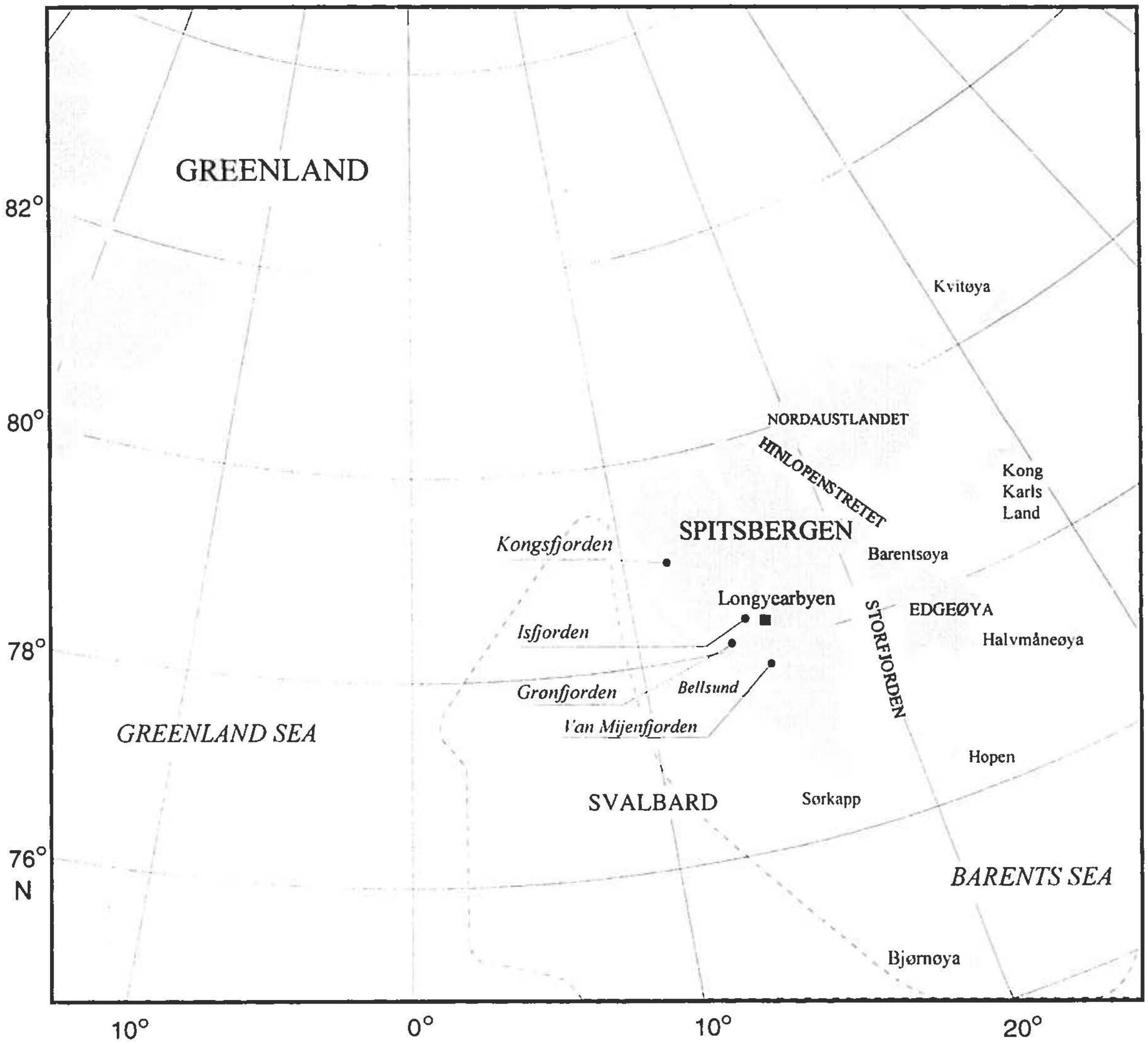

Fig. 1. Map of Svalbard with maximal extension of the drift ice indicated (from Vinje 1985).

line, except Bjørnøya and Hopen, was covered at least once as part of a 30-hour aerial survey. This survey was primarily designed for walruses but had white whales as secondary targets. Large parts of the northern and south-eastern coasts were covered two or three times.

Results

The first episode of white whale hunting at Svalbard was by the Russians in the 18th and early 19th centuries. Little is known about numbers taken, but we do know the sites of the Russian combined trapping and whaling stations. These stations were primarily situated in the fjords of the west coast of Spitsbergen (Storå 1987). The best known of the Russian catches was taken in 1818 at Sørkapp, the southernmost point of Spitsbergen, when a wintering crew supposedly caught 1200 white whales (Isachsen 1916–1919).

The Norwegian white whale hunt at Svalbard started in 1866. The most important hunting areas were the fjords along the west coast of Spitsbergen and Hinlopenstretet (Ingebrigtsen, cited by Hjort 1902). During the first four years a total of somewhat more than 800 animals was caught, while in 1870 alone about twice this number was caught (Wollebæk 1901). Norwegian catches for the years from 1871 to 1940 amount to approximately 9000 whales (Anonymous 1882–1921, Wollebæk 1901, Lønø & Øynes 1961). Thus a total minimum catch of about 11 400 white whales was recorded from 1866 to 1940, although it must be noted that a few of these were actually

Fig. 2. Netting of white whales at Svalbard in 1958. In addition to the methods of killing mentioned in the text, the whales were sometimes also killed instantaneously by the pressure emitted from underwater explosions of dynamite (*cf.* Lønø & Øynes 1961). Photo: O. Lønø.

taken in the White Sea and at Novaya Zemlya. The main method of catching was to trap part of a herd in a seine and then to kill individual animals and drag them ashore. Another common method was to shoot the whales in shallow water and harpoon them by hand. A significant number of killed whales must have been lost.

The final whaling episode lasted from 1945 to 1960 and is well documented by Lønø & Øynes (1961). In this period 3281 white whales were caught in Svalbard, while only 1290 were recorded in the official statistics. Lønø & Øynes (1961) indicated that most of the whales were killed along the west coast of Spitsbergen and relatively few were taken in Hinlopenstretet and Storfjorden.

Several large herds of migrating white whales have been obseved in Svalbard. In September of one of the years between 1910 and 1920 the trapper Hilmar Nøis observed a herd of whales at Grønfjorden that he claimed was 32 km long; it must have consisted of thousands of whales (Berset 1953). On 27 September 1947 a herd of at least 1000 whales was observed swimming southwards at Halvmåneøya (Lønø & Øynes 1961). The largest migrating spring herd ever reported was observed in Kongsfjorden on 15 May 1952, when an estimated 10 000–12 000 whales were said to have been seen feeding on polar cod (*Boreogadus saida*) (Wahl 1978). However Lønø & Øynes (1961) suggested that this number may have been rather overestimated. A small part of the herd, 402 animals, was caught. Of these 399 were adult males and three were females. During the following two weeks another 367 males were caught in the same area. On 27 May 1959 a herd of about 800 whales was seen at Grønfjorden (Lønø & Øynes 1961)

Two herds of four and 123 whales were detected on the photographs from Isfjorden taken in summer 1990. On the first aerial survey, 31 May 1992, no white whales were seen in the northern and eastern areas of Svalbard. On the second survey, 30 June, two herds were seen in Isfjorden. One contained at least 35 animals, five of which were calves, while the other was probably an all-male herd of 42 whales. On the surveys of 1–11 September only one white whale was seen off the northeast coast of Edgeøya on 1 September.

Discussion

According to whalers and early naturalists white whales were common along the coasts of Svalbard and were frequently found in shallow waters in the inner fjord areas at the mouths of glacial rivers (Malmgren 1863, Kükenthal 1900, Nathorst 1900, Collett 1911–12) and at glacier fronts where they fed on polar cod (Kolthoff 1903, Grieg 1921). According to Ingebrigtsen (cited by Hjort 1902) the distribution of white whales varied according to the prevailing weather and ice conditions. In northeasterly winds they were found in Storfjorden and in southerly winds in Bellsund. In periods with heavy ice along the northern coasts they aggregated in the ice-free fjords along the northwest corner of Spitsbergen. Even though white whales were mainly expected to be found in nearshore waters, they were also observed in the pack ice in the Greenland Sea (Wells 1876, Kolthoff 1903).

White whales were believed to arrive at Svalbard in large herds in April or May (Hjort 1902, Collett 1911–12). Some of these were mixed herds while others consisted only of adult males (Lønø & Øynes 1961). Some of these herds frequented the fjord areas but most continued migrating eastwards (Collett 1911–12). When all fjords and coastal waters of Svalbard froze and became filled with ice, the white whales were forced to move out of the area and were believed to migrate southwestwards to southern Greenland and eastern Canada (Hjort 1902, Collett 1911–12). The finding of American rifle bullets in many of the white whales killed in Svalbard were taken as proof of this (Ingebrigtsen, cited by Hjort 1902).

Lønø & Øynes (1961), however, believed that white whales from Svalbard migrated eastwards into the Barents Sea. They considered the observations of these whales by Norwegian sealers along the Barents Sea pack-ice edge from early April onwards to indicate such a migration. In extreme ice years when the pack-ice edge in the Barents Sea moved far south, as it did in 1902/03 when the ice limit was in a straight line from Spitsbergen to the Kola Peninsula, large groups of white whales occurred along the Norwegian coast and many hundreds were caught there in January (Collett 1911–12, Lønø & Øynes 1961).

During recent years white whales have first been seen in April-May, mainly in nearshore areas and in fjords along the west coast of Spitsbergen and in Storfjorden. They have been less numerous along the northern coasts (Svein Rundtom Lufttransport, Longyearbyen, pers. comm.).

Observations of white whales recorded in the NP-fauna-data-base, noted from occasional interviews with trappers or made directly by the authors, are consistent with the information reported by white whale hunters. White whales have been most often observed in shallow waters near the mouths of rivers or at glacier fronts. Many of the major rivers in Svalbard are in the fjords of western Spitsbergen, especially in Isfjorden and Van Mijenfjorden. It is in these same areas that white whales are most frequently sighted. Any conclusion from these observations may, however, be somewhat biased as these fjords are where Svalbard's inhabitants live. This is especially true in the case of Longyearbyen. In summer large numbers of white whales can regularly be seen at the mouth of the Adventelva, the river just outside town.

If the theory that white whales arrived at Svalbard from the west is correct, then the herds would probably have followed the ice edge across the Greenland Sea in April or May. If so, they would have arrived at the northwest corner of Spitsbergen and split, with some herds moving southwards and others eastwards along the northern coasts. If unable to continue along the northern coasts because of heavy ice, the herds might have continued southwards. This could explain the occasionally very large herds observed along the northwest coast of Spitsbergen in May. Present knowledge does not, however, allow any conclusions as to the migratory routes of white whales to and from Svalbard. DNA studies and satellite telemetry could shed light on this subject.

Some white whales may winter in Svalbard. One of the crew at Isfjord Radio, situated at the mouth of Isfjorden, has observed white whales in winter, when there has been open water (Gustav Halsvik, Longyearbyen, pers. comm.). This information is supported by trappers from the north coast of Spitsbergen who have heard whales blowing in the pack ice. However in total winter darkness the animals could not be seen and might have been other species (Hans Bjelke pers. comm.).

Nearly 15 000 whales have been registered as killed in one century of Norwegian white whale hunting. This number must be considered a minimum since the official statistics are not very accurate. According to Iversen (1930) the numbers given for the Russian catch in the 18th and 19th centuries may well be too high, since white whale hides usually were split in two. It is therefore probable that the actual catch quoted by Isachsen (1916–1919) was 600 whales, with 1200 half-hides being recorded. If the pre-1940 statistics are as inaccurate as those after 1945 (Lønø & Øynes 1961) then the number of white whales actually killed in Svalbard is significantly greater than 15 000 animals.

At the turn of the last century catches of white whales were insignificant compared to those of the 1870s (Wollebæk 1901, Collett 1911–12). According to Ingebrigtsen (cited by Hjort 1902) the numbers of white whales in Svalbard had been dramatically reduced due to hunting. He believed that in 1891 there were not more than 400–500 whales left in Svalbard. These whales were believed to be site tenacious and to visit the same areas every year.

It is not possible to reach any conclusions about population size based on the data presently available. However since white whales have been protected during the last 30 years in Norwegian waters, the population at Svalbard is assumed to be secure. Further research on white whales in Norwegian waters is needed.

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Exploitation and status

Massauna Kristiansen at the edge in Hvalsund, Avanersuaq, NW Greenland. Photo: R. Dietz.

Prehistoric exploitation of white whales (*Delphinapterus leucas*) and narwhals (*Monodon monoceros*) in the eastern Canadian Arctic

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Zooarchaeological data relating to prehistoric Paleoeskimo (ca. 4000–1000 B.P.) and Neoeskimo (ca. 1000 B.P. to historic times) use of white whales (*Delphinapterus leucos*) and narwhals (*Monodon monoceros*) in the eastern Canadian Arctic are reviewed. Remains of these two species are extremely rare in Paleoeskimo sites, probably because of the lack of a sophisticated whale-hunting technology.

While white whale and narwhal remains are more common in Neoeskimo sites, they nevertheless make up relatively insignificant portions of the total faunal assemblages. Since Neoeskimos possessed a sophisticated whaling technology, the problem becomes one of explaining the general paucity of such remains. Four potential factors are addressed: a) taphonomy, b) processing and transport, c) lack of appropriate archaeological data and d) lack of these two species in the diet of Inuit during prehistoric and early historic times.

Key words:
White whale, beluga, *Delphinapterus leucas*, narwhal, *Monodon monoceros*, hunting, archaeology, Paleoeskimo, Thule Eskimo.

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Introduction

The hunting of white whales (*Delphinapterus leucas*) and narwhals (*Monodon monoceros*) is an important activity in many Inuit communities in the eastern Canadian Arctic, and a growing body of literature relates to this hunting in the context of whale population assessment and hunt management (*e.g.* Reeves & Mitchell 1987a, 1987b, Richard 1991a, 1991b, Richard *et al.* 1990, Richard & Pike 1993). Furthermore, ethnographic sources (*e.g.* Boas 1888, Mathiassen 1928, McGhee 1974) and major land-use and occupancy projects, based largely on oral history, document at least some use of white whales and narwhals by early historic Inuit societies in many areas of the Canadian Arctic (see *e.g.* Freeman 1976, Brice-Bennett 1977, Riewe 1992).

Small-whale hunting by prehistoric inhabitants of the eastern Canadian Arctic, however, has been virtually ignored. Instead, research into prehistoric whaling has focused almost exclusively on the nature and extent of the use of large baleen whales, primarily the bowhead (*Balaena mysticetus*; see *e.g.* reviews by McCartney 1984, Maxwell 1985, Savelle & McCartney 1990, McCartney & Savelle 1993). As a result, summaries of the prehistory of this region note that small cetaceans were certainly a part of the diet of coastal groups during much of the period of prehistoric occupation (*e.g.* Maxwell 1984, 1985, McGhee 1978), but do so primarily on the basis of circumstantial evidence, scattered references to occasional white whale or narwhal bone elements from archaeological sites, or ethnographic analogy.

While acknowledging that the lack of research on the hunting of white whales and narwhals in this context often results from the general paucity of identifiable small whale remains in prehistoric sites, we nevertheless lack any summary or overview of (1) the archaeological evidence for the use of these species (however limited that evidence may be), (2) how such use may have influenced other aspects of the societies or, alternatively, (3) why such abundant and potentially useful resources would have been, for the most part, ignored. Accordingly, this paper attempts to provide a synthesis of archaeological data relating to white whale and narwhal use in the

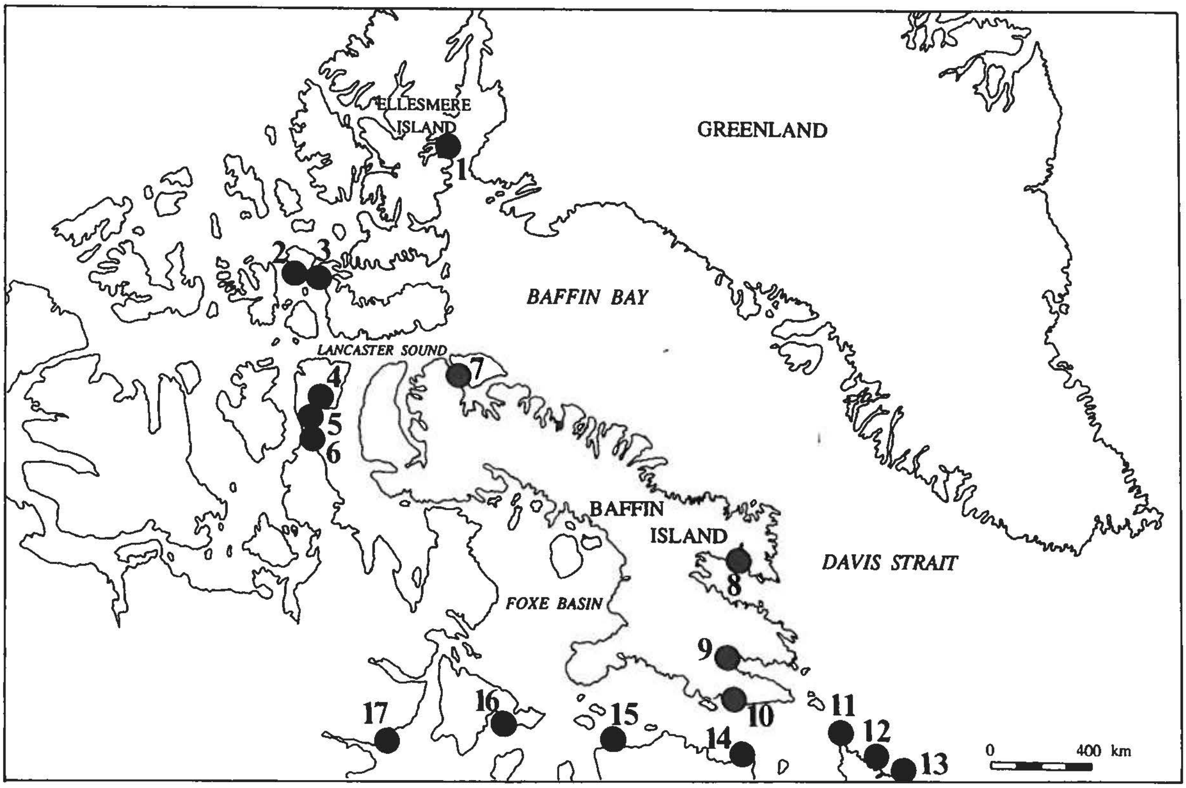

Fig. 1. Locations of archaeological sites or site complexes listed in Tables 1–12.
1. Ellesmere Island. 2. Port Refuge. 3. Porden Point. 4. Learmonth. 5. Cape Garry. 6. Hazard Inlet. 7. Navy Board Inlet. 8. Cumberland Sound. 9. Peale Point. 10. Talaguak. 11. Akulialuk. 12. Avayalik. 13. Koliktalik. 14. Diana Bay. 15. Tyara. 16. T-1 (Native Point). 17. Silumiut.

eastern Canadian Arctic. These data are then interpreted in the context of the historic and modern harvesting of these two species by Inuit.

Archaeological sites in the eastern Canadian Arctic are emphasized over those in Greenland because data from the Canadian sites are more amenable to geographical and temporal comparisons. However, when appropriate, data from Greenland are also incorporated. Furthermore, this study includes only those sites a) which lie within the historic, and by analogy prehistoric, ranges of white whales and narwhals and b) for which quantifiable faunal data are available. These sites are indicated in Fig. 1.

Archaeological evidence

Two major cultural complexes are recognized in the eastern Canadian Arctic and Greenland: Paleoeskimo and Neoeskimo. Both of these complexes are described in summary fashion in Maxwell (1985), Dumond (1987), and various papers in Damas (1984).

Paleoeskimo

Paleoeskimo incorporates the Independence I (ca. 4000–3700 B.P.), PreDorset (ca. 3700–2800 B.P.), Sarqaq (ca. 4000–2800 B.P.), Independence II (ca. 2000–1500 B.P.) and Dorset (ca. 2800–1000 B.P.) cultures. It originated to the west, in Alaska or possibly northeastern Asia. Coastal sites relating to this cultural complex occur throughout the Canadian High Arctic, along Hudson Bay and Hudson Strait, and in Labrador and Greenland. Although no whaling gear comparable in sophistication to that of Neoeskimo cultures (see below) has been identified, all the cultures listed above apparently possessed efficient sea-mammal harpoons, and Dorset, at least, apparently possessed some form of kayak (Maxwell 1985:137). Furthermore, it has been suggested that at least one type of large harpoon head (so far found only at an Early Dorset site in the Igloolik area) may have been used for hunting white whales (Maxwell 1985:115).

Unfortunately, we have relatively little information on faunal material from Paleoeskimo sites. While much of this lack of information is due to the generally poor organic preservation at many of the sites, it must also be admitted that much of the material that has been recovered has either not been identified or has not been described in detail in published work. Tables 1–6 provide summaries of the faunal material from representative coastal Paleoeskimo sites in the eastern Canadian Arctic. Although the level of identification and quantification is not always consistent, the number of identified specimens per taxon (NISP) can be used for comparisons in a rather gross fashion, as can the minimum number of individual animals per taxon (MNI).

Not unexpectedly, sea mammal remains predominate, with seals (and where differentiated, ringed seals; *Phoca hispida*) being by far the most common, followed in most areas by walruses (*Odobenus rosmarus*), and locally by caribou (*Rangifer tarandus*), foxes (*Alopex lagopus*) or birds. White whales and narwhals, on the other hand, are extremely rare. Bones identifiable to either of these two species, or indeterminate "small whale" species, have been reported at only three sites: Nunguvik in Navy Board Inlet, Tyara in northern Quebec and Avayalik-1 in northern Labrador, with NISP percentages ranging from 0.3% to 4.2%. Maxwell (1985:84) also referred to white whale remains from the Pre-Dorset Arnapik (northern Hudson Bay) and Port Refuge (Grinnell Peninsula, Devon Island) sites, which he interpreted as evidence of the hunting of small whales. However these remains consisted of only one vertebral disc and a narwhal tusk fragment, respectively.

In western Greenland preservation of faunal materials at Paleoeskimo sites is generally poor. Fitzhugh's (1984) summary of the archaeological data from Paleoeskimo sites in this region makes no reference to the hunting of small whales.

Neoeskimo

Neoeskimo includes the prehistoric Thule and the early historic and modern Inuit of the eastern Canadian Arctic and Greenland. For the purposes of this paper only the prehistoric Thule Eskimo culture will be considered.

Thule culture was originally defined and described by Mathiassen (1927) who, on the basis of structural whale bone in Thule dwellings, considered the hunting of bowhead whales a hallmark of the culture. Since Mathiassen's pioneering study, the initial development of Thule culture in Alaska prior to 1000 B.P., the migration of Thule Eskimos from Alaska across northern Canada into Greenland and the subsequent decline of the human population and abandonment of the High Arctic approximately 400–600 B.P., have all been related directly to the availability of bowhead whales (see *e.g.* McGhee 1969/70, McCartney 1977, and summaries in Maxwell 1985, Savelle & McCartney 1990). While some scholars, most notably Freeman (1979), have questioned the nature and extent of bowhead whaling by Thule Eskimos, there can be little doubt that bowheads played an extremely important role in the Thule diet, and consequently in their settlement systems, social organization and ideology (see *e.g.* McCartney 1980, Savelle & McCartney 1988, 1990, McCartney & Savelle 1993).

One component of Thule material culture directly related to bowhead whaling was the sophisticated whaling-gear complex. Items associated with this complex included specialized whaling harpoons and whaling lances, inflatable seal-skin floats, and kayaks and umiaks (*cf.* Maxwell 1985). Because Thule possessed a sophisticated whaling technology suitable for capturing bowheads, it has often been assumed that smaller cetaceans (primarily white whales and narwhals) were also hunted (or otherwise acquired) on a regular basis (Mitchell & Reeves 1981: 667 citing Kumlien 1879 and Schledermann 1975, Maxwell 1985: 263, Breton & Smith 1990:7). Although no specialized whaling equipment designed specifically for white whales or narwhals has been recognized, the assumption has been that the whaling gear used for bowheads would also have been used for these species, as would have the smaller "generic" harpoons, lances and related material (Maxwell 1985: 265–273).

Considerably more faunal material is available from Thule sites than from earlier Paleoeskimo sites, due in large part to the better preservation of organic material. Tables 7–12 provide summaries of faunal materials from representative coastal Thule sites in the eastern Canadian Arctic. As for the Paleoeskimo sites, the level of identification and quantification is not always consistent, but again the NISP and the MNI can be used for comparisons in a rather gross fashion. These tables do not include bowhead remains, since most such remains are incorporated within structures, making it less straightforward to judge these animals' role in the diet. However, the omission of bowhead remains is not a major concern, since the purpose of the comparisons presented here is to establish the relative importance of smaller cetaceans, compared with non-cetacean species, in the diet.

It is immediately apparent from the tables that, although white whale and narwhal remains are considerably more common in Neoeskimo sites than they are in Paleoeskimo sites, they still form very minor components of the assemblages relative to other species, whether based on NISP or MNI percentages. As previously noted by Savelle & McCartney (1988), ringed seal remains dominate almost all faunal assemblages from coastal Thule sites, with caribou, fox and bearded seal (*Erignathus barbatus*) remains often constituting secondary, but important, components (as discussed previously, this does not include bowhead whale elements). Thus, on the basis of recovered faunal material only, it could be suggested that white whales and narwhals contributed little to the diet of Thule Eskimos.

While comparative data from Greenland are not presented, the situation there is generally similar to that in the eastern Canadian Arctic. Mathiassen (1934:179), in commenting on the subsistence of, for example, prehis-

Table 1. Faunal remains from Paleoeskimo sites, Ellesmere Island.

	Sarqaq (Schledermann 1989)		
TAXA	NISP	%	MNI
White whale	–	–	–
Narwhal	–	–	–
Small whale indet.	–	–	–
Ringed seal	192	7.0	–
Harbor seal	–	–	–
Harp seal	6	0.2	–
Small seal	1947	71.5	–
Bearded seal	274	9.9	–
Large seal	60	2.2	–
Walrus	–	–	–
Caribou	2	<0.1	–
Musk-ox	127	4.7	–
Moose	–	–	–
Bear (polar/grizzly)	1	<0.1	–
Fox (arctic/red)	12	0.4	–
Dog	–	–	–
Wolf	–	–	–
Canid indet.	–	–	–
Wolverine	1	<0.1	–
Arctic Hare	15	0.6	–
Lemming	–	–	–
Birds	87	3.2	–
Fish	–	–	–
Shellfish	–	–	–
Ground squirrel	–	–	–
TOTAL	2724	100.0	–

Table 1. continued

	"Transitional" (Schledermann 1989)		
TAXA	NISP	%	MNI
White whale	–	–	–
Narwhal	–	–	–
Small whale indet.	–	–	–
Ringed seal	–	–	–
Harbor seal	–	–	–
Harp seal	–	–	–
Small seal	5	71.4	–
Bearded seal	–	–	–
Large seal	1	14.3	–
Walrus	1	14.3	–
Caribou	–	–	–
Musk-ox	–	–	–
Moose	–	–	–
Bear (polar/grizzly)	–	–	–
Fox (arctic/red)	–	–	–
Dog	–	–	–
Wolf	–	–	–
Canid indet.	–	–	–
Wolverine	–	–	–
Arctic Hare	–	–	–
Lemming	–	–	–
Birds	–	–	–
Fish	–	–	–
Shellfish	–	–	–
Ground squirrel	–	–	–
TOTAL	7	100.0	–

Table 1. continued

	Pre-Dorset (Schledermann 1989)		
TAXA	NISP	%	MNI
White whale	–	–	–
Narwhal	–	–	–
Small whale indet.	–	–	–
Ringed seal	–	–	–
Harbor seal	–	–	–
Harp seal	–	–	–
Small seal	303	76.9	–
Bearded seal	5	1.3	–
Large seal	49	12.4	–
Walrus	2	0.5	–
Caribou	2	0.5	–
Musk-ox	–	–	–
Moose	–	–	–
Bear (polar/grizzly)	–	–	–
Fox (arctic/red)	8	2.0	–
Dog	–	–	–
Wolf	–	–	–
Canid indet.	–	–	–
Wolverine	–	–	–
Arctic Hare	8	2.0	–
Lemming	–	–	–
Birds	17	4.3	–
Fish	–	–	–
Shellfish	–	–	–
Ground squirrel	–	–	–
TOTAL	394	99.9	–

Table 1. continued

	Early Dorset (Schledermann 1989)		
TAXA	NISP	%	MNI
White whale	–	–	–
Narwhal	–	–	–
Small whale indet.	–	–	–
Ringed seal	1	<0.1	–
Harbor seal	–	–	–
Harp seal	–	–	–
Small seal	780	54.5	–
Bearded seal	1	<0.1	–
Large seal	102	7.1	–
Walrus	78	5.5	–
Caribou	–	–	–
Musk-ox	–	–	–
Moose	–	–	–
Bear (polar/grizzly)	5	0.4	–
Fox (arctic/red)	66	4.6	–
Dog	–	–	–
Wolf		–	–
Canid indet.	1	<0.1	–
Wolverine	–	–	–
Arctic Hare	3	0.2	–
Lemming	–	–	–
Birds	395	27.6	–
Fish	–	–	–
Shellfish	–	–	–
Ground squirrel	–	–	–
TOTAL	1432	100.00	–

Table 1. continued

TAXA	Late Dorset (Schledermann 1989) NISP	%	MNI
White whale	–	–	–
Narwhal	–	–	–
Small whale indet.	–	–	–
Ringed seal	4	<0.1	–
Harbor seal	–	–	–
Harp seal	–	–	–
Small seal	1044	30.8	–
Bearded seal	33	1.0	–
Large seal	69	2.0	–
Walrus	107	3.2	–
Caribou	–	–	–
Musk-ox	11	0.3	–
Moose	–	–	–
Bear (polar/grizzly)	51	1.5	–
Fox (arctic/red)	219	6.5	–
Dog	–	–	–
Wolf	–	–	–
Canid indet.	4	<0.1	–
Wolverine	–	–	–
Arctic Hare	188	5.6	–
Lemming	30	0.9	–
Birds	1618	47.8	–
Fish	9	0.3	–
Shellfish	–	–	–
Ground squirrel	–	–	–
TOTAL	3387	100.0	–

Table 1. continued

TAXA	Other Paleoeskimo (Schledermann 1989) NISP	%	MNI
White whale	–	–	–
Narwhal	–	–	–
Small whale indet.	–	–	–
Ringed seal	–	–	–
Harbor seal	–	–	–
Harp seal	–	–	–
Small seal	1056	91.7	–
Bearded seal	5	0.4	–
Large seal	11	1.0	–
Walrus	9	0.8	–
Caribou	1	<0.1	–
Musk-ox	–	–	–
Moose	–	–	–
Bear (polar/grizzly)	2	0.2	–
Fox (arctic/red)	60	5.2	–
Dog	–	–	–
Wolf	–	–	–
Canid indet.	–	–	–
Wolverine	–	–	–
Arctic Hare	–	–	–
Lemmings	–	–	–
Birds	8	0.7	–
Fish	–	–	–
Shellfish	–	–	–
Ground squirrel	–	–	–
TOTAL	1152	100.0	–

Table 2. Faunal remains from Paleoeskimo sites, Grinnell Peninsula, Devon Island.

	Independence I Port Refuge (McGhee 1979)				Independence II Port Refuge (McGhee 1981)			
TAXA	NISP	%	MNI	%	NISP	%	MNI	%
White whale	–	–	–	–	–	–	–	–
Narwhal	–	–	–	–	–	–	–	–
Small whale indet.	–	–	–	–	–	–	–	–
Ringed seal	928	81.5	36	48.6	1335	93.2	18	62.1
Harbor seal	–	–	–	–	–	–	–	–
harp seal	–	–	–	–	–	–	–	–
Small seal	–	–	–	–	–	–	–	–
Bearded seal	49	4.3	6	8.1	4	0.3	1	3.4
Large seal	–	–	–	–	–	–	–	–
Walrus	–	–	–	–	1	0.1	1	3.4
Caribou	9	0.8	2	2.7	7	0.5	2	6.9
Musk-ox	–	–	–	–	–	–	–	–
Moose	–	–	–	–	–	–	–	–
Bear (polar/grizzly)	–	–	–	–	2	0.1	1	3.4
Fox (arctic/red)	92	8.1	12	16.2	80	5.6	4	13.8
Dog	–	–	–	–	–	–	–	–
Wolf	–	–	–	–	–	–	–	–
Canid indet.	1	<0.1	1	1.4	–	–	–	–
Wolverine	–	–	–	–	–	–	–	–
Arctic Hare	–	–	–	–	–	–	–	–
Lemming	–	–	–	–	–	–	–	–
Birds	60	5.3	17	23.0	3	0.2	2	6.9
Fish	–	–	–	–	–	–	–	–
Shellfish	–	–	–	–	–	–	–	–
Ground squirrel	–	–	–	–	–	–	–	–
TOTAL	1139	100.0	74	100.0	1432	100.0	29	99.9

Table 3. Faunal remains from Paleoeskimo sites, Navy Board Inlet, northern Baffin Island.

	Early Dorset (Mary-Rousselière 1976)			Middle Dorset (Mary-Rousselière 1976)			Late Dorset (Mary-Rousselière 1976)		
TAXA	NISP	%	MNI	NISP	%	MNI	NISP	%	MNI
White whale	–	–	–	–	–	–	–	–	–
Narwhal	–	–	–	–	–	–	–	–	–
Small whale indet.	79	4.2	–	–	–	–	22	2.8	–
Ringed seal	–	–	–	–	–	–	–	–	–
Harbor seal	–	–	–	–	–	–	–	–	–
Har seal	–	–	–	–	–	–	–	–	–
Small seal	474	25.4	–	13,208	83.9	–	147	18.6	–
Bearded seal	9	0.5	–	63	0.4	–	75	9.3	–
Large seal	–	–	–	–	–	–	–	–	–
Walrus	249	13.3	–	6	<0.1	–	50	6.3	–
Caribou	1044	55.9	–	1,181	7.5	–	302	37.9	–
Musk-ox	–	–	–	–	–	–	–	–	–
Moose	–	–	–	–	–	–	–	–	–
Bear (polar/grizzly)	–	–	–	2	<0.1	–	4	0.5	–
Fox (arctic/red)	–	–	–	693	4.4	–	31	3.9	–
Dog	–	–	–	–	–	–	2	0.2	–
Wolf	–	–	–	–	–	–	–	–	–
Canid indet.	–	–	–	–	–	–	–	–	–
Wolverine	–	–	–	–	–	–	–	–	–
Arctic Hare	–	–	–	394	2.5	–	6	0.7	–
Lemming	–	–	–	–	–	–	–	–	–
Birds	6	0.3	–	63	0.4	–	151	19.1	–
Fish	–	–	–	126	0.8	–	–	–	–
Shellfish	–	–	–	–	–	–	–	–	–
Ground squirrel	–	–	–	–	–	–	–	–	–
TOTAL	1861	99.6	–	15,736	100.0	–	788	99.3	–

Table 4. Faunal remains from Paleoeskimo sites (Middle Dorset), northern Labrador.

	Koliktalik-1 (Cox & Spiess 1980)			Akulialuk (Cox & Spiess 1980)			Avayalik-1 (Cox & Spiess 1980)		
TAXA*	NISP	%	MNI	NISP	%	MNI	NISP	%	MNI
White whale	–	–	–	–	–	–	–	–	–
Narwhal	–	–	–	–	–	–	–	–	–
Small whale indet.	–	–	–	–	–	–	6	0.3	–
Ringed seal	–	–	–	–	–	–	–	–	–
Harbor seal	–	–	–	–	–	–	–	–	–
Harp seal	–	–	–	–	–	–	–	–	–
Small seal	5223	98.3	–	609	98.5	–	898	52.9	–
Bearded seal	38	0.7	–	–	–	–	52	3.1	–
Large seal	–	–	–	–	–	–	–	–	–
Walrus	31	0.6	–	3	0.5	–	596	35.1	–
Caribou	3	0.1	–	5	0.8	–	28	1.6	–
Musk-ox	–	–	–	–	–	–	–	–	–
Moose	–	–	–	–	–	–	–	–	–
Bear (polar/grizzly)	6	0.1	–	1	0.2	–	42	2.5	–
Fox (arctic/red)	7	0.1	–	1	0.2	–	72	4.2	–
Dog	–	–	–	–	–	–	–	–	–
Wolf	–	–	–	–	–	–	–	–	–
Canid indet.	7	0.1	–	–	–	–	2	0.1	–
Wolverine	–	–	–	–	–	–	–	–	–
Arctic Hare	–	–	–	–	–	–	–	–	–
Lemming	–	–	–	–	–	–	–	–	–
Birds	–	–	–	–	–	–	–	–	–
Fish	–	–	–	–	–	–	–	–	–
Shellfish	–	–	–	–	–	–	–	–	–
Ground squirrel	–	–	–	–	–	–	–	–	–
TOTAL	5315	100.0	–	618	100.0	–	1696	99.8	–

*Mammalian bones only

Table 5. Faunal remains from Paleoeskimo sites (Dorset), northern Quebec.

	Diana Bay (Julien 1980)			Tyara (Taylor 1968)		
TAXA	NISP	%	MNI	NISP	%	MNI
White whale	–	–	–	46	1.9	–
Narwhal	–	–	–	–	–	–
Small whale indet.	–	–	–	–	–	–
Ringed seal	7	1.1	–	–	–	–
Harbor seal	–	–	–	–	–	–
Harp seal	–	–	–	–	–	–
Small seal	296	46.5	–	679	28.3	–
Bearded seal	15	2.4	–	589	24.5	–
Large seal	–	–	–	–	–	–
Walrus	44	6.9	–	445	18.5	–
Caribou	238	37.4	–	207	8.6	–
Musk-ox	–	–	–	–	–	–
Moose	–	–	–	–	–	–
Bear (polar/grizzly)	28	4.4	–	75	3.1	–
Fox (arctic/red)	–	–	–	130	5.4	–
Dog	–	–	–	–	–	–
Wolf	–	–	–	–	–	–
Canid indet.	–	–	–	–	–	–
Wolverine	–	–	–	–	–	–
Arctic Hare	–	–	–	–	–	
Lemming	–	–	–	–	–	–
Birds	8	1.3	–	231	9.6	–
Fish	–	–	–	–	–	–
Shellfish	–	–	–	–	–	–
Ground squirrel	–	–	–	–	–	–
TOTAL	636	100.0	–	2402	99.9	–

Table 6. Faunal remains from the T-1 Paleoeskimo site (Dorset), Southampton Island.

	(Cox & Spiess 1980)		
TAXA*	NISP	%	MNI
White whale	–	–	–
Narwhal	–	–	–
Small whale indet.	–	–	–
Ringed seal	–	–	–
Harbor seal	–	–	–
Harp seal	–	–	–
Small seal	2426	62.6	–
Bearded seal	304	7.8	–
Walrus	438	11.3	–
Caribou	29	0.7	–
Musk-ox	–	–	–
Moose	–	–	–
Bear (polar/grizzly)	17	0.4	–
Fox (arctic/red)	659	17.0	–
Dog	–	–	–
Wolf	–	–	–
Canid indet.	–	–	–
Wolverine	–	–	–
Arctic Hare	–	–	–
Lemming	–	–	–
Birds	–	–	–
Fish	–	–	–
Shellfish	–	–	–
Ground squirrel	–	–	–
TOTAL	3873	99.8	–

*Mammalian bone only

toric Neoeskimo groups in the Disko Bugt region, concluded that sealing was "the principal occupation", that caribou were next in importance after seals and bowheads, and that walruses, narwhals and white whales were "caught occasionally, but scarcely in any great numbers."

Interpretation

There are at least four possible reasons for the general paucity of white whale and narwhal remains from archaeological sites in the eastern Canadian Arctic, each of which will be discussed in turn.

Taphonomy

Organic decay and chemical and mechanical weathering (see *e.g.* Lyman 1984, 1985) are the most important taphonomic factors that affect faunal assemblages. However, these factors are unlikely to have caused a decrease in the relative abundance of white whale and narwhal remains at the various sites, since the bones of most of the other species represented in the same faunal assemblages are thinner, less dense or more delicate (*cf.* Wall 1983).

Table 7. Faunal remains from Thule sites, Ellesmere Island.

TAXA	(McCullough 1989) NISP	%	MNI	%
White whale	–	–	–	–
Narwhal	–	–	–	–
Small whale indet.	–	–	–	–
Ringed seal	–	–	–	–
Harbor seal	–	–	–	–
Harp seal	–	–	–	–
Small seal	10,197	65.3	238	44.8
Bearded seal	–	–	–	–
Large seal	379	2.4	34	6.4
Walrus	1097	7.0	53	10.0
Caribou	7	<0.1	–	–
Musk-ox	148	0.9	24	4.5
Moose	–	–	–	–
Bear (polar/grizzly)	357	2.3	35	6.6
Fox (arctic/red)	2073	13.3	76	14.3
Dog	–	–	–	–
Wolf	–	–	–	–
Canid indet.	1015	6.5	55	10.4
Wolverine	–	–	–	–
Arctic Hare	86	0.6	15	2.8
Lemming	1	<0.1	1	0.2
Birds	270	1.7	–	–
Fish	–	–	–	–
Shellfish	–	–	–	–
Ground squirrel	–	–	–	–
TOTAL	15,630	100.0	531	100.0

The reverse outcome should in fact be expected – that is, the white whale and narwhal would be over-represented relative to other species (except the bowhead) in comparison to the faunal assemblage as originally deposited.

Processing and Transport

It might be argued that given the size and weight of individual white whales and narwhals, relatively few of their bone elements would have originally been transported from the kill site to the residential site (*i.e.* place of consumption). Instead much of the mattak (edible skin), meat and blubber would have been selectively removed (culled) and transported (see *e.g.* Figs 2 & 3), leaving almost complete skeletons at the kill sites (Fig. 4). Culling and transport are important considerations (see *e.g.* Binford 1978, Metcalfe & Jones 1988, O'Connell *et al.* 1988), and there is no doubt that some culling would have taken place. However there are several lines of argument that could be made against selective culling and transport being primary determinants in this context.

First, "traditional" Inuit societies that engaged in intensive white whale hunting have been documented both ethnographically and archaeologically in the Mackenzie Delta region of the western Canadian Arctic. McGhee (1974), citing ethnohistorical accounts, described inten-

Table 8. Faunal remains from Thule sites, Porden Point, Grinnell Peninsula, Devon Island.

TAXA	(Park 1983) NISP	%	MNI	(Park 1989) NISP	%	MNI	%
White whale	–	–	–	17	0.2	3	0.8
Narwhal	–	–	–	–	–	–	–
Small whale indet.	1	0.1	–	–	–	–	–
Ringed seal	315	33.8	–	–	–	–	–
Harbor seal	–	–	–	–	–	–	–
Harp seal	6	0.6	–	–	–	–	–
Small seal	332	35.6	–	8654	80.3	171	44.2
Bearded seal	15	1.6	–	64	0.6	12	3.1
Large seal	–	–	–	–	–	–	–
Walrus	1	0.1	–	45	0.4	11	2.8
Caribou	19	2.0	–	119	1.1	13	3.4
Musk-ox	2	0.2	–	10	0.1	6	1.5
Moose	–	–	–	–	–	–	–
Bear (polar/grizzly)	12	1.3	–	132	1.2	17	4.4
Fox (arctic/red)	194	20.8	–	1250	11.6	47	12.1
Dog	6	0.6	–	193	1.8	19	4.9
Wolf	–	–	–	2	<0.1	1	0.3
Canid indet.	13	1.4	–	–	–	–	–
Wolverine	–	–	–	–	–	–	–
Arctic Hare	–	–	–	13	0.1	6	1.5
Lemming	–	–	–	–	–	–	–
Birds	17	1.8	–	257	2.4	71	18.4
Fish	–	–	–	27	0.2	10	2.6
Shellfish	–	–	–	–	–	–	–
Ground squirrel	–	–	–	–	–	–	–
TOTAL	933	99.9	–	10,783	100.0	387	100.0

Table 9. Faunal remains from Thule sites, Somerset Island.

	Learmonth (Taylor & McGhee 1979)			Learmonth (Rick 1980)				Cape Garry (Rick 1980)				Hazard Inlet (Whitridge 1992)			
TAXA	NISP	%	MNI	NISP	%	MNI	%	NISP	%	MNI	%	NISP	%	MNI	%
White whale	10	0.3	–	–	–	–	–	–	–	–	–	–	–	–	–
Narwhal	3	0.1	–	–	–	–	–	–	–	–	–	–	–	–	–
Small whale indet.	–	–	–	–	–	–	–	–	–	–	–	6	0.1	1	0.6
Ringed seal	2,155	63.9	–	850	57.1	19	19.2	2,100	73.4	32	21.2	7230	76.6	77	43.5
Harbor seal	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Harp seal	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Small seal	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Bearded seal	207	6.1	–	9	0.6	2	2.0	19	0.7	3	2.0	50	0.5	3	1.7
Large seal	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Walrus	113	3.4	–	4	0.3	1	1.0	1	<0.1	1	0.7	1	<0.1	1	0.6
Caribou	270	8.0	–	45	3.0	2	2.0	42	1.5	3	2.0	93	1.0	3	1.7
Musk-ox	4	0.1	–	24	1.6	3	3.0	9	0.3	3	2.0	2	<0.1	1	0.6
Moose	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Bear (polar/grizzly)	105	3.1	–	25	1.7	5	5.1	21	0.7	2	1.3	13	0.1	2	1.1
Fox (arctic/red)	137	4.1	–	400	26.9	37	37.4	410	14.3	59	39.1	1071	11.4	20	11.3
Dog	–	–	–	–	–	–	–	–	–	–	–	7	0.1	3	1.7
Wolf	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Canid indet.	146	4.3	–	28	1.9	4	4.0	55	1.9	11	7.3	111	1.2	1	0.6
Wolverine	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Arctic Hare	43	1.3	–	2	0.1	1	1.0	1	<0.1	1	0.7	32	0.3	3	1.7
Lemming	–	–	–	1	<0.1	1	1.0	70	2.5	4	2.6	150	1.6	16	9.0
Birds	180	5.3	–	101	6.8	24	24.3	133	4.6	31	20.5	654	6.9	45	25.4
Fish	–	–	–	–	–	–	–	1	<0.1	1	0.7	14	0.1	1	0.6
Shellfish	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ground squirrel	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
TOTAL	3,373	100.0	–	1,489	100.0	99	100.0	2.862	99.9	151	100.1	9434	99.9	177	100.1

Table 10. Faunal remains from the Nungavik site (early to late Thule), Navy Board Inlet, northern Baffin Island.

	Nungavik 52 (early Thule) (Mary-Rousselière 1976)			Nungavik 42 (early Thule) (Mary-Rousselière 1976)			Nungavik 15, 17, 21 (late Thule) (Mary-Rousselière 1976)		
TAXA	NISP	%	MNI	NISP	%	MNI	NISP	%	MNI
White whale	–	–	–	–	–	–	–	–	–
Narwhal	–	–	–	–	–	–	–	–	–
Small whale indet.	20	1.0	–	43	3.7	–	49	5.8	–
Ringed seal	–	–	–	–	–	–	–	–	–
Harbor seal	–	–	–	–	–	–	–	–	–
Harp seal	–	–	–	–	–	–	–	–	–
Small seal	776	37.0	–	640	54.9	–	471	56.3	–
Bearded seal	35	1.7	–	56	4.8	–	26	3.1	–
Large seal	–	–	–	–	–	–	–	–	–
Walrus	119	5.7	–	45	3.8	–	113	13.5	–
Caribou	1118	53.3	–	376	32.2	–	171	20.4	–
Musk-ox	–	–	–	–	–	–	–	–	–
Moose	–	–	–	–	–	–	–	–	–
Bear (polar/grizzly)	2	0.1	–	1	0.1	–	7	0.8	–
Fox (arctic/red)	–	–	–	3	0.3	–	–	–	–
Dog	9	0.4	–	1	0.1	–	–	< –	–
Wolf	–	–	–	–	–	–	–	–	–
Canid indet.	–	–	–	–	–	–	–	–	–
Wolverine	–	–	–	–	–	–	–	–	–
Arctic Hare	–	–	–	1	0.1	–	–	–	–
Lemming	–	–	–	–	–	–	–	–	–
Birds	18	0.9	–	–	–	–	–	–	–
Fish	–	–	–	–	–	–	–	–	–
Shellfish	–	–	–	–	–	–	–	–	–
Ground squirrel	–	–	–	–	–	–	–	–	–
TOTAL	2097	100.1	–	1166	100.0	–	837	99.9	–

Table 11. Faunal remains from Thule sites, southern and eastern Baffin Island.

	Cumberland Sound (Schledermann 1975)				Peale Pt. (Stenton 1983)				Talaguak (Sabo 1981)			
TAXA	NISP	%	MNI	%	NISP	%	MNI	%	NISP	%	MNI	%
White whale	15	0.4	2	1.6	39	0.4	4	1.2	4	0.2	2	1.0
Narwhal	–	–	–	–	5	0.1	1	0.3	–	–	–	–
Small whale indet.	–	–	–	–	–	–	–	–	–	–	–	–
Ringed seal	3469	93.6	92	72.4	7,400	78.3	191	57.5	1,864	46.1	112	57.1
Harbor seal	–	–	–	–	–	–	–	–	–	–	–	–
Harp seal	55	1.5	7	5.5	48	0.5	17	5.1	–	–	–	–
Small seal	–	–	–	–	–	–	–	–	–	–	–	–
Bearded seal	26	0.7	4	3.2	166	1.8	13	3.9	153	3.8	10	5.1
Large seal	–	–	–	–	–	–	–	–	–	–	–	
Walrus	–	–	–	–	43	0.5	3	0.9	–	–	6	3.1
Caribou	103	2.8	5	3.9	1,241	13.1	43	13.0	1,823	45.1	28	14.3
Musk-ox	–	–	–	–	–	–	–	–	–	–	–	–
Moose	–	–	–	–	–	–	–	–	–	–	–	–
Bear (polar/grizzly)	1	<0.1	1	0.8	11	0.1	3	0.9	11	0.3	5	2.6
Fox (arctic/red)	–	–	–	–	50	0.5	14	4.2	43	1.1	8	4.1
Dog	33	0.9	14	11.0	407	4.3	30	9.0	–	–	–	–
Wolf	–	–	–	–	1	<0.1	1	0.3	–	–	–	–
Canid indet.	–	–	–	–	–	–	–	–	59	1.5	12	6.1
Wolverine	–	–	–	–	–	–	–	–	–	–	–	–
Arctic Hare	3	0.1	1	0.8	1	<0.1	1	0.3	2	<0.1	2	1.0
Lemming	–	–	–	–	3	<0.1	2	0.6	–	–	–	–
Birds	1	<0.1	1	0.8	33	0.3	9	2.7	84	2.1	11	5.6
Fish	–	–	–	–	–	–	–	–	–	–	–	–
Shellfish	–	–	–	–	–	–	–	–	–	–	–	–
Ground squirrel	–	–	–	–	–	–	–	–	–	–	–	–
TOTAL	3706	100.0	127	100.0	9,448	100.0	332	99.9	4,045	100.0	196	100.0

Table 12. Faunal remains from the Silimiut site (Thule), northwest Hudson Bay.

	(Staab 1979)			
TAXA	NISP	%	MNI	%
White whale	–	–	–	–
Narwhal	–	–	–	–
Small whale indet.	–	–	–	–
Ringed seal	11,177	61.0	309	41.6
Harbor seal	31	0.2	13	1.7
Harp seal	–	–	–	–
Small seal	–	–	–	–
Bearded seal	1,204	6.6	54	7.3
Walrus	706	3.9	34	4.6
Caribou	4,310	23.5	150	20.2
Musk-ox	113	0.6	11	1.5
Moose	–	–	–	–
Bear (polar/grizzly)	–	–	–	–
Fox (arctic/red)	243	1.3	27	3.6
Dog	92	0.5	21	2.8
Wolf	53	0.3	8	1.1
Canid indet.	59	0.3	14	1.9
Wolverine	3	0	3	0.4
Arctic Hare	5	0	4	0.5
Lemming	–	–	–	–
Birds	133	0.7	45	6.1
Fish	108	0.6	17	2.3
Shellfish	81	0.4	33	4.5
Ground squirrel	–	–	–	–
TOTAL	18,318	99.9	743	100.1

sive hunting of white whales by two Mackenzie Inuit groups, the Kupugmiut and Kittegaryumiut. Both of these groups employed a system of driving whales into shallow water where they became trapped or grounded. McGhee excavated two late prehistoric and early historic coastal winter residential sites in the area historically occupied by these groups, and the recovered faunal remains are summarized in Table 13. The differences between these assemblages and those from the eastern Canadian Arctic are striking. NISP percentages for white whales range from 62% to 87% in McGhee's assemblages, which contrast sharply with the range of 0.0% to 2.1% for eastern Canadian Arctic sites. While MNI percentages were not provided by McGhee, there is no doubt that white whales would comprise the bulk of the diet represented by the faunal assemblages. Similarly 2266 (31%) of the 7343 bone elements recovered from the prehistoric Gupuk residential site, also in the Mackenzie Delta, were from white whales (Friesen & Arnold 1993). The above two examples suggest that intensive (that is, through the use of mass killing techniques) white whale hunting can indeed result in faunal assemblages dominated by white whales.

Second, sites for processing or caching white whales and narwhals have yet to be identified in the eastern Canadian Arctic (see also below). While taphonomic factors such as dispersal of carcasses by tides, currents or scavengers are important in this context, we would still

Fig. 2. Processing narwhals close to the kill site, Creswell Bay, Somerset Island, August 1989. The processing site is approximately 3 km from the residential site. Photo: J. M. Savelle.

expect at least an occasional special-purpose processing or caching site to have been recognized (see *e.g.* Fig. 4).

Lack of Appropriate Archaeological Data

The argument could be made that archaeologists have not addressed the problem of white whale and narwhal hunting in a systematic fashion. In other words, archaeological projects have been conducted with other, very different, research goals, and thus any data relating to the use of white whales or narwhals have been collected only incidentally. Recognizable primary processing or caching sites, or summer and fall camps located specifically for the hunting of white whales or narwhals (and thus probably containing abundant remains of these whales), for example, may exist, but appropriate surveys have not been made to locate them. In this regard it is significant that all of the faunal material summarized in Tables 7–12 is from winter residential sites.

With this problem in mind, two related projects have recently been initiated. The first is the detailed survey and excavation of summer and fall, as well as winter, Thule residential features on southeastern Somerset Island begun by the author in 1988. These coastal features are well within the present range of white whales and narwhals. Of over 10 000 animal bones from these features thus far identified, less than two dozen can be positively identified as either white whale or narwhal.

The second project has involved aerial and ground surveys to locate prehistoric archaeological sites which might relate to intensive white whale use in particular. These surveys were conducted in collaboration with Allen McCartney (University of Arkansas, Fayetteville, Arkansas) in 1988, and with Thomas G. Smith (Pacific Biological Station, Nanaimo, British Columbia) in 1991, 1992 and 1993. They concentrated upon the detailed examination of areas near known seasonal concentrations of white whales along the coasts of Somerset Island and southern Devon Island. These concentrations are centered primarily in major estuaries and bays (see Figs 5 & 6; see also Sergeant & Brodie 1975, Smith *et al.* 1985), many of which could have functioned as natural "traps". Given that white whales are at least to some extent site tenacious (Caron & Smith 1990), it seems reasonable to suggest that similar concentrations occurred at the same sites during much of the recent prehistoric period (*i.e.* 1000

Fig. 3. Narwhal mattak and blubber in a cache at Creswell Bay, Somerset Island, August 1989. The caching site is approximately 1.5 km from the residential site. Photo: J. M. Savelle.

B.P. onwards). The rationale for these surveys was that if prehistoric Inuit were exploiting white whales to any significant degree in the Somerset Island-southern Devon Island area, they would have tended to do so at localities of major accessible concentrations. The remains of whaling camps and processing and caching sites would be expected adjacent to these localities.

At only one locality, Fellfoot Point on the southeastern corner of Maxwell Bay, was there any evidence of extensive prehistoric white whale use. A site at this locality consists of at least 15 shallow, semi-subterranean dwellings, most of which are probably Thule, with at least 10 white whale skulls in apparent association. If the skulls are indeed associated with the Thule dwellings, this site is unique within the surveyed areas. Otherwise, the surveys have yielded no evidence of significant white whale (or narwhal) use. Furthermore, at the sites in the surveyed areas for which we have quantitative data (Learmonth and Cape Garry, adjacent to the Creswell River white whale concentration – see Fig. 1 & Table 9) white whale and narwhal bone elements range from 0.0% to 0.4% of the NISP for the total assemblages.

Contribution to Diet

The final, and certainly the most parsimonious line of argument, is simply that the white whale and the narwhal rarely formed a significant part of the diet of prehistoric Inuit of the eastern Canadian Arctic. Given the archaeological data and discussions thereof presented above, this would seem to be a reasonable interpretation. However, here we are faced with a situation, alluded to above, in which we have very little data from summer or fall sites – the recent study of Thule sites on southeastern Somerset Island being an exception. It is precisely at these sites that we would expect the majority of white whale and narwhal remains if these species were being hunted to any significant degree.

Discussion

The archaeological data available at present are inadequate to draw any firm conclusions regarding the nature and extent of white whale and narwhal use by prehistoric Inuit in the eastern Canadian Arctic. Clearly, additional

Fig. 4. Narwhal remains at Creswell Bay several years after processing. This processing site is approximately 1.5 km from the contemporaneous residential site. August 1993. Photo: J. M. Savelle.

research designed specifically with this goal in mind is needed. The potential problems of taphonomy, processing and transport, and inadequate surveys and excavation will need to be addressed. Detailed studies of processing and transport, and of "seasonal" summer and fall sites, are especially critical in this regard. However, if the overall lack of white whale and narwhal bones at archaeological sites is taken to suggest that (with some exceptions) these species did not contribute significantly to the diets of prehistoric inhabitants of the eastern Canadian Arctic, the question arises of why such abundant and valuable resources would have been largely ignored.

For Paleoeskimo groups the answer would appear to relate primarily to technology. Specifically, Paleoeskimos lacked an elaborate whaling technology. Although watercraft, perhaps kayaks, may have been used at least by Dorset Eskimos, there is no evidence that Paleoeskimos made extensive use of boats. While other large sea mammals such as walruses and bearded seals could have been taken without specialized equipment, the capture of white whales and narwhals without boats, harpoons and floats would probably have been extremely difficult.

Thule Eskimos, on the other hand, possessed sophisticated whaling gear such as specialized harpoons and lances, floats and possibly drags, and kayaks and umiaks (large open boats traditionally associated with whale hunting – see *e.g.* Maxwell 1985, Dumond 1987). Although most of these were originally designed for large baleen whales, such gear could be, and was, used for white whales and narwhals during the historic period (see *e.g.* Lyon 1824, Birket-Smith 1924, Nelson 1969).

If in fact Thule Eskimos were not actively hunting white whales and narwhals, one possible explanation may lie in the scheduling of subsistence activities. Hunter-gatherer societies in marginal areas that rely primarily on storage, as do many arctic groups, and certainly as the prehistoric Thule did, typically follow structured and predictable (but relatively inflexible) annual rounds (*cf.* Bettinger 1991: 69–70). It has been suggested that hunter-gatherer subsistence behaviour, as reflected by these annual rounds, can be considered optimizing behaviour (*cf.* Winterhalder 1981, Bettinger 1991). Since, for the most part, prehistoric Thule subsistence in the eastern Canadian Arctic was based on the bowhead whale, residential and logistical organization during the open-water whaling season would have been focused specifically on that resource (see *e.g.* Savelle 1987, Savelle & McCartney 1988). Accordingly, other resources, although seasonally available and harvestable with Thule technology, would have been essentially ignored during the bowhead

Table 13. Faunal remains from late prehistoric and early historic sites on the Mackenzie Delta reported by McGhee (1974).

	Kittigazuit			
	M-1 NISP = 338	M-2 NISP = 177	M-4 NISP = 1357	'Old House' NISP = 217
white whale	80%	79%	87%	81%
caribou	17%	13%	7%	12%
waterfowl	2%	4%	3%	4%
ringed seal	1%	3%	2%	–
moose	–	0.5%	1%	–
fox	–	–	–	3%
	Radio Creek NISP = 386			
white whale	62%			
caribou	30%			
waterfowl	present			
ringed seal	present			
fox	2%			
wolf	3%			
'bird'	present			

whaling season (unless they could be "co-harvested" within the residential and logistical constraints imposed by bowhead hunting – see *e.g.* Nelson 1969: 213). In those areas (*e.g.* most of the Canadian High Arctic Islands) where bowheads, white whales and narwhals are all available during approximately the same period (late

Fig. 5. White whale concentration at an estuary near Wadworth Island, northwestern Somerset Island (see Fig. 6). Photo: J. M. Savelle.

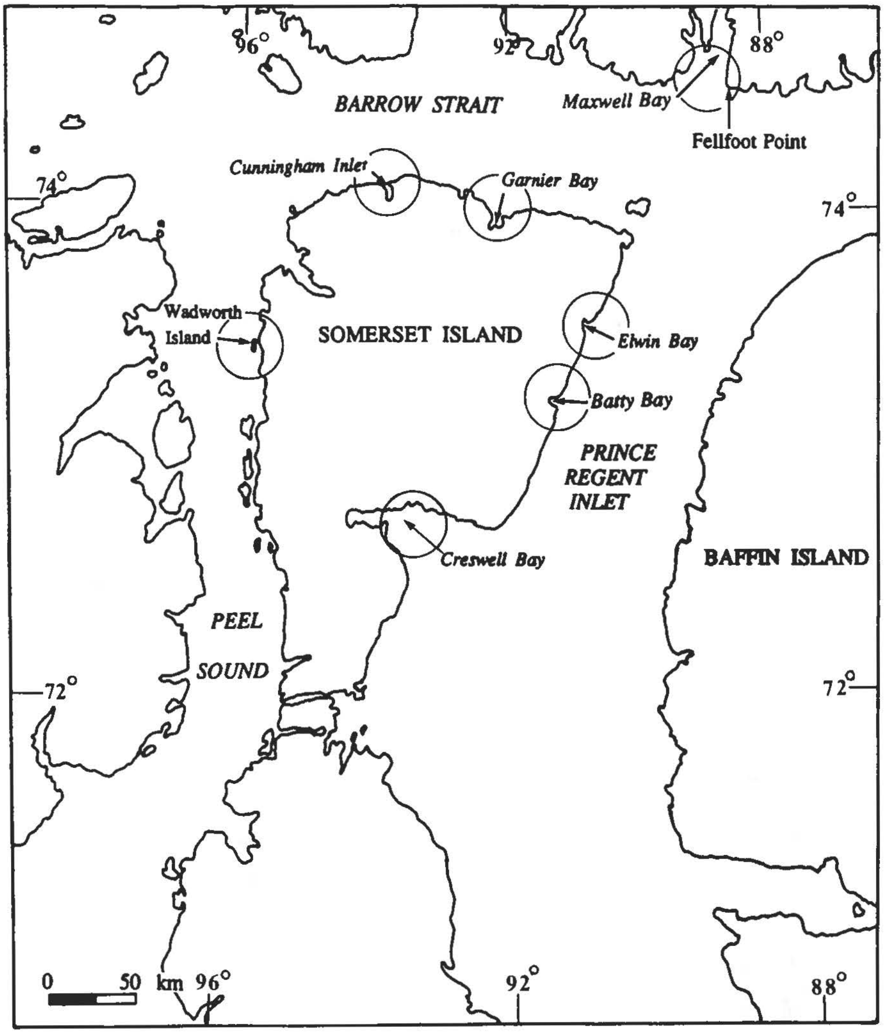

Fig. 6. Locations of known major white whale concentrations (indicated by circles) along the coasts of Somerset and southwest Devon islands that were surveyed for archaeological sites (data from Sergeant & Brodie 1975, Smith *et al.* 1985, T. G. Smith 1992 pers. comm.).

summer and early fall), any major effort to acquire smaller whales would have lessened the chances of success in the bowhead hunt.

If the suggestion that most Thule groups ignored white whales and narwhals is correct, the question arises of why the hunting of these species in the eastern Canadian Arctic (and Greenland) was apparently quite common during the early historic period (*i.e.* at the time of first contact by explorers, missionaries, ethnographers, *etc.*)

The most parsimonious explanation relates to bowhead whale availability. Specifically, it has been suggested by several authors (see *e.g.* McGhee 1969/70, McCartney 1977) that deteriorating climatic conditions beginning approximately 800 years B.P. and culminating in what has been termed the Little Ice Age of approximately 400–100 B.P., resulted in a decrease in the abundance and predictability of bowhead whales. Consequently, Thule expanded their diet breadth to include a) an increased diversity of harvested resources and b) an increased use of resources that had previously been ranked as secondary (see *e.g.* Savelle & McCartney 1988). Accordingly, white whale and narwhal use would have increased amongst those groups that occasionally harvested these species, and possibly would have added to the diet of those groups that had not harvested them at all.

The above scenario, of course, is based on the premise that there was substantial use of white whales and narwhals by many traditional Inuit societies during the early historic period. While beyond the scope of this paper, a detailed investigation of early historic sources may suggest that it was mainly after the introduction of new technologies (*e.g.* firearms, nets, motorized boats) that allowed more efficient whale harvesting, and the development of European and Euroamerican markets for whale products, that substantial white whale and narwhal hunting took place.

Conclusions

Identifiable remains of white whales and narwhals are, with very few exceptions, absent at Paleoeskimo (ca. 4000–1000 B.P.), and rare at Thule Eskimo (ca. 1000–400 B.P.), archaeological sites in the eastern Canadian Arctic. The lack of remains of these species at Paleoeskimo sites can most readily be explained by the lack of an appropriate whaling technology.

Thule Eskimos, on the other hand, possessed a sophisticated whaling technology. The paucity of white whale and narwhal remains at Thule sites can more readily be attributed to one, or more, of the following: a) taphonomic factors, b) processing and transport, c) lack of surveys for, and excavations of, appropriate sites, or d) a relatively low contribution to the Thule diet due to scheduling conflicts with other, higher-ranked resources, primarily the bowhead whale.

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Commercial aspects of the exploitation of narwhals (*Monodon monoceros*) in Greenland, with emphasis on tusk exports

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Reeves, R. R. and Heide-Jørgensen, M. P. 1994. Commercial aspects of the exploitation of narwhals (*Monodon monoceros*) in Greenland, with emphasis on tusk exports. – Meddr. Grønland, Biosci. 39: 119–134. Copenhagen 1994-04-22.

This study presents and evaluates data on recent commercial exchanges in narwhal (*Monodon monoceros*) products, particularly tusks, from Greenland. No evidence was found of an export trade in narwhal blubber or skin (mattak), but since the mid-1960s mattak has been sold to the Royal Greenland Trade Department (or more recently Royal Greenland Production) for re-sale within Greenland. Since 1977 the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) has required documentation for the international trade in narwhal tusks. The Greenland Home Rule Government assumed responsibility for this documentation beginning in 1985. More than 90% of the tusks exported with CITES permits issued by the Home Rule Government have given Denmark as the declared destination. Of the total tusks re-exported from Denmark with CITES documentation between 1985 and 1992, approximately two-thirds had the United Kingdom as the declared destination. The monetary value of an "average" tusk-bearing narwhal to a Greenlandic hunter in 1990 was estimated as 7632 Dkr (1272 US dollars). This estimate includes the tusk (6 kg), mattak (80 kg) and meat (46 kg) that were sold but makes no allowance for the products consumed by the hunter and his family. The cash value of narwhal products has not diminished in spite of high inflation in Greenland since the late 1960s.

Key words:
Narwhal, *Monodon monoceros*, tusks, exports, commercial trade.

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Introduction

The narwhal (*Monodon monoceros*) has long been an important game animal in Greenland. It provided several essential items for the Inuit who, since more than a thousand years ago, subsisted along the narrow strips of habitable land between the ice cap and the sea. In this ancient economy the most important products from narwhals were probably blubber for lamp fuel, red meat for human and dog food, skin (mattak), liver and heart for human food and sinew for thread.

In this paper we focus on the commercial distribution of narwhal tusks that originate in Greenland and are exported. The domestic selling of narwhal mattak (skin with adhering blubber) and red meat is also considered, but in less detail. Our main objectives are to: (1) provide a brief historical context for the current trade in narwhal products, (2) specifically examine the nature and extent of the Greenlandic narwhal tusk trade since 1985 when permits became a requirement for exports, (3) evaluate the present economic significance of narwhal products in Greenland, (4) review legal aspects of the commerce in narwhal products and (5) consider the potential conservation significance of such trade.

Materials and methods

For historical information we relied on published sources and a few unpublished reports with limited distribution. For recent information (since 1985) we also depended on our own observations in Greenland and on data obtained from the files of the Greenland Home Rule Secretariat (Grønlands Hjemmestyre Sekretariatet, Nuuk) and the

Danish National Forest and Nature Agency (Skov- og Naturstyrelsen, Ministry of the Environment, Copenhagen).

We examined the export permits issued under the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) by the Home Rule Government in the years 1985, 1986 (part only), 1988 and 1989. Data were extracted from the 1986 (missing part), 1987, 1990, 1991 and 1992 permits on our behalf by H. Thing, H. Lykke, K. Mortensen and P. Nielsen of the Home Rule Government's Environment and Nature Section (Miljø- og Naturafdelingen), Department of Health and Environment (Direktoratet for Sundhed og Miljø). For each permit examined we recorded the permit number, date issued, kind and number of items (*e.g.* tusks, carvings) and declared export destination. For some of the permits we also obtained information on the weight, length and condition (broken or not) of tusks, or on the more exact character of carvings (*e.g.* necklaces, crochet needles, letter knives, tupilaks).

Re-export data from Denmark for the period 1 January 1985 to 31 December 1992 were supplied to us by the National Forest and Nature Agency as lists, usually including destination, date, number of items, purpose (*e.g.* trade, exhibition, scientific, personal) and origin (mostly Greenland but occasionally Canada). For some of the entries, information was also given on total weight of the shipment, the original export permit number from the country of origin and the Danish re-export permit number. The Agency also provided lists of the numbers of narwhal tusks and carvings imported by Denmark in the years 1985–1990 and a more detailed list of imports recorded in 1992. The latter includes, for each transaction, the type of item, quantity, purpose, country of origin, declared destination and permit number (if available).

As part of this study we also searched the annual reports on wildlife trade published by the European Community (Commission of the European Communities 1987–92), and we received from TRAFFIC International, Cambridge, UK, a list, compiled from the annual reports of the CITES Parties (K. Lochen, TRAFFIC International, pers. comm. July 1993), showing all CITES transactions involving narwhal products, 1979–1991 (current to 6 July 1993). The data from these sources were used to supplement and evaluate the data obtained directly from the national CITES authorities in Greenland and Denmark.

For tabulating export, import and re-export data, we treated the source closest to the initial documentation as the most authoritative. In other words, we preferred to use information obtained by examining the CITES permits ourselves. As a second choice we relied on extracts provided directly to us by the national CITES authorities. Only when the information could not be obtained from one of these procedures did we depend on tertiary sources such as the TRAFFIC International compilation. Slight differences are unavoidable between lists made by different persons examining the same permits. For example, it is sometimes unclear whether an item described on a permit as a "little tooth" is in fact a small erupted tusk, a tusk tip or even an embedded (unerupted) tooth. It is not possible to judge whether a tusk tip came from a particular broken tusk, in which case two separate transactions could refer to the tusk products of a single whale. It is also unclear how such items as "scraps" of ivory, parts of "teeth" and tusk pieces should be listed. They are not carvings or craft items but neither are they whole tusks. As far as we know, bidental skulls ("double-tuskers") are generally listed as two tusks even though each set represents only one killed whale.

We made enquiries to all local stores of the Greenland Trade Department (Kalaallit Niuerfiat, or KNI) concerning purchases and sales of narwhal tusks and to all Royal Greenland Production facilities concerning purchases and sales of mattak and meat (*cf.* Heide-Jørgensen 1994). We attempted to obtain more information on purchases of narwhal tusks by the Royal Greenland Trade Department between 1957 and 1985 but were advised that such statistics were not available in the Department's archives (N.-C. Urne Fischer, KNI, Nuuk, and U. Scheppelern, KNI, Copenhagen, pers. comm.).

Results

Historical development of trade in narwhal products

Barter in Greenland and the early overseas trade

Greenlanders probably bartered narwhal tusks among themselves long before the first contact with Europeans. As Crantz (1820: 160) explained:

> ... since the Southlanders have no whales, while the inhabitants of the north coast are in want of wood, numerous companies of Greenlanders make every summer, a voyage of from five hundred to one thousand miles out of the south, or even from the east coast, to Disko, in new kajaks and large boats. They barter their lading of wood for the horns of the narwhal, teeth, bones, and the sinews of the whale, which they in part sell again during their return homewards.

Although Crantz's experience was as a visitor to Greenland in the early 1760s (well after Danish colonization had begun), the bartering described in this passage would not have required any external impetus and was probably indigenous to Greenlandic society.

Narwhal tusks from Greenland have been in international trade for hundreds of years. Although walrus tusks and polar bear hides were their export staples, the Norse colonists in southern Greenland almost certainly provided some, or most, of the narwhal tusks that reached

Fig. 1. Map of Greenland showing places mentioned in the text.

Europe in the Middle Ages to become coveted as "unicorn horns" (Shepard 1930). The nature and scale of these early shipments are poorly documented. Shepard (1930: 254) estimated that only about 20 whole narwhal tusks were well known in Europe by the late 1500s. Referring to the wreck of a ship with narwhal tusks on board near Iceland in 1126 he remarked:

> How many cargoes such as this were brought safely to port in later years no one can say, for they belonged to a business in which it did not pay to advertise. There were not enough of them, at any rate, to glut the market, nor did they come in frequently enough to attract the slightest attention in Europe.

Narwhal skulls found buried together in the chancel of a Norse cathedral in southern Greenland suggest that they, like walrus skulls, could have been kept occasionally as hunting trophies by the Norsemen (McGovern 1985). Alternatively, these skulls may simply have been in storage for trade.

The demise of the Norse colonies by about 1500 was followed by a century or so of virtual isolation of Greenland from Europe. Not until the 1600s did Danish-Norwegian and Dutch ships begin making regular visits to southern and western Greenland for whaling and trading. When the St. Peter entered Itilleq Fjord (Fig. 1) in 1652 the Inuit came out from shore to barter fish, sealskin clothing and narwhal tusks in exchange for nails, knives and needles. Gad (1971: 238) inferred from this incident that such exchanges were typical. He quoted from the vessel's logbook entry of 7 July:

Fig. 2. Hunters at Uummannaq posing for a photograph early this century with the head of a large tusked narwhal. Photo: A. Bertelsen. Copyright Arktisk Institut, Denmark.

... otherwise when coming on board, the Greenlanders will point to the sun and beat their chests shouting 'Elevout', and when our sailors did the like, then they immediately came quite close and shouted 'tuacha', which is unicorn ....

At least two Danish trading ships returned to Copenhagen in 1652 with cargoes that prominently included narwhal tusks (Dalgård 1962: 409). A voyage of 1653 returned with 343 Danish pounds (172 kg) of narwhal tusks; nine complete tusks in this shipment weighed, in total, 88.5 Danish pounds (44 kg; Bencard 1989). Some of these tusks may have been intended for use in the construction of the famous throne at Rosenborg Palace (*cf.* Rosing 1986, Bruemmer 1993).

There is no way to guess how many narwhal tusks were taken out of Greenland during the seventeenth and eighteenth centuries. They were obtained at least occasionally by European whalers involved in the Davis Strait fishery for bowhead whales (*Balaena mysticetus*) that began in the early eighteenth century (Gad 1973). Particularly after 1814 when the British began whaling for bowheads on the west (Canadian) side of Davis Strait and Baffin Bay, narwhal tusks in the whaling returns could indicate catches and trade off either Greenland or Baffin Island (Reeves & Mitchell 1987a). Few commercial whalers hunted narwhals themselves, but many of them obtained tusks and skins through barter with the Inuit. Not all of the narwhal tusks leaving the arctic regions were destined for Europe. For example Dutch commerce with Greenland had an Oriental connection: many narwhal tusks secured by Dutch whaling and trading vessels apparently ended up in Japanese collections and medicine shops (Shepard 1930).

Official exports after 1774

Establishment of the Royal Greenland Trade Department (Kongelige Grønlandske Handel, KGH) in 1774 was the culmination of Danish efforts to create a trade monopoly in Greenland (Tejsen 1977). Most of the produce shipped to Denmark by KGH, on an exclusive basis, initially consisted of train oil (oil from marine mammals), baleen (whalebone), polar bear and fox hides, sealskins, narwhal and walrus ivory and eider down (see Fig. 2). The KGH monopoly continued until 1953 when Greenland became

Table 1. Amount of narwhal ivory (kg) purchased by KGH, by year and district or municipality (after 1952). Sources: Anon. (1909–58) and KNI (1991–1992, see text).

Year District	1908/ 09	1909/ 10	1910/ 11	1911/ 12	1912/ 13	1913/ 14	1914/ 15	1915/ 16	1916/ 17	1917/ 18	1918/ 19	1919/ 20	1920/ 21	1921/ 22	1922/ 23	1923/ 24	1924/ 25	1925/ 26	1926/ 27	1927/ 28	1928/ 29	1929/ 30	1930/ 31	1931/ 32	1933	1934	1935
Sisimiut																											
Aasiaat	6,5	21	4,5	7	8,5	119	45,5	85,5	4,5			1	1	2	9	5			5			4				1	1
Qasigiannguit	16	5,5			11,5	6	72	241			3													2			
Ilulissat	8,5	15					45,5	116																			
Ritenbenk		5		13	4		29	13			131							5									
Qullissat																											2
Qeqertarsuaq				3	14	5,5	850	29	3			14															
Uummannaq	78	95,5	92	48	96,5	47	84	124	271	317	65	64	29	36	17	33	8	20	2	4							
Upernavik	139	72	78	57,5	91,5	66	114,5	196	148		71	193	82	46	117	132	136	99	76	138	136	82	99	207	3–17,7		33
Avanersuaq																											
Tasiilaq																											
Ittoqqortoormiit																				15	29	14	3	5			
East Greenland																				15	29	14	3	5			
West Greenland	248	214	174,5	128,5	226	243,5	1240,5	804,5	426,5	317	270	272	112	84	143	170	144	124	83	142	136	86	99	209	3–17,7	1	36
Total	248	214	174,5	128,5	226	243,5	1240,5	804,5	426,5	317	271	272	112	84	143	170	144	124	83	157	165	100	102	214	3–17,7	1	36

Table 1. Continued.

Year District/ Municipality	1936	1936/ 37	1937	1937/ 38	1938	1938/ 39	1939	1939/ 40	1940/ 41	1941/ 42	1942/ 43	1943/ 44	1944/ 45	1945/ 46	1946/ 47	1947	1947/ 48	1948/ 49	1949/ 50	1950/ 51	1951/ 52	1953	1954	1955	1956	1957	Sum	Mean	1991	1992
Maniitsoq																												6,7	6,7	
Sisimiut																											0		0	0
Aasiaat																											331	18	55	6,6
Qasigiannguit																											357	45	0	0
Ilulissat												9		5						5	8						212	27	0	0
Ritenbenk	2	3																									205	23		
Qullissat							13	65				74,5		13											5		173	29		
Qeqertarsuaq								5						7													931	103	12	0
Uummannaq	1	16			1	13	1	8	8	8	13		2		8			3							197	9	1819	54		404
Upernavik	7	123	8	23	17	114		61	53	50	34	196,9	97		49		69	41	11	14							3582	85		20
Avanersuaq					39	242	75	244	288	138	240	82,2	100	122	173	141	285	227	344	131		87	87	142	75	180	3367	168		143
Tasiilaq																														
Ittoqqortoormiit	3		10																	4	7						90	10	0	0
East Greenland		48		45																4	7						170	19	0	0
West Greenland	10	142	8	23	57	369	89	383	349	196	287	362,6	199	147	230	141	354	271	355	150	139	87	87	142	284	189	11181	211		
Total	13	190	18	68	57	369	89	383	349	196	287	362,6	199	147	230	141	354	271	355	154	146	87	87	142	284	189	11251	212	73,4	580,3

Table 2. Declared export destinations of raw narwhal tusks from Greenland, 1985–1992. Source: Greenland Home Rule. Note that there are some discrepancies between the data shown here and those in Reeves (1993a: table 3), particulary for 1991. The 1991 figures in Reeves (1993a) are from country totals provided by A. Andersen (*in litt.*, 9 April 1992) whereas those given here for 1991 and 1992 are from data provided by P. Nielsen (*in litt.*, 9 August 1993).

Year	DK	JP	CA	NO	FO	DE	SE	CH	FR	GB	BE	IT
1985	42	0	3	0	1	0	2	0	1	0	0	0
1986	93	11	1	1	2	0	0	2	1	0	0	0
1987	90	1	0	1	1	2	0	0	0	4	0	0
1988	158	2	3	4	0	0	1	0	2	0	0	0
1989	153	3	0	1	2	4	2	3	0	0	1	0
1990	325	3	0	0	0	1	3	0	0	0	0	2
1991	271	1	0	1	0	3	1	0	9	0	0	2
1992	180	2	1	0	0	0	0	0	0	0	0	0
TOT.	1312	23	8	8	6	10	9	5	13	4	1	4

Abbreviations used in Tables 2 and 4: AT, Austria; AU, Australia; BE, Belgium; CA, Canada; CH, Switzerland; CS, Czechoslovakia; DE, (West) Germany; DK, Denmark; ES, Spain; FI, Finland; FO, Faroe Islands; FR, France; GB, United Kingdom; IS, Iceland; IT, Italy; JP, Japan; MA, Morocco; MC, Monaco; NO, Norway; NZ, New Zealand; PH, Philippines; PL, Poland; SE, Sweden; GL, Greenland; US, United States; XX, Unknown.

a Danish county and was granted equal status with the rest of the kingdom. Although the monopoly has been legally abolished, KGH (renamed KNI after 1986) continues to dominate international trade and much of the internal trade in Greenland, particularly north of Disko Bugt (Fig. 1). Its stores remain the chief financial and exchange centers in most villages.

Rink (1877: 313) stated that the average quantity of narwhal tusks exported annually from Greenland (south of 73°N) in the period 1853–1872 was 550 Danish pounds (275 kg). Vibe's (1967: fig. 44) summary of KGH purchases from 1800 to the 1950s does not include data from the Disko Bugt region where, judging by Rink's statement and the data in Table 1, considerable numbers of narwhal tusks were often traded. Published tables of trade statistics have many inconsistencies. For example the yearly amounts of narwhal tusks listed, by district, for the years 1908/09 to 1957 in Anonymous (1909–58; see Table 1) differ from the yearly country-wide compilations listed for 1915/16 to 1938/39 in Anonymous (1946: table 302, p. 806).

Amounts of narwhal tusks sold (in kg, by year) are published for the Avanersuaq (Thule) area only for the years 1938–1957, and amounts reported for the district during this time far exceed the combined totals for other districts in most years (Table 1). The lack of data from Avanersuaq for years before 1938 and after 1957 certainly does not mean that there was no catch. Rather, an annual catch of 125–250 narwhals has been assumed for this district on the basis of reported catches in 1961–1964 (Kapel 1977, Heide-Jørgensen 1994). Born & Olesen (1986) assumed an annual catch of 150 whales (range: 110–274) based on estimated landings given in the Hunters' Lists of Game. The published lists only occasionally give figures for amounts of narwhal tusks traded on the east coast of Greenland (Table 1), where the annual catch in recent years has been estimated at at least about 80 narwhals (Dietz *et al.* 1994).

There was a substantial market for narwhal (and white whale, *Delphinapterus leucas*) skins in British and European tanneries during the nineteenth and early twentieth centuries (Mitchell & Reeves 1981, Reeves & Mitchell 1987b). Although white whale skins obtained in the net fisheries at Maniitsoq (Sukkertoppen) and Kangersuatsiaq (Prøven) were purchased and exported through KGH (Oldendow 1935, Anonymous 1909–58, 1944), we are not aware that KGH bought narwhal skins for export.

White whale blubber was often purchased and exported (Anonymous 1963). For some years pinniped blubber is not distinguished from cetacean blubber in the statistics, but for most years separate amounts are listed for blubber from white whales. Some narwhal blubber could have been lumped with that from white whales for statistical purposes, but we have found no documentation confirming that it was. Nor have we attempted here to evaluate the influence that blubber sales might have had on narwhal hunting effort. In any event blubber could only have been landed when the whales or seals were near a storage facility, and this would rarely have been the case for narwhals taken and flensed in the ice of Disko Bugt or in more northern areas that had no blubber-storage facilities.

Internal markets

Kapel & Petersen (1982: 71) described the present internal trade in hunting products as "a development of the traditional distribution system in an adaptation to modern conditions". Although the traditional distribution system, based on sharing and gifting, and interpreted to include the sending of food to relatives living in towns, continues to some extent in Greenland (Hertz & Kapel 1986, Dahl 1989, Caulfield 1993), traditional foods, including narwhal mattak and meat, are also distributed widely within Greenland on a cash basis.

Table 3. Comparison of number of whole tusks exported from Greenland to Denmark vs. the number imported by Denmark, 1985–1992.

	Greenland Exports[1]	Danish Imports[2]
1985	42	47
1986	93	100
1987	90	80
1988	158	157
1989	153	148
1990	325	389
1991	271	243
1992	180	182
Totals	1312	1346

[1] Data from Greenland Home Rule (Greenland).
[2] Data from National Forest and Nature Agency (Denmark).

Mattak began to be purchased as early as 1965 (Heide-Jørgensen 1994). Based on his observations during a brief visit to the Avanersuaq area Bruemmer (1971) guessed that about 80% of the mattak obtained from narwhals and white whales was sold to KGH. Some of the frozen mattak was later bought back by local Inuit at twice the price that the hunters had received for it. He also stated that an unspecified portion of the sinew and frozen mattak was exported to southern Greenland. Although sinew is no longer purchased, mattak and meat continue to be purchased from hunters; they are frozen and shipped south for sale in the fishing and herding districts (Born 1987, Heide-Jørgensen 1994). Consumer prices for frozen narwhal and white whale meat are moderate, while those for frozen mattak are fairly high relative to the prices for imported and other locally-produced foods available in the shops (Reeves 1993a, personal observations).

Recent exports of narwhal tusks

Detailed information on tusk exports from Greenland is available only beginning in 1985 when Greenland withdrew from the European Community (EC). Such withdrawal placed Greenland outside Denmark's customs area and therefore made it necessary for CITES export permits to be issued by Greenland Home Rule.

The vast majority (more than 90%) of the raw (unworked) tusks from Greenland entering international trade (with CITES documentation) have been exported initially to Denmark (Table 2). For the period 1 January 1985 to 31 December 1992 a total of approximately 1312 narwhal tusks covered by Greenland CITES export permits had Denmark as the declared destination. Declared exports from Greenland and declared imports by Denmark do not match exactly but are in rough agreement most years (Table 3).

Some tusks, especially those with Denmark as the declared destination, are shipped in bulk for re-selling. For example Home Rule data for 1990 show that 215 of the 335 exported tusks (64%) were covered by permits issued to KNI for consignments ranging in size from 4 to 60 tusks. The estimated rates of export for re-sale in other years are lower. If one assumes that lots of three or more tusks represent shipments for re-sale (ruling out those for which we could identify the exporter as a private individual), the percentages of tusks exported for re-sale are 40% in 1985, 19% in 1986, 11% in 1987, 42% in 1988 and 31% in 1989. The 1991 and 1992 data suggest that no more than 30–45% of the tusks exported in these years were for re-sale. Some retail shops (*e.g.* the post office in Ilulissat – Jakobshavn) ship tusks to Denmark on the customer's behalf, then arrange for them to be forwarded to their final destination (P. Nielsen pers. comm., August 1993). Thus some of the shipments that we have assumed to be for re-sale may actually consist of tusks that have already been purchased by individuals and are simply being handled, in bulk, by intermediaries to spare customers the trouble of carrying them home.

Re-exportation of narwhal tusks

At least 742 tusks were re-exported from Denmark with CITES documentation between 1980 and 1992 (Table 4). Of 451 re-exported tusks for which we have detailed information 430 were re-exported for "trade", 14 for "personal" and 7 for "exhibition" or "zoo" purposes. We have the Greenland export-permit numbers (indicating the year of issue) for 331 of the 742 re-exported tusks. For this sample 186 tusks (56%) were re-exported in the same calendar year as the export permit, and 140 (42%) were re-exported in the calendar year following that of the export permit. Re-exported tusks were shipped in lots of one to 20. If it is assumed that shipments of three or more tusks represent transactions with the intention to re-sell (the "3-tusk criterion"), then 404, or nearly 90%, of the 451 tusks were shipped for resale. Of the 164 re-export shipments documented 55 (34%) were for resale according to our 3-tusk criterion. A particularly high proportion of these shipments (73%) went to the UK. Of the 539 tusks re-exported between 1985 and 1992, 356 (66%) had the UK as their declared destination.

We did not make an extensive search for information on re-exportation by countries other than Denmark. Some of the Greenlandic tusks imported by Switzerland have been re-exported to Japan (Reeves 1993a). Of 91 tusks (of any origin) re-exported from the UK under CITES between 1979 and 1984, Italy was the declared destination for 46 and Switzerland for 14 (Reeves 1993a). Since the UK reported importing 388 tusks from Canada and only two from Denmark during 1979–1984 (Reeves 1993a) most of the tusks re-exported by the UK in these years presumably originated in Canada rather than Greenland. The published lists of exports and re-exports by EC

Table 4. Declared re-export destinations of raw narwhal tusks from Denmark, 1980–1992. Sources: 1980–1984, TRAFFIC International; 1985–1992, National Forest and Nature Agency. Data for 1980–1984 are probably incomplete, as indicated by "-" in cells for which no information is available in CITES records.

Year	GB	JP	CH	FR	BE	DE	ES	IT	AT	AU	MA	NO	PL	SE	US	CA	GL	IS	MC	PH	XX	CS	Tot
1980	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	2
1981	–	–	4	–	–	–	–	–	–	–	–	–	–	–	1	126	–	–	–	–	–	–	131
1982	1	–	10	–	–	25	–	5	2	–	–	–	–	–	–	2	–	–	–	–	–	–	45
1983	–	–	2	–	–	–	–	5	2	–	–	–	–	–	1	3	–	–	–	–	–	–	13
1984	3	–	3	–	–	2	–	–	2	–	–	–	–	–	1	1	–	–	–	–	–	–	12
1985	6	4	1	1	0	1	0	0	3	0	0	0	0	0	1	0	0	0	0	0	0	0	17
1986	15	2	1	3	0	1	0	0	2	0	0	1	0	1	0	0	0	0	0	0	0	0	26
1987	12	1	2	0	0	0	0	2	0	2	0	0	0	0	1	0	2	0	0	0	0	0	22
1988	30	0	0	0	0	1	0	0	0	1	2	1	0	1	0	1	0	1	0	0	0	0	38
1989	63	11	1	1	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	79
1990	109	0	15	3	15	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	2	0	147
1991	55	1	7	0	10	3	0	19	0	0	0	3	0	0	0	0	0	0	12	1	1	0	112
1992	66	1	11	4	2	5	0	0	1	0	0	1	0	1	0	0	3	0	0	0	0	3	98
Tot	360	20	57	12	28	38	1	32	12	3	2	6	1	4	5	135	6	1	12	1	3	3	742

countries for the years 1985–1989 (Commission of the European Communities 1987–92) only cover shipments to non-EC countries. Judging by these lists and the TRAFFIC International data for 1990 and 1991 Denmark has been the only EC country regularly re-exporting tusks outside the Community.

Recent exports of carvings and other craft items

A large variety of items are carved or crafted in Greenland using narwhal tusks. CITES export permits are required for these items as they are for whole tusks. The data in Table 5 provide an idea of the nature and scale of craft exports. As with raw tusks, Denmark was the principal declared export destination for worked narwhal ivory. Occasionally items made from Greenlandic narwhal tusks have been exported from Denmark back to Greenland. For example 266 carvings in 1987 and one in 1990 were shipped from Denmark to Greenland for "trade" purposes, and two items in 1989 were sent as personal effects.

Damaged tusks and tusk pieces are often sold for use in carving, and this ivory is sometimes exported. For example a consignment of four broken tusks exported to Denmark in 1990 (Export Permit 26.4/100) was declared as being for use in domestic crafts by a certified Greenlandic artist. In 1992 three consignments of "scrap" were imported to Denmark, and one of these consisted of 45 pieces of tusk (Export Permit GL 71/92, Import Permit F 267 P, DK9124532). Some of the carvings made from narwhal ivory are actually made from embedded teeth rather than from tusks. This applies particularly to crochet needles but may also apply to many of the other small items.

Prices of narwhal products

The prices of narwhal products in Greenland have generally increased through time (Table 6). However, much of the increase can be attributed to inflation, which has been high in Greenland for the past 25 years (Hertz & Kapel 1986, Born 1987). The prices paid to hunters by KNI for tusks were stable at 725 Dkr (ca 121 US dollars) per kg for A-quality and 200 Dkr (ca 33 US dollars) per kg for B-quality (broken) tusks from 1990 to August 1993.

In practice, local KNI stores in the smaller towns often pay hunters A-quality prices for B-quality tusks. Also, purchasers sometimes recognize quality classifications between A and B (Henning Thing *in litt.*, 24 September 1990). KNI's mark-up for retail sales of narwhal tusks in Greenland was 65% in 1990 (H. Thing *in litt.*, 24 September 1990). The retail price of undamaged whole tusks at the post office in Ilulissat in August 1993 was 1300 Dkr (ca 186 US dollars) per kg, indicating a net mark-up of nearly 80% over the price paid to hunters.

The combined value of mattak, meat and tusks makes the narwhal one of the more important cash-generating game animals in Greenland (Bruemmer 1971, Born 1987, Heide-Jørgensen 1990, 1994). Born & Olesen (1986) estimated that during the mid 1980s a hunter could receive 5000 to 15 000 Dkr by selling the products of a single narwhal. We made a similar estimate based on data from a large purchase of narwhal products by KNI at Uummannaq in 1990, when the reported narwhal catch for this municipality was 1019 animals (Greenland Statistical Office data). The 306 tusks purchased by KNI weighed a total of 1848 kg (R. Fleischer *in litt.*) for an average of about 6 kg per tusk. The average price paid was 538 Dkr (90 US dollars) per kg (R. Fleischer *in litt.*) so an average tusk would have been purchased for about 3228 Dkr (538 US dollars). Royal Greenland Production purchased 81 500 kg of narwhal mattak at Uummannaq

Table 5. Carvings and other craft items made from narwhal ivory that were declared on CITES export permits from Greenland, 1984–1992 (all data from Greenland Home Rule). Note that raw tusks are sometimes declared on the same permits as are one or more craft items. Jewelry pieces can include necklaces, bracelets, ear or finger rings, brooches and pendants. Carved figures can be of bears, sleds, kayaks or hunting implements. A tupilak is a small figurine.

Year	No. Permits	No. Items	Declared Destination
1984	1	3 tupilaks	Canada
1985	3	4 tupilaks	Canada
	6	9 tupilaks 2 necklaces 2 lampstands	Denmark
1986	17	35 tupilaks 2 crochet needles 5 necklaces 1 kayak paddle	Denmark
	1	5 tupilaks	Canada
	2	7 tupilaks, knives, buttons (for exhibit) 1 carving	Japan
	1	1 tupilak	W. Germany
1987	40	15 carved figures 123 tupilaks 5 pieces of jewelry 2 utensil handles	Denmark
	1	1 tupilak	Venezuela
	2	6 tupilaks	Canada
1988	51	86 tupilaks 13 pieces of jewelry 1 lampstand 57 carved figures 1 "souvenir" 1 crochet needle 2 flagstands	Denmark
	1	1 tupilak	Hungary
	1	6 tupilaks	France
	1	1 carving	Sweden
1989	38	90 tupilaks 32 carved figures 3 "souvenirs" 21 pieces of jewelry	Denmark
		5 tupilaks	Sweden
	1	5 carvings	Norway
1990	25	4 letter knives 46 tupilaks 14 carved figures 11 pieces of jewelry 2 "games"	Denmark
1991	50	87 tupilaks 45 carved figures 48 pieces of jewelry 4 napkin rings 4 crochet needles 1 lampstand 1 knife handle 1 tusk tip 3 tusk pieces 1 "little tusk"	Denmark
1992	67	57 tupilaks 1 rib 1 bone 4 lampstands 57 carved figures 56 pieces of jewelry 5 crochet or other needles 3 letter knives 2 toys 61 "diverse" items ("scrap"?) 2 pieces of tusk	Denmark
	1	1 tupilak	Canada

(K. L. Rasmussen *in litt.*) for an average of about 80 kg per whale. At the official price of 47.52 Dkr (8 US dollars) per kg this would mean that an average narwhal provided about 3800 Dkr (634 US dollars) worth of mattak. Royal Greenland Production bought 46 555 kg of narwhal meat at Uummannaq for 13 Dkr (2.17 US dollars) per kg. The average amount of meat sold per whale was about 46 kg so hunters received about 598 Dkr (100 US dollars) for the meat of each narwhal caught. These data suggest that an average tusked narwhal provided approximately 7632 Dkr (1272 US dollars) to the hunter.

An adult male narwhal can be considerably larger and thus more valuable than our "average" specimen. Hay & Mansfield (1989) gave the following maximal values from their Canadian sample of narwhals: 8 kg of ivory, 140 kg of mattak and 450 kg of meat. At the unit prices quoted above, an animal of these maximal dimensions would have been worth more than 16 800 Dkr (2800 US dollars) in 1990.

Discussion

Historical development of trade in narwhal products

Vibe (1967: 73) expressed the opinion that KGH data provided a fairly complete record of ivory production through 1950: "... it is safe to assume that the greater part of the Narwhal tusks acquired have landed in the stores". Although he provided no information on exchange values or prices, Vibe (1967) claimed that narwhal tusks (Fig. 3) had always been good trading commodities. By the late 1960s and early 1970s large, unbroken tusks were sometimes sold privately, *i.e.* without KGH involvement (Hansen 1970, Bruemmer 1971). The steadily expanding presence of non-Greenlanders, *e.g.* scientists, engineers, aviators, tourists, military personnel and school teachers, since the 1950s (see Lyck & Taagholt 1987) has created more opportunities for direct sales of tusks. Thus KNI data are much less complete as a record of the actual numbers of tusks sold nowadays than they were 25 and more years ago. Although we have not attempted a comprehensive review of the scattered and sometimes contradictory historical information on the trade in narwhal products, we believe that such a study would be an interesting and useful contribution.

Trends in narwhal tusk exports

We believe that the low number of tusk exports attributed to Greenland before 1985 (*cf.* Payne 1988, Klinowska 1991) is largely a reporting artifact rather than an accurate indication of little trading activity. Some, possibly

Fig. 3. Inughuit in the Avanersuaq (Thule) area with narwhals taken during the mid 1920s. Photos: P. Freuchen: Arktisk Institut, Denmark.

Table 6. Official prices paid to hunters for narwhal products in Greenland (Dkr/kg). Inflation-adjusted prices in parentheses are expressed in 1971 Dkr. Note that "unpublished data" are from KNI (tusk prices) or Royal Greenland Production (mattak and meat prices).

Year	A-tusks[2]	B-tusks[2]	Mattak	Meat	Source
Mid 1960s[1]			1.00		Bruemmer (1971)
			(1.45)		
1968	45.00		7.50	2.00	Hansen (1970)
	(52.65)		(8.78)	(2.34)	
1971		45.00[3]	7.50		Bruemmer (1971)
		(45.00)	(7.50)		
1984	715.00		35.00	25.00	Born (1987)
	(185.23)		(9.06)	(6.48)	
1985	500.00				Born (1987)
	(118.76)				
1990	725.00	200.00	47.52	13.00	H. Thing *in litt.*; unpublished data
	(133.32)	(36.77)	(8.74)	(2.39)	
1991	725.00	200.00	50.00	13.00	Unpublished data
	(127.54)	(35.18)	(8.80)	(2.29)	
1992	725.00	200.00	50.00	13.00	Unpublished data
	(125.50)	(34.62)	(8.66)	(2.24)	
1993	725.00	200.00	51.10	11.00	Unpublished data

[1] "Just a few years ago" (Bruemmer 1971).

[2] A-tusks have unbroken tips; B-tusks have broken tips.

[3] Bruemmer (1971) referred to a single price paid for tusks by KGH but noted that "they get only the broken tusks". "Good" tusks were sold for 50–100 dollars (Canadian?) "to local Danes (legally) or at the Air Base (illegally".

much, of the increase in reported exports from Greenland in the years after 1985 is due to changes in the reporting system. According to Home Rule authorities, by 1987 the export of narwhal tusks and ivory carvings from Greenland to Denmark was being "strictly monitored according to CITES rules: export permits from Greenlandic authorities, import permits from Danish authorities" (Trolle 1987). If this assessment is correct, then trends in the number of tusks covered by CITES export permits since 1986 should reflect actual trends in the rate of export.

The data shown in Table 2 indicate an increase in tusk exports in 1988/1989, a peak in 1990, a slight decline in 1991 and a further decline in 1992. We are unable to fully explain these developments. Such a short time series should, in any event, not be interpreted to represent long-term trends. Improved reporting procedures (notwithstanding the statement by Trolle, quoted above) could be a partial explanation of the apparent increase in the late 1980s. Also, as has been noted by others (Kapel 1977, Born & Olesen 1986, Heide-Jørgensen 1994, Siegstad & Heide-Jørgensen 1994), there can be strong fluctuations in the catch of narwhals in West Greenland due, at least in part, to the exceptional hunting opportunities provided periodically by ice entrapment (sassat) and oceanographic factors. The spike in tusk exports in 1990 may be related to the exceptional catch of 1019 narwhals in the Uummannaq area that year (see above). This catch was made possible by an unusual occurrence of narwhals in November just before freeze-up in Uummannaq.

Lyck (1990) called for a more integrated and "dynamic" economy in Greenland, suggesting, for example, that markets for seal products be expanded within Greenland and that further dependence on external markets be avoided. However there appears to be little potential for internalizing the market for narwhal tusks. Danish expatriates working temporarily in Greenland often acquire tusks, which they eventually take back to Denmark as personal effects. Narwhal tusks are sometimes given as gifts to foreign dignitaries or business colleagues. Sales to tourists and other visitors, along with bulk or wholesale shipments mainly to Denmark, are the other primary means of disposing of whole narwhal tusks.

The carving industry provides a strong internal demand for ivory, and narwhal tusks and embedded teeth are used by some Greenlandic carvers. In 1993 at least two shops in Nuuk-Godthåb (Santa's Work Shop and KNI) and one in Ilulissat (post office) were selling raw narwhal ivory in 5–15 cm sawed chunks at 280 DKr (40 US dollars) per kg. Sperm whale (*Physeter catodon*) teeth imported from Japan were traditionally used to make tupilaks, but with the decline and closure of Japanese whaling for sperm whales this supply of ivory is no longer available. Caribou antler, walrus ivory and narwhal ivory have become the main ingredients for tupilaks as well as for jewelry and figurines. An illustrated flyer was produced by KGH to promote sales of tupilaks made from narwhal ivory (Rosing no date). Some of the market for carvings may be internal, but we assume that many if not most of the carvings are eventually exported.

The claim was made recently that narwhals are "at risk" because of the international ban on trade in elephant ivory under CITES (Bradstock 1990). It seems unlikely that narwhal ivory would be a good substitute for elephant ivory in the Asian carving industry because of its relative hardness and brittleness (Jardine 1837, Degerbøl & Freuchen 1935). However two Early Netsuke carvings of narwhal ivory are in the British Museum (accession numbers HG 222 and 224, dated to the Qing Dynasty) so it has played at least a minor role in this Oriental craft. Also, the use of narwhal teeth as substitutes for sperm whale teeth in tupilak production in Greenland demonstrates some degree of interchangeability among ivories. The CITES data that we have examined do not suggest that inferior or broken narwhal tusks have been exported to Japan at a proportionally high rate. Rather, most of the tusks exported to Japan in recent years apparently have been large ones. Of 211 tusks exported to Japan from Canada between 1986 and 1990, 135 (64%) were at least 2 m and a further 40 (19%) at least 1.7 m long (unpubl. data from Canadian CITES permits, Hull, Québec – *cf.* Reeves 1992). All 39 of the tusks exported commercially from Canada to Japan in 1992 were 1.9–2.9 m long (R. R. Campbell *in litt.*, 14 July 1993). The only tusk exported to Japan from Greenland for which we know the length was 2.48 m long (Export Permit no. 057/89).

Trends in re-exportation of narwhal tusks

The most striking feature of the Danish re-export data (Table 4) is the large number of tusks shipped to the UK. Prior to the closing of the UK market for Canadian narwhal tusks under EC regulations in 1984 (see below) the UK was the major importer of tusks from Canada; few tusks have been exported from Canada to the UK since 1984 (Reeves 1992, 1993a). It would appear that after a period of adjustment (ca 1984–1987) importers based in the UK began importing more tusks from Greenland (via Denmark) as a replacement for imports from Canada. Of 73 re-export permits issued by Denmark for shipments to the UK between 1 January 1985 and 31 December 1992, 40 involved lots of three or more tusks (range: 3–20) (data from National Forest and Nature Agency). Although such "bulk" shipments (accounting for 85% of the total tusks re-exported to the UK) suggest that a high proportion of those imported to the UK is for re-sale, very little re-exportation by the UK has been documented under CITES since 1979 (Reeves 1993a).

Discrepancies and inconsistencies in reporting

As anyone who has worked on trade-documentation problems knows, it is easy to detect discrepancies and inconsistencies. While there are some obvious differences in the reports of Greenlandic tusk exports to Denmark vs. the reports of Danish imports (Table 3), we do not consider them major. Among the possible explanations, apart from simple coding errors, are the following: (1) Permits sometimes expire, get withdrawn or are otherwise not used. (2) Permits issued in one reporting year can be used in another, so exportation and importation of the same consignment can be recorded in different reporting years. (3) Some imports destined for re-exportation might be kept in bonded warehouses and thus would never officially "enter" the country at all. A few minor inconsistencies are also revealed by comparing the import and re-export data obtained directly from the National Forest and Nature Agency with those published by Commission of the European Communities (1987–92) and with those appearing in the TRAFFIC International list.

Although we are not aware that any illegal exports have been documented, it would be naive to assume that all whole tusks and craft items leaving Greenland are covered by CITES permits. Thus the export data shown in our tables probably under-represent the actual volume of international trade in narwhal products, especially the trade in jewelry and other small craft items.

Controls on narwhal hunting and trade

KGH's trade monopoly, which lasted until 1953, provided virtual regulation of the export trade in hunting products. It prevented competitive stimulation of narwhal exploitation such as occurred in northern Baffin Island in the 1910s and 1920s (Mitchell & Reeves 1981). Moreover KGH deliberately refrained from developing commercial markets for certain hunting products. For example the shop in the Avanersuaq area refused to purchase narwhal blubber because of concern that doing so would lead to critical winter shortages of fuel, food and dog food among the Inughuit (Vibe 1950: 83).

Customary hunting regulations emanating from local communities in Greenland were codified beginning in the early twentieth century (Qujaakitsoq 1990). These are recorded in "Nalunaerutit-Grønlandsk Lovsamling" and "Grønlandsk Lovregister". Such regulations relate mainly to hunting technology and practices; they have rarely involved explicit limitations on catches or hunting effort (Kapel & Petersen 1982). Regarding narwhals specifically, Greenlandic laws neither limit harvests nor restrict the uses of hunting products within Greenland. The regulations governing narwhal and white whale hunting were consolidated in Home Rule Law (Hjemmestyrets bekendtgørelse) No. 10 issued in July 1992 (Anonymous 1992), and revised in No. 21 issued in July 1993 (Anonymous 1993). These regulations define hunter eligibility, designate closed areas, specify approved hunting, processing and transporting methods and establish procedures for the reporting of catches and the collecting of lower jaws from caught whales. Any export of narwhal or white whale products requires approval from the Home Rule Government. Commercial exportation of meat from all cetaceans is prohibited under Greenland Home Rule Law (para. 6(3) in Bekendtgørelse 33, Nal. D, 1985, p. 263–266).

Greenland's special relationship with Denmark has meant that its interests have been represented in most international agreements by the Danish government. Because of Denmark's membership in the International Whaling Commission (IWC) the exploitation of "large" whales, including the minke whale (*Balaenoptera acutorostrata*), in Greenlandic waters has been subject to IWC regulation. Narwhals, however, are not included in the Commission's schedule of whaling regulations, and the responsibility to manage the hunt for this species rests with national, regional and local authorities.

Denmark joined CITES in 1977. The narwhal's listing in Appendix II of this convention has meant that although international trade is allowed, it must be documented with permits issued by the exporting country (Wijnstekers 1990). Greenland was granted home rule in 1979 but remained within the Danish customs area until 1985, so the exportation of narwhal tusks to Denmark was technically not international trade before 1985. Narwhal tusks leaving Greenland required CITES permits only if they were being exported directly from Greenland to a country other than Denmark. We have not seen any CITES documentation of Greenlandic exports prior to 1985.

EC Regulations 3626/82 and 3418/83 effectively prohibit commercial trade by treating all species of Cetacea as if they were in Appendix I of CITES. Since 1984 these EC regulations have had a dramatic effect on Canada's export trade in narwhal tusks (Reeves 1992). An explicit exemption, however, was given in Regulation 3626/82 to the parts and derivatives of Appendix II species "taken by the people of Greenland under licence granted by the competent authorities of Greenland or Denmark" (Anonymous 1982). Thus the importation of Greenlandic narwhal tusks by EC countries has been allowed to continue under the normal Appendix II provisions. A proposal sponsored by the Federal Republic of Germany to move the narwhal into CITES Appendix I was defeated at the biennial meeting of parties in April-May 1985, and no further proposal has been made to change the narwhal's status under CITES.

In addition to the CITES permit requirements and the EC regulations, imports to the United States were prohibited under the Marine Mammal Protection Act of 1972. In spite of this prohibition narwhal tusks destined for the United States have appeared occasionally in published CITES export, import and re-export records (Tables 2 and 4, Commission of the European Communities 1987–92, Canadian Wildlife Service 1978–93, Reeves 1993a).

Recent and current monetary value of narwhals

The increasingly open and monetized character of the Greenlandic economy has made it vulnerable to fluctuations in external demand for hunting products. An important development of the past decade has been the sharp decline in hunter prices for sealskins – an indirect result of actions taken by animal protectionists to halt the commercial hunt for harp seals (*Phoca groenlandica*) and hooded seals (*Cystophora cristata*) (Hertz & Kapel 1986, Wenzel 1991). By early 1984 the narwhal hunt had "come to play a critical role in the ability [of hunters in the Avanersuaq area] to pay the installments on village houses and boats, to pay for heating oil, gasoline, ammunition, radios, cloth for anoraks, and other items ..." (Silis 1984: 527). Born (1987) interpreted the increase in mattak purchases by KGH in the Avanersuaq area during the mid 1980s as compensatory for the declining value of sealskins.

The decline in 1985 in the price offered by KGH for narwhal tusks, from 715 to 500 Dkr per kg, is said to have been caused by "a reduced market outside Greenland probably related to import restrictions enforced in 1984 by the EEC" (Born 1987: 122), even though, as noted above, Greenlandic products were exempt from the EC regulations. A steeper decline in hunter prices for narwhal tusks occurred in Canada during 1984–1985, but this was reversed as the decline in exports to EC countries (especially the UK) was offset in the late 1980s and early 1990s by increases in exports to Japan and Switzerland (Reeves 1992, Canadian Wildlife Service 1978–93).

Our estimate of the value of an "average" narwhal in Greenland in 1990 – 7632 Dkr (1272 US dollars; see above) – is conservative for the following reasons: (a) Some of the mattak would have been sold informally at high prices without involvement of Royal Greenland Production. (b) Some, and perhaps the best, of the tusks would have been kept by the hunters to be sold directly to tourists and other visitors. Private sales are sometimes at unit prices much higher than those offered by KNI. (c) Some of the mattak and meat would have been consumed by the hunters and their families outside the cash-mediated marketing system. Thus the average yields of mattak and meat from the catch at Uummannaq are underestimated when based only on the amounts sold. An imputed value equivalent to the foregone earnings could be added to our estimate of the cash value.

At the prevailing prices of the late 1960s and early 1970s the "average" narwhal as defined above (80 kg of mattak at 7.50 Dkr, 6 kg of tusk at 45.00 Dkr, and 46 kg of meat at 2.00 Dkr – see Table 6) would have been worth 962 Dkr, which would have bought approximately 2400 litres of kerosene (see kerosene price curve in Hertz & Kapel 1986: fig. 3). At the prevailing rates in 1985 (35 Dkr per kg for mattak, 500 Dkr per kg for tusks and 25 Dkr per kg for meat – Born 1987) the "average" narwhal would have been worth 6950 Dkr, enough to buy about 2100 litres of kerosene. Using the 1984 price of 750 Dkr rather than the lowered 1985 price of 500 Dkr per kg for tusks (Born 1987) the money made from an "average" narwhal (8450 Dkr) would have bought about 2600 litres of kerosene. From this analysis it can be concluded that the actual "purchasing power" of narwhal products to a Greenlandic hunter was little different in the mid 1980s from what it had been in the late 1960s and early 1970s.

Using the official consumer price index for Greenland (Greenland Statistical Office, Nuuk) instead of the kerosene price as an index, the real value of narwhal products (including only mattak, tusk and meat that is sold) is seen to have increased by somewhat less than 1.5 times between the late 1960s/early 1970s and 1990 (*i.e.* from about 960 to about 1400 Dkr, expressed in 1971 Dkr, for an "average" narwhal; using 1990 unit prices paid to hunters of 538, 47.52 and 13 Dkr per kg for tusk, mattak and meat, respectively). It should be noted that in 1971 sinew was also sold to KGH (Bruemmer 1971), but it is no longer of any commercial value.

Conclusions

Persons concerned with wildlife conservation have used a dichotomy – commercial vs. subsistence – to define and characterize different hunting and fishing regimes (*cf.* Berkes 1988, Wenzel 1991). Some scientists have denied the appropriateness of this approach for analyzing Greenlandic (and certain other) hunting (Kapel & Petersen 1982, Hertz & Kapel 1986, Freeman 1993). They have argued that hunting in Greenland is not oriented towards profit maximization but rather that money has merely facilitated the continuation of a traditional country-wide distribution system and allowed modern hunters to outfit themselves efficiently. Dahl (1989) claimed that rising prices for hunting products do not necessarily lead to intensified hunting. Rather, the intensity of hunting is, according to Dahl, governed primarily by structural features of the hunting communities rather than by external demand factors. Similar arguments have been made concerning seal hunting in Canada (Wenzel 1989, 1991).

From a strictly biological point of view, with the health of the whale stock (*i.e.* its capacity for renewal, or its probability of persistence) as the paramount concern, questions as to how hunting products are consumed and distributed (whether it is "subsistence" or "commercial") or as to how the animals are taken (whether by "traditional" or "modern" means) have no intrinsic relevance (although in the case of hunting methods, these can help determine the amount of hunting loss due to sinking and escapement). What is most important for conservation is to ensure that the rate of hunting removals is sustainable on a long-term basis. In the absence of reliable estimates of sustainable yield from the stock(s) of narwhals available to Greenlandic hunters, and given the lack of any formal system for limiting the size of harvests (such as a quota, for example), it is appropriate to be concerned about the sensitivity of hunting effort to demand factors such as the sales of mattak and tusks.

The human population of Greenland has more than doubled since the mid 1950s, and the trend of rapid increase has continued until recently (Lyck & Taagholt 1987). This inevitably has placed greater demands on the country's resources. Since narwhal mattak and meat are consumed both in the hunting communities and in the towns, and since mattak, in particular, is highly esteemed by most Greenlanders (and some non-Greenlanders), the aggregate demand for these products has remained strong and may have increased through the years (*cf.* Born 1987).

Little is known about the size and character of the worldwide demand for narwhal tusks. Much of it is clearly for large unbroken tusks to be kept as souvenirs or ornaments. There is also considerable demand for the carvings and other craft items made from small or broken tusks and tusk pieces (Table 5). Extreme price fluctuations for Canadian narwhal tusks have been interpreted as reflecting the vagaries of market developments, restrictive trade policies and macroeconomic trends (Mitchell & Reeves 1981, Reeves 1992). Prices and sales of Greenlandic tusks and ivory products are undoubtedly influenced by similar forces.

We recognize that the processes which determine hunting effort and success may be complex. Ice and weather can play an important role by influencing the movements of whales and thus their availability to the hunters (*e.g.* see Siegstad & Heide-Jørgensen 1994 for a discussion of ice entrapments). Born *et al.* (1994) suggested that annual differences in prey distribution could help explain year-to-year variability in the movements and abundance of narwhals in Inglefield Bredning. Some hunters are more skilled than others, and this can be an especially important factor in kayak hunting, which usually accounts for a large proportion of the Greenlandic narwhal catch. It is reasonable to assume that prices and opportunities for selling products affect the ways that hunters decide to allocate effort. Also, the cash value of different products (*e.g.* tusks and mattak) may affect the extent to which hunters hunt selectively for whales of a particular size, age or sex (*cf.* Reeves 1993b).

The Canada-Greenland Joint Commission on Conservation and Management of Narwhal and Beluga met for the first time in January 1991 and has met annually since then to discuss problems of mutual concern. As this commission seeks to develop a narwhal conservation program it will need to take account of the mixed character of narwhal hunting (both subsistence and commercial; see Dahl 1989) and the openness of markets for narwhal products. At present we are unable to say to what degree hunting effort is sensitive to market factors, such as the domestic demand for mattak in both Canada and Greenland and the international demand for tusks and carvings. However market factors certainly could provide an incentive for intensified hunting. This paper should provide a benchmark for assessing future trends in the commerce in narwhal products originating in Greenland.

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Distribution, exploitation and population status of white whales (*Delphinapterus leucas*) and narwhals (*Monodon monoceros*) in West Greenland

MADS P. HEIDE-JØRGENSEN

Heide-Jørgensen, M. P. 1994. Distribution, exploitation and population status of white whales (*Delphinapterus leucas*) and narwhals (*Monodon monoceros*) in West Greenland. – Meddr Grønland, Biosci. 39: 135–149. Copenhagen 1994-04-22.

Historic and present distribution of narwhals (*Monodon monoceros*) and white whales (*Delphinapterus leucas*) in West Greenland is reviewed. The distribution of white whales changed early in this century. They initially disappeared from Nuuk District and later, during the 1920s, from Maniitsoq District. Southwest Greenland (south of 65°N) is no longer a part of the winter or spring distribution of Baffin Bay white whales. Possible reasons for this change are discussed. No large-scale changes in distribution of narwhals have been detected. The major products from narwhals and white whales traded in Greenland are mattak (= whale skin) and narwhal tusks. The mean yield of mattak per whale is estimated to be about 67 and 133 kg per white whale in the municipalities of Upernavik and Qeqertarsuaq, respectively, and 89 kg per narwhal in the municipality of Avanersuaq. Annual reported catches were approximately 900 white whales and 300 narwhals in West Greenland during 1970–1980. After 1980 the catch reporting system became less reliable and it had virtually collapsed by 1991. However, some statistics of catches during the 1980s are reliable, some are available from other sources and others can be calculated from purchases of mattak. The estimated catches of white whales during the 1980s indicate one of two scenarios: either 1) the population estimates from 1981 seriously underestimated the actual population size, or 2) the population has been declining during the 1980s. For narwhals the catches are smaller and the population estimates higher, albeit subject to large variability.

Key words:
White whale, beluga, *Delphinapterus leucas*, narwhal, *Monodon monoceros*, Greenland.

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Introduction

Narwhals (*Monodon monoceros*) and white whales (*Delphinapterus leucas*) have been exploited for centuries by Inuit. Although the evidence from archaeological excavations is still meagre (*cf.* Savelle 1994), these small whales have probably been hunted in Greenland since the earliest settlement by Inuit. The abundance, coastal habits and nutritional value of white whales and narwhals make them attractive game animals for "subsistence" hunters. The colonisation of the Arctic by Europeans and Americans during the 18th, 19th and first half of the 20th centuries also introduced the commercial exploitation of whales, including white whales and to some extent narwhals. This had detrimental effects on some stocks of white whales in Canada and Greenland (Mitchell & Reeves 1981). Catches of monodontids used to be optional, but with the increased dependency on a monetary economy catches of narwhals and white whales have become critically important to some Inuit hunting communities in northwestern Greenland (Born 1987a, Dahl 1990). Trade with products from these whales provides the most important cash income in some of these communities. The combined value of mattak (= whale skin) from narwhals and white whales exceeds the total revenue obtained from the sale of all other edible hunting products in Greenland today. The cash income from the sale of mattak and narwhal tusks enables hunters to buy boats, hunting gear, kerosene and other imported articles. Also

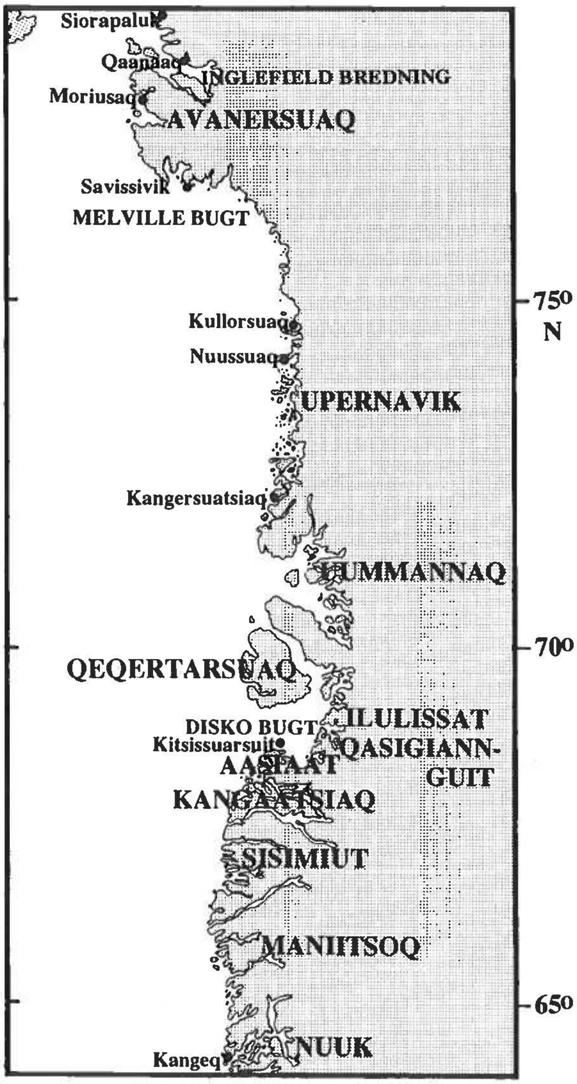

Fig. 1. Municipalities, settlements and bays in West Greenland mentioned in the text.

of major importance is the contribution of whale meat and mattak to the basic food supplies for humans and dogs.

In this paper I consider the white whales and narwhals that spend the summer in the Canadian High Arctic and in Northwest Greenland to belong to Baffin Bay populations. The whales in these populations overwinter primarily in northern Baffin Bay, southward along the west coast of Greenland and in Davis Strait.

I describe current and past distribution of narwhals and white whales in West Greenland and examine the recent harvesting regime in detail. The possible impacts of recent hunting on the population development of both species in West Greenland and the Canadian High Arctic are examined.

Materials and methods

Data on recent and historic distribution and catches

Official catch statistics are available for some years and areas from the annual description of the situation in Greenland (Anon. 1896–1908, Anon. 1909–1931) and from the Hunters' List of Game (HLG, Anon. 1953–1988). Statistics on trade in mattak were obtained from the Greenland Statistical Yearbook for the period 1966–1986 (Anon. 1953–1988). Data on deliveries of mattak for processing at fish factories after 1986 were obtained by sending questionnaires to 19 landing sites, to the central administration of the fish industry, Royal Greenland Production, and to the Greenland Statistical Office. The official statistics from Royal Greenland and the Greenland Statistical Office did not distinguish between mattak from narwhals and white whales until 1991, but some information about the species landed was obtained from the questionnaires or by asking factory employees. Information about the purchases of narwhal tusks by the Greenland Trade Department (KNI; earlier referred to as KGH = Royal Greenland Trade Department) was presented in Reeves & Heide-Jørgensen (1994).

Between 1989 and 1992 I interviewed hunters and other residents of hunting communities to obtain data on catches of white whales and narwhals. I also compiled newspaper articles mentioning large catches. Furthermore, biologists from the Greenland Fisheries Research Institute (GFRI) witnessed some hunting events and flensing situations.

Information about Canadian removals of white whales and narwhals in the Baffin Bay region before 1988 was extracted from Strong (1989) and from Anon. (1991, 1992a, 1992b, 1993) for catches between 1988 and 1991.

Weight of mattak

In September-October 1991 the mattak from 28 white whales killed at Kullorsuaq in the municipality of Upernavik (Fig. 1) was weighed. Additionally, mattak was weighed from four white whales taken at Qeqertarsuaq (Godhavn) in May 1992. In both cases the hunters were asked to flense the white whales in the same manner as they normally do when they sell the mattak. The mattak from the body, excluding the flukes, flippers, and head region, was lifted using a crane aboard the research vessel *Adolf Jensen*. It was then weighed to the nearest kg with a Salter DC-2 digital scale. The total weight and the body length (in a straight line, tip of snout to fluke notch) of the whales were measured before flensing started (see also Heide-Jørgensen & Teilmann 1994).

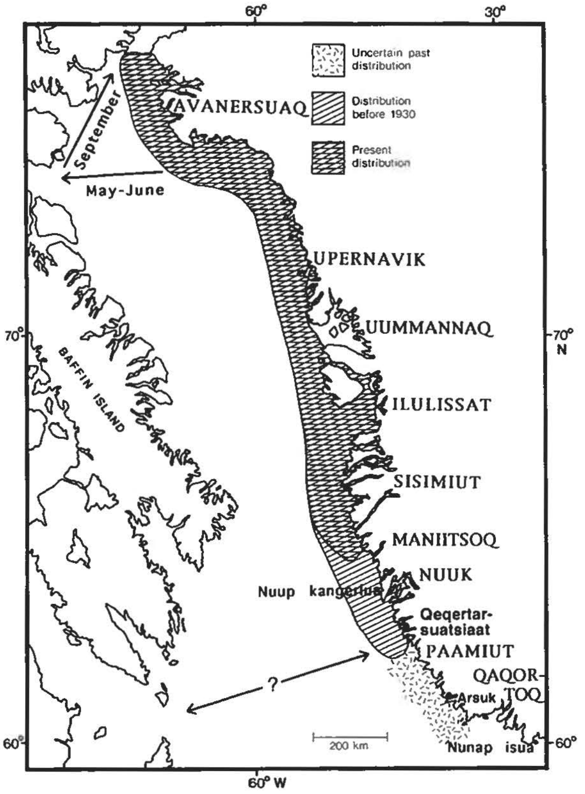

Fig. 2. Historic and present distribution of white whales in West Greenland with likely routes of migrations indicated with arrows.

Trends in population size

The size of the "Baffin Bay population" of white whales was estimated in 1981 at the summer concentration areas in Canada (Smith *et al.* 1985). The number of narwhals in Baffin Bay and Davis Strait was estimated in spring 1979 (Koski & Davis 1994) and the summer concentrations of narwhals in the Canadian High Arctic and in Northwest Greenland were estimated in 1984 (Born 1986, Richard *et al.* 1994). Estimated net recruitment rates were used for simulating the effects on the populations of the documented catch levels.

Plausible population trends can be calculated by adding the net recruitment to an estimate of the population size and subtracting the annual mortality due to hunting:

(1) $N_{t+1} = N_t - K_t + R_t (N_t - FK_t)$ (Smith 1983)

where population size (N) in year t + 1 is calculated from population size in year t (N_t), minus the mortality caused by hunting (K_t), plus the net recruitment rate of the population at time t (R_t) multiplied by N_t minus F times the hunting mortality (K_t). The factor F is incorporated because it is assumed that some proportion of the whales killed in year t would have reproduced during the year of the kill (Smith 1983). Most of the catch of white whales and narwhals in West Greenland is made after the peak season of reproduction (April-May), hence a crude estimate of 0.25 was used for F.

Results

Distribution and catches of white whales until 1930

Winge (1902) made an extensive review of 18th and 19th century literature on marine mammals in Greenland. According to his sources white whales migrated south along the west coast in October and arrived at Qeqertarsuaq (Godhavn; Fig. 1) in October or later, and at Nuuk (Godthåb) in December. The southward movement of white whales in the autumn rarely extended past Qeqertarsuatsiaat (Fiskenæsset, Fig. 2). However, reports of white whales as frequent visitors at Arsuk and the catch statistics from Paamiut (Frederikshåb) and Qaqortoq (Julianehåb) districts (Table 1) both show that white whales occurred frequently and in relatively large numbers in South Greenland in the 19th century (Winge 1902). The

Table 1. Catches of white whales in districts and (after 1952) municipalities in southwestern Greenland during 1874–1891 and 1971–1987. Data for 1874–1891 from Winge (1902) and data from 1971–1987 from present study.

District/municipality	1874–1891			1971–1987		
	Years with reported catches	Mean of catches	Range of catches	Years with reported catches	Mean of catches	Range of catches
Qaqortoq	12	5	1–13	0	0	0
Paamiut	17	9	2–15	2	2	1–2
Nuuk	17	203	77–336	15	28	1–78
Maniitsoq	17	283	163–525	15	12	2–45
Sisimiut	17	140	71–240	15	86	25–135

Table 2. Catches of white whales in seven areas during 1894–1951 (Anon. 1896–1908, 1909–1931, 1938, 1944, 1948). The catches are given per district except for the towns and settlements in Disko Bugt that are lumped together, and the drive fishery station at Kangersuatsiaq in Upernavik District that is shown separately.

Year	Nuuk	Maniitsoq	Sisimiut	Disko Bugt	Uummannaq	Kanger-suatsiaq	Upernavik	TOTAL
1894–95	>200							>200
1896–97				'poor catch in all areas'				
1897–98				'generally good catches'				
1898–99		'varying catches; in Uummannaq poor catches but large catches in Upernavik'						
1906–07	ca. 400							400
1907–08		90		150				240
1908–09	109							109
1909–10	161							161
1910–11	98							98
1911–12	300							300
1912–13		'good catch'						
1913–14	530	66						596
1914–15	ca. 670							670
1915–16	200	300			100			600
1916–17	300	150						450
1917–18		150			60			210
1918		'a few'						
1919		'good catch'						
1919–20	400	700		40				1140
1920–21	200	'very good catch'						200
1922	380	1000		50	25			1455
1923		874						874
1924		950			100			1050
1925		950			50		50	1050
1926		1500					25	1525
1927		700			100	150	100	1050
1928		100						100
1929		76			Uummannaq and Upernavik >1000			>1076
1926–29						1744		
1930		33				311		344
1931				40	200	268	107	615
1932				183	108	610	105	1006
1933						90	106	196
1934–35	1	24	13			240	12	290
1935–36	1	8	47					56
1936–37	4	2	65	20		48		139
1937–38		4	41	49		22		116
1938–39	1	7	8	19		127		162
1939–40	4	2	34	178	83		351	652
1940–41	2	3	99	186	139		351	780
1941–42	1	1	78	326	133		120	659
1942–43		1	36	380	146		127	690
1943–44		3	27	146	63		28	267
1944–45		1	20	324	27		328	700
1945–46	1	1	56	238	13		28	337
1946–47		5	11	207	63	57	70	413
1947–48			9	189	8	54	36	296
1948						122		122
1949						no catch		
1950						24		24
1951						17		17

mean of the annual catches during 1874–1891 in West Greenland south of 66°N was 638 (range 648–1010, sum 10 851). The largest numbers were taken in Maniitsoq (Sukkertoppen) District, but even Nuuk District had large catches (Table 1).

Large numbers of white whales were frequently seen in fjords in West Greenland between 61°N and 63°N during the winter, although their main distribution was farther north, particularly in the fjords of Nuuk and Maniitsoq districts (Fig. 2, Bendixen 1921). The whales were reported to start their northward migration from February until early April. Most whales left the fjords in May, but some remained until June-July (Winge 1902, Degerbøl & Nielsen 1930). Møller (1928, 1964) stated that white

Fig. 3. Flensing of white whales caught in the drive fishery in Nuup kangerlua (Godthåb Fjord) around 1920 (above, Copyright: Arktisk Institut) and at Nuussuaq, Upernavik, in October 1990 (below, Photo: M. P. Heide-Jørgensen).

whales arrived in Nuuk in late October, wintered in Nuup kangerlua (Godthåb Fjord, Fig. 2), and usually left the fjord in April, May or June. This is confirmed by observations of several white whales in leads in the ice during the latter half of November 1914, daily catches of white whales in Nuup kangerlua in January 1915, catches of 42 during 16–20 February and frequent observations and catches between 20 April and 1 May 1914 (J. Noe-Nygård *in litt.*). The season of the catches in Nuuk is known for 12 of the years between 1894 and 1922 (Table 2). In 11 of the years (2769 white whales in total) the catches took place during spring and early summer, usually during May-June. Only once (70 white whales in 1914–15) was the catch reported to have taken place in winter.

Møller (1928) stated that the occurrence of white whales in Nuup kangerlua changed dramatically. After perhaps 1920 they began to leave the fjord earlier in the spring and were caught only occasionally. No catches were reported in Nuuk between 1922 and 1934 and low numbers (<5 per year) have been reported since 1934 (Table 2).

Degerbøl & Nielsen (1930) confirmed the southward movement of white whales in the autumn (October) described by Winge (1902), but they mentioned another pulse of migrating white whales that arrived in South Greenland in December. These animals were said to be fatter and in better condition than the autumn arrivals, and they often carried fresh bullet wounds and shells said to have been of Canadian origin (Degerbøl & Nielsen 1930).

White whales were hunted in Nuuk District (and perhaps throughout Greenland) exclusively by kayak and hand harpoon until the mid 19th century (Møller 1928). During the late 1800s rifles, and after 1900 motorboats, became increasingly used for chasing and killing white whales. With motorboats white whales could be driven in Nuup kangerlua and chased into a shallow bay to be killed (Fig. 3; Møller 1964).

Large-scale netting and driving of white whales was introduced in South Greenland at the beginning of the 20th century. In 1923 it was decided to limit the netting of white whales at Nuuk to the inhabitants of Nuuk and the nearby settlement Kangeq (Fig. 1), but by that time the groups of white whales were already reported to be small (Anon. 1924). A drive-net fishery was started in Maniitsoq District in 1917 and particularly large catches were made during 1917–1930 (Table 2). In one year the catch in this fishery reached 1488 whales (Degerbøl & Nielsen 1930), and the cumulative catch during 1917–1930 was in the magnitude of 8000–10 000 (Table 2). A decline in catches was evident during the late 1920s. Before 1917 catches in three of four years were reported to have been in the spring (Anon. 1896–1908, Anon. 1909–1931). After 1917 the whales were mainly taken in Maniitsoq District on their southward migration from mid October till early December (Degerbøl & Nielsen 1930).

Netting of white whales was initiated at Kangersuatsiaq (Sydprøven, Upernavik District, Fig. 1) in 1925. In 1930 the overall impact of the netting and driving activities stirred a heated debate in the Greenland Council (Nordgrønlands Landsraad) between hunters, especially those from the districts north of Disko Bugt, and the Royal Greenland Trade Department (KGH) that oversaw the white whale fishery (Anon. 1933, 1944). Several representatives from the northern districts claimed that the timing of migrations of white whales had changed significantly in Uummannaq and Upernavik districts. It was claimed that after the introduction of motorboats and netting at Kangersuatsiaq, white whales arrived later and stayed for a shorter period, especially during the summer. On the other hand, it was claimed by KGH that the white whales changed their routes of migrations and that their disappearance in Nuuk and Maniitsoq districts was caused by the increased sea temperature after 1926. The decision to abandon the net fishery at Kangersuatsiaq, stated in the summary of the negotiations in the Greenland Council (Anon. 1933), was never implemented (Anon. 1947, Table 2).

Distribution and catches of white whales after 1930

Since 1930 white whales have rarely been seen south of Sisimiut (Holsteinsborg), although they are sometimes listed in the HLG from Maniitsoq, Nuuk and Paamiut (Table 1). The white whale catches reported from these towns have probably been made further north by hunters who pursue white whales from fishing vessels (Kapel 1977). Vibe (1967) stated that white whales were rarely seen in Nuuk around 1940 and that only five were caught in Maniitsoq during 1935–38. However, pods of white whales were occasionally seen in Nuup kangerlua in winter and spring 1993 (Bjørn Rosing, Greenland Home Rule, *in litt.*).

The major wintering ground for white whales off West Greenland at present seems to be along the coast from 67°N to 69°N, as documented by recent aerial surveys (Heide-Jørgensen *et al.* 1993). The timing of the autumn and spring movements of white whales along West Greenland seems identical to that documented by Winge (1902) and Degerbøl & Nielsen (1930), except that the movements no longer extend as far south as they did before 1930 and that white whales are rarely seen in June south of Uummannaq.

White whales were abundant in Avanersuaq (Thule) District in the summers of 1939–41 and small numbers winter in open water in the northern part of Baffin Bay (the "North Water") where they were sometimes caught along the ice edge in Avanersuaq as early as February (Vibe 1950). A few hundred white whales were observed during aerial surveys of leads and cracks in the North Water in March-April 1978 and March 1979 (Finley & Renaud 1980). One adult white whale was seen from the ice edge in Avanersuaq on 26 April 1985 (Heide-Jørgensen unpubl. data).

Summer observations of white whales in West Greenland are rare, but small pods are occasionally seen in the municipalities of Uummannaq and Upernavik in July-August. One observation of a white whale near Nunap isua (Kap Farvel, Fig. 2) in August 1988 (Reeves 1990) must be considered a straggler of unknown origin. In Nuup kangerlua two pods, both of 12–15 white whales, were seen on 30 June 1993 (B. Rosing, *in litt.*). On 9 September 1987, 25–30 white whales were observed in Uummannaq (Heide-Jørgensen & Leatherwood 1987).

In Avanersuaq a few white whales (< 10 per year) are taken in July-August but the largest catches are now taken in September-October just prior to the catches in the municipality of Upernavik. For instance on 3 October

Table 3. Catches of narwhals and white whales in the Baffin Bay region, 1954–1992.

Year	Narwhals				White whales			
	West Greenland (1)	Estimates W. Grl. (2)	Canada (3)	Total Baffin Bay (1+2+3)	West Greenland (1)	Estimates W. Grl. (2)	Canada (3)	Total Baffin Bay (1+2+3)
1954	47			47	1874		0	1874
1955	195		48	243	300		14	314
1956	318		113	431	424		85	509
1957	74		215	289	503		109	612
1958	73		282	355	225		97	322
1959	57		77	134	309		149	458
1960	332		234	566	216		81	297
1961*	203		197	400	345		36	381
1962*	213		198	411	329		78	407
1963*	317		85	402	229		86	315
1964*	319		90	409	207		53	260
1965	99		78	177	429		49	478
1966	110		168	278	561		125	686
1967	140			140	594		1	595
1968	472			472	1250		0	1250
1969	204			204	978		0	978
1970	322			322	1509		0	1509
1971	186			186	737		36	773
1972	107		26	133	823		0	823
1973	199		372	571	1067		136	1203
1974	147		152	299	917		144	1061
1975	117	149	271	537	607	47	55	709
1976	115	141	297	553	1175	37	58	1270
1977	253	134	255	642	804	36	61	901
1978	612		261	873	719		48	767
1979	377		288	665	741		86	827
1980	462		324	786	889		16	905
1981	609		366	975	1017		158	1175
1982	461		382	843	894		101	995
1983	439		333	772	601		106	707
1984	666		258	924	763		123	886
1985	256		298	554	611		120	731
1986	237		256	643	360	75	75	510
1987	505	50	157	812	606	90	58	754
1988		500	228	728		275	91	366
1989		600	285	885		457	52	509
1990	1046	150	253	1449		1000	47	1047
1991			340	340		550	54	604
1992		250		250		750		750

* indicates that a report was received from the municipality of Avanersuaq.
Greenlandic data from 1954–1974 from Hunters' List of Game with estimates from Kapel (1977). Data and estimates from 1975–1977 from Kapel (1983), 1978–79 from Kapel & Larsen (1984), 1980–82 (Kapel 1985), 1983–84 (Born & Kapel 1986), 1985 (Born 1987b), 1986–87 from Greenland Home Rule Authority and 1988–90 from estimates made by biologists from Greenland Fisheries Research Institute. Data from Canada from Strong (1989) and Anon. (1991, 1992a, 1992b, 1993). For white whales Canadian catches include the settlements of Clyde River, Pond Inlet, Arctic Bay, Grise Fiord, Resolute, Creswell Bay, Spence Bay, Hall Beach, Igloolik and Pelly Bay. For narwhals Canadian catches also include the settlements of Broughton Island, Pangnirtung, Iqaluit, and Gjoa Haven. Canadian catches were reported from 1 April to 31 March but all catches were assumed to occur in the first calendar year. Total catches for Baffin Bay include catches from West Greenland, "estimates" and Canada.

1985, 39 white whales were taken in Siorapaluk, two days later 20 were shot in Qaanaaq, and the following day another 50 were taken in Moriusaq (Fig. 1). The first white whales of the season were taken in the municipality of Upernavik on 9 October (R. Dietz, Greenland Environmental Research Institute, *in litt.*). Again in 1991 approximately 50 white whales were taken in Qaanaaq on 20 September and the catches at Kullorsuaq began on 30 September (Heide-Jørgensen unpubl. data).

After 1930 reported catches in West Greenland south of 68°N vanished in Nuuk and Maniitsoq districts (Table 2). The reported catches south of Aasiaat (Egedesminde) District (Fig. 1) remained low (1934–1947: annual average less than 50, Table 2), and most were probably caught in the municipality of Sisimiut north of their previous autumn and winter occurrence (Fig. 2). The drive-net fishery at Kangersuatsiaq in Upernavik was maintained

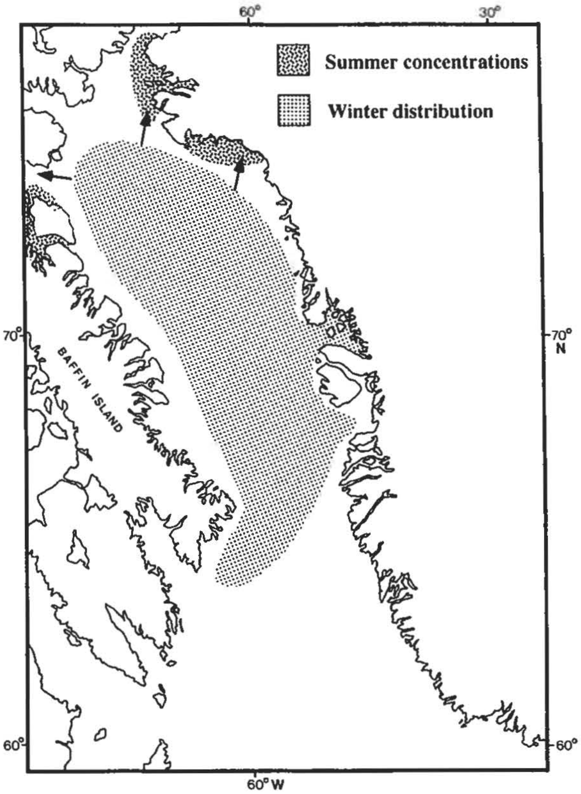

Fig. 4. Distribution of narwhals in West Greenland. Dotted areas indicate major summering grounds, hatched areas indicate wintering grounds.

with varying success until 1951 with a pause during World War II (Table 2).

The reported catch of white whales in West Greenland during 1970–1980 was about 900 whales per year (Table 3). After approximately 1980 the reporting system became progressively less reliable, as several settlements did not report their catches and known catches did not appear in the statistics (Table 3). A contributing factor to this development was the change in hunting methods. During the 1980s more large cutters became involved in catches in "foreign municipalities" and more white whales were caught by co-operative hunting (drive fishery; Fig. 3) involving many hunters, perhaps from several settlements (this study). These changes created uncertainty about who should be responsible for reporting catches.

Distribution and catches of narwhals

Narwhals are present in the offshore pack ice of central Davis Strait and southern Baffin Bay during March (Koski & Davis 1994; Fig. 4). They are also seen and caught during winter and spring along the West Greenland coast where they are particularly abundant at the southern entrance to Disko Bugt. Narwhals are rarely seen or caught south of Aasiaat (Fig. 1). This is also evident from the statistics on trade in narwhal tusks: none were purchased by KGH in districts south of Aasiaat during 1908–1957 (Reeves & Heide-Jørgensen 1994).

Some narwhals winter in the "North Water" polynia and they are sometimes seen and caught along the ice edge in the municipality of Avanersuaq as early as February (Vibe 1950, Finley & Renaud 1980, J. Danielsen pers. comm.). Narwhals are particularly abundant in July through September in Inglefield Bredning (Kangerlussuaq) in Avanersuaq and in Melville Bugt (Qimusseriarsuaq) north of Upernavik (Meldgaard & Kapel 1981, Born 1986, 1987b). During October and November narwhals are frequently seen in Upernavik municipality and particularly in Uummannaq municipality where large catches have been made in recent years. No conspicuous changes in the overall distribution of narwhals have been observed during the last 100–200 years (Winge 1902, Oldendow 1935). Some hunters claimed in 1930 that narwhals had changed their migration routes during the 1920s (?) such that they were no longer abundant in Disko Bugt, but in the northern part of Upernavik the occurrence and relative abundance remained unchanged (Anon. 1933).

The average reported catch of narwhals during 1970–1980 was approximately 270 per year for West Greenland (Table 2). As in the case of white whales the reliability of the narwhal catch statistics declined during the 1980s and no complete catch statistics have been received from Avanersuaq since the 1960s (Table 2).

During one week in November 1989 about 400–450 narwhals were killed in the municipality of Uummannaq according to local sources (Arne Niemann pers. comm., Grønlandsposten 1989), and about 25 tons of mattak was sold (Kjeld L. Rasmussen, Royal Greenland, Uummannaq *in litt.*). In the official catch statistics 275 narwhals were reported for November and 57 for December in Uummannaq. In 1990 1046 narwhals were reported in the catch statistics and of these, 1019 were taken in Uummannaq during an extraordinarily large catch beginning on 29 October and continuing throughout November 1990 (Greenland Statistical Office *in litt.*). From this catch 306 narwhal tusks were sold to KNI (Rudolf Fleischer, KNI Uummannaq, *in litt.*) and 81.5 tons of narwhal mattak and 46.6 tons of narwhal meat were purchased by Royal Greenland during November to January (K. L. Rasmussen *in litt.*). Additionally some narwhals were caught in January and February 1991 in small sassat (ice entrapments) and 9.0 tons of mattak was purchased (*ibid.*). In the autumn of 1991 4.2 tons of mattak was purchased in Uummannaq and low numbers of narwhals were reported to have been caught.

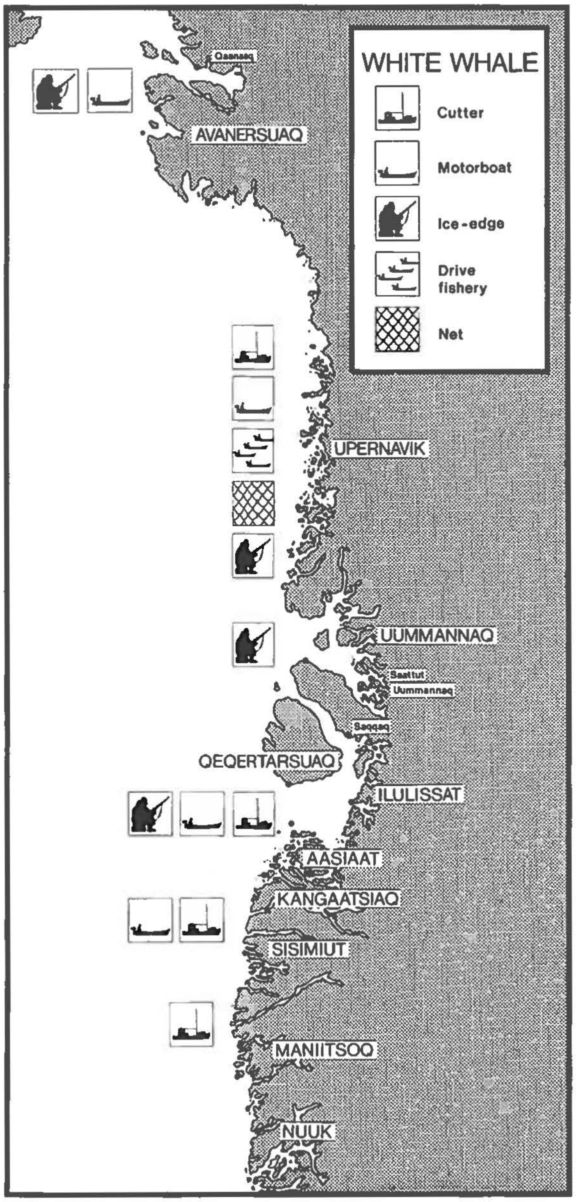

Fig. 5. Most important methods of hunting white whales in the municipalities along West Greenland.

Present methods for catching white whales and narwhals

A variety of methods for catching white whales and narwhals are used by hunters in Greenland. The following is a compilation of information on present hunting methods that I have collected during visits to the hunting areas (also see Thomsen 1993):

White whales are caught in nets, in a drive fishery in the autumn, from the fast ice edge and from cutters in open water (Fig. 5). Harpooning from kayak is rare as most hunters consider it too difficult to approach white whales from kayak. Netting with 80 m-long nets with mesh diameters of 40 × 40 cm and a depth of 3–6 m is responsible for small and infrequent catches in the municipalities from Qeqertarsuaq to Avanersuaq. The nets are set either in open water in the autumn or in the leads and cracks in the fast ice in late spring in Disko Bugt. During the 1980s the drive fishery for white whales in the municipality of Upernavik provided the largest catches of white whales. There are a number of shallow bays and inlets in

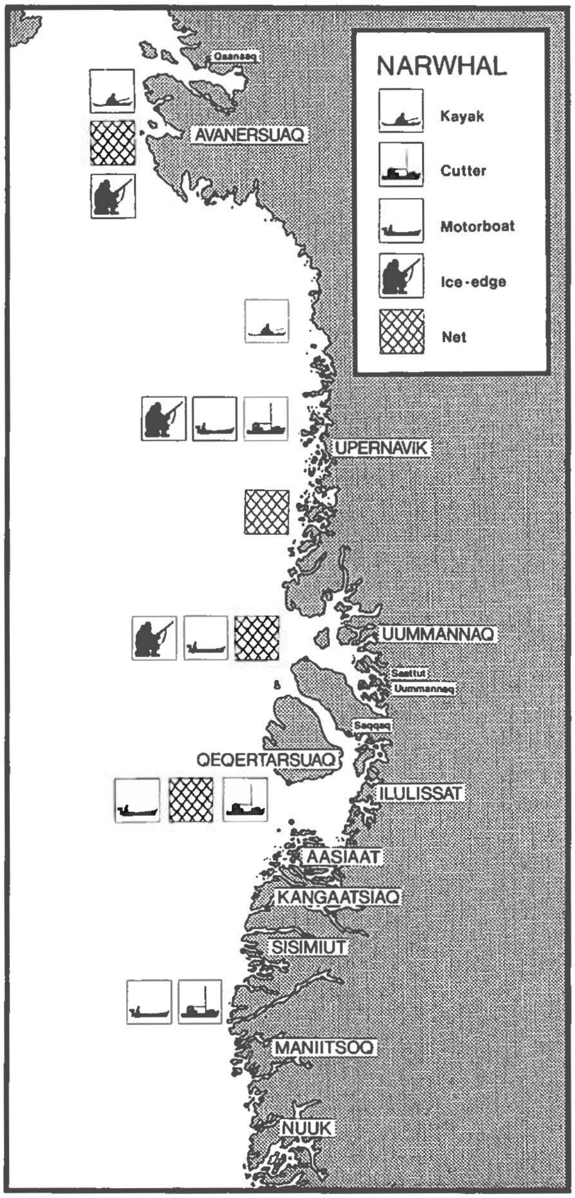

Fig. 6. Most important methods of hunting narwhals in the municipalities along West Greenland.

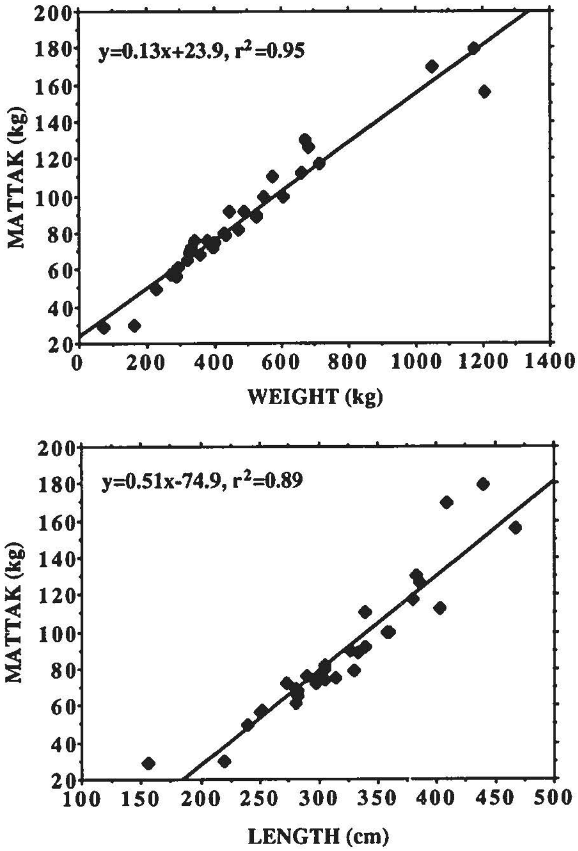

Fig. 7. Yield of mattak for white whales of different length and weight (N = 28). The data are from catches of white whales at Kullorsuaq, Upernavik, in September-October 1991.

the archipelago of Upernavik that are frequently used for this hunt, especially between 73°N and 74°30'N (Fig. 5). The present technique of driving the whales with outboard-powered dinghies is of relatively recent origin as these boats have only been available in Upernavik since the early 1970s. However, the driving of whales with slower motorboats was also practised at Nuuk and Maniitsoq in the first three decades of this century (Fig. 3). Catches from cutters are made primarily in the Disko Bugt area and in the municipality of Sisimiut although white whales are also sometimes taken from cutters in the Upernavik area (Fig. 5).

During the open-water season narwhals are taken from kayaks in the municipality of Avanersuaq and the northern part of the municipality of Upernavik (Fig. 6). Netting of narwhals is also allowed in Avanersuaq after 1 September, but weather and ice conditions often make such netting of narwhals difficult. Netting of narwhals is also practised in Upernavik and Uummannaq especially during November before new ice forms. Large catches of narwhals have recently been made in Uummannaq during November when most narwhals are taken by shooting and harpooning from dinghies. In spring narwhals are chased from dinghies in the loose packice in the entrance to Disko Bugt, especially at Kitsissuarsuit (Hunde Ejland, Fig. 1) and Qeqertarsuaq. In Uummannaq, Upernavik and Avanersuaq narwhals are taken from kayaks along the fast-ice edge during spring.

Sassat or ice entrapments of both narwhals and white whales frequently occur in Disko Bugt and an entrapment in January 1990 resulted in a catch of an estimated 500 white whales (Siegstad & Heide-Jørgensen 1994).

Yield of mattak per whale

The amount of mattak per white whale is linearly related to both the standard body length and the total body mass of the whale (Fig. 7). The mean amount of mattak per whale landed during an autumn catch in Upernavik in 1991 was 79 kg/whale (95% CI 70–88). However this is an overestimate as some of the blubber attached to the skin is removed before the mattak is sold. When the mattak is sold for processing at the fish factories it is required that about 1 cm of blubber be attached to the skin. Simple tests in the field showed that this may reduce the amount of mattak by 10–20% of the values measured in this study. Thus the mean amount of landed mattak per whale during the drive fishery in Upernavik in the autumn is probably closer to 70 kg/whale. The weights of the tails of 9 whales averaged 12 kg.

Three males and one female measured in May at Qeqertarsuaq produced a mean of 156 kg of mattak. Approximately 15% should be subtracted to estimate the mean yield: 133 kg of mattak. White whales taken in Qeqertarsuaq in the spring include animals of a much larger size than those taken in the drive fishery in Upernavik in the autumn (Heide-Jørgensen & Teilmann 1994).

Narwhals reach larger asymptotic lengths and weights at physical maturity than white whales (Hay & Mansfield 1989). It is therefore expected that narwhals generally provide more mattak than white whales. The mean length of 41 narwhals killed in Avanersuaq in 1984 and 1985 was 365 cm (SD = 105, Greenland Environmental Research Institute, unpubl. data). Following the regression in Fig. 7 this corresponds to 105 kg of mattak per whale, from which about 15% should be subtracted to account for blubber that is removed before the mattak is sold. Hence my best estimate of the amount of mattak landed per narwhal in Avanersuaq is about 90 kg. Similarly, Reeves (1993) estimated that 89 kg was landed per narwhal in Arctic Bay.

Utilisation of hunting products

Blubber and skins of white whales were sold to KGH for export to Denmark until 1962 (Reeves & Heide-Jørgensen 1994). In the official statistics only blubber and skins

Table 4. Amounts of mattak from narwhals and white whales sold in West Greenland (1965–1992).

Year	Mattak sold in tons					Total
	ILU	QEQ	UUM	UPV	AVAN	
1965					1.5	1.5
1966				0.1	5.3	5.4
1967				0.1	3.9	4.0
1976					11	
1977					14	
1978					6	
1979					14	
1980					14	
1981				25.0	26.5	51.5
1982				21.2	24.0	45.2
1983				21.1	12.8	33.9
1984				20.7	21.9	42.6
1985				5.8		
1986				1.7		
1987	0	0	4.4	32.6	?	37.0
1988	0	4.9	7.3	27.3	2.4	41.9
1989	0	0.8	31.0	19.3	?	51.1
1990	16.4	2.3	63.6	18.5	9.2	110.0
1991	0	1.4	29.4	26.1	15.1	72.0
1992	0.8	6.7	13.3	46.3	12.2	79.3

Data from Anon. (1967, 1968a, 1968b), Greenland Statistical Office, Royal Greenland Production, Valdemar A.m.b.a. (Adam Kristensen, Innarsuit, pers. comm.) and Born (1987a). The municipalities are abbreviated as follows: ILU = Ilulissat, QEQ = Qeqertarsuaq, UUM = Uummannaq, UPV = Upernavik, AVAN = Avanersuaq.

of white whales are listed, but it is possible that the figures include some blubber and skins from narwhals. Since the 1960s mattak, tusks and to some extent meat have been the primary trade items from the white whale and narwhal hunting in Greenland. Mattak was first purchased by KGH in Avanersuaq in 1965 (Table 4). Although the statistics on the mattak trade are incomplete, it appears that the importance of this trade has increased in parallel with the increase in prices paid for mattak. The price paid to the hunters for mattak was 50 Dkr/kg in 1993 (Royal Greenland Production *in litt.*).

A portion of the mattak obtained from narwhals and white whales is sold to local fish factories, where it is packed, frozen and shipped to the larger towns in South Greenland. The number of white whales killed (observed or reported) and the amount of mattak sold are linearly correlated (Fig. 8), with a mean corresponding to a rate of about 65% of the mattak obtained from white whales in Upernavik being purchased (Fig. 8). This correlation can be used to calculate a rough estimate of the catches from the statistics on purchases of mattak, which are usually more reliable than the catch statistics *per se*.

There have been no purchases of mattak at Royal Greenland plants in Qasigiannguit (Christianshåb), Maniitsoq, Kangaatsiaq, Sisimiut or Aasiaat during the 1980s. Almost all mattak purchased in Qeqertarsuaq, Ilulissat (Jakobshavn) and Upernavik is from white whales, whereas narwhal mattak is traded primarily in Avanersuaq and Uummannaq.

Most of the tusks from narwhals are sold privately or to the KNI for export to Denmark (see Reeves & Heide-Jørgensen 1994).

Catches calculated from the purchase of mattak

The mean weight of mattak (narwhals and white whales, combined) purchased in Avanersuaq during 1976–1981 was 14 tons per year. The catch of white whales in Avanersuaq (excl. Moriussaq and Savissivik) in 1985, 1986 and 1987 was 70–80 white whales per year (Jörn Byrsing and Navarana Qaviaq pers. comm.) and mattak from these would amount to about 5 tons. Subtracting this amount from the total mattak purchased gives an estimate of about 100 narwhals caught, assuming a mean mattak yield of 90 kg per whale and that all of the mattak obtained was sold. It is more likely that only a portion of the mattak was sold and that the rest was consumed locally. If the proportion sold follows the prediction in Fig. 8, then the total catch of narwhals has been about 195 per year in Avanersuaq during 1976–1987.

Trends in population status estimated from the catch statistics and population size estimates

Catch reporting is incomplete in West Greenland. In particular, the municipality of Avanersuaq only infrequently report catches. For proper population assessment precise numbers of removals are mandatory. To correct the reported catches 75 white whales can be added for

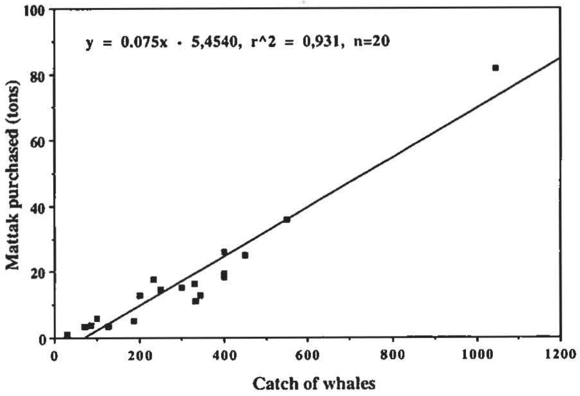

Fig. 8. Correlation between catches of white whales and narwhals and the amount of mattak sold to fish factories per catch.

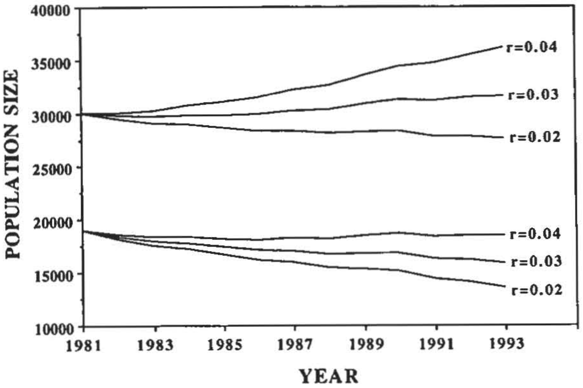

Fig. 9. Trends in the size of the Baffin Bay population of white whales during the 1980s with removals as revealed by the hunting statistics (Canada and Greenland combined), net recruitment rates (r) of 0.02, 0.03 and 0.04 and population estimates in 1981 of 18 600 white whales (Smith *et al.* 1985) or 30 000.

1985 through 1987 for Avanersuaq (see above). Furthermore, 195 narwhals (as calculated above) can be added annually for the 1980s and 1990s, again to account for unreported catches in Avanersuaq. For 1961 through 1964, which are the only years with complete reporting, Avanersuaq reported an average catch of 217 narwhals per year (Kapel 1977).

During the summer of 1981 Smith *et al.* (1985) conducted an aerial "strip-census" of white whales in the Canadian High Arctic where most of the Baffin Bay population of white whales is believed to summer. They estimated 12 000 (95% CI 6 300–18 600) white whales in this area at the time of the survey but made no corrections for submerged whales.

Vital population parameters have been estimated for white whales from Alaska (Burns & Seaman 1986), the Saint Lawrence River (Béland *et al.* 1988), Hudson Strait and Hudson Bay (Sergeant 1981, Doidge 1990) and West Greenland (Heide-Jørgensen & Teilmann 1994). The estimates of net recruitment are generally within the range 0.02–0.04; some of the authors have claimed that the true value is in the upper end of this range. Sergeant (1981) calculated the net recruitment as 0.05 on the basis of 17 years with constant catches of white whales in western Hudson Bay. However the critical assumption of a closed population was not met in his study.

Combining the current estimates of population size with the combined catch statistics for Baffin Bay (Table 3) and the values for the net recruitment reveals a declining trend in the population if this was smaller than about 20 000 white whales in 1981 (Fig. 9). Only a Baffin Bay population of more than 30 000 white whales, with a net recruitment rate of at least 0.03, could have sustained the reported catches without declining.

Visual aerial surveys of Baffin Bay and Davis Strait showed that narwhals are widely dispersed in the heavy pack ice during March through July (Koski & Davis 1994). Based on surveys in May-July 1979 Koski & Davis (1994) estimated that some 34 363 narwhals (SE 8 282) were present in the Baffin Bay pack ice. To this should be added narwhals in areas east and north of the surveyed area, plus whales that were submerged during the passage of the airplane.

Aerial photographic surveys of the Canadian High Arctic summering grounds carried out in 1984 revealed an estimate of 18 000 (90% CI 15 000–21 000) narwhals present at the surface during the survey (Richard *et al.* 1994). At the same time land-based counts of narwhals in Inglefield Bredning in northwestern Greenland produced a figure of about 4 000 narwhals (Born 1986). The sum of these two estimates provides a minimal figure of 18 000 narwhals in northern Baffin Bay and the high Arctic archipelago of Canada. To this estimate should be added figures for unsurveyed areas of Melville Bugt and Smith Sound and a correction factor for whales that did not appear on the photographs due to submergence.

The net recruitment rate of narwhals was recently estimated as no larger than 0.03–0.04 (Kingsley 1989). Narwhals are believed to have vital parameters that resemble those of white whales. It therefore would not be surprising if the net recruitment rates were found to be similar as well.

By applying the range of values for net recruitment, catches after 1979 and a combined estimate of 22 000 in 1984 to equation 1, it appears that the narwhal population could sustain recent catch levels only if it was larger than 22 000 in 1984. For the point estimate of 34 000 narwhals in 1979 (Koski & Davis 1994) the catches can be sustained if the net recruitment exceeds 0.03 (Fig. 10).

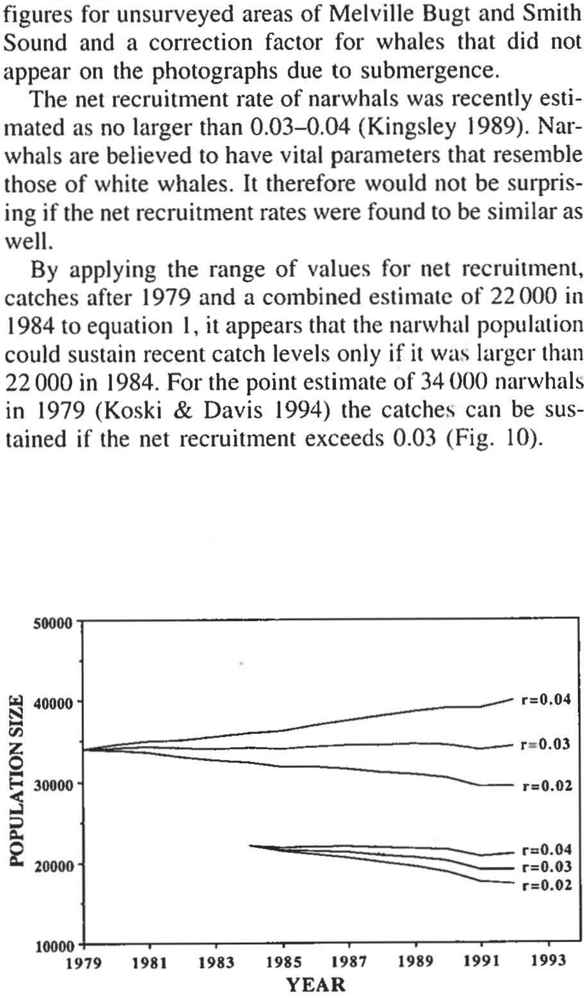

Fig. 10. Trends in the size of the Baffin Bay population of narwhals during the 1980s with removals as revealed by the hunting statistics (Canada and Greenland combined), net recruitment rates (r) of 0.02, 0.03 and 0.04 and point estimates of 22 000 narwhals in 1984 (Born 1986, Richard *et al.* 1994) or 34 000 in 1979 (Koski & Davis 1994).

Discussion

Changes in distribution of white whales

White whales were previously present, at least seasonally, in large numbers in Southwest and South Greenland (south of 65°N). Those that wintered along southwestern Greenland came from the north and were part of a southward movement in the autumn, similar to the present situation. The origin (*i.e.* main summer distribution) of the whales that occurred in southwestern Greenland south of Qeqertarsuatsiaat (63°N) is less certain as Degerbøl & Nielsen (1930) suggested that at least some of them came from Canada. The present situation is clearly different: white whales are rarely seen or caught south of Sisimiut (67°N). The most likely explanation for the change in distribution is the exploitation on the southern wintering grounds. Intensive hunting may have depleted the stock wintering south of 63°N, and especially the drive fishery at Nuuk and the drive-net fishery at Maniitsoq may have severely reduced the number of whales wintering in Maniitsoq and Nuuk districts after 1930. The catch statistics show a brief peak followed by an obvious decline in all three areas (Nuuk, Maniitsoq and Kangersuatsiaq) with organised drive fisheries.

The sea temperature in southwestern Greenland (63°N) gradually declined from 1876 to 1920, after which time it increased rapidly and remained high until the late 1960s. Cold conditions have developed rapidly since the 1960s (Buch 1990). It could be speculated that the higher sea temperatures in South Greenland after 1920 contributed to a change in white whale distribution, with less whales present in South Greenland. However the decline in sea temperatures after 1968, that was just as pronounced as the increase in the 1920s (Smidt 1983), did not result in an increased abundance of white whales in South Greenland.

Eastern Canadian stocks of white whales were also severely reduced during the 1920s and 1930s (Mitchell & Reeves 1981, Reeves & Mitchell 1987a, 1987b). In Cumberland Sound reported catches in the drive fishery during 1920–39 totalled 5 242 whales and by the late 1930s the population was probably depleted (Brodie 1971, Mitchell & Reeves 1981, Reeves & Mitchell 1987a).

The collapses of stocks of white whales off southwestern Greenland and in Cumberland Sound and Ungava Bay may have been mutually reinforcing if the stocks were connected by movement of animals across Davis Strait. Recently white whales have been observed in the middle of Davis Strait in March and mid-May (Mitchell & Reeves 1981), suggesting some exchange between stocks in eastern and western Baffin Bay and Davis Strait. Mixing among neighbouring stocks in southern Davis Strait and perhaps the Labrador Sea is more likely to have occurred before commercial exploitation started, especially during winter months when distance between white whale concentrations in eastern Canada and West Greenland is shortest (Richard *et al.* 1990).

Catches

The largest catches of white whales during the 1980s were made in the drive fishery in the municipality of Upernavik. The catch due to ice entrapment in Disko Bugt in 1990 exceeded the catch in Upernavik, but this was an exceptional event. Kapel (1977) reported three ice entrapments between 1954 and 1975, all in Disko Bugt, with catches of 425, 342 and 260 white whales. Some unusually large autumn catches of narwhals have also been made recently in Uummannaq. The reason for the sudden appearance of large numbers of narwhals in Uummannaq remains obscure. Favourable weather and ice conditions during November may partly explain the rise in catches, but also the sudden abundance of prey species and the disturbance from trawlers offshore have been suggested as contributing factors.

Born (1987a) estimated that 150 narwhals were taken annually in the municipality of Avanersuaq during the 1980s. This may be an underestimate as my calculations suggest that at least 150 have been taken to balance the purchases of mattak, and some additional catch would have been needed to provide for local mattak consumption. Correcting for the local consumption gives a total estimated catch of about 195 per year in Avanersuaq.

Official catch statistics for both white whales and narwhals are incomplete. As the catches show large fluctuations from year to year, catch statistics can not be corrected unless detailed data from each area are available. Annual catches during the late 1980s were probably in the magnitude of 500–1000 white whales and 500 narwhals in West Greenland. To this should be added the proportion of whales that are killed-but-lost.

Trends in population size

The calculations of population trends based on catch statistics, estimated population sizes and estimated net recruitment rates are subject to various uncertainties. The population sizes may be underestimates because the entire distributions of white whales and narwhals have not been covered in any of the surveys. Some of the unsurveyed areas may, however, be of marginal importance. Also, the estimates from aerial surveys are not adjusted to account for the whales that were submerged during the passage of the aircraft. Removals are usually under-reported as hunting loss is never included and some areas and settlements report their catches only infrequently. Among these is the municipality of Avanersuaq, where it was possible to estimate catches from sources other than the Hunters' List of Game. In other areas, where under-reporting may be less obvious, not enough information is available to estimate actual removals.

It is not possible, at present, to apply a simple correction factor to survey estimates to account for submerged whales (*cf.* Koski & Davis 1994) and only unsubstantiated estimates of hunting loss rates in West Greenland are presently available (*e.g.* IWC 1980: 127). Born (1987a) and this study represent the first attempts to quantify under-reporting of narwhals in Avanersuaq. Under-reporting in other areas and for white whales remains to be quantified. It is nevertheless clear that the Baffin Bay white whale population would have had to be considerably larger than the 1981 population estimate to have sustained the reported catches and purchases of mattak since then. It seems unlikely that the extensive surveys conducted in the Canadian High Arctic in 1981 would have resulted in a population estimate that is only half or less of the true population size. It must be concluded that white whales are probably being harvested above the replacement yield and that a decline in the population size has taken place during the 1980s. This is also supported by systematic aerial surveys of the wintering stock of white whales off West Greenland that indicate a 30% decline in relative abundance from 1982 to 1991 (Heide-Jørgensen *et al.* 1993).

The Baffin Bay white whale population may be especially vulnerable to overexploitation because of the whales' coastal habits. During the autumn they move south along the west coast of Greenland, passing near a number of settlements with intensive white whale hunting and where especially females are taken in large numbers (Heide-Jørgensen & Teilmann 1994). These coastal areas may act as "bottlenecks" for the whale population. The recent increase in price of the much-desired mattak, combined with improved hunting equipment (fast dinghies with outboard engines), has increased the hunting pressure on the white whales.

Narwhals are taken in smaller numbers in Greenland and they are more difficult to find and pursue. The projection of the narwhal population seems to be more stable than that of white whales although some narwhal catches in some recent years may have exceeded the replacement yield. Overexploitation of narwhals in Greenland is less likely to happen because they are found farther offshore than white whales, and their range at any time of the year is much larger than that of white whales. However, this may not be true for Canada, where deep-water concentrations of narwhals are found near shore in areas and periods where considerable hunting takes place.

The uncertainties of the status of both the white whale and narwhal populations warrant more thorough study so that catches can be adjusted to sustainable levels and further declines can be prevented.

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Ice entrapments of narwhals (*Monodon monoceros*) and white whales (*Delphinapterus leucas*) in Greenland

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Siegstad, H. & Heide-Jørgensen, M. P. 1994. Ice entrapments of narwhals (*Monodon monoceros*) and white whales (*Delphinapterus leucas*) in Greenland. – Meddr Grønland, Biosci. 39: 151–160. Copenhagen 1994-04-22.

Information on historical and recent ice entrapments of narwhals (*Monodon monoceros*) and white whales (*Delphinapterus leucas*) in Greenland is presented. Most entrapments occur in the inner parts of Disko Bugt where both narwhals and white whales are caught. In this area entrapments happened under particular weather conditions and at certain sites at intervals of two to three years during the 1970s and 1980s. In the Uummannaq and Upernavik areas entrapments occurred less frequently and usually involved only narwhals. No entrapments were documented in East Greenland. The data suggest that whales sometimes die in entrapments that are not discovered by hunters and that ice entrapments may be regarded as contributing to the natural mortality of narwhals and white whales. These large-scale, periodic die-off events probably affect long-term population trends and represent a concern for the management of arctic whale stocks.

Key words:
Narwhal, *Monodon monoceros*, white whale, beluga, *Delphinapterus leucas*, ice entrapment, sassat, Baffin Bay, Greenland.

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Introduction

Arctic whales are periodically entrapped by ice, especially in periods with extremely low temperatures when fast ice forms rapidly. Among the arctic whales, narwhals (*Monodon monoceros*) and white whales (*Delphinapterus leucas*) seem to be particularly vulnerable to ice entrapment. Bowheads (*Balaena mysticetus*) were occasionally reported in ice entrapments in the past in Greenland and elsewhere (Mitchell & Reeves 1982) but a recent review concluded that relatively few bowheads die from ice entrapment (Philo *et al.* 1993). In Baffin Bay and Davis Strait the depleted status of the stock of bowheads (Reeves *et al.* 1983) may help explain the absence of recent entrapments.

Porsild (1916, 1918) provided the first detailed description of ice entrapments of whales in Greenland (Fig. 1), although the phenomenon had been recognized for more than a century (Egede 1788, Gad 1973, Glahn 1991). Porsild (1916) used the Greenlandic word "savssat" ("sassat" in modern Greenlandic) to describe an event in which "whales and birds are surprised by sudden low temperatures [and] they congregate in large herds in the remaining holes in the ice to breathe". We found that "ice entrapment of whales" requires a more restrictive definition as both white whales and narwhals often naturally occur in leads and cracks in dense ice. It is somehow arbitrarily decided when the animals are lethally (or otherwise dangerously) entrapped. For this compilation we decided that an entrapment of whales is ultimately fatal. Thus a true "ice entrapment" event occurs only when the whales are unable or unwilling at any given instant to escape from a restricted open-water reservoir that is surrounded by fast ice or pack ice. This definition is necessary because arctic whales live for the major part of the year in areas with heavy pack ice where they are often found in surroundings that 'at first glance' may look like an entrapment but in fact is their preferred habitat. For instance narwhals that winter in the Baffin Bay area show a strong preference for areas with more than 9/10 of pack ice (Koski & Davis 1994) where they may live for months in relatively small leads and cracks.

The significance to the whale populations of mortality caused by ice entrapment has been dicussed by several investigators (Mitchell & Reeves 1981, Brodie 1982,

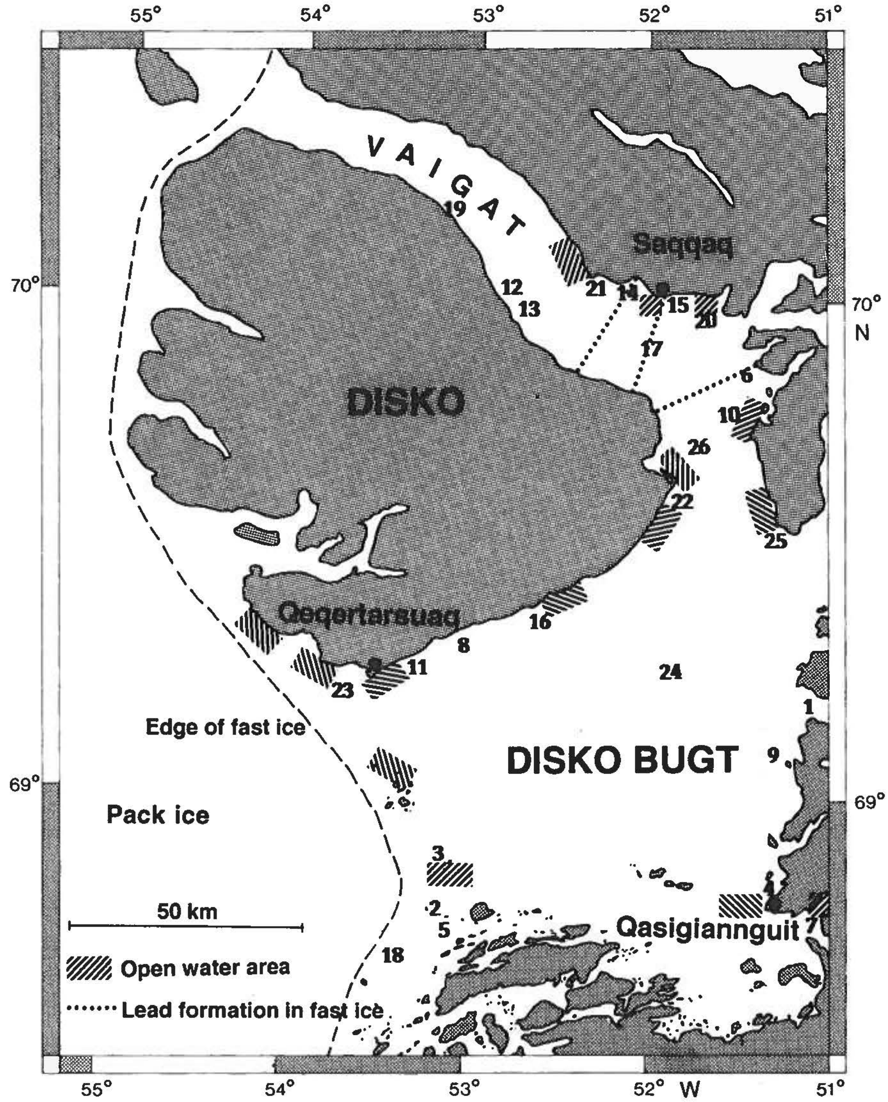
Fig. 1. Flensing of narwhal taken in sassat in Disko Bugt during February 1915. Photo: M. Porsild. Copyright Arktisk Institut. Denmark.

Burns & Seaman 1986, Ivashin & Shevlyagin 1987). When discovered by hunters, entrapped whales are subjected to intensive hunting (*e.g.* Mitchell & Reeves 1981). In this paper we summarize data on the frequency and distribution of ice entrapments in Greenland. Some information on the survival of entrapped whales is also presented. We discuss ice entrapment of whale populations as a factor contributing to both natural and hunting mortality.

Materials and methods

Published sources (*e.g.* scientific literature, newspapers) were consulted for information on ice entrapments. All available issues of local newspapers from Ilulissat/Jakobshavn ("Iluliarmioq": 1954–1992), Qeqertarsuaq/Godhavn ("Qaqaliaq": 1962–1992), Vaigat ("Qulleq": 1954–1972), Uummannaq ("Nasiffik": 1936–1992) and Upernavik ("Qimusseq": 1953–1992) were searched for reports on sassat's. Information on ice entrapments of whales throughout Greenland was obtained through extensive interviews with hunters and fishermen conducted under the project "Inventory of Renewable Resources in Greenland" (Siegstad 1991). During the course of that project all municipalities in Greenland were visited by one of the authors (HS) and hunters with particular insight into the past occurrence of whales were interviewed. To obtain information on numbers caught in ice entrapments the Hunters' List of Game was also consulted (Anon. 1953–1987). However, large catches in winter months were not used as indications of ice entrapments unless auxiliary information so suggested. Entrapments of narwhals in the Uummannaq area and white whales in Disko Bugt in 1984 were witnessed by one of us (HS). A large entrapment of white whales in 1990 in Disko Bugt was visited by research staff, who collected biological specimens including lower jaws. Ages of thirteen entrapped white whales were estimated by counting dentinal growth layers in teeth from the lower jaw (Heide-Jørgensen *et al.* 1994) and sex was determined by chromosomal analyses (Palsbøll *et al.* 1992). Data on purchases of whale skin ("mattak") at fish processing plants were used to estimate numbers of whales killed in some sassat's.

Fig. 2. Map of the Disko Bugt region showing positions of ice entrapments (keyed to nos. in Table 1), and areas where leads and open water in the fast ice are frequently found during January-March. The information on open-water areas and leads was collected during the project "Inventory of Renewable Resources in Greenland".



Results

Occurrence and distribution of entrapments in Greenlandic waters

Narwhals are present year-round along the coast of East Greenland and in the Greenland Sea. During the open-water season they are frequently present in the fjords of East Greenland (Dietz *et al.* 1994). White whales are only occasionally observed in East Greenland and these may be stragglers from West Greenland or from Svalbard (Dietz *et al.* 1994). No published accounts or descriptions from hunters of ice entrapments in East Greenland have come to our attention. This may be due partly to the low abundance of whales and partly to the extreme mobility of the coastal sea ice and the predictability of the formation of fast ice in the fjords of East Greenland.

In West Greenland ice entrapments have been reported from the municipalities in Disko Bugt and from Uummannaq and Upernavik municipalities (Tables 1 and 2, Figs 2 and 3). Ice entrapments occur relatively frequently in Disko Bugt but less frequently in Uummannaq and Upernavik municipalities. In Disko Bugt narwhals and white whales can be found in mixed or single-species entrapments (Table 1, Fig. 2). In the Ummannaq and Upernavik areas usually only narwhals are entrapped (Table 2, Fig. 3).

The entrapments in Disko Bugt are remarkably uniform in their geographical distribution. Particular currents and patterns of ice formation may determine the localities of the entrapments (Fig. 2). In Disko Bugt freeze-up rarely occurs until December and March is

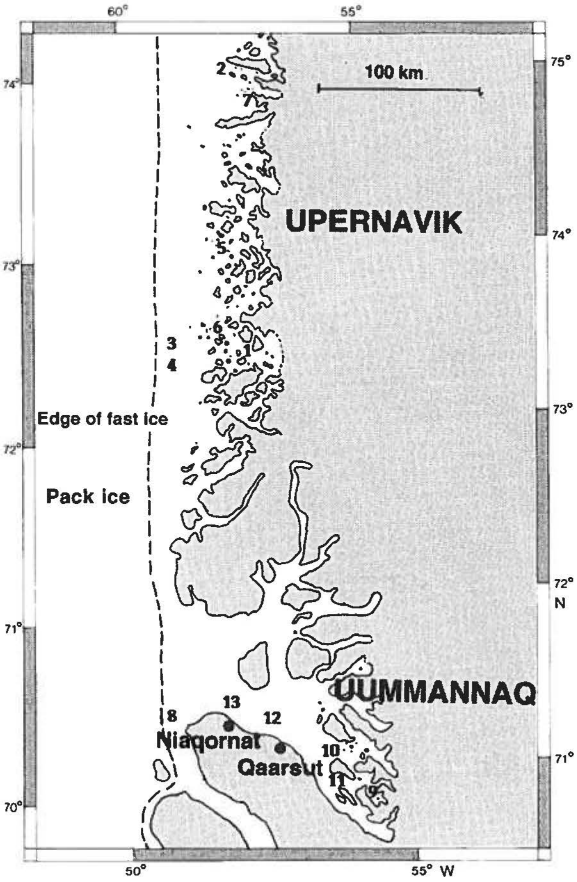


Fig. 3. Map of the municipalities of Uummannaq and Upernavik showing positions of ice entrapments (keyed to nos. in Table 2).

generally the coldest month. Whales are usually entrapped in the period January to March and occasionally in April (Tables 1 and 2). A period with stable and cold weather normally precedes an entrapment, and hunters often expect the entrapments to occur during certain ice and temperature conditions (see below).

The largest entrapment reported from Greenland took place in 1955 when an estimated 3 000 white whales were landed by the hunters (Table 1, Fig. 2; No. 17). This event was described in detail by Golodnoff (1956) and the size of the catch was estimated by a local inhabitant of Saqqaq who had witnessed several entrapments (Hannibal Fencker *in litt.*). The entrapment had been expected by the hunters because, after a period with open water early in January, the air temperature suddenly dropped and remained near −30°C. Within a week the sound of Vaigat (Sullorsuaq) was covered with fast ice except for a narrow lead 0.5–1 m wide extending across the Vaigat from Saqqaq to Disko (the island of Qeqertarsuaq). The white whales were discovered in this lead in late January (Golodnoff 1956).

Recent entrapments of white whales and narwhals

April 1988: At "Per Dams skib" close to the town of Qeqertarsuaq (Godhavn, Table 1, Fig. 2; No. 8) 100–150 white whales were entrapped. It is uncertain whether the presence of outboard motor boats actually scared the whales into the ice. A large proportion of the killed whales floated and could be recovered, so hunting loss was considered minimal. It was suggested by some hunters that the entrapped whales were primarily females with calves because it was more difficult for them to leave the area than it was for the mature males (Hans Christian Petersen, Greenland Home Rule, Nuuk, pers. comm.). The amount of mattak purchased after this entrapment was 10.3 tons (Niels Bjerregaard, Royal Greenland, Qeqertarsuaq *in litt.*). The mattak yield from a sample of four white whales taken in Qeqertarsuaq in May 1992 ranged between 100 and 150 kg per whale (Heide-Jørgensen unpubl. data). This is considerably higher than the estimated yield for white whales taken in Upernavik (Heide-Jørgensen 1994). The difference is explained mainly by the larger size of the whales taken in spring at Qeqertarsuaq (Heide-Jørgensen & Teilmann 1994). Nevertheless, the purchased amount of mattak corresponds to a kill of at least 100 white whales if all mattak was sold.

February 1990: After a cold period with almost no wind that began in mid January and lasted till mid February (Fig. 4), ice cover in Disko Bugt was extensive and thick. In late January and early February a large herd of white whales was discovered close to the eastern part of Disko (Table 1, Fig. 2; No. 26). The whales were in a lead 5 m wide and 5–10 km long. Hunters from several settlements and towns within Disko Bugt and even some from the municipality of Uummannaq participated in the catch. Figures indicating a total catch of between 300 and 1000 were frequently mentioned, but no exact data on catches or losses are available. The purchases of mattak totalled 9.4 tons at Ilulissat and 6.4 tons at Saqqaq (Per Lyster, Greenland Statistical Office, Nuuk *in litt.*). Assuming that each whale produced an average of 75 kg of mattak (see Heide-Jørgensen 1994) then a minimum of 210 whales would have been taken to produce this amount of mattak. Additionally, some mattak was sold locally or consumed by local people. Using an equation developed by Heide-Jørgensen (1994) showing the relationship between the amount of mattak purchased and the catch of whales per settlement, we can estimate a combined catch in Ilulissat and Saqqaq of 285 white whales. Mattak was also delivered to other villages (*e.g.* Qeqertarsuaq/Godhavn and Qasigiannguit/Christianshåb), so a more likely estimate of the total catch is around 400 white whales. There are no estimates of the loss rate (*i.e.* whales killed but not retrieved) but it is likely to have been high as the air temperature was low (-30°C) and there was little daylight.

Table 1. Ice entrapments of narwhals and white whales in Disko Bugt. See Fig. 2 for localities. HLG is Hunters' List of Game (Anon 1953–1988).

Year	Month	No.	Position	Comments	Source
1738	January	1	Ice Fjord at Ilulissat	More than 100 white whales	Egede 1788
1750		2	Near Aasiaat	More than 1000 *D.leucas* and 21 bowheads	Gad 1969
1803	March to April	3	Near Kronprinsens Ejland	"A fantastic entrapment comprising both *M.monoceros* and *D.leucas*"	Gad 1976
1860	April	4	Near Qasigiannguit	"Hundreds" of *D.leucas* and *M.monoceros*	Brown 1868
1898	April	5	Near Aasiaat	22 *M.monoceros* or *D.leucas*	Anon. 1944, Kapel 1979
1899	May	6	Nuak in Ritenbenk district	80 *M.monoceros* or *D. leucas*	Anon. 1944, Kapel 1979
1915	January	7	Akulleq	6 *D.leucas*	Porsild 1918
1915	February	8	Between Qeqertarsuaq and Aamaruutissat	More than 1000 *M.monoceros* were caught in two sassat	Porsild 1918, Anon. 1944, Rosendahl 1957
1915	March	9	Ilimanaq in Qasigiannguit	About 130 *M.monoceros*	Porsild 1918, Anon. 1944
1915	April	10	Ritenbenk	25–33 *D.leucas*	Porsild 1918, Anon. 1944
1920			Sisimiut	40 *M.monoceros* and/or *D.leucas*	Anon. 1944, Kapel 1979
1933		10	Ritenbenk	About 100 *M.monoceros* and/or *D.leucas*	Anon. 1944, Kapel 1979
1934	March	11	Qeqertarsuaq	About 50 *M.monoceros* and/or *D.leucas*	Anon. 1944, Kapel 1979
1935		12	Qullissat	About 100 *M.monoceros* and/or *D.leucas*	Anon. 1944, Kapel 1979
1943	March	13	Qullissat-Ujarasussuk	340 *D.leucas* and *M.monoceros*	Fencker *in litt.*, Anon. 1943
1945	February	14	At Taartuna	*M.monoceros* and *D.leucas*-no other information	Fencker *in litt.*
1951	February	15	Saqqaq	HLG (February): 85 *M.monoceros* and 173 *D. leucas*	Fencker *in litt.*, Golodnoff 1956
1952	March	16	Aamaruutissat	About 450 *M.monoceros*	Anon. 1988a
1955	January	17	Saqqaq-Sioraleq in a 30 km long lead	More than 3000 *D.leucas*	Fencker *in litt.*, Anon. 1955, 1961, Golodnoff 1956
1960		18	Aasiaat	About 100 *M.monoceros* and/or *D.leucas*	Anon. 1961
1967	March	14	Taartuna	Mixed *M.monoceros* and *D.leucas*, the ice broke after one week – few days later a new sassat was discovered – this time with only *D.leucas*. HLG (March): 31 *M.monoceros* and 3 *D.leucas*	Fencker *in litt.*,
1968	February	19	Northwest of Qullissat at Kuusinerssuaq	Both *M.monoceros* and *D.leucas* – 600 HLG (February): 161 *M.monoceros* and 234 *D.leucas*	Berliner 1968, Fencker *in litt.* Kapel 1977
1969	January	20	East of Saqqaq	Only *M.monoceros* – no information on numbers	Fencker *in litt.*
1970	January	21	Nuunguaq NW of Saqqaq	Only *M.monoceros*. (Kapel: > 100 caught)	Fencker *in litt.*, Kapel 1977
1970	January	22	Nuuk at Disko Island	1000 *D.leucas*. (Kapel: > 340 caught)	Anon. 1970a, 1970b, Kapel 1977
1970	April	12	Northwest of Qullissat	Only *D.leucas* – less than 50	Fencker *in litt.*
1976	January	23	Qeqertarsuaq	HLG (for the town): 479 *D.leucas* in early January and 147 *D.leucas* in late January (and 15+12 for Kangerluk). "More than 500 caught off Brededal"	Kapel unpubl.
1982	February	24	Between Aamaruutissat Ilulissat	Between 50–200 *D.leucas* caught	Born *in litt.*
1982	April	4	At Qasigiannguit	45 *M.monoceros* caught. The animals were found under air-filled cupolas in the ice	Born *in litt.*
1984	February	22	Marraat (Mudderbugten)	About 200 *D.leucas*	Anon. 1984
1984	April	25	Niaqornarsuk	20 *D.leucas* caught-the animals disappeared	Witnessed by H. Siegstad
1988	April	8	Between Qeqertarsuaq and Aamaruutissat	About 100–150 *D.leucas*	Anon. 1988b
1990	January	26	Between Marraat and Appat	About 500 *D.leucas* caught	Anon. 1990a, 1990b, 1990c

The mean estimated age of a sample of the entrapped white whales was 13.9 years (range 5.5–24, N = 6) for females and 10.5 years (range 1.5–17, N = 7) for males, which indicates that mature whales of both sexes are present in Disko Bugt in winter and that they are susceptible to entrapments.

January 1991: In mid January groups of narwhals were discovered entrapped in the outer parts of the municipality of Uummannaq off Niaqornat; 26 were caught and one was lost (Table 2; J. Tobiassen pers. comm.).

Mortality of entrapped narwhals in Uummannaq

A small entrapment of 8 narwhals was discovered on 29 April 1984 between Qaarsut and Niaqornat in Uummannaq (Table 2, No. 12; Fig. 3). The whales were found in a small open-water area (about 3 m^2) in the fast ice approximately 5 km from shore. During searches with mirrors under the ice a further 25–30 dead narwhals could be seen frozen into the underside of the fast ice. A few of these were grappled and hauled onto the ice (Fig. 5). They had all been dead for a considerable time and were

Table 2. Ice entrapments of narwhals and white whales in the Upernavik and Uummannaq areas. See Fig. 3 for localities. IRR = "Inventory of Renewable Resources in Greenland".

Year	Month	No	Position	Comments	Source
Upernavik					
1920–30		1	Aappilattoq	A sassat saved a starving settlement	Siegstad unpubl.
1939		2	North of Nuussuaq Amdrup Isle	100 *M.monoceros* killed in a lead	IRR, Anon. 1940 Kapel 1979
1948		3	West of Upernavik	About 200 *M.monoceros*	IRR
1956		4	West of Upernavik	100–150 *M.monoceros*	Knudsen 1958, Anon. 1961 Kapel 1977
1958		5	North of Tasiusaq	*M.monoceros*– no information on number	IRR
1960–63		6	Northwest of Upernavik at Pututaasaq	10 *M.monoceros*	IRR
1968	January		Upernavik area	Caught about 50 *M.monoceros*	Kapel 1977
1969	March	7	Illulik	60 *M.monoceros*	IRR, Haller 1986
Uummannaq					
1781			150 km N of Uummannaq	No information on species	Gad 1973
1917		8	Nuussuaq	No information on number and species	Bertelsen *et al.* 1921
1922		9	Sermilik	About 25 *M.monoceros* or *D.leucas*	Anon. 1944 Kapel 1979
1956	December	10	Uummannaq town	Caught 250 *M.monoceros*	Hadrup 1971, Kapel 1977, Anon. 1961
1961	April			272 *M.monoceros*	Anon. 1962, Kapel 1977
1968	January	11	West of Uummannaq	84 *M.monoceros*	Kapel 1977, Anon. 1968
1984	Late April	12	North of Ikorfaat	8 *M.monoceros* caught and 25–30 *M.monoceros* found dead under the ice	Witnessed by H. Siegstad
1991	January	13	North of Niaqornat	26 *M.monoceros*	J. Tobiassen 1991 (pers. comm.)

partly decomposed. A large tusk-bearing narwhal was found 50–100 m from shore in the tidal zone between the fast ice and the land-fast ice foot approximately 5 km away from the breathing hole. When hauled onto the ice this whale appeared decomposed and amphipods had been feeding heavily on the mattak.

During the same period Greenland sharks (*Somniosus microcephalus*) caught at the ice edge 50 km east of the sassat had meat from marine mammals in their stomachs, indicating that they may have been feeding on dead narwhals.

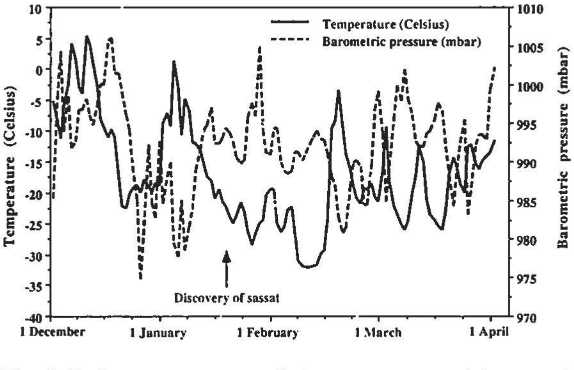


Fig. 4. Daily measurements of air temperature and barometric pressure in Ilulissat during December 1989 through March 1990. (Source: Grønlands Forundersøgelser).

Discussion

Limitations of the study

Our search for reports on ice entrapments primarily covered published sources. Hence some ice entrapments that were not reported, or that were reported but not published, may have escaped our notice. However, our sample of entrapment reports offers a consistent description of the geographical distribution of entrapments and for the past decade or two the frequency of discovered entrapments is probably also reliably described. Most observations of whale entrapment stem from discoveries by hunters. In winters when weather conditions favour ice entrapments hunters will search for whales in areas with open water and where whales are known to have been entrapped previously. These searches are usually effective because ice fog, visible at long distances, is emitted from the open water. After entrapped whales are found, they are invariably subjected to intensive hunting.

Thomsen (1993) recently presented a study of Inuit knowledge of narwhals and white whales. Her study reveals a similar picture of the frequency and general distribution of ice entrapments. The discrepancies between her study and ours may be attributed to different definitions of ice entrapment (see Introduction) and to the fact that her study was based on human recall rather than written sources.

Fig. 5. Narwhals frozen into the fast ice and discovered in late April 1984 (Table 2; No. 12) in Uummannaq. Photo: H. Siegstad.

Weather conditions during an entrapment

Narwhals and white whales are in danger of becoming ice-entrapped when air temperatures are low and new ice is rapidly forming. Factors responsible for an entrapment could include a group of whales' lack of experience with dangerous ice conditions, their preoccupation with exploiting a concentration of prey, or simply a failure to respond quickly enough to a rapid change of environmental conditions. In West Greenland the entrapments occur most frequently in the northern part of the area influenced by the influx of Atlantic water. South of Disko Bugt open water can usually be found along the coast during the winter. The weather situation for an entrapment in 1990 is in accordance with descriptions from previous incidents of entrapment in Disko Bugt: a period with open water early in January is suddenly reversed when a period with extremely low temperatures and no wind results in rapid freezing of the sea surface (Porsild 1918, Golodnoff 1956).

Destiny of entrapped whales

The discovery of dead narwhals frozen into the fast ice in the Uummannaq area suggests that when whales are trapped well inside the persistent fjord ice they are at risk of dying when the last open water freezes. However, the definition of an ice entrapment is important when considering the whales' ability to survive. The entrapment at Qeqertarsuaq in April 1988 was probably a short-term entrapment in deteriorating ice conditions as the spring break-up of land-fast ice was progressing. No new ice was forming during daytime because of the elevation of the sun in mid April and this entrapment must therefore be considered temporary, with limited or no mortality of whales expected due to the entrapment itself. However, as the whales were discovered by hunters, they experienced high mortality from the hunt.

The pertinent question is whether the whales that are killed by hunters would have died anyway because of their lack of access to open water. If the whales usually survive an entrapment, then the mortality caused by hunting should be considered additive to the natural mortality. It seems likely that there is no simple solution to this problem. The survival of entrapped whales depends entirely on the persistence of the ice conditions and the time of the year. Generally, we feel confident that whales that are entrapped early in winter with the prospect of continued low temperatures and increasing ice coverage have a high probability of dying regardless of whether they are hunted or not. This may often be the case for entrapments in the eastern parts of the Uummannaq area and perhaps also in the eastern parts of Disko Bugt. Entrapments later in the season in areas where ice conditions are likely to change within a few weeks will probably always be survived by the whales. This may be the case for entrapments in the western parts of Disko Bugt and Uummannaq, and in the Upernavik area.

The observation of dead narwhals frozen into the fast ice in the vicinity of a small open-water area suggests that entrapment can be fatal even when the whales are not hunted. Degerbøl & Freuchen (1935) and Mitchell & Reeves (1981) mentioned similar incidents in which narwhals were found late in the season in the fast ice in northern Canada. Freeman (1968) described ice entrapments of white whales near Grise Fiord where the whales were discovered in the autumn and were hunted throughout the winter. The animals became progressively thinner and in poorer condition during the winter, suggesting that they would have eventually succumbed to starvation if they had not been killed by the hunters. Lowry *et al.* (1987) listed the relatively few entrapments of white whales in Alaska and described two incidents, both in April, when entrapped white whales died from natural causes. In both incidents polar bears were observed to prey upon or scavenge from the entrapped whales.

Population effects

If entrapment mortality is usually a part of natural mortality then it must constitute a major proportion of this mortality. The numbers of dead whales at some entrapments are high relative to the estimates of population size. The white whale population centered in Baffin Bay is in the magnitude of 10 000 to 20 000 and less likely to be 30 000 (Smith *et al.* 1985). When 500 whales die in an entrapment it constitutes a mortality of 2–5%, which is a high instantaneous mortality rate for an odontocete. Independent estimates of annual mortality rates for white whales are in the range of 2–4% (Beland *et al.* 1988, Doidge 1990). To balance this periodic pulse in mortality the remaining population would need to have a reduced natural mortality during the rest of the year and in the preceding and succeeding years.

Other marine mammals do experience pulses of mass mortality that greatly exceed the natural mortality for normal years. The most dramatic example is the mass die-off of harbour seals, *Phoca vitulina*, in the North Sea area during 1988 when more than 18 000 seals died during six months, corresponding to an instantaneous mortality rate of 60% in some areas (Heide-Jørgensen *et al.* 1992). Various odontocetes mass strand, particularly *Globicephala spp.*, *Pseudorca crassidens*, and *Physeter catodon* (Sergeant 1982). Also, walruses (*Odobenus rosmarus*) sometimes die in unusually large numbers because of overcrowding at haul-out sites (Fay & Kelly 1980). These mass die-offs certainly exceed the natural mortalities and have pronounced effects on long-term population trends (Harwood & Hall 1990). The population-regulating effects of density-dependent changes in reproduction and mortality rates are masked by the mass die-offs caused by epizootics or stranding events, and this may also be true for the mass die-offs of narwhals and white whales caused by ice entrapment.

From a management point of view, the mass die-offs are particularly intriguing as most predictions about stock responses to exploitation assume relatively constant population parameters. If unpredictable catastrophic mortalities, independent of the population size, were to be incorporated into a management scheme, the result could be that the margins or surpluses available for exploitation are surprisingly small. This could be true regardless of whether the entrapped and hunted whales would have succumbed from natural causes alone. Entrapments provide unpredictable opportunities for windfall catches of unusually large numbers of whales. The population effects of such events should be carefully monitored to allow rapid adjustments in the hunt-management scheme.

Acknowledgements

We wish to thank the hunters and fishermen in Greenland for sharing with us their hard-won knowledge about ice entrapments of whales during the project "Inventory of Renewable Resources in Greenland". This study was jointly financed by Aage V. Jensen's Charity Foundation and by the Greenland Home Rule. A. E. Kristensen collected the samples from the ice entrapment in Disko Bugt in 1990 and F. O. Kapel provided additional information on entrapments.

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Habitat use and behaviour

White whales in pack ice off Central West Greenland. Photo: M. P. Heide-Jørgensen.

Summer distribution and movements of narwhals (*Monodon monoceros*) in Eclipse Sound and adjacent waters, North Baffin Island, N.W.T.

MICHAEL C. S. KINGSLEY, HOLLY J. CLEATOR and MALCOLM A. RAMSAY

Kingsley, M. C. S., Cleator H. J., & Ramsay, M. A. 1994. Summer distribution and movements of narwhals (*Monodon monoceros*) in Eclipse Sound and adjacent waters, North Baffin Island, N.W.T. – Meddr Grønland, Biosci. 39: 163–174. Copenhagen 1994-04-22.

Each year from 1987 to 1991 and in 1993, 3–6 helicopter surveys were flown in August to study the distribution and movements of narwhals (*Monodon monoceros*) in their summering grounds in western Eclipse Sound, Milne Inlet, Koluktoo Bay and Tremblay Sound. Their summer distribution is influenced by ice cover. They prefer waters that while giving them shelter from the wind, are over deep bottoms. Narwhals associate with ice in Eclipse Sound, a large expanse of water, while it persists, but do not frequent Tremblay Sound, a narrow fjord, when it has ice cover. When Eclipse Sound is ice-free, narwhals frequent smaller water bodies. Favoured areas in the ice-free season have in common the characteristics of being steep-sided and deep. Narwhals associate in small groups, but these groups aggregate to form larger herds that generally move together. In the short term, movements and distribution are greatly affected by the near presence of killer whales (*Orcinus orca*), which narwhals seek to avoid.

Key words:
Narwhal, *Monodon monoceros*, distribution, behaviour, Baffin Island, killer whale, *Orcinus orca*.

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Introduction

Narwhals (*Monodon monoceros*) occupy fjord complexes during the open-water season (Mansfield *et al.* 1975, Silverman 1979, Born 1986, Koski & Davis 1994). Females with young show special preference for the heads of fjords (Vibe 1950). It is not known for certain what factors influence the distribution and movements of narwhals at that time of year, although tidal cycles, feeding, calving, ice conditions and hunting have all been suggested (Vibe 1950, Finley 1976, Silverman 1979).

Knowledge of the distribution and movements of narwhals in their summering grounds is of practical interest for several reasons. 1) It potentially provides insight about why whales occupy their summer habitat. 2) It may aid in identifying types of habitat that should be given special protection. 3) Distributions that are difficult to explain can cause researchers to investigate seemingly unlikely, or less directly related, factors for an explanation. 4) It can lead to more effective design of aerial surveys for population estimation. Mass movements may also affect the precision of aerial census surveys which may take several days to complete.

We flew aerial surveys in western Eclipse Sound and two adjoining fjord systems (Fig. 1) in August 1987–1993 to study narwhal distribution and movements. We were particularly interested in the influence of ice cover and wind. Observations of killer whales (*Orcinus orca*) were also noted. Survey observations were complemented by incidental observations made in the course of vocalisation, behaviour and radio-tagging studies in Tremblay Sound in 1984–1987 and 1989–1991 and in southern Milne Inlet in 1988 and 1993.

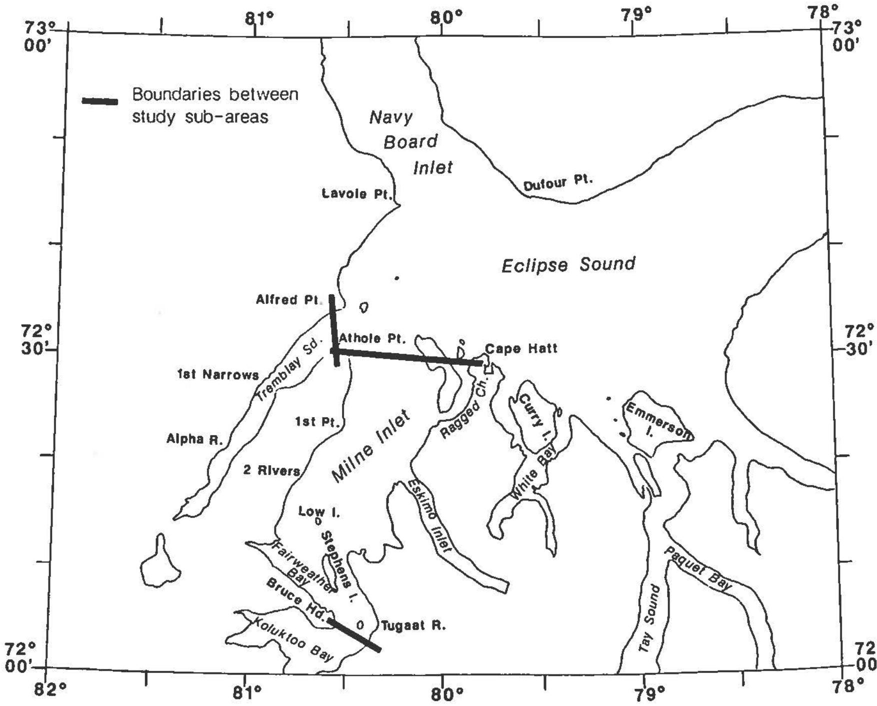

Fig. 1. Study area in northern Baffin Island.

Materials and methods

Study area

The full survey route sampled the western end of Eclipse Sound, Tremblay Sound, Koluktoo Bay and Milne Inlet (Fig. 2). Some surveys flown in early August, before fuel had been cached within the survey area, could not cover the full route. Three surveys in 1988 were prevented by bad weather from flying the full route in Eclipse Sound. In two surveys each in 1989, 1990 and 1991 the route in Milne Inlet was varied to cover the western near-shore waters more thoroughly, fewer transects being flown from side to side. The southern end of Navy Board Inlet was crossed by a single transect.

Weather and ice conditions

In most years Tremblay Sound, Koluktoo Bay and Milne Inlet are cleared of ice by river inflows while the ice in Eclipse Sound remains fast. When the ice in Eclipse Sound breaks up, north or northeast winds can sometimes drive ice into Milne Inlet and Tremblay Sound, where it may stay until south winds cause clearing. The surveys described here took place after the ice in Eclipse Sound had broken up. In 1987 this break-up occurred 2–3 weeks later than usual. Mean ice cover was 25% (SD 33%, N = 220) for the four surveys in 1987; 8% of the ice was multi-year. In the first survey that year Tremblay Sound had 15% ice cover and Koluktoo Bay had no ice, while Eclipse Sound had 57% ice cover and Milne Inlet averaged 41%. During the following three surveys in 1987, Eclipse Sound had less ice cover, while in the other three bodies of water the ice cover increased in the second survey and then decreased in the third and fourth.

Break-up of the sea ice occurred early in 1988 and 1989, and no ice was recorded on any survey. In 1990 there was ice in southwestern Eclipse Sound, northern Tremblay Sound and northern Milne Inlet during the first survey on 2 August, but southern Tremblay Sound and southern Milne Inlet were ice-free. This ice cover had cleared by the time of the next survey on 12 August. In 1991 the last ice disappeared during the first week of August. In 1993 Koluktoo Bay and Tremblay Sound were clear of ice, and Eclipse Sound had only light ice cover on 16 August. Continuous north winds moved the ice out of Navy Board Inlet, increased the ice cover in Eclipse Sound and brought heavy multi-year pack ice to Tremblay Sound from 17 August and to southern Milne Inlet from 19 August.

Strong winds affect all aspects of aerial survey for marine mammals, so light winds were preferred. However as one objective of the surveys was to determine if narwhals select summering areas that will give them shelter during windy periods, we flew several surveys when wind speeds exceeded 8 m/s. One of four surveys in

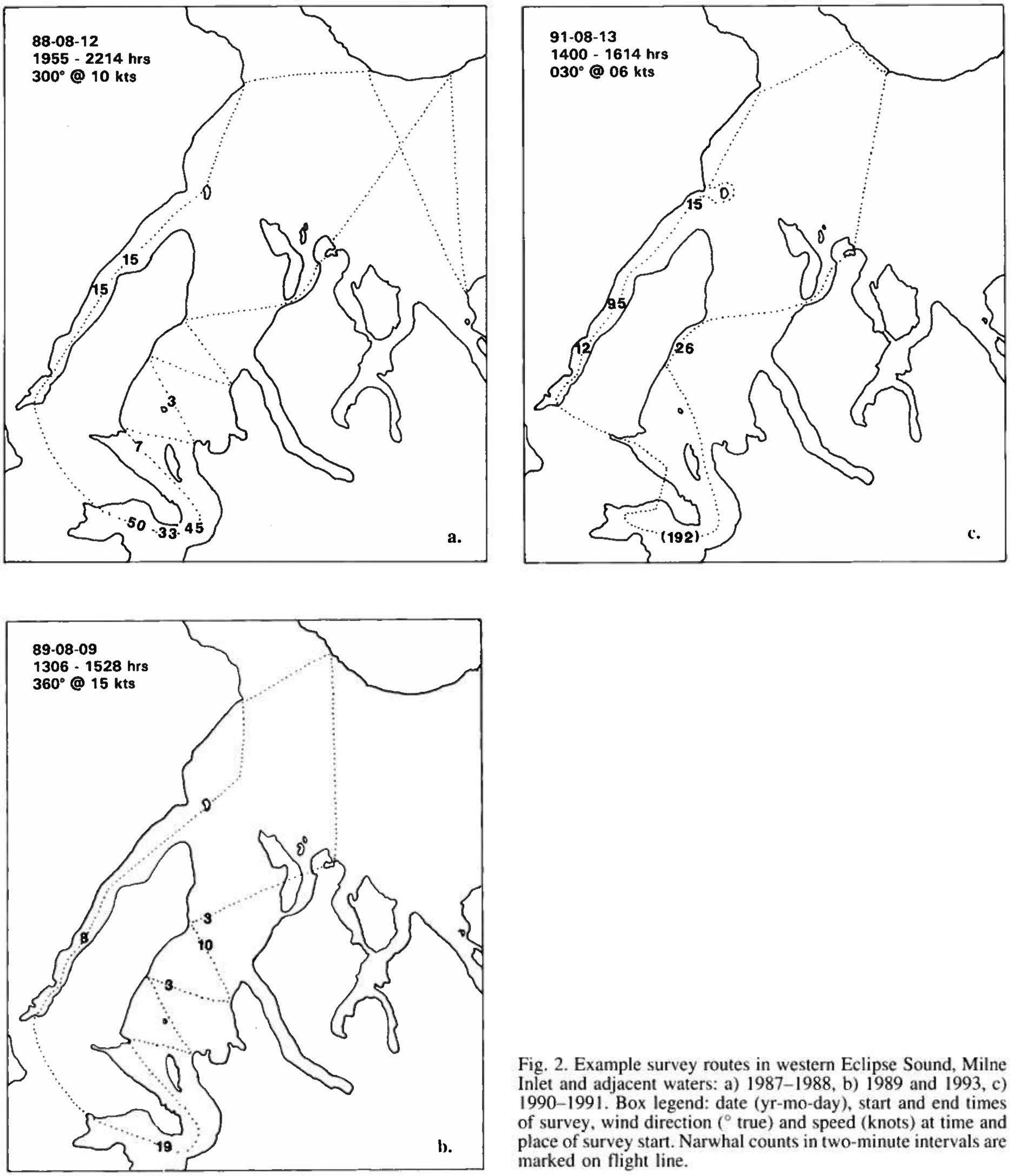

Fig. 2. Example survey routes in western Eclipse Sound, Milne Inlet and adjacent waters: a) 1987–1988, b) 1989 and 1993, c) 1990–1991. Box legend: date (yr-mo-day), start and end times of survey, wind direction (° true) and speed (knots) at time and place of survey start. Narwhal counts in two-minute intervals are marked on flight line.

1987 and three of six surveys in 1988 deviated from the planned pattern because of high winds or fog. Of the four water bodies surveyed Eclipse Sound was the largest and the most prone to bad weather.

Survey methods

Surveys were flown in a Bell 206 "Jet Ranger" helicopter at an indicated airspeed of 166–176 km/h and at altitudes of 244 or (usually) 305 m above sea level (a.s.l.). We found that if we flew below 244 m narwhals reacted so

Table 1. Mean sizes for cow-calf groups and for other narwhal groups by water body, western Eclipse Sound and adjacent waters, 1987–88 and 1993.

	No. of Individuals	No. of Groups	Group Size	
			Mean	SD
Cow-calf groups				
Eclipse Sound	6	3	2.0	0
Koluktoo Bay	128	58	2.2	0.7
Milne Inlet	146	70	2.1	1.0
Tremblay Sd	83	25	3.3	2.7
Total	363	156	2.3	1.4
All other groups				
Eclipse Sound	133	64	2.1	1.6
Koluktoo Bay	339	163	2.1	1.7
Milne Inlet	452	203	2.2	2.0
Tremblay Sd	471	193	2.4	2.0
Total	1395	623	2.2	1.9

quickly to the helicopter that we could not get accurate counts; even at 305 m a.s.l. narwhals on the flight track reacted to the helicopter by starting to dive even before the helicopter passed over them. However flying higher would have decreased our ability to identify and count animals.

In 1987 and 1988 observers sat in the back seat of the helicopter and scanned a 690 m strip on each side of the aircraft for narwhals. The surveyed strip was defined by window marks that had been established by triangulation while the aircraft was on the ground. The number and age class (calf, *i.e.* young of the year, older juvenile or adult) were recorded; when time permitted, sex (tusked or non-tusked), activity (localized or directed) and direction of movement (if any) were also recorded. We identified calves as very small animals (about, or less than, half of adult length) swimming very close to another whale. Whales within one body length of each other were considered to comprise a group. Four types of group were distinguished: adult all male; adult all female; mixed male and female; and "cow-calf" groups, consisting of females with calves and other accompanying animals, including older juveniles, females without young and occasional adult males. Data were tabulated for periods of two minutes (transect intervals) during a survey; at the cruising speed of the helicopter each interval would have covered approximately 7.8 km^2. In 1987 a third observer sat in the front seat and recorded weather, ice conditions and waypoint times. In 1988 one of the observers in the back seat recorded that information. Wind speed and direction, cloud cover (in tenths) and type, and temperature were recorded at the start of each survey and updated as required. Ice cover (in tenths) and ice types (first-year and multi-year) were recorded for each two-minute interval.

From 1989 through 1993 most surveys were carried out by a single observer in the left front seat of the helicopter who recorded ice cover, sea state and counts of narwhals on a 500 m strip below and to the left of the aircraft for an estimated interval area of 3 km^2. Narwhal observations were recorded, with their times, as they occurred; so were changes in ice cover or sea state. The time was also recorded when each navigational waypoint was passed. Two-minute interval data were constructed after the flight from the timed records. For some surveys supplementary observations were made by another observer in the right rear seat. They were not included in the quantitative analyses but were included in the presence-absence contingency table analyses. Four primary observers carried out the surveys reported here: Verbeek and Ramsay in 1987; Cleator, Ramsay and Kingsley in 1988; Kingsley in 1989, 1990 and 1993; and Ramsay or Kingsley in 1991.

Data analysis

Dummy-variable stepwise linear regression (Draper & Smith 1981) was used to examine the data set for consistent patterns of narwhal density or distribution due to year, date, water body, ice cover or sea state, including the effects of the presence of ice in Eclipse Sound on narwhal numbers in other water bodies. In order to at least partly stabilise the variance of the data, which was highly skewed, the fourth root of the two-minute-interval counts was used as the dependent variable. Strict critical levels were used, usually 0.01%, to identify effects, because of the large size of the data set and the problem of non-independence (serial correlation) of two-minute intervals. These results were interpreted to give information on the directions (increase or decrease) of density variations due to the factors listed above.

The association between ice cover and narwhal distribution was also examined using contingency tables of the presence or absence of narwhals in one water body and of ice in the same or a different one, treating each survey as an observational unit. Contingency coefficients and chi-squared statistics were calculated.

Results

Group size and composition

As calves are much smaller than adults, the observers had no difficulty distinguishing them from adults but they were harder to see. The presence or absence of a tusk was not always easy to determine, so all groups other than cow-calf groups were pooled for analysis of group size. Mean group sizes were small – mostly 2.0–2.4; the largest group sizes were in Tremblay Sound where cow-calf groups averaged 3.3 (Table 1). Variation in group

Table 2. Mean narwhal density per two-minute survey interval and mean ice cover on survey lines for Eclipse Sound, Tremblay Sound, Milne Inlet and Koluktoo Bay, 1987–1993.

Date (Aug.)	Eclipse Sound			Tremblay Sound		
	No. of intervals	Mean (SD) narwhals/ interval	Mean ice cover (%)	No. of intervals	Mean (SD) narwhals/ interval	Mean ice cover (%)
87–06	30	0.43 (1.15)	57.6	6	0.17 (0.37)	15.0
87–15	30	1.23 (3.40)	17.0	7	0.0	55.7
87–20	30	0.0	0	7	1.86 (4.55)	38.6
87–24	18	0.22 (0.71)	0.5	6	14.00 (18.62)	0
88–02	6	0.50 (1.12)	0	8	14.13 (27.37)	0
88–08	3	0.33 (0.47)	0	5	0.80 (1.17)	0
88–12	26	0.0	0	6	5.00 (7.07)	0
88–16	29	1.31 (5.52)	0	8	2.63 (5.07)	0
88–19	2	0.0	0	8	29.63 (40.25)	0
88–23	27	0.04 (0.19)	0	8	6.88 (9.80)	0
89–04	23	0.09 (0.41)	5.7	7	21.00 (51.44)	0
89–09	17	0.0	0	12	0.67 (2.24)	0
89–18	35	0.0	0	13	5.77 (19.41)	0
90–02	20	5.20 (10.92)	16.5	5	0.0	16.0
90–12	15	0.0	0	9	1.33 (2.87)	0
90–16	15	0.0	0	7	2.29 (5.60)	0
91–07	10	0.0	0	12	30.75 (27.77)	0
91–11	9	0.0	0	11	5.91 (11.62)	0
91–13	15	0.0	0	9	13.89 (29.19)	0
91–15	22	0.0	0	7	9.43 (21.89)	0
91–17	16	0.0	0	6	5.83 (12.60)	0
93–17	16	0.0	9.4	9	0.0	28.9
93–19	16	0.31 (1.21)	10.0	9	0.0	20.0
93–21	14	1.36 (4.89)	17.9	10	0.0	44.0
93–23	14	1.29 (3.88)	12.1	7	0.0	17.1

Date (Aug.)	Milne Inlet			Koluktoo Bay		
	No. of intervals	Mean (SD) narwhals/ interval	Mean ice cover (%)	No. of intervals	Mean (SD) narwhals/ interval	Mean ice cover (%)
87–06	17	0.47 (1.24)	41.2	4	9.75 (15.17)	0
87–15	17	0.24 (0.94)	49.4	4	6.75 (7.79)	22.5
87–20	16	5.88 (8.77)	10.6	4	3.25 (1.92)	17.5
87–24	17	7.63 (14.76)	3.5	4	0.0	0
88–02	17	6.24 (24.94)	0	4	15.25 (25.84)	0
88–08	17	0.29 (0.82)	0	5	3.40 (3.44)	0
88–12	18	0.56 (1.71)	0	4	32.0 (19.48)	0
88–16	18	0.89 (1.66)	0	4	2.25 (2.86)	0
88–19	18	0.0	0	4	38.50 (44.12)	0
88–23	20	0.55 (1.96)	0	4	8.0 (6.44)	0
89–04	19	0.26 (0.78)	5.8	6	38.33 (53.14)	0
89–09	16	1.0 (2.9)	0	7	2.71 (5.20)	0
89–18	20	14.25 (26.75)	0	4	60.75 (63.18)	0
90–02	4	10.5 (6.22)	57.5	0		
90–12	14	3.43 (8.95)	0	3	17.0 (11.78)	0
90–16	15	1.2 (4.49)	0	5	0.40 (0.80)	0
91–07	12	0.0	0	4	35.5 (41.72)	0
91–11	17	0.0	0	5	9.0 (18.00)	0
91–13	14	2.0 (4.90)	0	4	48.0 (33.94)	0
91–15	14	0.50 (1.24)	0	6	21.5 (22.61)	0
91–17	23	11.34 (50.93)	0	4	0.0	0
93–17	22	1.77 (4.58)	1.8	5	14.2 (17.39)	0
93–19	18	0.0	5.0	5	0.0	0
93–21	16	9.38 (24.63)	8.1	5	0.0	0
93–23	17	4.06 (7.19)	5.3	6	0.0	0

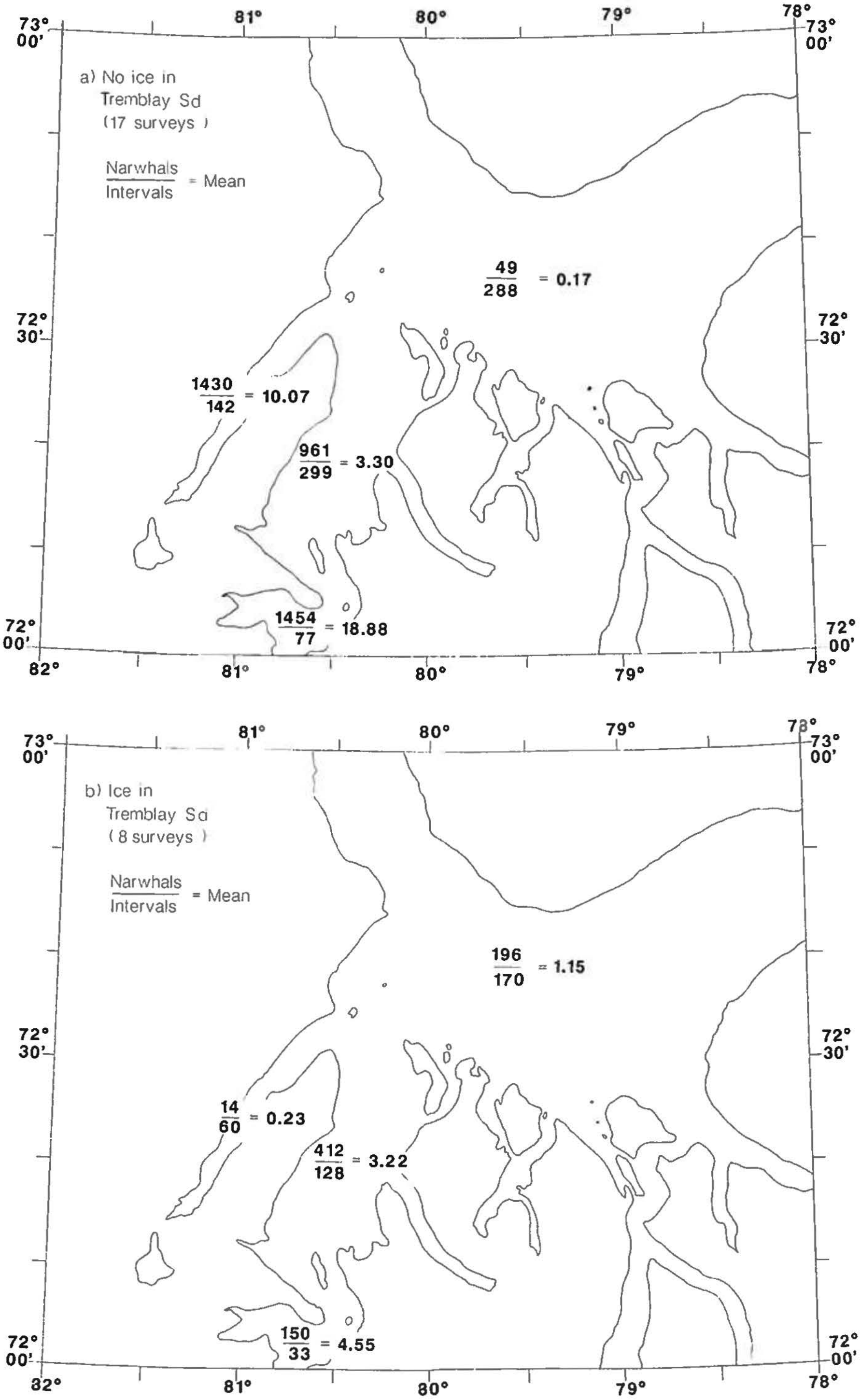

Fig. 3. Summary distribution of narwhals in the survey area: a) after ice had cleared from study area and b) when pack ice was present in Tremblay Sound or Eclipse Sound.

size was so large that differences were not statistically significant.

Cow-calf pairs or groups averaged overall 20.0% of the total groups classified, and accounted on average for 20.6% of individual whales. Calves were 9.6% of classified individuals, and accompanying whales were 11.0%. In Koluktoo Bay and Milne Inlet females with young formed the same proportion of groups (26.2% and 25.6%; $Chi^2_1 = 0.02$) and of individuals (27.4% and 24.4%; $Chi^2_1 = 1.23$) classified (Table 1). In Eclipse Sound, where few narwhals were counted or classified, females and young formed a smaller proportion of groups (4.5%) and of individuals (4.3%). In Tremblay Sound females and young formed 11.5% of groups and 15.0% of individuals classified, between the Milne Inlet-Koluktoo Bay values and those for Eclipse Sound.

Distribution and movements of narwhals

Survey totals of narwhals seen ranged from 5 to more than 600. The survey mean number of narwhals per 2-min. survey interval ranged from 0.1 to 13.4. The numbers of narwhals recorded varied between surveys both within and between years; however the dummy-variable regression selected only the survey of 2 August 1990, when many narwhals were seen in the ice in Eclipse Sound, as being different from the others.

The mean number of narwhals/interval also varied significantly between water bodies (Table 2, Fig. 3). Eclipse Sound had the lowest overall mean, 0.54/interval, Milne Inlet 3.30, Tremblay Sound 7.15 and Koluktoo Bay the highest, 14.58. In 1988 Eclipse Sound had the lowest mean number of narwhals/interval in five of six surveys, and in 1989–1991, other years in which the ice cleared early, few narwhals were counted in Eclipse Sound. An exception was the first survey in 1990, on 2 August, when Eclipse Sound still had 16% average ice cover and a mean of 5.2 narwhals/interval was recorded. The ice did not clear until very late in 1987 and Eclipse Sound had the lowest mean narwhals/interval in only one survey out of four; 1993 was also a late ice year, and narwhals were observed in Eclipse Sound, in the pack ice, in three surveys out of four. In the late ice years of 1987 and 1993 no narwhals were sighted in Tremblay Sound in 5 surveys out of 8, and fewer than usual (1.5% and 16.7% of the weighted mean narwhals/interval for 19 surveys on which narwhals were sighted in Tremblay Sound) in two others. Only in the last survey in 1987, when the ice had left, did we record normal numbers (125.7% of the mean). In 1988 narwhals were relatively abundant in Tremblay Sound: it ranked second to Koluktoo Bay. In 1991 Tremblay Sound, south of the First Narrows, was continuously, and densely, frequented (Table 2). In most surveys Koluktoo Bay had large numbers of whales, usually densely distributed in the same small area. The fitted dummy-variable regression model confirmed these results, with positive coefficients for the dummy variables "water body is Koluktoo Bay" and "water body is Tremblay Sound", and a negative coefficient for the variable "water body is Eclipse Sound".

The aggregated results of the 6 years of surveys showed a consistent pattern of distribution in the open-water season. There were three preferred centres of aggregation. One was the northern part of eastern Koluktoo Bay, under the southern face of Bruce Head. Distribution in this area sometimes extended eastward around the point of Bruce Head and into southern Milne Inlet (which had on average 5.76 narwhals/interval) or toward western Koluktoo Bay. A second preferred area was Tremblay Sound, south of the First Narrows. On most surveys narwhals were observed there, and they were present in this area throughout August in 1991. A less favoured extension of this area was in the mouth of Tremblay Sound north of the First Narrows as far as Alfred Point. We seldom saw narwhals south of the Alpha River. The third area was in west central Milne Inlet. Narwhals were usually recorded within the area defined by Low Island, Two Rivers and First Point (mean 4.01 narwhals/interval in western Milne Inlet).

Areas where we rarely saw narwhals during the open-water season included eastern and northern Milne Inlet (mean 0.93 narwhals/interval). They were often absent from eastern and northern Milne Inlet when they were concentrated on the western side. We also counted few narwhals (mean 0.56 /interval) in Eclipse Sound in the open-water season. The most likely part of Eclipse Sound to be frequented by narwhals was north of Cape Hatt and Ragged Island. Northwestern Eclipse Sound and southern Navy Board Inlet were less frequented: we only twice, out of 19 flights that went into this area, saw narwhals to the northwest of a line from Alfred Point to the southernmost point of Bylot Island.

The areas frequented by narwhals in Milne Inlet and Koluktoo Bay, within which narwhals were observed on surveys, form a continuum stretching from northeastern Koluktoo Bay round Bruce Head, northwestward toward Two Rivers and First Point, and further north up the west side of Milne Inlet. Narwhal movements were observed from camps and capture sites, and from survey aircraft, between different parts of this range. Live-capture teams stationed on Bruce Head in 1988 and 1993 recorded movements round the point, which is used as a netting and hunting site by Inuit. North-south directional movements of narwhals in western Milne Inlet were seen from the survey helicopter. Many narwhals were observed in northeastern Koluktoo Bay, sheltered by Bruce Head from the light north wind that was blowing, at 2100 h on 14 August 1988 during a flight to track a VHF radio. Another flight at 1100 h on the next day found no narwhals in that area, exposed to the south wind that had arisen; narwhals were found in central Milne Inlet in calm water. First Point in western Milne Inlet is a site used by Inuit for narwhal hunting camps, because narwhals pass close along shore in this area.

Ice cover

After ice cover disappeared, narwhals were distributed differently from how they were when ice was still present (Fig. 3). Contingency table analysis of the relation between the presence of ice and the presence of whales in Eclipse Sound, treating each survey as an observational unit, showed a positive association (coefficient of contingency (CC) 51%; $Chi^2_1 = 6.5^*$). The same analysis for Tremblay Sound showed a strong negative association (CC −82%; $Chi^2_1 = 16.8^{***}$). Ice cover in Eclipse Sound was associated with ice cover in Tremblay Sound (c.c. 78%). Contingency table analysis for narwhals and ice in Milne Inlet (CC 11%) and Koluktoo Bay (7%) did not give significant results because Koluktoo Bay very seldom had ice cover, whether narwhals were seen there or not, and Milne Inlet almost always had narwhals, regardless of ice cover. However the presence of whales in Koluktoo Bay was negatively associated with the presence of ice in Eclipse Sound (CC −50%; $Chi^2_1 = 6.0^*$). The results of dummy-variable regression identified two ice cover factors that affected distribution: ice-cover in Tremblay Sound appeared to be associated with lower narwhal density in Tremblay Sound, and ice cover in Eclipse Sound appeared to be associated with lower narwhal density in Koluktoo Bay. The positive association of ice and narwhals in Eclipse Sound was not evident in the results of dummy-variable regression because densities in Eclipse Sound were never high, even when ice was present. There was no association of narwhals with high ice cover within Eclipse Sound.

Wind speed

The Beaufort sea state was entered into the regression analyses. Increasing sea state reduced narwhal sightings (dummy variable "Beaufort > 1" had coefficient −0.14, P = 0.38%).

Killer whales

Killer whales influence the behaviour and distribution of narwhals (Reeves & Mitchell 1988). They occur in the study area when the waters are ice-free; according to Reeves & Mitchell (1988) they do so "on a regular basis". In Eclipse Sound on 30 August 1980, 30–40 killer whales cooperatively attacked a herd of "over 300" narwhals, killing at least one (Steltner *et al.* 1984.) Reports and records available to us for 1984–1991 and 1993 indicate the presence of killer whales in the Eclipse Sound area as follows: 1985 – Campbell *et al.* (1988), J. Ford (Vancouver Public Aquarium, pers. comm.); 1988 – reports from hunters on 16 August, while we were on Bruce Head, of killer whales in southern Milne Inlet; 1990 – 5 killer whales were reported in the straits of Pond Inlet in the evening of 7 August; and 1991 – 15 killer whales were sighted in the strait east of Stephens Island on a survey on 17 August.

Unusual behaviour and distribution that we observed to be associated with the presence of killer whales included (1) unusually rapid directed movement round Bruce Head into Koluktoo Bay, seen from shore on the evening of 16 August 1988 and (2) crowding of narwhals in to Fairweather Bay, where they were not seen at any other time, on 17 August 1991.

Discussion

Group size and composition

Compared with our overall mean group size of 2.3 (N = 597), Koski & Davis (1979) calculated a larger mean group size (2.9, N = 165) from aerial-survey data collected in Milne Inlet on 24 August 1978. They also reported larger group sizes in coastal and ice-edge areas both within (2.5) and outside (2.9) Lancaster Sound (Koski & Davis 1994). Silverman (1979) calculated a much larger average group size of 4.1 (N = 635) from cliff-top observations in Tremblay Sound in August 1977 and 1978. The sampling system used in these observations was to record "total numbers of narwhals passing by, group size, group composition. . ." (Silverman 1979, p. 11). However observations from the land are comparable with observations from the air only if all groups in a study area are regularly recorded by scan sampling. If each group that passes, or comes within sight, is recorded once, then observations from slow-moving or stationary platforms will record a larger proportion of travelling groups. If narwhals in directed travel tended to aggregate into larger groups (*cf.* Silverman 1979, p. 102), this would raise the estimate of mean group size for land-based data and make caution necessary in comparing them with aerial-survey data. Our subjective impression from shore-based observations in Tremblay Sound and at Bruce Head was that travelling groups, especially of males, were larger and disproportionately evident. In contrast, cow-calf pairs were so cryptic that they were caught several times in live-capture nets before those watching the nets were aware that any narwhals were close by. Other aspects of behaviour and factors such as ice conditions, prey distribution and density of narwhals may also influence group size (Silverman 1979) and account for differences in mean group size between studies. We noted that mean group size sometimes varied between surveys in the same area in the same year.

Silverman (1979) reported that sex and age segregation does not usually take place between herds, but that narwhals seem rather to form segregated groups within herds. However our results from 1987–88 and 1993 indicate that while cow-calf groups comprised 27% of narwhals seen in Koluktoo Bay and 24% in Milne Inlet (Table 1), in Eclipse Sound this proportion was about 4%. In Tremblay Sound, overall, an intermediate proportion was observed. These observations support the hypothesis that females and young are a smaller proportion of narwhals seen in the exposed waters of Eclipse Sound than in more sheltered waters. The population of white whales (*Delphinapterus leucas*) in the St Lawrence estuary, where group composition has been intensively studied in the entire summering area, tends to segregate into a component of adult males inhabiting the deeper, colder northeastern part of the range, and cow-calf and mixed groups in warmer, shallower water (Michaud 1993).

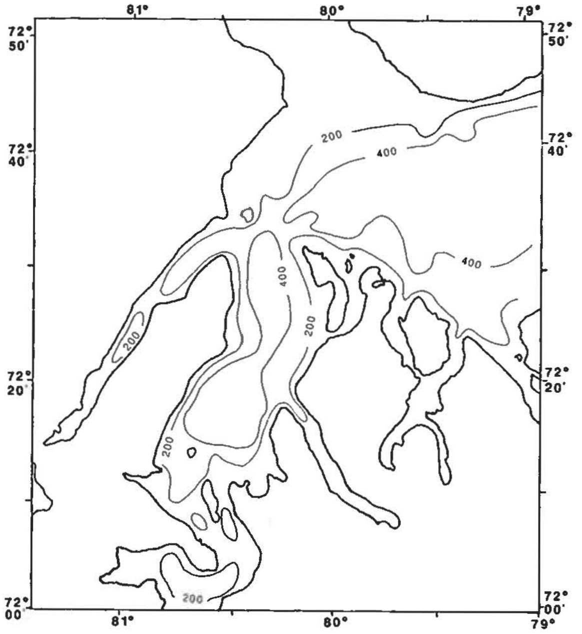

Fig. 4. Bathymetry of Eclipse Sound, Milne Inlet and adjacent waters.

Koski & Davis (1994) estimated 7.8% to 9% young of the year in selected observations made by expert observers in summer aerial surveys flown at 45, 90 or 150 m a.s.l. There were 10.3% "neonates" (young of the year) and 6.3% "calves" (defined by Silverman (1979, p. 25) as one- or two-year-olds) among 1469 narwhals classified in cliff-top observations in Tremblay Sound in 1977–78 (Silverman 1979, Table 10). We estimated 9.6% calves but, flying as high as we did, may have missed some calves; we also may have misidentified some small yearlings as calves. These estimates are consistent with models of monodontid population dynamics which indicate gross annual birth rates of 7% to 14% (Hay 1984, Burns & Seaman 1985, Kingsley 1989).

Finley & Gibb (1982) suggested that the preference of narwhals for particular areas in and around Eclipse Sound in summer may be related to calving. July and August constitute the calving period for narwhals (Hay 1984), and it has been suggested that protected fjords and inlets may be important for rearing young (Silverman 1979). Our survey data showed that cow-calf groups were more common in Koluktoo Bay, Milne Inlet and Tremblay Sound than in Eclipse Sound, supporting this suggestion.

Numbers, distribution and movements

These surveys were not designed to estimate absolute abundance. The survey route was not an unbiased sample of the study area. In Tremblay Sound and Koluktoo Bay we were surveying areas where high densities were expected. Only in Milne Inlet and Eclipse Sound did we fly a survey pattern that was independent of the expected distribution of whales. The survey pattern in Milne Inlet used promontories of land as survey waypoints and therefore may have under-sampled nearshore waters.

Numbers of narwhals in any summering area vary from year to year (Koski & Davis 1994, Born *et al.* 1994). In this series of surveys the number counted varied also from survey to survey within years, partly because of variation in viewing conditions. For example during the 19 August 1988 survey the lack of wind and relatively low and diffuse light made narwhals appear light-coloured against a background of dark water. The calm, high-contrast conditions facilitated detection and probably contributed to the high numbers recorded in that survey. However variations were also caused by the movement of herds of narwhals into and out of the survey area, or onto and off the survey transect pattern, between surveys.

Fallis *et al.* (1983) flew aerial surveys for narwhals in Koluktoo Bay, Milne Inlet and Tremblay Sound on 12 August 1975 and 11 August 1976. Their counts were comparable to ours except for a cow-calf group, or herd, of nearly 200 that they saw in the mouth of Tremblay Sound in 1975. This is larger than any group recorded during our surveys. Koski & Davis (1979) counted 507 narwhals while surveying all of Milne Inlet on 24 August 1978. We counted up to 143 narwhals in the Inlet in 1987–88, and 340 on 18 August 1989.

We expected that strong winds would reduce the counts of narwhals. We also hypothesised that narwhals, accustomed for much of the year to the calmer water found in pack ice, would seek sheltered waters in windy weather. Beaufort sea state entered into the dummy-variable stepwise regression with a significant negative coefficient. However several possible factors are confounded in this result: 1) rough water makes marine mammals, even at the surface, hard to see; 2) in rough water, narwhals may spend more time at depth below the zone of wave turbulence and be less visible for this reason; 3) the distribution of narwhals may change in windy weather if narwhals actively seek sheltered calm water. We have difficulty separating these factors using our data set. Fluctuations in the number of narwhals that could be counted in Inglefield Bredning, Greenland, were associated with variations in sea state (Born 1986).

Narwhals preferred some bodies of water in the study area over others. Koluktoo Bay had the highest mean number of narwhals/interval, and Tremblay Sound, when ice-free, was also much frequented. Eclipse Sound, the largest water body, had the lowest density. Deep water is found in almost all parts of our study area. Both Tremblay Sound and Koluktoo Bay are more than 200 m deep and are bounded by steep underwater slopes (Fig. 4). Deep water in Tremblay Sound, and the steep western shore, extend north to Alfred Point. Milne Inlet is also steep underwater on its west side. However there are some parts of the study area that are not as deep. Southern Navy Board Inlet, where we never observed narwhals, and northwestern Eclipse Sound and eastern Milne Inlet, where we rarely saw them, are shallower, with shelving shores. Narwhals apparently do not occur in Eskimo Inlet, which is shallow, but they have been reported in Tay Sound (Miller 1954). Born (1986) cited local knowledge that narwhals do not frequent the shallow Olrik, McCormick and Robertson fjords in the municipality of Avanersuaq (Thule area), where white whales occur instead. The distribution of narwhals in other summering areas of the Canadian high Arctic in 1984 appeared to be related to water depth: narwhals were more concentrated near the deepest areas of water bodies (Richard *et al.* 1994). "Narwhals characteristically have a deep-water distribution in the Arctic" (Sergeant 1979). The narwhal is physiologically adapted to deep diving, with oxygen-storage capabilities that have been evaluated, from physiological parameters such as the myoglobin content of muscle, as permitting aerobic dives lasting about 20 min (Williams *et al.* 1987). Dive data obtained from satellite-linked time-depth recorders in 1991 and 1993 indicate that narwhals make repeated dives to the bottom of deep fjords in summer (Martin *et al.* in press, Kingsley unpubl. data). It is possible that these areas provide a feeding niche where deep-diving narwhals experience less competition from other arctic marine mammals, Sergeant (1979), comparing narwhals with white whales, found that narwhals feed in deeper water, perhaps because they have a competitive advantage there. The distribution of food stocks has been suggested as influencing the summer distribution of white whales in Alaskan waters (Seaman & Burns 1981). We have no data on the distribution of food stocks in our study area at this time of year, and analyses of stomach contents of animals taken by hunters have suggested that narwhals feed little in the Eclipse Sound area during the open-water season (Mansfield *et al.* 1975, Finley & Gibb 1982, Weaver & Walker 1988). If these data are unbiased, preference shown by narwhals for this area may not be related to feeding (Finley & Gibb 1982). However regurgitation might account for the absence of food in the stomachs of some narwhals killed by hunters (Vibe 1950). In summer narwhals in Inglefield Bredning are reported to feed on polar cod (*Boreogadus saida*), arctic cod (*Arctogadus glacialis*), Greenland halibut (*Reinhardtius hippoglossoides*) and shrimp (Vibe 1950, Heide-Jørgensen *et al.* 1994). Satellite-radio-tagged narwhals in Tremblay Sound in 1991 spent 70% of their time diving deep, possibly related to feeding (Martin *et al.* in press).

Narwhals have been reported to move into and out of fjords throughout the summer (Silverman 1979); this tendency was also apparent from our shore-based observations in Tremblay Sound during 1984–1987 (Kingsley unpubl. data). Livecapture teams working or camped on the extremity of Bruce Head also noted movements, sometimes apparently of significant numbers of narwhals, round the point into or out of Koluktoo Bay. Reports of narwhals in Inglefield Bredning (Born 1986, Born *et al.* 1994) also emphasized movement from one sector of the observation area to another or into and out of tributary fjords. Vibe (1950) and Silverman (1979) suggested that these movements into and out of fjords may be related to foraging activities or to the tidal cycle. Our ground-based observations agreed with those of others, but our aerial-survey results did not entirely agree. On 16 out of 16 surveys made when Tremblay Sound was ice-free, narwhals were found there, and in Koluktoo Bay on 14 of 15 surveys flown when Eclipse Sound was ice-free. Other information was obtained from satellite-radio-tag data: in 1991 two of two radio-tagged female narwhals stayed continuously for three weeks between Alpha River and Athole Point in Tremblay Sound; they did not leave Tremblay Sound (Kingsley unpubl. data). Conversely a sub-adult male narwhal radio-tagged at Bruce Head on 24 August 1993 stayed within radio-shot of the tagging site for two days. He then moved to western Milne Inlet, and five days later into central Eclipse Sound (Kingsley unpubl. data).

We have some evidence that narwhals do move into and out of Koluktoo Bay, backed up by indications of where they go – into southern and western Milne Inlet. But if narwhals move out of Tremblay Sound, we have little indication of their destination, whether north to Navy Board Inlet, round Athole Point into Milne Inlet, or northeast into central Milne Inlet. We frequently surveyed the western coast of Eclipse Sound, and crossed the southern end of Navy Board Inlet, without seeing narwhals, but we did not survey the inshore waters around Athole Point. We once saw narwhals close inshore in western Milne Inlet north of First Point. Information from local hunters is conflicting. Some say that narwhals from Tremblay Sound move north along the western shore of Eclipse Sound into central Navy Board Inlet, and there are traditional summer-season narwhal hunting camps – Kaunak and Komukouri – on the western shore of Eclipse Sound (Finley *et al.* 1980, Finley & Miller 1982). However other hunters say that the narwhals hunted at Low Point (Nadluat) in central Navy Board Inlet are part of a separate group that moves within a region extending further north towards Lancaster Sound.

Distribution relative to ice

Finley (1976) reported that in the late summer narwhals strongly prefer water containing pan ice, and Silverman (1979) suggested that they may do so because the ice offers protection from wind and predators. As long as ice remained in Eclipse Sound, narwhals were found there, usually associated with the ice. However the association of narwhals with ice cover, in this study, only applied to Eclipse Sound. Ice cover in Tremblay Sound, which usually coincided with ice cover in Eclipse Sound, had a clear negative effect on narwhals, and they stayed out of

Tremblay Sound when it was ice-covered. Narwhals may prefer wide, deep waters like Eclipse Sound, but, finding themselves exposed to predators or rough weather when such areas are ice-free, move then into more enclosed areas. Alternatively narwhals may have a preference for steep shorelines of deep narrow inlets, but avoid such areas when they are infested with ice because they perceive a danger of ice entrapment. The observation of a negative association between narwhal presence in Koluktoo Bay and ice cover in Eclipse Sound is an indication, but not proof, that the former hypothesis is more likely. Additional support for it is given by the winter distribution of narwhals, which tends to favour offshore ice-covered waters (Koski & Davis 1994).

Narwhals may move into areas recently cleared of ice to take advantage of newly-available food sources. This may be especially important for nursing females. Although adult males lead major northward and westward spring migrations into the Canadian Arctic archipelago (Greendale & Brousseau-Greendale 1976), our observations from shore in Tremblay Sound in 1984–86 (Kingsley unpubl. data) indicated that females with young were usually the first animals to arrive there once the ice disappeared.

Distribution and movements relative to wind

Once the ice in the study area disappeared, the narwhals seemed to seek out smaller bodies of water (*e.g.* Koluktoo Bay) or areas containing islands or other topographical irregularities (*e.g.* southern end of Milne Inlet) that offered shelter from the wind, from a variety of directions, without the whales having to travel very far. The results of dummy-variable regression indicated that fewer narwhals were seen when the Beaufort sea state was higher. However, known visibility biases are confounded with possible behavioural biases, making interpretation of this result difficult. Two observations support the hypothesis that the distribution of narwhals may be affected by wind. First, while narwhals were usually found in Koluktoo Bay, they consistently favoured the calmer water under the south face of Bruce Head and avoided the rougher water where north winds blew down through the pass further to the west. Second, narwhals moved from Koluktoo Bay into Milne Inlet between 2100 h on 14 August 1988 and 1100 h on 15 August apparently in response to a change in wind direction. On the evening of 14 August we saw narwhals in calm water in northern Koluktoo Bay; the wind then was from the north and the high ridge sheltered the bay. On the next day the wind was from the south. Koluktoo Bay was exposed to it, and the water was rough. During a helicopter flight to locate a VHF radio transmitter that we had attached to a narwhal the day before, we saw no narwhals in Koluktoo Bay, but many in central and western Milne Inlet, where the water was quite calm. On 16 August narwhals were still in southern Milne Inlet, and the wind was still blowing from the south.

Movements in response to killer whales

The proximity of killer whales affects the behaviour of other marine mammals. Ringed seals are said to haul out on land only when killer whales are near, and narwhals are said by the Inuit to have a suite of characteristic behaviour patterns when avoiding killer whales. This includes moving into heavy ice or close to ice edges or shorelines, and slow, quiet movement (Reeves & Mitchell 1988, Finley *et al.* 1990). Long-finned pilot whales (*Globicephala melas*) have been reported to "hide" from killer whales by swimming very close to a shoreline (Bloch & Lockyer 1988), and what succeeds for one prey species may serve another. Our observations indicate that narwhals may also crowd into small bays, that they do not usually frequent, when killer whales are nearby. We observed more than 200 narwhals crowded into Fairweather Bay, southwestern Milne Inlet, when killer whales were east of Stephens Island in 1991. Narwhals were also reported by local hunters to use Z Lagoon at Cape Hatt when killer whales were in the vicinity. On 24 August 1987 200–300 narwhals were reported to be in Z Lagoon, but we had no confirmed sighting of killer whales in the area at the time. All our surveys passed over Cape Hatt, but we did not see narwhals in Z Lagoon in any other survey.

Although killer whales, as a species, are adept at hunting in ice-infested waters, it has been suggested that in eastern Canadian and Greenlandic waters they are less apt to enter ice fields than in Antarctic or Alaskan waters (Heide-Jørgensen 1988). Whether or not this is so, narwhals could be harder for killer whales to detect in ice-covered waters than in open waters. And if swimming close to shore helps narwhals to avoid detection by killer whales, then areas with complex shorelines should be favoured.

Conclusions

Narwhals favour larger, deeper water bodies as long as ice cover persists, probably because the ice cover helps them to avoid predators, perhaps also because it shelters them from wind, although this is still unproven. When ice cover disappears, they seek smaller water bodies but prefer those that are deep and bounded by steep shores. They tend not to use the smaller water bodies as long as ice cover persists in the larger ones. Although the distribution of narwhals is usually predictable, it is highly clumped, and may change over short periods of time. Reaction to the presence of killer whales causes the distribution to become more clumped and less predictable. The indications for aerial survey are two-fold: 1) careful stratification and 2) multi-aircraft surveys to complete surveys in a short time.

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Herd composition and behaviour of white whales (*Delphinapterus leucas*) in two Canadian arctic estuaries

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White whales occupy the Nastapoka River and Cunningham Inlet estuaries in northeastern Canada each summer. They arrive at the Nastapoka in late June and at Cunningham in mid-July, where numbers build to maxima of 260 and 1750, respectively. Distribution of whales in both estuaries is influenced mainly by the state of the mixed semi-diurnal tides and, to a certain extent, by river outflow and date. Few adult males appear to be present in the estuaries, the herd being composed mainly of females with calves and weaned juveniles. Limited evidence suggests that the basic social units of herds are matrilines consisting of adult nursing females accompanied by older female offspring. The age structure of the herd changes seasonally with an increasing proportion of nursing pairs. Behaviour was grouped into four activity classes. These are descriptive and are not intended to imply functions, which remain somewhat obscure. Much of the nearshore behaviour appears to be related to the processes of shedding old skin and growing of new epidermis. Strong philopatry and physiological dependence of white whales on estuaries indicate that these are important habitats which must be managed and preserved in order to conserve the species.

Key words:
White whale, beluga, *Delphinapterus leucas*, herd composition, behaviour.

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Introduction

Each summer certain estuaries and smaller stream outlets in northeastern Canada are visited by white whales, *Delphinapterus leucas*. During periods of several days and weeks, the whales expose themselves to water that is warmer and fresher than the ocean. Some of these sites are traditional places of summer aggregation for large numbers of white whales. It appears that these assemblages consist largely of females and their calves, and evidence indicates that the same animals return to the sites from year to year (Caron & Smith 1990). This site fidelity to areas where white whales appear to undergo a synchronous moult (St. Aubin *et al.* 1990), and where newborn calves are nurtured for the first month of a prolonged lactation period (Doidge 1990), strongly suggests that these sites are seasonally a critical part of their habitat.

All estuaries share the common features of low salinity and relatively warm waters, but vary in their size and bathymetry and the degree to which they provide opportunities for observing the behaviour of the whales in them.

We describe and compare the composition of the herds and behaviour seen at two different estuaries: the Nastapoka River in eastern Hudson Bay and Cunningham Inlet on the north coast of Somerset Island. The Nastapoka is a small estuary, which during our studies was hunted on most weekends by Inuit from communities along the eastern Hudson Bay coast. In contrast Cunningham Inlet is a much larger area, somewhat enclosed from the sea, which is totally undisturbed by hunters or traffic.

Materials and methods

In both study areas white whales were observed from a position 6 m above water level atop aluminum towers,

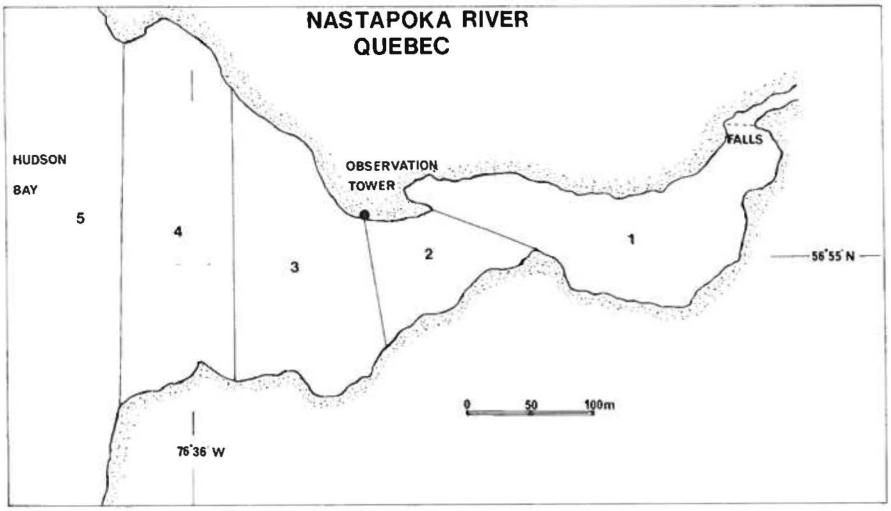

Figure 1. Study area at the Nastapoka River, eastern Hudson Bay, Canada.

and at Cunningham also from a 32-m high observation hut on the adjacent shoreline (Figs 1 & 2) (Sjare & Smith 1986). Binoculars, spotting telescopes and cassette tape recorders were used during these observations.

Both scan and focal animal sampling (Altmann 1974) were used to enumerate and document whale behaviour (Caron & Smith 1990). We compiled an ethogram of both nearshore (Smith *et al.* 1992) and offshore behaviour using these two sampling methods.

The sampling period at the Nastapoka was from 20 July to 13 August in 1983 and from 21 June to 2 September in 1984. Sampling at Cunningham was in the years 1980–1987 between mid June and 15 August.

Regular observations were made at 0900, 1100, 1300, 1500, 1700, 1900 and 2100 hr. These included total counts of white whales in the inlet. Scan and focal samples were taken during the intervening hours whenever the opportunities were available. Speed estimates of travelling white whales were made from the 32-m high observation point at Cunningham Inlet using vertical and horizontal angles from a theodolite and a stop watch.

At the Nastapoka tidal height was read from a tide gauge accurate to 5 cm, located in a small adjacent bay approximately 100 m from the observation tower. Water temperature was recorded from a temperature probe fixed to the bottom of the estuary in the middle of quadrat 3 and was relayed to a YSI tele-thermometer in the tower. Wind speed and wind direction were read from a portable weather station. Other factors influencing observations such as the state of the water surface, water clarity and light conditions were recorded on an ordinal scale of 1 to 4. A value of 1 indicated a choppy water surface, opaque water and strong glare, 4 indicated calm and flat surface, clear water and diffuse light. A count index variable, on an ordinal scale of 1 to 4 (worst to best), was created to measure the observer's confidence in the count value, which also represents a subjective measurement of observer fatigue.

The environmental variables were: the total number of whales present in the estuary at the time of observation, the time elapsed since the return of the first whale to the estuary after an evacuation, the time elapsed since the last hunt, and the median position of the distribution of the herd in the estuary. All variables were recorded immediately after the observation sessions. Sessions were of variable length depending on the number of whales present; they lasted until all whales had been counted in the study area.

Age structure of the herd was documented by recording the size categories of animals during the scan samples. Calves were assigned to different length categories based on the body length in proportion to that of accompanying or adjacent adult white females, and these length categories were in turn assigned to age classes (Caron & Smith 1990: table 1). Adult males were identified by their large size and heavy lateral musculature.

In constructing the ethogram we have in most cases employed terms previously used in descriptions of the activities of cetaceans. We purposely avoided implying functions in our terminology.

Study sites

The Nastapoka estuary is located at 56°55'N, 76°36'W on the east side of Hudson Bay. The estuary is only 1.3 km long, measured from the river mouth, which opens to the ocean, to a 30 m-high waterfall. It runs east-west and is 0.2 km at its widest (Fig. 1). Maximum tidal amplitude in the estuary was 5.2 m during June to August. Salinities and temperatures taken at mid-tide in the estuary during July and August ranged from 0 to 15 ppm and 6.6°C to 16.1°C. Because of its topography Lamothe (1983) classified this as a submerged delta estuary, but our measure-

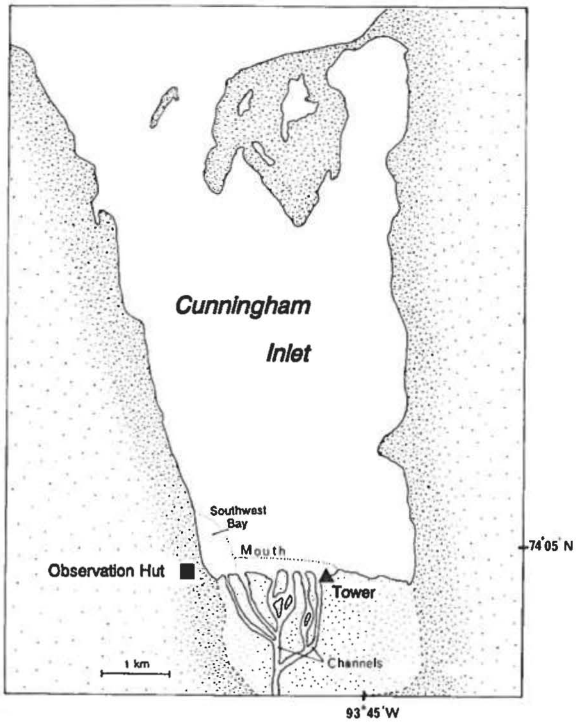

Figure 2. Study area with observation points at Cunningham Inlet on the north coast of Somerset Island, N.W.T., Canada.

ments indicate two distinct water masses which categorize it as a salt wedge estuary (Pickard 1979).

Peak discharges of the Nastapoka River occurred in June to September (468.6 m^3/sec) with an average monthly discharge of 268 m^3/sec over 20 years (Lamothe 1983).

Cunningham Inlet is on the north coast of Somerset Island, Northwest Territories at 74°05'N, 93°45'W. The inlet is 7.5 km long with a maximum width of 5.2 km; it thus covers a much larger area than the Nastapoka estuary (Fig. 2). The head of the inlet consists of a 3.2 km-wide delta deposited by the Cunningham River, which has a drainage area of some 2600 km^2. During the unmeasured maximum outflow in July, the Cunningham River enters the inlet via two major channels. Since 1980 these channels have changed position several times due to sediment deposits and ice scouring.

Cunningham Inlet has a maximum depth of 42 m. Tides during July and August range from 0.8 to 2.1 m in mean maximum amplitude. In July there is strong vertical stratification throughout the inlet. A marked halocline exists from the surface to a 3 m depth (3 to 30 ppm), and there is an even more pronounced thermocline (6–8°C at the surface to 1° to 8°C at 3 m of depth) (Morrison & Taylor 1978). Stronger and more frequent winds in August turn the Inlet into a partially mixed estuary.

Results

Seasonal occupation and numbers

In eastern Hudson Bay the shore-fast ice usually breaks up by mid-June. In 1984, when observers were present prior to the arrival of white whales, the animals were first observed in the Nastapoka estuary on 23 June and were still present on 2 September when our observations ended. Maximum numbers counted at the Nastapoka were 245 on 27 July 1983 and 260 on 25 August 1984. During 1984, herd size gradually increased during July and August, then started to decrease into September.

In the high arctic, the ice along northern Somerset Island, adjacent to Cunningham Inlet, begins to break up in early July. Even when most of Cunningham Inlet remains ice-covered, except for the area melted by the river outflow, white whales penetrate into the inlet. In seven seasons the date of first occupation varied from 8 to 21 July and in five seasons the date of departure varied from 3 to 16 August. Annual dates of these events are

Table 1. Spearman rank correlation coefficients between the environmental factors and the median position of the white whale herd in the Nastapoka estuary in 1984.

Environmental factor	Correlation Coefficient (!R!)	Probability of a greater !R!	Number of Observations
Tide	0.39845	.0001	349
Total count	0.33728	0.0001	351
Water surface	0.32272	0.0001	351
Estuary time	0.23086	0.0001	272
Hunt time	0.21195	0.0004	272
Wind speed	0.16976	0.0014	351
Wind dir. (Sine)	0.14865	0.0053	351
Water clarity	0.12183	0.0224	351
Count index	0.11870	0.0262	351
Temperature of freshwater	0.11371	0.0332	351
Time of day	0.06737	0.2080	351

Table 2. Contingency table of the age structure of the Nastapoka herd in different quadrats (Q) of the estuary during the 1984 season using scan sampling. A deviation statistic Z was calculated for each cell and compared with the critical value of Z (3.0256) given a significance level of 0.05. Cell values which are significantly different from the expected value are marked with an asterisk.

	Q1	Q2	Q3	Q4
Age class	Obs. (percent) Z statistic	Obs. (percent) Z statistic	Obs. (percent) Z statistic	Obs. (percent) Z statistic
Neonate	1278 (20.5%) 2.8693	2486 (19.9%) 1.8354	1258 (17.6%) *3.2546	1369 (18.2%) 2.0722
1/2	931 (15.2%) 0.4266	1992 (16.0%) 1.6207	1125 (15.8%) 0.7899	1074 (14.3%) 2.5852
2/3	649 (10.6%) 1.9505	1581 (12.7%) *4.1051	888 (12.5%) 2.5527	671 (8.9%) *7.2206
3/4	606 (9.9%) *7.1721	1773 (14.2%) *4.4626	1045 (14.7%) *4.2657	814 (10.8%) *5.0958
White	2663 (43.5%) 2.7609	4644 (37.2%) *7.9141	2818 (39.5%) 2.4331	3584 (47.7%) *8.6139

$X^2 = 342.4939$, DF = 12, $P < 0.005$.

directly influenced by the timing and pattern of ice break-up in the adjacent Barrow Strait, which is quite variable from year to year (Prinsenberg & Bennett 1987, Gorman 1988). Cunningham Inlet was occupied by white whales for periods varying from 27 to 38 days each summer (N = 5 seasons). Peak numbers ranged from 760 to 1750 whales, and the seasonal daily peaks varied from 17 July to 7 August (N = 7 seasons).

Factors influencing distribution

In both estuaries the daily pattern of distribution of white whales was strongly influenced by tides. Generally white whales moved farthest into the estuaries as the tide rose and either dispersed into offshore areas or left the estuary completely as the tide ebbed.

At the Nastapoka the median position of the white whale herd was most influenced by the state of the tide. Other influencing factors included the total number of whales present (total count), the water surface condition (water surface), the time of day (estuary time) and amount of time elapsed after the last hunting disturbance (hunt time) (Table 1).

At Cunningham white whales dispersed into the deeper waters of the Inlet on the ebb tide and could still be seen by observers, but we could not verify whether some left the Inlet completely. Analyses on factors influencing the number of whales in the mouth quadrat of Cunningham Inlet, which is analogous to the inner quadrats of the Nastapoka site, indicate that date had the greatest influence on whale numbers during 5 years of systematic observations. The importance of the other factors were highly variable. Both river flow and tide influenced the number of whales in the mouth and channel quadrats.

The upper channels of the Cunningham River can only be reached by the whales on a rising tide. Date had a noticeable influence on numbers in the channel, especially since it was related to high tides which occurred in the latter part of July.

Herd composition and social groups

At the Nastapoka estuary, where in 1984 our data set was sufficiently large, 19% of the herd consisted of neonates, 15% were yearling (1/2 length) calves, 24% were older juveniles (2/3 and 3/4 length) and 42% were white adults (Caron & Smith 1990: table 2). The sex ratio of adults was calculated by assuming that: (1) since the gestation period is >1 year, nursing neonates and 1/2 length calves (yearlings) must each have one mother present in the Nastapoka herd, and (2) since lactation lasts for up to 2 years, an adult seen with a 2/3 length calf (2 or 3 years old) was assumed to be that calf's mother. The sum of neonates, 1/2 length calves and white animals with 2/3 length calves gave a conservative estimate of 35% sexually mature females. A small percentage of large grey animals accompanied by neonates and therefore assumed to be sexually mature (3%) was subtracted, giving 32.1% adult white females. Subtracting this from the total whites in the area gives a maximum estimate of 10% adult males, and an adult sex ratio of 1 (male): 3.2 (females) in the Nastapoka estuary.

Age structure in the Nastapoka varied between quadrat areas. Juvenile (2/3 and 3/4 length) age classes penetrated higher upstream while large, solitary adults individuals were most often found at the seaward end of the estuary. Females with neonates and yearlings (1/2 length) were most frequent in the middle quadrats (Table 2).

Age structure also varied seasonally, with a decrease of the juvenile age class (2/3 and 3/4 length) in mid-summer

Table 3. Contingency table of the age structure variation of the Nastapoka herd over the 1984 season. The dates listed are mean values of dates for blocs of equal sample size. A deviation statistic Z was calculated for each cell and compared with the critical value of Z (3.0256) given a significance level of 0.05. Cell values which are significantly different from the expected value are marked with an asterisk.

	17 July	7 August	20 August	29 August
Age class	Obs. (percent) Z statistic	Obs. (percent) Z statistic	Obs. (percent) Z statistic	Obs. (percent) Z statistic
Neonate	1455 (17.4%) *3.9657	1733 (20.4%) 2.5837	1670 (20.0%) 1.6840	1542 (18.9%) 0.6223
1/2	1143 (13.7%) *4.2544	1474 (17.4%) *4.5117	1257 (15.1%) 0.7863	1254 (15.4%) 0.0187
2/3	1484 (17.8%) *14.2083	736 (8.7%) *8.4982	547 (6.6%) *17.3304	1022 (12.5%) 3.0170
3/4	910 (10.9%) *5.1238	1226 (14.4%) *4.2706	1029 (12.3%) 1.0690	1077 (13.2%) 1.1922
White	3355 (40.2%) 1.6985	3310 (39.0%) *3.5317	3844 (46.1%) *6.7856	3259 (40.0%) 2.0206

$X^2 = 703.7002$, DF = 12, $P < 0.005$.

and a sharp increase towards the end. Neonates and yearlings were fewer during the first quarter, but reached constant levels for the remainder of the season (Table 3).

At Cunningham Inlet during 1980–87 we obtained age structures from two quadrats analogous to the Nastapoka river: the mouth and channel quadrats. We also documented the age structure in Southwest Bay quadrats, a quiet part of the inlet outside of the influence of flowing fresh water, which had no counterpart in the Nastapoka study area.

Males were infrequently seen at Cunningham and were noted usually as groups consisting of 10–15 large white adults. These pods appeared to be transient and would come and go throughout the period of estuarine occupation by other white whales.

Comparing all the quadrats at Cunningham Inlet using an analysis of variance revealed no significant differences in the age structure ($F = 0.6074$, $P > 0.6947$). A seasonal trend of an increasing 0+ age group for individual years of 1980, 1981, 1982 and 1983 was significant ($F = 37.88$, $P < 0.0001$), as were the combined suckling calves (0+ and yearling calves) for all years together ($F = 12.60$, $P < 0.0011$).

Focal samples seem to indicate that females with young calves actively avoid contact with adult males in the nearshore areas. To investigate this relationship we examined the effect of adult male presence on the neonate-to-adult female ratio and the suckling calf (neonate and 1/2 length) – to the adult female ratio. Surprisingly there was a significant positive relationship between both ratios and the presence of adult males ($F = 13.82$, $P < 0.007$ and $F = 5.92$, $P < 0.0193$, respectively). Further regression analysis, which sought to remove the influence of date on this relationship, showed a much weaker relationship of neonates to the presence of males ($F = 0.346$, $P = 0.91$), but a significant effect on the percentage of yearling calves (1/2 length) ($F = 4.38$, $P < 0.0432$).

Ethogram

The ethogram describes the action patterns in four classes of activity: locomotor, non-locomotor and comfort, emergent and surface, and interactive (Table 4).

Locomotor behaviour of white whales involves normal swimming, often with synchronous diving and surfacing when whales are travelling in groups. Swimming speeds measured at Cunningham Inlet, usually when adult whales were travelling in a directed manner toward the offshore areas, varied from 0.9 to 8.1 km/h (Fig. 3).

In shallow water and in areas occupied by large numbers of whales the usual swimming pattern would often be altered. Instead of rolling gently to the surface, only the blowhole only would emerge from the water as a whale raised its head to breathe.

Leaping, often called porpoising, occurred very infrequently and for only short periods at the beginning of quick swimming. It was seen occasionally at Cunningham Inlet, when a sudden mass movement out of river channels occurred (Sjare and Smith 1986). In the Nastapoka this behaviour was also observed when whales were fleeing from Inuit hunters.

Skimming is used to describe white whales swimming with their heads out of the water. White whales are the only northern cetacean species with unfused cervical vertebrae (Kleinenberg *et al.* 1969) similar to the platanistoid river dolphins (Martin 1990). This allows white whales to raise their head completely clear of the water. Individuals have been seen to swim in this position for up to 30 minutes in Cunningham Inlet. Our impression was

Table 4. Ethogram of white whale behaviours seen at the Nastapoka River estuary and Cunningham Inlet, Northwest Territories.

Activity Class	Action pattern	Description
Locomotor	Normal swimming	Forward motion with the blowhole region of the head exposed and a gentle roll of the back above the surface during breathing.
	Head raising	Raising only the head and blowhole clear of the surface to breathe while moving forward.
	Leaping (porpoising)	During fast movement forward. Projecting the anterior end of the body and re-entering head-first during the initial thrust of the sequence. Never done frequently; never prolonged.
	Skimming	Slow forward swimming with the neck bent upwards, lifting the full face, including the underside of the jaws, above the surface of the water.
	Side swimming	Moving forward with body oriented laterally to the water surface.
	Back swimming	Moving forward with the dorsum towards the sea bottom.
Non-locomotor and Comfort	Sounding	At the initiation of a prolonged dive the body bends sharply downward midventrally, exposing the mid-dorsum, but not raising the flukes above the surface.
	Sounding with tail up	Initiation of a prolonged dive with flukes and caudal peduncle appearing above the surface.
	Mud stirring	In depths of several meters or more diving to contact the sea bottom and rubbing all parts of the body. Mud is often seen to adhere briefly to the body after such dives.
	Partial Stranding	In a normal swimming position while in full contact with the bottom. Parts of the dorsum are continuously exposed to the air including the blowhole. Occasional lifting of the flukes and head, or both, completely clear of the water. Whales can be completely motionless or actively rubbing on the substrate in this position.
Surface and Emergent	Breaching	Projecting the body in a forward motion obliquely out of the water and falling on the water surface on the side, front or back.
	Spinning	Breaching in a forward motion and spinning through at least 270° before reentering the water.
	Body slapping	Emerging vertically and falling backward slapping the water with the back often repeatedly.
	Spy hopping	Raising the head and neck vertically out of the water.
	Pitch poling	In the same position as a spy hop, but with rotation around the axis of the body.
	Tail standing	Raising the body vertically out of the water to the area posterior to the flippers and maintaining position briefly by vigorous tail movement.
	Tail waving	Moving the tail (caudal peduncle and flukes) from side to side above the water surface with the rest of the body submerged.
Interactive	Head bobbing	Moving the head up and down above the water surface.
	Head slapping	Hitting the water surface with the chin and throat.
	Flipper slapping	Hitting the surface with the ventral surface of the flipper.
	Tail slapping	Striking the surface with the ventral surface of the flukes.
	Mouthing	Touching, biting or holding any part of another whale with the mouth. These are often head to head or head to genital region contacts.
	Head butting	Pushing or butting against other whales with the head.
	Milling	Active interactions, often among juveniles, involving chasing, rolling and tumbling. Most often seen in shallow areas 2–4 m deep and also involving contact with the sea bottom.
	Sexual activity	During close contact usually involving milling behaviour. Erections are seen.
	Riding	Usually neonates or yearlings position themselves over the backs of adult females and probably benefit from the laminar flow to maintain their position.
	Suckling	Both neonates and yearlings are seen to dive repeatedly to the genital area of adult females, which usually maintain a normal swimming position, but sometimes turns slightly sideways. Usually observed in quiet nearshore areas away from other whales.
	Carrying objects	Carrying objects either in their mouths or on their heads or backs.

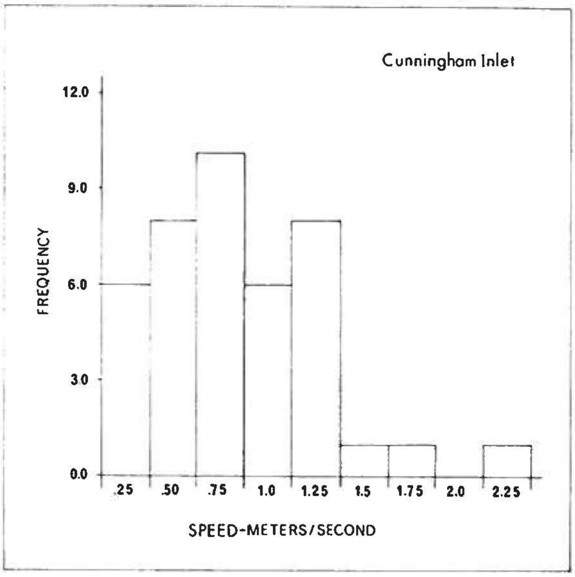

Figure 3. Speed of adult white whales (N = 41) swimming in a directed manner within Cunningham Inlet, N.W.T., Canada.

that this occurred more frequently in groups of whales that had just arrived in the estuary, but we cannot verify the impression with data.

Both side swimming and back swimming occurred only for short intervals and could only be seen when white whales were in the shallow waters near the observation points. In most cases these postures were assumed as the white whales visually investigated and sometimes echolocated on hydrophones or the observation tower. Back swimming may have involved the rubbing of the dorsal skin on the sea bottom.

Prolonged dives were observed offshore in Cunningham Inlet in water depths of up to 42 m. Focal samples, of what was presumed to be the same whale, revealed two types of action pattern which we have called sounding. The most common was when whales initiated a dive with a pronounced midbody bend exposing the mid-dorsum above the surface. Less frequently a sounding also resulted in the caudal peduncle and flukes breaking the surface. Neither of these action patterns is thought to be distinct enough to indicate unequivocally that a prolonged or deep dive has begun. We caution that more detailed observations are needed in order to use such action patterns as indicators of feeding or foraging dives.

Mud stirring in water depths of several metres or more appears to be directly involved with abrasion of the skin surfaces during the moult process, but feeding cannot definitely be excluded. Partial stranding in the flowing fresh water of the river channels is also related to rubbing of the skin surfaces on the abrasive substrates (St. Aubin *et al.* 1990, Smith *et al.* 1992). Occasionally animals which have lingered too long on an ebbing tide in shallow water strand completely. Usually they are left in a pool 10–30 cm deep, with parts of their bodies continuously exposed to the air. Sometimes they are left in deeper pools where they can submerge completely, but cannot escape to the sea. On the several occasions when we observed white whales completely stranded out of the water, they were all able to escape on the next high tide. It did not appear that exposure to elevated ambient air temperatures resulted in burning or desiccation of the skin, and the whales remained vigorous throughout the maximum 18 hours of stranding. Infrequently such strandings result in mortality from predation by polar bears (*Ursus maritimus*; Smith & Sjare 1990).

Behaviour classified as surface and emergent occurred in the deeper areas of the estuaries. Although many other white whales were in the estuaries, our observations of these action patterns were of single whales. These patterns have been described for other cetaceans. They have rarely been noted for white whales in captivity (Defran & Pryor 1980), possibly because of the limited depth of the aquarium tanks.

Interactive behaviour was documented near our observation points in the inshore areas, but it could also be seen offshore. Slapping of the water surface with various parts of the body was common and occurred when animals were close to each other and during interactions such as chasing or rubbing. Visual signalling was probably involved in close, head to head encounters, in which up and down movements of the heads were seen. Actual contacts involved use of the mouth to touch, hold or bite parts of another whale. Head butting observed in the nearshore areas of Cunningham Inlet commonly involved groups of adult male white whales. It infrequently resulted in "rosette formation", previously described for such species as the sperm whales (*Physeter catodon*; Nishiwaki 1962).

Neonate and yearling calves remained close to their mothers at all times. Occasionally we were able to follow triads of adult females with either a neonate or a yearling accompanied by a larger grey animal. On two such occasions we observed the white adult, which we presumed to be the mother, leave her neonate in the care of the large grey individual. Because of the large number of whales and the lack of individually identifying characteristics, we could not obtain much information on these groups which might be family units.

Both neonates and yearlings appear to benefit from the laminar flow effect created by their mothers' swimming. The smaller calves remain in the area above the dorsal ridge as far back as the beginning of the caudal peduncle, as their mother swims about one meter below the surface. Neonates breathe more frequently than their mother and are able to take quick breaths without actively swimming (Williams *et al.* 1992) simply by changing the angle of their tail surfaces while being passively propelled.

In nearshore areas close to our observation points, neonatal, yearling and possibly 2+-year-old calves were seen in position to be suckled. It was usually difficult to ascertain whether nursing actually occurred because it is such a brief event (Hewlett 1978).

White whales near shore were seen to carry inanimate objects both in their mouths and on their backs. Whales held flat stones in their mouths on several occasions while swimming in the river channels of Cunningham Inlet. They also carried objects, on the backs and near the head region, including planks and other flotsam. This might relate to succorant maternal behavior in response to perinatal mortality (Smith & Sleno 1986).

Almost all of the action patterns were observed in both study areas. Only the stranding, mud stirring and carrying of objects were missing from the behaviourial repertoire at the Nastapoka River.

Discussion

In appearance and size the Nastapoka and Cunningham Inlet estuaries are quite different. Within the small area of the Nastapoka, white whales are constantly exposed to the significant river outflow and are never far from the open ocean. At Cunningham Inlet they are able to move from the delta areas of fast-flowing river water to quieter and warmer waters within the enclosed inlet, and yet remain somewhat distant from the open sea areas of Barrow Strait.

Because of these different sighting conditions, our documentation of detailed action patterns was different at the Cunningham Inlet and Nastapoka estuaries. The rubbing behaviour, for example, which appears to be a principal action pattern related to the mouth and channel areas of Cunningham Inlet (Smith *et al.* 1992), could not be easily detected in the deeper fast-flowing waters of the Nastapoka. It was probably occurring there since epidermal moult was clearly evident (St. Aubin *et al.* 1990), but the rubbing behaviour (Smith *et al.* 1992) was almost totally obscured. We would also expect this behaviour to occur in other estuaries, such as those of western Hudson Bay and the Mackenzie River, where sighting conditions, because of lack of good observation points or muddy waters, prevent close observations.

Herd structure at the two estuaries in our study appears similar. Adult males, which appear to maintain tight pods of 10–15 individuals, are a small component of the estuarine aggregations. They appear to remain in estuaries only for short periods compared with the younger whales. Focal samples indicate that adult females, especially those with neonates, avoid close contact with large males in the nearshore areas of the estuaries. Age-structure data, however, do not support this conclusion, but instead point to a positive correlation of adult males, at least with the number of female-yearling pairs. Date appears to play a large role in this correlation, with adult males and female-neonate pairs both increasing as the season progresses.

In both areas the proportions of females with suckling calves, both neonates and yearlings, increases as the season progresses. No calving or behaviour which could be associated with parturition has ever been observed in either estuary and we conclude that births occur prior to the females' arrival in the nearshore waters. This conclusion is consistent with evidence from other recent studies of reproductive cycles which indicate that the season of births is between April and July (Heide-Jørgensen & Teilmann 1994, Doidge 1990a). The argument that estuaries provide a thermal advantage for calving (Sergeant 1973) has been refuted by Doidge (1990b).

The difficulty of following individuals, pairs or groups in crowded estuaries has resulted in a low yield of information on herd structure. The close association of calves with their mothers for two and possibly more years is obvious. There are strong indications that adult-neonate pairs are accompanied by large grey calves who might assist in the care of the newborn or yearling calves. The sex of large grey animals was usually not discernible to the observer. However, in one instance we were able to attach satellite transmitters to a large white female and a large grey female captured together in a river channel, where they had become entrapped together on the ebbing tide. These animals stayed together for at least 21 days as they travelled away from Cunningham Inlet in the Barrow Strait area. Location data during this period indicated that they remained together as they travelled over a considerable distance both offshore and in coastal areas. All of the 5 unaccompanied grey calves captured at Cunningham Inlet during our satellite tagging program have been females ranging in length from 250 to 340 cm. These data might be taken to indicate that the basic herd structure is along matrilines similar to those suggested for other long-lived cetacean species (Baker *et al.* 1990, Bigg *et al.* 1990, Hoelzel *et al.* 1991).

The functions of individual behavioural patterns are difficult to understand. Surface observations of behaviour, occurring offshore at some distance from the observer, are subject to misinterpretation. These surface observations usually consist of what essentially is the beginning of an underwater behaviour, providing weak data from which to infer functions. Even the simple observations of sounding will not give quantitative data on foraging effort for studies of energetics. These answers are more likely to be provided by the application of telemetry (Martin & Smith 1992) in combination with physiological measurements and a detailed knowledge of regional biological oceanography (Welch *et al.* 1992).

Marine mammals remain elusive to researchers attempting to understand how they thrive in the oceanic environment. Our restricted windows of access for observing such species, coupled with their great mobility through vast unpopulated areas, makes the research task difficult. The period of estuarine aggregation provides only a glimpse of how white whales behave and of the composition of their herds. The important late winter period when mating and calving occur (Heide-Jørgensen & Teilmann 1994, Doidge 1990a) will remain obscure for some time to come. It is vital, however, to underline the importance of estuaries as areas of particular biological significance. These are areas of traditional occupation where fidelity to site is strong (Caron & Smith 1990) and is probably developed through a learning process, in animals which remain in family groups over a prolonged period. The strong dependence of white whales on specific estuaries, which appear to be limited in number, has led to the depletion of many populations in Canada (Finley *et al.* 1982, Pippard 1985, Reeves & Mitchell 1989, Richard 1991) and the extirpation or cessation of use of at least one large estuarine area of aggregation at the Great Whale River (Francis 1977, Finley 1982) and possibly one other in Ungava Bay (Smith & Hammill 1986, Reeves & Mitchell 1989).

White whales are the most vulnerable of arctic marine mammals under present harvest regimes and should be the subject of continuing conservation action. Five of seven Canadian white whale stocks are considered either endangered, threatened or vulnerable (Finley *et al.* 1982, Pippard 1985, Reeves and Mitchell 1989, Richard 1991, International Whaling Commission 1992, Doidge & Finley in press). The strong philopatry of discrete white whale stocks to specific estuaries makes them subject to severe overexploitation and loss of critical habitat, both major ingredients of past man-mediated ecological disasters.

Acknowledgements

We wish to acknowledge the efforts made by the late Louise Caron in her study of the Nastapoka white whales. The behavioural studies at both the Nastapoka estuary and Cunningham Inlet were supported by the World Wildlife Fund, Canada, Whales Beneath the Ice program and the Arctic Biological Station, Department of Fisheries and Oceans. Our long-term studies at Cunningham Inlet have been made possible by the Polar Continental Shelf Project, Department of Energy, Mines and Resources, through their provision of continuing logistic support and aircraft time. We thank Gary Sleno, George Horonowitsch, Walter Klenner, Becky Sjare, Kathy Frost, and Bill Doidge for their contributions to the field studies. Peter Olesiuk, Pacific Biological Station, Department of Fisheries and Oceans, aided with the statistical analyses.

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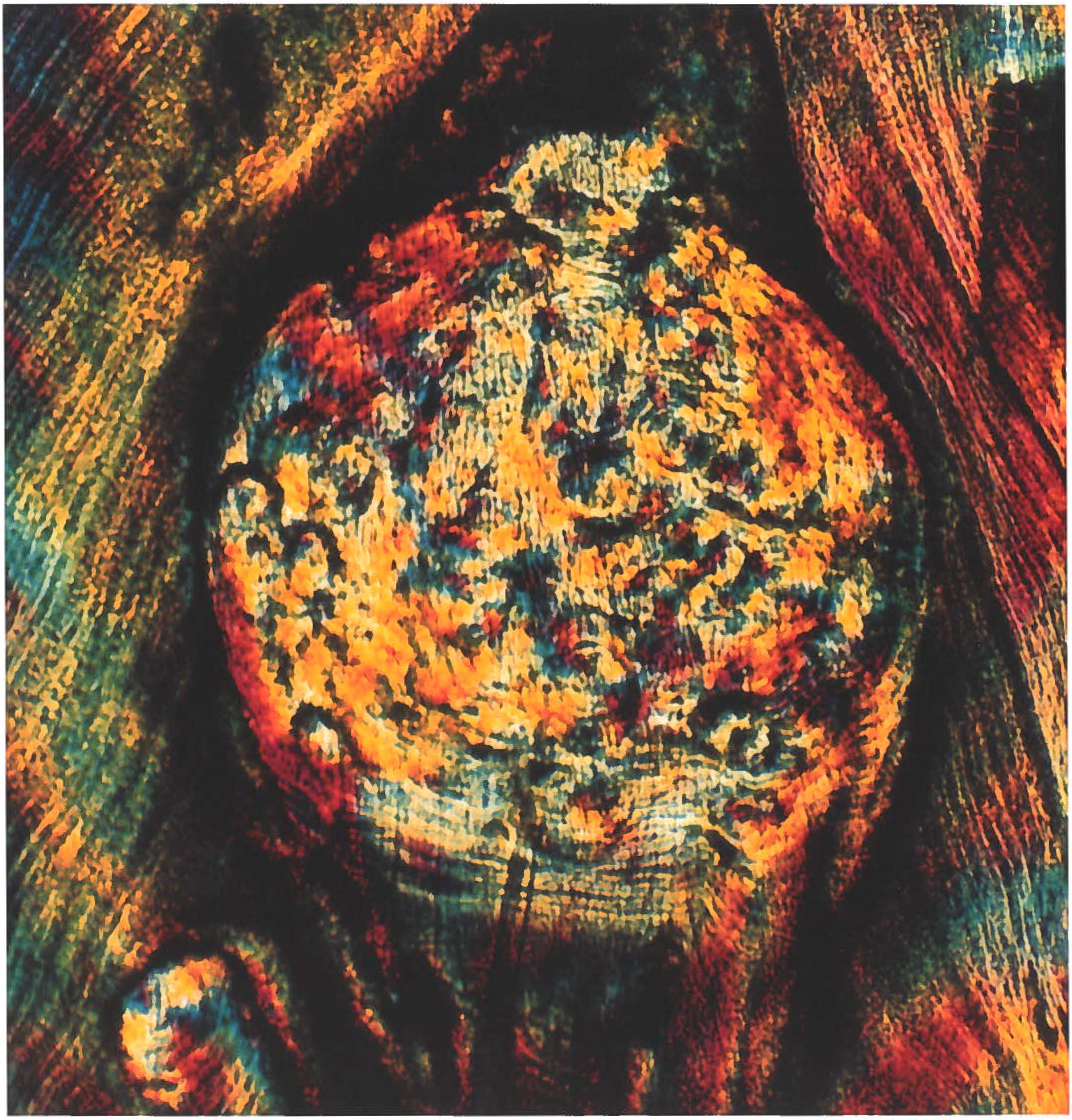
Life history, stock identity and toxicology



Pulp stone in the dentine of white whale teeth viewed in polarized light. Photo: J. Jensen.

Age estimation of white whales (*Delphinapterus leucas*) from Greenland

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Heide-Jørgensen, M. P., Jensen, J., Larsen, A. H., Teilmann, J. and Neurohr, B. 1994. Age estimation of white whales (*Delphinapterus leucas*) from Greenland. – Meddr Grønland, Biosci. 39: 187–193. Copenhagen 1994-04-22.

Various techniques of displaying growth layer groups (GLGs) in teeth from white whales, *Delphinapterus leucas*, from Greenland were tested. The dentine and cementum in unprepared longitudinal thick sections (150–200μm) displayed under transmitted polarized light microscope generally provided the simplest and clearest display of GLGs. Teeth taken from the lower jaw of white whales in West Greenland show significant wear at a much earlier age than teeth of white whales from northern Québec, the White Sea and the Kara Sea. The least worn teeth are usually positioned towards the rear of the lower jaw (tooth numbers 7–9). They give the highest number of GLGs and thus most accurately reflect the age of the whale. Teeth from one white whale that was captured when approximately three years old and maintained in captivity for 15 years showed 30–36 GLGs. This finding adds to the evidence that two GLGs are deposited annually in the teeth of white whales.

Key words:
White whale, *Delphinapterus leucas*, Greenland, age estimation.

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Introduction

In studies of vital parameters and life history it is critically important to use reliable techniques of age estimation. This also applies to studies in which the goal is to evaluate changes in age structure due to exploitation or to analyse the accumulation of contaminants by various age classes within a population.

A number of studies of white whales, *Delphinapterus leucas*, have used longitudinal sections of teeth for displaying dentine growth layer groups (GLGs) to estimate ages of the whales. One growth layer group (GLG) is assumed to consist of a dark and a translucent layer. Longitudinally bisected, polished teeth were examined under reflected light with a dissecting microscope by Sergeant (1973), Brodie (1982) and Goren *et al.* (1987). Finley *et al.* (1982) stained the bisected teeth with haematoxylin before examining them in a microscope with reflected light. Participants in a workshop on odontocete age determination found that bisected teeth were difficult to "read" and they therefore etched the teeth in 10% formic acid (Perrin & Myrick 1980). However, etching failed to improve the readability of the teeth. Instead, longitudinal sections of 25–300 μm were examined under a microscope with transmitted light or under a microfiche reader (Perrin & Myrick 1980, Burns & Seaman 1986). Doidge (1990a) also used unstained 300 μm longitudinal midsections of teeth of white whales from northern Québec. Goren *et al.* (1987) prepared 100 μm sections for scanning with a microdensitometer. These same authors also prepared 250–300 μm sections, bathed them in 5% formic acid and examined them with a scanning electron microscope. However, this method did not prove satisfactory.

The present study evaluates different tooth preparation procedures, examines differences in wear between teeth taken from the same white whale, considers sexual dimorphism in the dimensions of teeth and identifies differences in tooth wear between populations. Teeth from a "known-age" captive white whale were used for validating our age estimation techniques.

Table 1. Counts of growth layer groups (GLGs) in dentine in unstained and stained thin sections and unprepared thick sections from 13 white whales. '+' indicates that the teeth were worn and only minimum counts of GLGs could be obtained. Numbers in parentheses indicate the position of the teeth in the jaw.

Whale ID no.	Unstained thin sections	Toluidine blue thin sections	Unprepared thick sections
1104	8 (8)	8 (8)	+ 8 (1)
1114	7 (8)	7 (8)	7 (1)
1172	5 (8)	5 (8)	5 (1)
1176	6 (8)	6 (8)	6 (1)
1178	13 (8)	13 (8)	13 (1)
1181	10 (8)	10 (8)	+ 8 (1)
1182	17 (6)	17 (6)	+13 (1)
1185	11 (7)	11 (7)	11 (1)
1186	10 (8)	10 (8)	+10 (1)
1495	+16 (least worn)	+24 (least worn)	+24 (least worn)
1496	+15 (7)	+15 (7)	+20 (1)
1498	+20 (least worn)	+35 (least worn)	+30 (least worn)
1499	+24 (8)	+30 (8)	+26 (8)

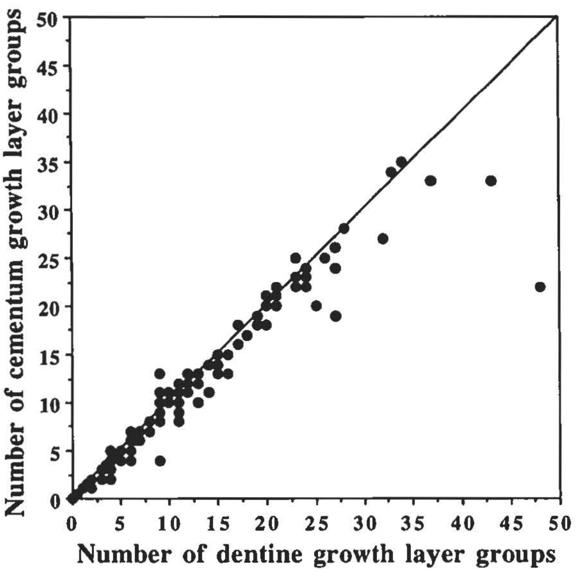

Fig. 2. Correlation between the number of dentine and cementum growth layer groups in white whale teeth.

Materials and methods

The entire lower jaws were collected from 44 white whales taken in the harvest by Inuit in West Greenland. It proved to be too time-consuming under field circumstances to collect the entire jaws from a larger sample of the catch. Instead, the lower jaws of 282 additional white whales were cut off with a saw. The jaws were kept frozen until extraction of teeth, which was done after boiling in water for 5 min or maceration in water at 40°C for a few days. As a standard, we numbered the teeth in each side of the lower jaw from 1 to 10, starting anteriorly. The effect of boiling versus maceration was tested on two whales in which the left side of the lower jaw was boiled and the right side was macerated.

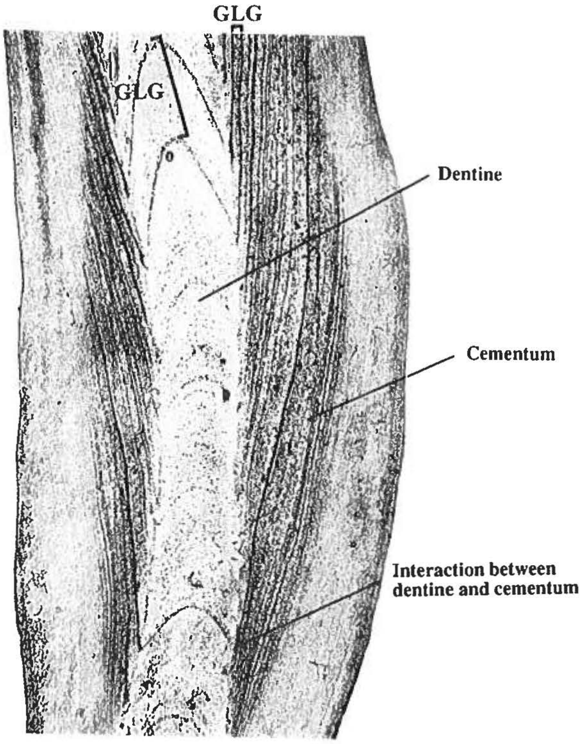

Fig. 1. Detail of white whale tooth showing the interaction between cementum and dentine.

Two types of section were prepared:

1) *Thin sections:* Teeth were decalcified for 2–20 days (depending on the size of the tooth) in 5% HNO_3. Central longitudinal thin sections (14 μm, 30 μm and 40 μm) were then cut with a freezing microtome at −22°C (Reichert Jung type 1206 and Frigomobil OM) and stained with toluidine blue following methods described by Dietz *et al.* (1991). The sections were mounted on glass slides. The thin sections were read both before and after staining with toluidine blue.

2) *Thick sections:* Unprepared longitudinal sections of 150–200 μm were cut with diamond wafering blades mounted on a Buehler Isomet lowspeed saw. When necessary, sections were polished by hand using wet 600-grit silicon carbide paper disks (3M) before examination under a microscope. Sections were kept in a mixture of alcohol and glycerin.

Counting of GLGs in both dentine and cementum was facilitated by the use of a transmitted light microscope (10 ×, Carl Zeiss Jenaval) with polarized light. Two or three trained readers examined all teeth independently. The number of GLGs in both dentine and cementum was

Table 2. Discrepancies in counts of growth layer groups (GLGs) in dentine and cementum of white whale teeth. Two or three independent observers counted the GLGs and the difference between the minimum and maximum counts was used as a qualifier (Q). In some cases a final age could not be determined (ND). The number of teeth (N(Q)) is shown for each qualifier.

	Dentine		Cementum	
Q	N(Q)	%	N(Q)	%
0	189	56	146	43
1	82	24	104	31
2	28	8	27	8
3	8	2	13	4
4	3	1	4	1
5	3	1	2	1
ND	27	8	44	13
		N = 340		

determined to be the mean of the readings, rounded upwards to the next whole number. Disagreement among the various readers was quantified as the difference between minimum and maximum values. This figure was used as a "qualifier" for the age estimation. Teeth in which a neonatal line could be detected were assumed to reveal a "complete age", whereas those where the neonatal line had disappeared due to apical wear were considered to provide only a "minimum age".

Teeth from a 372 cm female white whale that died on 26 July 1984 after 15 years in captivity at Duisburg Zoo, Germany, were used for validating the age estimation technique. The whale was estimated by her captor to have been 3 years old (length 294 cm) when captured in the Seal River near Churchill, western Hudson Bay, 5 August 1969 (Gewalt 1970). During maceration the teeth were mixed and no position numbers could be assigned to them when the cranium was deposited at the Institut für Haustierkunde in Kiel, Germany. Thus teeth from upper and lower jaws could not be distinguished, nor could the anterior and posterior teeth be identified. All teeth from this specimen are now being kept at the Greenland Fisheries Research Institute (ID no. 74). For age estimation four teeth, judged to be the least worn, were selected for sectioning (150–200 μm).

To test whether there was any difference in the number of GLGs in various teeth from the same animal, we prepared sections (150–200 μm) of 5 teeth from the same side of the jaw (usually nos 1, 3, 5, 7, 8) from 6 individuals with unworn teeth and 12 individuals with worn teeth (Figs 3 & 4).

The proportion of worn teeth in both males (N = 142) and females (N = 184) was calculated for the teeth from West Greenland. This proportion was compared with that for a sample from northern Québec (Doidge 1990b) and a large sample from the White and Kara seas. Ages for the latter sample had already been estimated and were made available to us by G.N. Ognetov (SEVPinro, Arkhangelsk). These ages were estimated by methods described in Ognetov (1985a, 1985b), which are consistent with methods described by Sergeant (1973). For both samples, ages were estimated on the assumption that 2 GLGs are deposited annually.

Mean age at tooth wear (MATW) was calculated by the technique described in DeMaster (1978).

Teeth from 206 individuals were measured to assess sexual dimorphism in tooth development. Weight, length, width and thickness were measured with a Sartorius labweight (1/10 g) and a digital micrometer (1/100 mm).

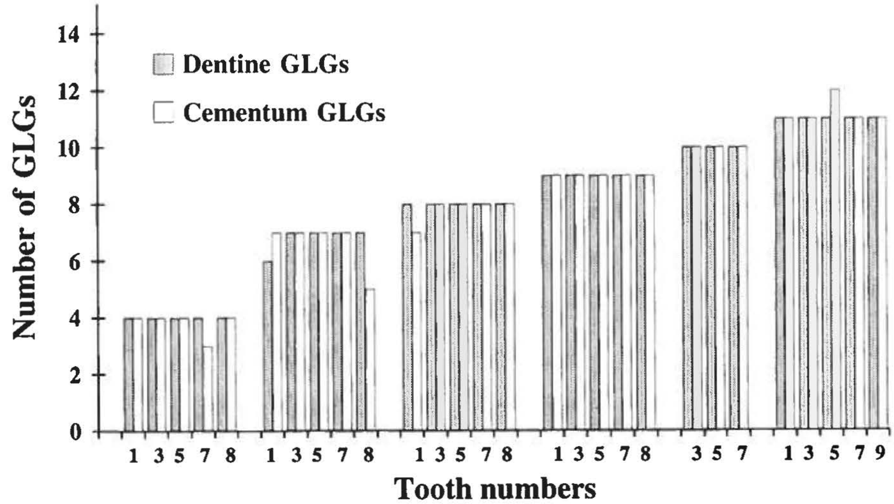

Fig. 3. Number of GLGs counted in unworn teeth from the lower jaws of six white whales from West Greenland.

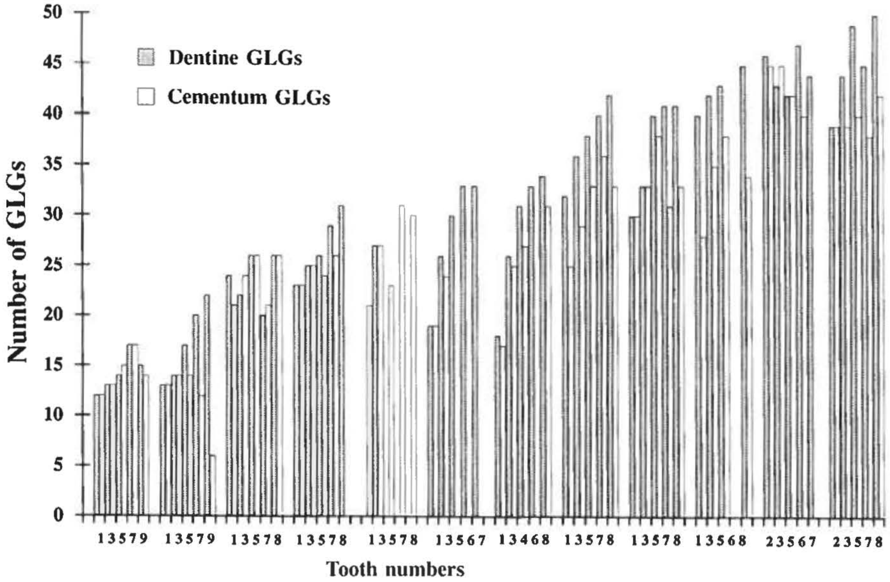

Fig. 4. Number of GLGs counted in worn teeth from the lower jaws of 12 white whales from West Greenland. The neonatal line could not be detected in any of these teeth.

Results and discussion

Preparation of teeth

There was no discernible difference in the readability of the unstained thick sections (150–200 μm) that had been boiled or macerated. Furthermore there was no obvious difference in using 14 μm, 30 μm or 40 μm thin sections, although it seemed that 14 μm sections were slightly easier to read. For younger teeth, unstained thin sections did not differ appreciably from those stained with toluidine. However, for older teeth, staining improved the readability. This effect can be seen with ID numbers 1495, 1498 and 1499 (Table 1), for which larger numbers of GLGs were counted in the stained sections.

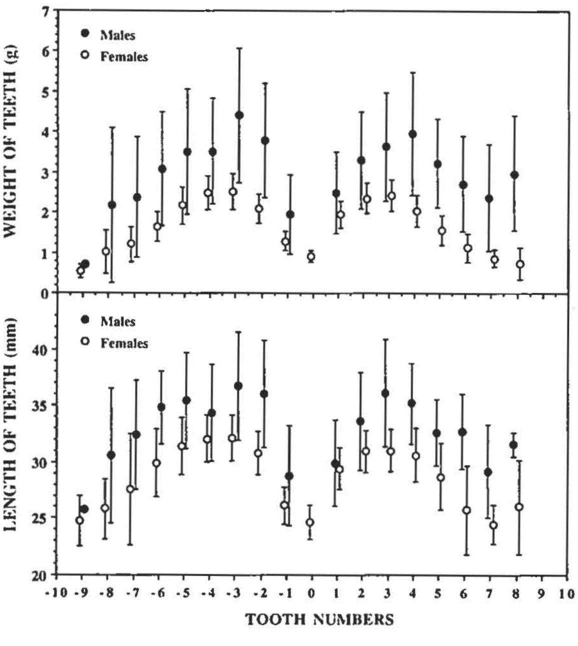

Fig. 5. Comparison of weight and length of white whale teeth from males (dots) and females (open circles) at different positions in the lower jaw. Only whales with more than 9 GLGs are shown and the vertical lines indicate 95% confidence limits. The teeth are shown from left (indicated by a minus) to right (plus).

The same tooth could not be used to make both thin sections and thick sections, so the comparison between these two methods cannot be conclusive. However, stained thin sections did provide higher GLG counts than unstained thick sections in 4 of 13 cases (Table 1). This could have been due to the fact that the teeth used for staining in 10 of the 13 cases were generally from positions farther back in the jaw than those used for thick sections. However, thick sections gave a higher number of GLGs in one case (ID no. 1496, Table 1).

The same numbers of dentine and cementum GLGs were counted in most teeth where the dentine and cementum "interacted" (Fig. 1). However, there were generally more readable GLGs in the dentine than in the cementum in both decalcified (Wilcoxon $P < 0.01$, $N = 20$) and unprepared sections (Wilcoxon $P < 0.001$, $N = 212$). This was especially pronounced in older animals (Fig. 2). For age estimation the tissue with the most readable GLGs was used. This was the dentine in most cases.

Eighty percent of the dentine GLG counts and 74% of the cementum counts deviated by less than a year (0–1 GLG, Table 2). Twelve percent of the dentine counts and 14% of the cementum counts deviated by one year or more (2–5 GLGs). In 8% of the dentine counts and 13% of the cementum counts the number of GLGs could not be determined exactly either because of a twist in the

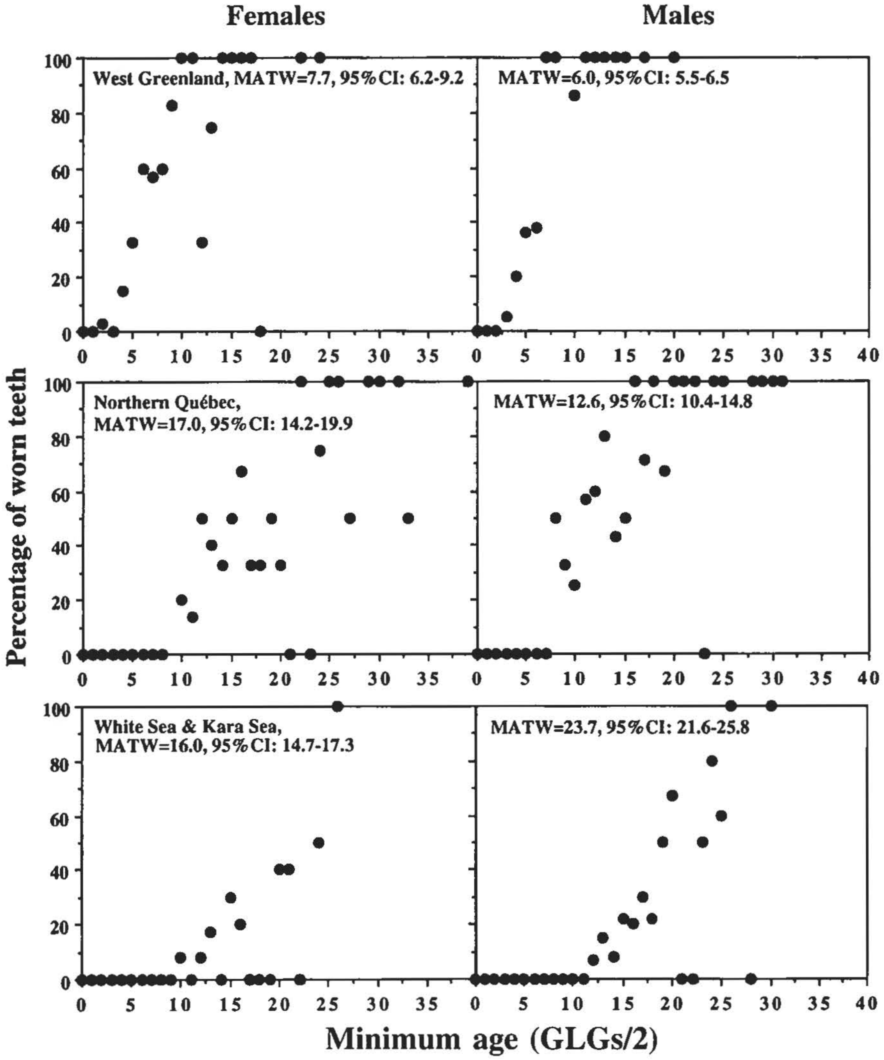

Fig. 6. Age at tooth wear in female and male white whales from West Greenland (this study), northern Québec (Doidge 1990b) and the White Sea and Kara Sea (Ognetov unpublished data). MATW indicates the mean age at tooth wear calculated according to DeMaster (1978).

tooth that made proper sectioning impossible, or because it was difficult to discern the GLGs (Table 2). In most cases it was possible to read at least one set of GLGs – either those in the dentine or those in the cementum – and therefore an age could be estimated for most whales.

Effects of tooth wear

Unworn teeth taken from different positions in the jaw showed no significant difference in the number of dentine or cementum layers (Fig. 3). However, in worn teeth there was a trend towards more dentine GLGs being present in teeth taken from the more posterior positions in the jaw (Fig. 4). The front teeth are usually worn, especially in older whales, but they often have easily distinguished GLGs in the dentine and cementum. The teeth in the middle of the jaw are usually the largest and they are less worn than the anterior teeth. The most posterior teeth tend to be the least worn, but because of their smaller size and vestigial form they are often difficult to read. In particular, the cementum GLGs are generally more difficult to discern in these rear teeth due to their smaller size (Figs 4 & 5). The closer spacing makes it difficult to distinguish the GLGs in these teeth. More dentine GLGs are present in the posterior teeth and thus they provide a better estimate of age than do the cementum GLGs for these teeth (Fig. 4).

Tooth wear is common in both sexes, but it appears and becomes more severe in males at slightly younger ages than in females (Fig. 6). However, male white whales from the White and Kara seas have a greater mean age at tooth wear (MATW) than females. The onset of tooth wear occurs at a much greater age in white whales from

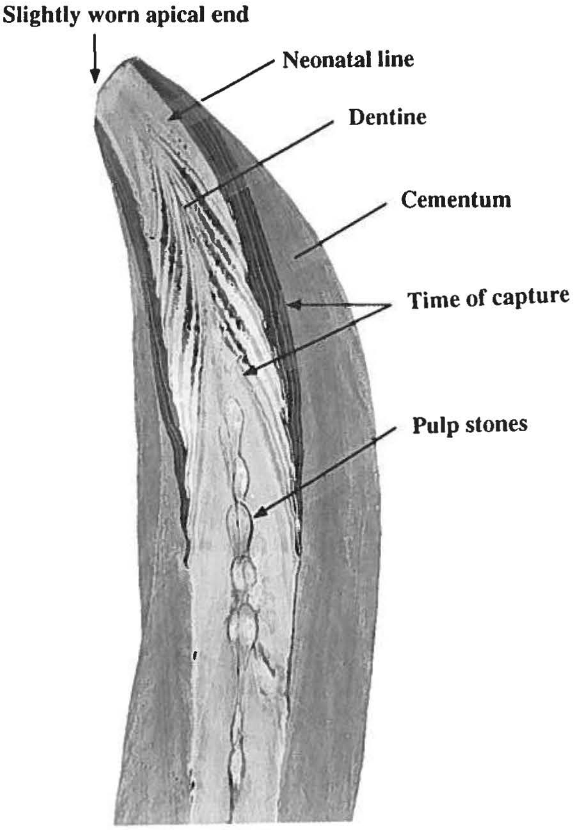

Fig. 7. Section of distal end of a tooth from a known-age white whale from western Hudson Bay. A distinct change in deposition of GLGs is evident after 6 GLGs.

the White and Kara seas (both males and females) than in white whales from West Greenland and northern Québec (Fig. 6). MATW is significantly lower for white whales from West Greenland compared with the other areas. Females from northern Québec have a MATW similar to that of females from the White and Kara seas but that of males differs greatly between the two areas (Fig. 6). These differences in tooth wear (which affects readability) must be taken into account when comparing age-related parameters between populations.

Pulp stones

Pulp stones appear occasionally in the dentine, but never in the cementum, of both males and females. Pulp stones are deposited in the pulp cavity (Fig. 7). None or several pulp stones could be found in teeth from whales of the same age and different sex. No meaningful pattern could be detected in the deposition of pulp stones.

Sexual dimorphism

Perrin & Myrick (1980) suggested that there were sexually dependent morphological differences in tooth development. Thus tooth measurements from 206 white whales were tested by discriminant analysis for evidence of sexual dimorphism, but no significant differences between males and females could be detected. However, teeth from male white whales with more than 9 GLGs are clearly larger than teeth from similar-aged females (Fig. 5).

Calibration of age

All four teeth from the captive whale had characteristics that clearly distinguished them from the teeth collected from white whales in West Greenland. In the four teeth a clear difference was evident in the distinctness of GLGs in both cementum and dentine after deposition of the sixth one (Fig. 7). The deposition pattern changed from a distinct one with well-defined dark and translucent zones through GLG 6 to a less pronounced layering pattern from GLG 7 to the death of the whale. A similar change was observed in the teeth of two other captive white whales (Brodie 1982, Goren *et al.* 1987). Brodie (1982) was unable to count the GLGs deposited after the time of capture in one specimen.

The neonatal line was present in three of the four teeth, and this made it possible to estimate the whale's "complete age". Two of the four teeth were difficult to read, but the estimated number of GLGs in the dentine of the two most readable teeth varied between 30 and 36. The GLGs in the cementum were even more difficult to read but also gave counts of between 30 and 36.

Despite the uncertainty in our GLG counts for this whale, they allow us to reinforce the conclusion of Sergeant (1973) and Brodie (1982) that 2 GLGs are deposited annually in the teeth of white whales. The only previous validation of annual deposition of 2 GLGs in the white whale was that by Goren *et al.* (1987). These last authors tested various techniques for estimating age from the teeth of a male white whale from Alaska whose known age at death was approximately 24 years. Approximately 40 GLGs could be counted consistently in this whale's teeth.

Recommended procedure for age estimation

We recommend that the less worn of tooth numbers 7 and 8 from either side of the lower jaw be selected for age estimation (Fig. 4), that unprepared thick longitudinal sections (150–200 μm) be used and that a transmitted-light microscope with polarized light be used for counting GLGs. Counts in the dentine seem to result in higher values and more reliable (*i.e.* more nearly complete) estimates of age than counts in the cementum (Fig. 2 & Table 2), although counts in the cementum can provide a valuable supplement. For whales with many GLGs, thin sections stained with toluidine could be used to supplement the thick sections (Table 1).

Acknowledgements

A. A. Hohn, C. Lockyer and R. R. Reeves offered useful comments on this report.

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Growth, reproduction, age structure and feeding habits of white whales (*Delphinapterus leucas*) in West Greenland waters

MADS P. HEIDE-JØRGENSEN and JONAS TEILMANN

Heide-Jørgensen, M. P. & Teilmann J. 1994. Growth, reproduction, age structure and feeding habits of white whales (*Delphinapterus leucas*) in West Greenland waters. Meddr Grønland, Biosci. 39: 195–212. Copenhagen 1994-04-22.

Reproductive organs, mandibular teeth, stomach contents and body measurements including total mass from white whales (*Delphinapterus leucas*) taken by Inuit hunters in West Greenland during 1985–1992 were analysed. Both sexes of white whales from West Greenland attain a greater length at physical maturity than do white whales from Alaska, Hudson Bay, northern Québec, the White Sea and the Kara Sea. Male white whales attain sexual maturity at 6–7 years. Size of testes and presence of spermatozoa suggest that mating takes place in May or perhaps later. Female white whales apparently become sexually mature at 4 to 7 years of age, but the negative bias of age estimates from whales whose teeth lack the neonatal line confounded our effort to estimate the age at sexual maturity. Gestation lasts at least 330 days, with implantation in May–June, and calves are likely to be born in April–May. The oldest white whales were taken in spring in Disko Bugt, whereas the herds taken in the Upernavik area in autumn usually consisted of immature whales and females with calves. The white whales taken in the current fishery in West Greenland are significantly smaller than those taken in the drive fishery in South Greenland in the 1910s and 1920s. The most likely explanations include changes in age distribution caused by the harvesting regime and changes in prey availability on the wintering grounds. Present diet of white whales in West Greenland includes polar cod (*Boreogadus saida*), arctic cod (*Arctogadus glacialis*), squids (Cephalopoda), and lanternfishes (Myctophidae) in the Upernavik area in the autumn and redfish (*Sebastes* sp.) and squids in Disko Bugt in the spring.

Key words:
White whale, beluga, *Delphinapterus leucas*, Greenland, growth, reproduction, age structure, feeding habits.

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Introduction

The white whale or beluga (*Delphinapterus leucas*) has been an important game animal in the Inuit hunting societies that have inhabited the west coast of Greenland for more than 2000 years. Nowadays it is among the most important of the marine mammals exploited in Greenland, and the annual catch of 500–1000 white whales often exceeds the combined catch of all other whale species in Greenland (Heide-Jørgensen 1990).

White whales arrive in the municipality of Upernavik (Fig. 1) in October during their southward autumn migration, and they are killed there in large numbers in a drive fishery (Heide-Jørgensen 1994). The present-day center of winter distribution of white whales off West Greenland is along the coast between 67°N and 69°N; white whales are rarely observed more than 70 km offshore (Heide-Jørgensen *et al.* 1993). The return spring migration northward begins in April when white whales are caught along the ice edge or in the loose pack ice of Disko Bugt (Kapel 1977). In May-June they are taken in open water in the Vaigat, northern Disko Bugt. The small catches during spring along the ice edge in Uummannaq, Upernavik and Avanersuaq municipalities suggest that the white whales cross Baffin Bay somewhere between Disko and the municipality of Avanersuaq on their migration to the eastern Canadian High Arctic.

Despite its historic and current importance in the Greenlandic subsistence economy, the life history and

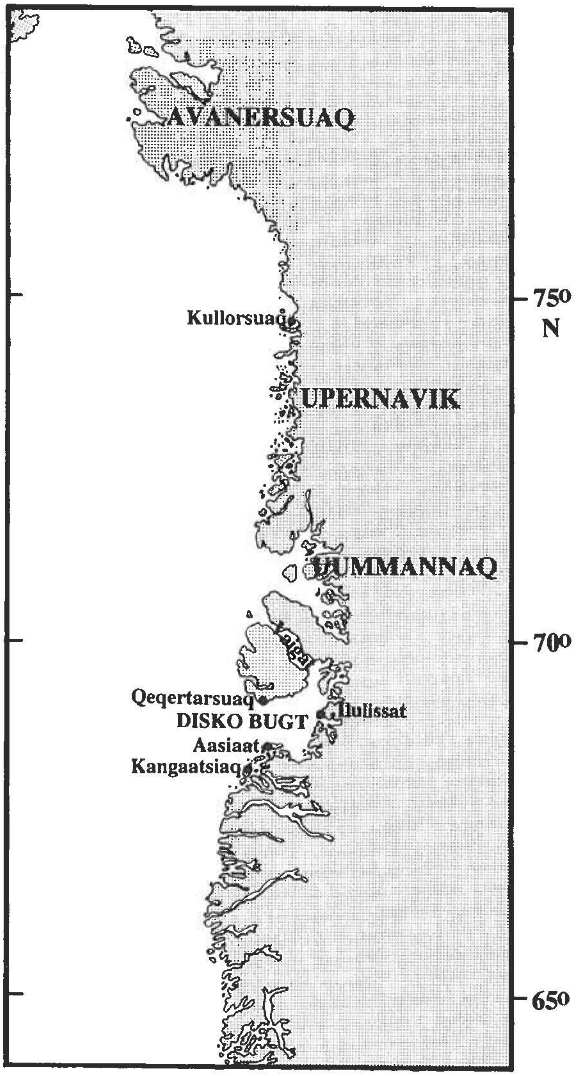


Fig. 1. Map of municipalities, settlements and sites mentioned in the text.

population structure of this white whale population is poorly documented. Degerbøl & Nielsen (1930) studied body growth and exploitation of white whales caught in a drive-net fishery in southwestern Greenland (south of 66°N), an area where these whales were formerly abundant (Heide-Jørgensen 1994). The history of white whale exploitation in Greenland has been described by Kapel (1975, 1977, *in* Reeves & Mitchell 1987) and Heide-Jørgensen (1994). Aerial surveys conducted in 1981, 1982, 1990 and 1991 documented the occurrence and population decline of white whales wintering off West Greenland (McLaren & Davis 1983, Heide-Jørgensen *et al.* 1993).

The present study was initiated to provide basic biological information on growth, maturation, reproduction, diet and age structure of white whales off West Greenland. Some of these features are compared with the results from similar studies in Alaska (Burns & Seaman 1986), Hudson Bay (Sergeant 1973, Doidge 1990a), northern Québec (Doidge 1990a) and the Sea of Okhotsk (Kleinenberg *et al.* 1969), and to results of similar but unpublished studies in the White and Kara seas (G.N. Ognetov, SEVPinro, Arkhangelsk, unpubl. data). Growth parameters are also compared with data for white whales taken in southwestern Greenland in the 1910s and 1920s (Degerbøl & Nielsen 1930).

Materials and methods

Samples from 381 white whales were collected from the Inuit catch in West Greenland during 1985–1992 (Table 1). The samples were collected by biologists who were present during flensing of the animals or by hunters trained to collect the samples.

Table 1. Samples collected from white whales in West Greenland, 1985-1992. Sex was not determined for all specimens. "Drive fishery" indicates whales were driven into shallow bays. "Ice entrapment" indicates whales were caught when trapped in the ice. "Ice edge" indicates whales were caught in spring primarily along the diffuse ice edge in Disko Bay and in the loose pack ice during breakup of fast ice.

Year	Month	Municipality	No. males	No. females	Total	Catch method
1985	October-November	Upernavik	13	20	35	Drive fishery
1986	March	Kangaatsiaq	7	0	7	Ice edge
1989	April	Qeqertarsuaq	6	0	6	Ice edge
1989	October	Upernavik	30	22	54	Drive fishery
1990	February	Ilulissat	7	6	13	Ice entrapment
1990	March-April	Aasiaat	3	7	10	Ice edge
1990	May	Ilulissat	5	0	5	Ice edge
1990	October	Upernavik	43	86	132	Drive fishery
1991	October-November	Upernavik	38	57	95	Drive fishery
1992	April-May	Qeqertarsuaq	15	7	24	Ice edge
TOTAL			167	205	381	

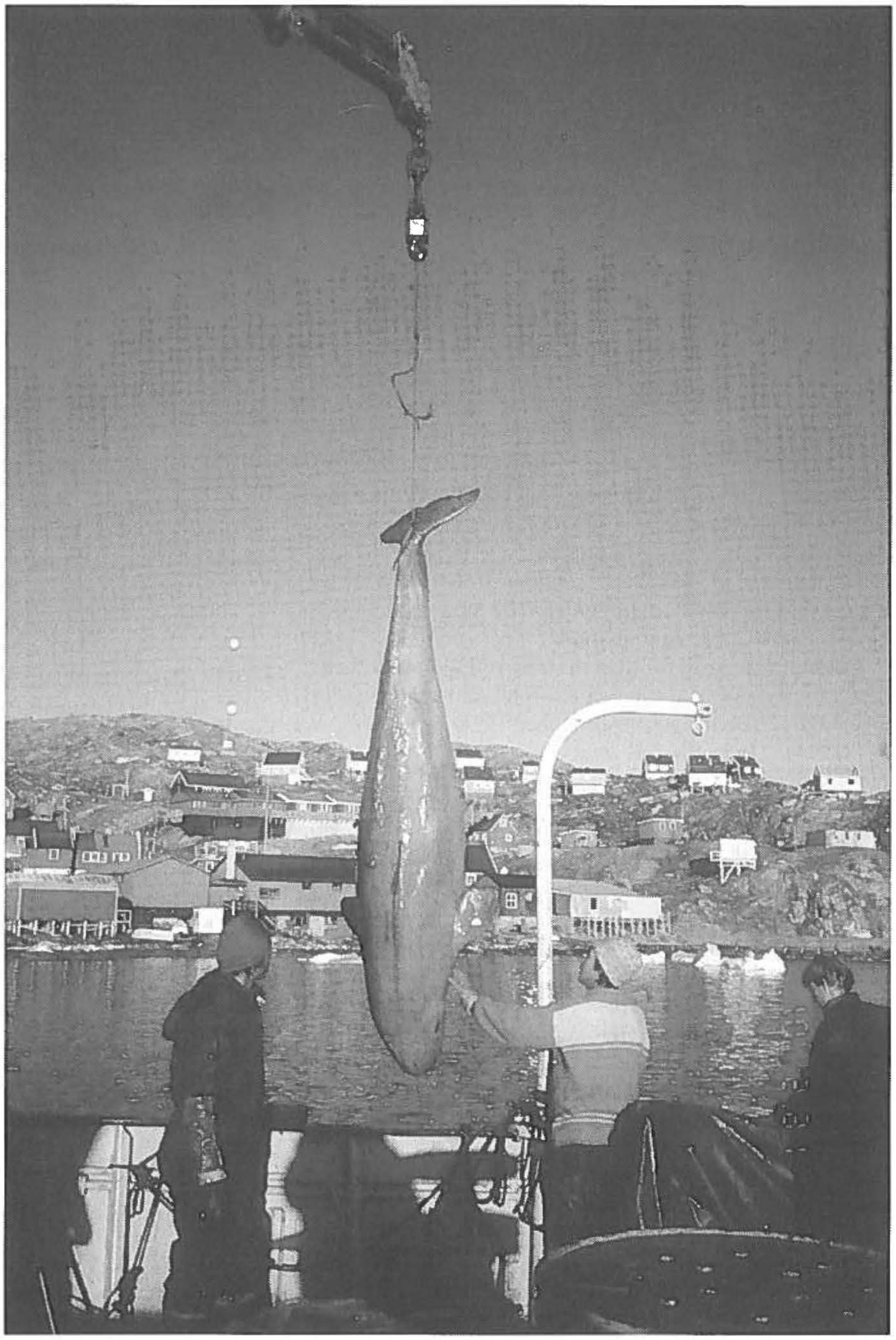


Fig. 2. Weighing of white whale onboard the research vessel *Adolf Jensen* in Kullorsuaq.

External examination and body measurements

Standard body length (SL) was measured to the nearest cm in a straight line along the side of the whale from the anterior tip of the lower jaw to the notch of the tail flukes. Dorsal curvilinear length was measured on a subsample of whales for comparison with SL. While being measured, the carcasses were lying on their sides on the beach. Fluke width (FW) was measured from tip to tip of the flukes in a straight line, also to the nearest cm. For some whales SL could not be obtained, but was calculated from the regression of FW on SL (see Fig. 8, later). Length of nipples and presence of exudates were noted, and mammary glands were examined for milk.

Between 30 September and 4 October 1991 measurements of total body mass were made of 97 white whales killed at Kullorsuaq in the municipality of Upernavik (Fig. 1). The entire, unopened whales were lifted aboard r/v *Adolf Jensen* using a crane (Fig. 2). They were then weighed to the nearest kilogram with a Salter DC-2 digital scale and length was measured when the whales were lying on the deck. Body mass and length were measured in the same way for three male and one female white whales killed at Qeqertarsuaq (Godhavn) between 9 and 14 May 1992.

Sex was determined by chromosomal analysis (Palsbøll *et al.* 1992) for 32 whales for which no reproductive organs were collected.

Age estimation

Teeth were extracted from lower jaws and stored frozen. Longitudinal sections of 150–200 μm were cut with a diamond wafering blade mounted on a Buehler Isomet lowspeed saw. If necessary, sections were polished by hand using wet 600 grit silicon carbide paper disks (3M) before microscopic examination.

Counting of growth layer groups (GLGs) was facilitated by the use of a transmitted light microscope (Carl Zeiss Jenaval) with polarization (see Heide-Jørgensen *et al.* 1994). Two trained readers examined all teeth independently. The mean of their combined counts of GLGs was used to estimate age. The term "complete age" is used for tooth sections in which all GLGs, including the neonatal line, could be counted. "Minimum age" refers to those teeth which did not contain a neonatal line because the apex of the tooth was worn. Two GLGs were assumed to be accumulated during one year (Heide-Jørgensen *et al.* 1994).

Growth of white whales from the Kara and White seas

For comparison with growth in white whales from West Greenland, data on growth of white whales from the Kara and White seas from G.N. Ognetov (SEVPinro, Arkhangelsk) were analysed. Length and age were estimated in similar ways as for the Greenland samples for 164 males and 40 females from the White Sea and 148 males and 218 females from the Kara Sea. A preliminary presentation of a subset of these data was given by Ognetov (1981).

Statistical analysis of growth data

Foetal length at age was described by a second-order polynomial. Length and body mass at age of *post-partum* whales was fitted to the following growth models:

von Bertalanffy:

$$SL = L_\infty * (1 - b * \exp(-k * x))$$

Gompertz

$$SL = L_\infty * (\exp(-b * \exp(-k * x)))$$

General Growth Equation:

$$W = W_\infty * (\exp(-b * \exp(-k * x)))^M$$

where SL is the standard length, W total body mass, L_∞ asymptotic standard length, W_∞ asymptotic body mass, and x age in years prorated for months, and where b, k and M are constants to be derived. The geometric relationship between standard length and body mass can be described as:

$$\text{body mass} = a * SL^b$$

where a and b are constants to be fitted.

Least-square estimation of parameters was carried out using the Quasi-Newton minimization in the Nonlin procedure of Systat (Wilkinson *et al.* 1992).

Male and female reproductive organs

Length, width, thickness and mass of testes and epididymides were measured. Right and left testes and epididymides were not distinguished. Sexual maturity in males was determined on the basis of presence of spermatozoa in histological sections of testes and epididymides. A subsample of testes and epididymides was measured before fixation in 5% seawater-buffered formalin. Large testes were cut into 2 cm sections before fixation.

Samples from the periphery and the core of midsections of the testes and midsections of epididymides were taken for histological examination. The samples were embedded in paraffin, microtome-sectioned at 6 μm, then stained with haematoxylin and eosin. The sections were examined for spermatogonad activity using a transmitted-light microscope. The diameters of ten circular seminiferous and epididymal tubules were measured, and the mean of each set of measurements calculated.

Uteri were cut off at the cervix, trimmed and opened, to accomodate later examination. Ligaments were removed before preservation in 5% seawater-buffered formalin for at least two weeks. A subsample was measured before fixation. Mass of the entire uterus, and diameter and thickness of the uterus wall at mid-length, were measured. The diameter and thickness at mid-length and the total length were measured for each uterine horn. Uteri were examined for foetuses and for evidence of pregnancies. Standard length, sex and body mass of foetuses were determined. Length and mass were measured for ovaries. After fixation the ovaries were sliced by hand in 2–3 mm sections and examined for numbers and sizes of corpora lutea (CL), corpora albicantia (CA) and follicles. Terminology of female reproduction follows Perrin & Donovan (1984). The diameter of these structures was

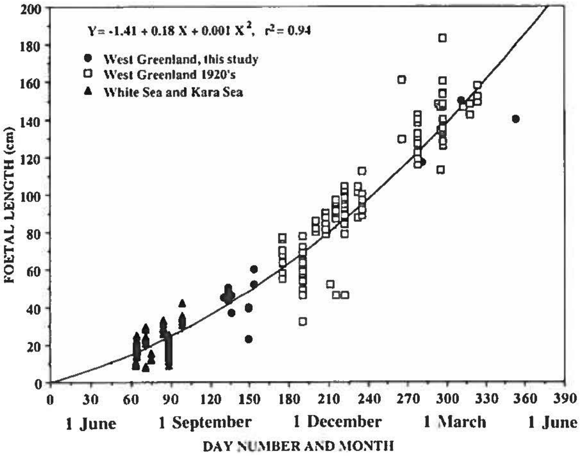


Fig. 3. Growth in length of white whale foetuses collected in West Greenland in 1985, 1989–92 (this study), in South Greenland in 1925–27 (Degerbøl & Nielsen 1930) and in the White and Kara seas between 1973 and 1984 (Ognetov 1985).

Table 3. Body mass-at-age of female and male white whales taken in West Greenland from 30 September to 4 October 1991.

	Females			Males		
Age (GLGs/2)	n	Mean mass (kg)	95% CI	n	Mean mass (kg)	95% CI
0–1	2	194	–	2	101	–
1–2	5	284	266–342	3	293	138–447
2–3	14	341	316–365	10	328	303–353
3–4	6	376	323–430	8	393	356–430
4–5	9	443	402–485	5	478	473–583
5–6	4	456	430–482	4	577	483–671
6–7	3	548	415–680	3	515	408–622
7–30	11	614	566–663	1	600	–

estimated by adding the largest and smallest diameter measured with a micrometer, then dividing the sum by two. Follicles of less than 1 mm were not measured. No attempt was made to distinguish between corpora atretica and CAs (Perrin & Donovan 1984).

Females were classified as mature if they had at least one ovarian corpus or if they were pregnant or lactating. Pregnancy was detected by the presence of a foetus. Lactation was identified by the presence of white creamy milk exuding from the nipples or mammary glands. Mature females which were neither pregnant nor lactating and had no other signs of recent delivery or mature follicles were considered resting.

Stomach contents

Stomachs of young, dark whales were examined for milk. For older whales, samples of the stomach contents were collected. Entire stomachs were collected from nine whales from the municipality of Upernavik in October 1990 and from four whales from Qeqertarsuaq in May 1992. Subsamples of 2–3 liters of stomach contents were collected from the municipality of Upernavik (n = 21) in 1985 and 1989 and from Qeqertarsuaq (n = 2) in 1989. Otoliths, squid beaks, invertebrate skeletons and other identifiable remains were classified to the lowest possible taxonomic level.

Table 2. Length-at-age of female and male white whales from West Greenland from late September through early November and from the White and Kara seas from July through September.

	West Greenland						White Sea and Kara Sea					
	Females			Males			Females			Males		
Age (GLGs/2)	n	Mean length (cm)	95% CI	n	Mean length (cm)	95% CI	n	Mean length (cm)	95% CI	n	Mean length (cm)	95% CI
0–1	6	212	186–238	7	186	153–219	6	197	187–207	14	191	178–205
1–2	11	251	236–266	14	251	230–272	10	225	208–243	15	237	220–254
2–3	33	277	271–283	29	274	269–280	17	268	260–276	17	271	262–280
3–4	23	303	293–312	20	302	293–311	13	301	287–314	17	311	295–328
4–5	16	312	301–322	13	318	307–328	20	306	296–316	14	309	298–319
5–6	9	327	317–337	11	341	329–353	14	319	304–334	11	332	318–345
6–7	18	349	340–358	7	372	332–412	18	342	334–350	13	357	342–371
7–8	17	349	340–358	4	421	356–486	8	350	327–372	12	369	357–381
8–9	10	355	338–372	1	385		24	354	348–360	13	380	366–395
9–10	11	363	350–375	5	436	365–506	17	358	351–366	25	378	370–387
10–11	11	368	347–388	8	444	405–483	13	361	352–370	27	395	386–404
11–12	8	369	339–398	4	456	424–488	9	371	353–389	21	397	385–408
12–13	6	375	350–401	5	461	441–480	13	369	355–383	15	400	388–412
13–14	7	383	363–403	3	463	413–514	12	368	357–379	13	412	400–424
>14	10	395	380–410	4	461	417–504	64	373	369–378	85	429	424–434

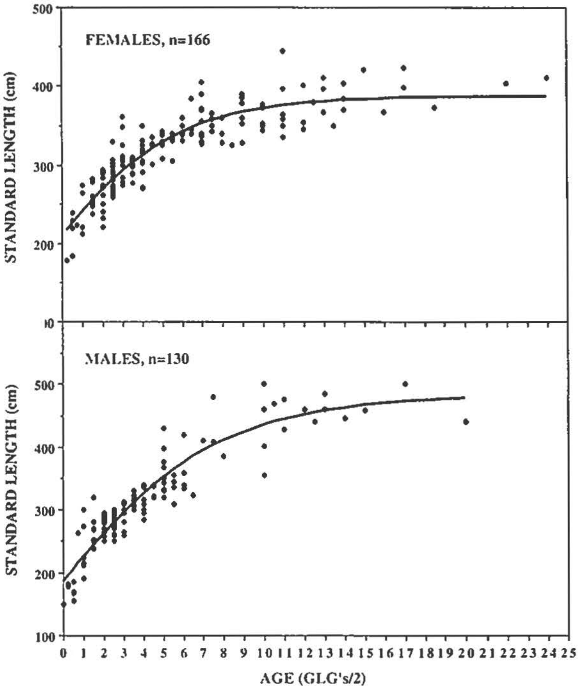


Fig. 4. Growth in length for female and male white whales from West Greenland. The curves are fitted by the Gompertz model (see Table 4 for parameters).

Results

Body growth

Foetal growth

Timing and growth in length of foetuses collected in autumn and spring (1985, 1989–92) are reasonably consistent with the foetal development described from Degerbøl & Nielsen's (1930) sample collected between 27 November and 12 April (1925–27; Fig. 3). However, the early growth of embryos is not represented in either of the two samples. To estimate the early growth we have used data from white whales taken in the White and Kara seas in July through September (1973–84; Ognetov 1985; Fig. 3). Backward extrapolation of the second-order polynomial fitted to the data from the White and Kara seas and West Greenland indicates that implantation takes place in May or early June.

The large variation in length of near-term foetuses (Degerbøl & Nielsen's and our samples) prevents exact estimation of body length and time of birth (Fig. 3). If the average length at birth is assumed to be 160 cm, then gestation apparently lasts 315 days and calves are likely to be born in mid April. However, the polynomial regression of foetal growth depicted in Fig. 3 does not account for a possible decline in growth in the last part of the foetal development. This may delay the peak of the parturitions.

That parturition can occur in May is confirmed by observations of a lactating female caught on 14 May 1992. She had a distended vulva, obvious placental scars

Table 4. Growth constants (b, k) and asymptotic length (L_∞) and body mass (W_∞) of female and male white whales from West Greenland and the White and Kara seas. Parameters were fitted to the Gompertz growth model and the General Growth Equation for M = 3. No convergence could be achieved for male body mass-at-age (n = 39; Fig. 5). Numbers in brackets indicate 95% confidence intervals and n indicates sample size.

Parameter	Length-at-age (cm)		Body mass-at-age (kg)
	Females	Males	Females
West Greenland:			
L_∞/W_∞	386 (374–398)	483 (458–509)	683 (617–748)
b	0.62 (0.56–0.67)	0.95 (0.89–1.01)	0.45 (0.38–0.51)
k	0.27 (0.21–0.32)	0.22 (0.18–0.26)	0.27 (0.18–0.35)
n	166	130	55
White Sea and Kara Sea:			
L_∞/W_∞	375 (370–379)	434 (427–441)	
b	0.65 (0.60–0.70)	0.75 (0.71–0.79)	
k	0.31 (0.27–0.34)	0.21 (0.19–0.23)	
n	258	312	

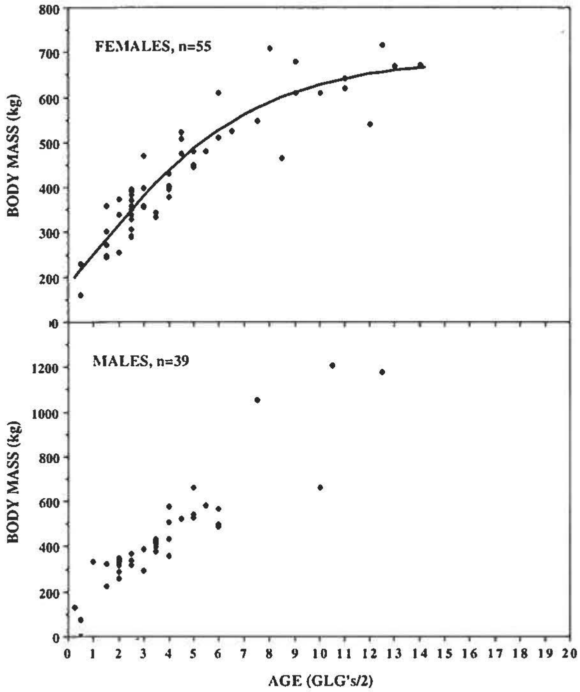


Fig. 5. Growth in body mass for female and male white whales from West Greenland. The curve for females is fitted by the General Growth Equation (see Table 4 for parameters). No convergence could be achieved for males. The three males exceeding 1000 kg were from May 1992 while all other males were from October 1991.

and a uterus mass (1877 g) that was intermediate between the average prègnant and the average lactating white whale (Table 8, later). She also had elevated levels of progesterone and prolactin (Høier & Heide-Jørgensen 1994). These characteristics allow us to infer that this whale had given birth recently.

Of ten foetuses with known sex, six were males. Only four foetuses were weighed; three from 2 October 1989 all had body masses of 2 kg with standard lengths of 43, 48 and 49 cm. One foetus from 17 October 1990 had a body mass of 300 g with a standard length of 23 cm.

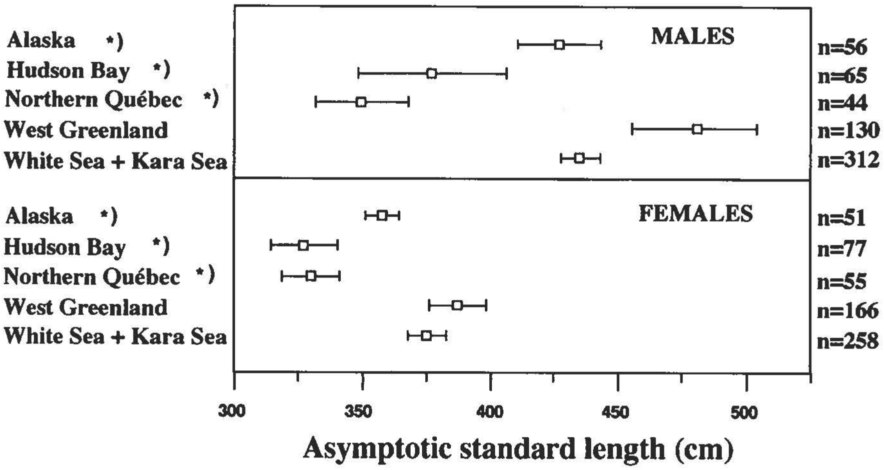
Growth in length and mass of West Greenland white whales

Dorsal curvilinear lengths were 4.6% (95% CI 3.0–6.3) larger than standard lengths. Rates of growth in standard length and body mass of immature white whales are similar in both sexes (Tables 2–3). In October male and female calves could be distinguished from whales older than one year on the basis of their body length. Some of the variation in lengths of whales in age class 0–1 can be attributed to difficulties in determining their exact ages.

Both von Bertalanffy and Gompertz growth models failed to account for less than 15% of the variation in the length-at-age data, and both showed significant differences in size between the sexes (t-test, $P < 0.05$; Fig. 4 & Table 2). The residual sums of squares were marginally smaller for the von Bertalanffy model, but this model slightly over-estimated the asymptotic length of males (L_∞ = 501 cm) which also had a larger standard error. Hence the Gompertz function was chosen for the estimation of growth parameters (Table 4). Growth rates seem to be approximately equal for both sexes until about 10 GLGs. Thereafter the rate of female growth declines while the male growth rate remains high for another 10–15 GLGs (Table 2).

The General Growth Equation (M = 3) fitted to body mass at age explained 99% of the variation in female mass, whereas convergence could not be reached for males (Fig. 5). Three males killed in May 1992 had body masses of more than 1000 kg, which is 400–500 kg more than females of similar age. They suggest the likely magnitude of the asymptotic mass in males. One male of 1050 kg from May was 30% heavier than a male of

Fig. 6. Asymptotic standard lengths with 95% confidence intervals for female and male white whales from various areas. Asymptotic lengths for Alaska, Hudson Bay and northern Québec were fitted by the Gompertz growth equation (Doidge 1990a).



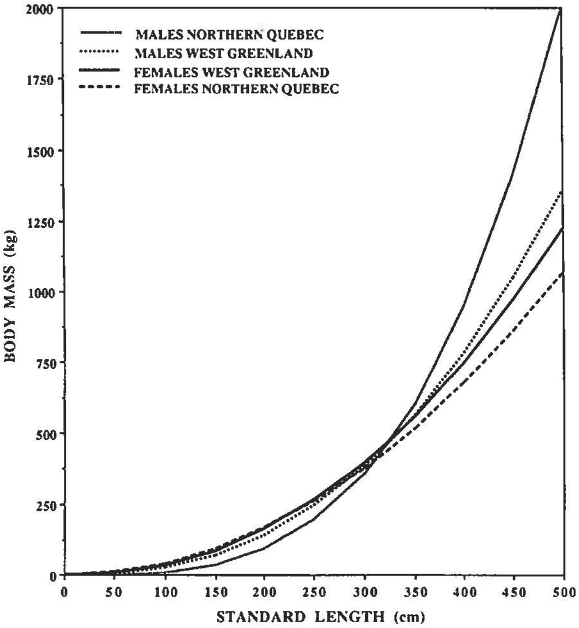


Fig. 7. Comparison of length-body mass relations between male and female white whales from two different populations: West Greenland (this study) and northern Québec (Doidge 1990a). The curve was fitted by the function: body mass = a* SL^b.

similar age and length from October; this could perhaps indicate the magnitude of seasonal variation in body mass.

Growth in white whales from other stocks

The asymptotic length of West Greenland white whales is compared to that of white whales from other areas (Fig. 6). Greenland white whales are significantly longer (t-test) than white whales from Alaska, Hudson Bay and northern Québec (see Doidge 1990a for data on the these stocks).

To allow comparison with the samples from all other areas the Gompertz growth model was chosen for predicting growth of white whales in the White and Kara seas. White whales from these seas reached identical asymptotic lengths and hence the growth data were pooled for each sex. Male white whales from the White and Kara seas were evidently smaller than male white whales from West Greenland, and they were not significantly larger than males from Alaska (t-test, $P > 0.05$; Fig. 6). Female white whales from Alaska were smaller than those from the White and Kara seas (Fig. 6, $P < 0.05$), which were, as in males, significantly ($P = 0.05$) smaller than West Greenland females.

The geometric relationships between length and body mass for male and female white whales from West Greenland were compared with those for white whales from northern Québec (Fig. 7), the area with the shortest white whales (Fig. 6). Male white whales from northern Québec had the closest to a cubic relationship between length and body mass (b = 3.37, 95% CI 2.60–4.14), whereas the

Table 5. Geometric relationship between body mass and standard length, body mass = a* SL^b. Numbers in brackets indicate 95% confidence intervals and n indicates sample size. The correlation (r^2) between body mass and SL was larger than 0.98 for all regressions. Data from northern Québec from Doidge (1990a).

	Body mass versus length Females	Males	Both sexes
West Greenland:			
a (x10^{-4})	13.68	2.95	5.14
b	2.21 (2.00–2.41)	2.47 (2.29–2.65)	2.37 (2.25–2.50)
n	57	41	98
Northern Québec:			
a (x10^{-4})	35.15	0.02	0.31
b	2.03 (1.35–2.71)	3.37 (2.68–4.10)	2.85 (2.59–3.12)
n	20	16	36

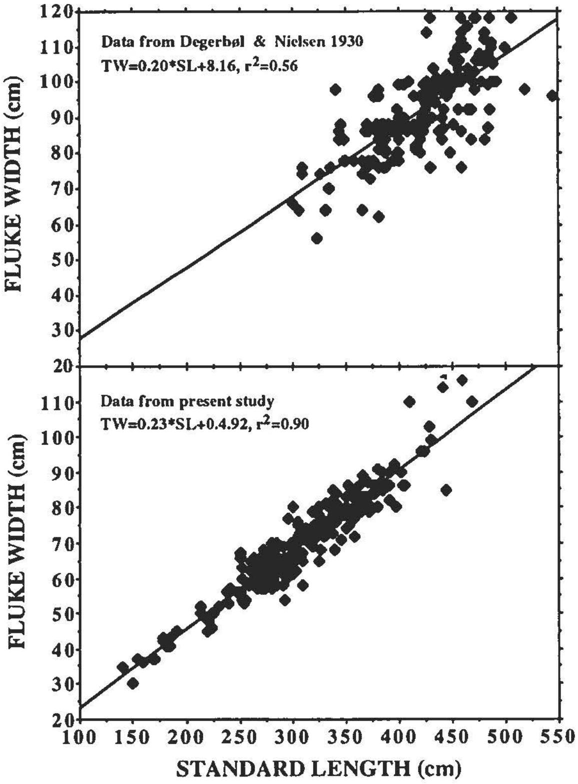


Fig. 8. Linear regressions of the width of the tail flukes (TW) on standard length for two sets of white whale samples. The uppermost figure shows measurements from the 1920s presented by Degerbøl & Nielsen (1930) from southwestern Greenland. The lower figure shows measurements from 1985–1992 from the present study.

Table 6. Comparison of testes and epididymides measurements and histology from immature and mature white whales. Right and left testes and epididymides were mixed together and all measurements were taken on formalin-fixed tissue.

	Mean	Immature whales 95% CI	n	Mean	Mature whales 95% CI	n
Testes						
Mass (g)	26.0	23.7–28.3	130	540.0	453.9–626.2	24
Length (cm)	7.4	7.2–7.7	133	19.6	18.4–20.7	23
Large diameter (cm)	2.4	2.4–2.5	134	6.7	6.2–7.1	23
Small diameter (cm)	1.9	1.8–2.0	134	5.3	4.9–5.8	23
Tubuli diameter (μm)	73	57–89	4	172	163–181	21
Epididymides						
Mass (g)	39.9	35.3–42.6	124	176.4	138.5–214.4	18
Length (cm)	15.0	14.3–15.7	124	29.4	26.2–32.6	20
Large diameter (cm)	2.4	2.2–2.5	126	3.6	3.1–4.0	23
Small diameter (cm)	1.0	1.0–1.1	126	1.8	1.4–2.2	23
Tubuli diameter (μm)	–	–	0	1544	1440–1647	22

exponent b was significantly smaller than 3.00 for females in northern Québec and for females and males in West Greenland (Table 5). Insufficient sample size, with no males larger than 885 kg, probably explains the different exponent for males from northern Québec.

Correlation between fluke width and standard length

Measurements of fluke width are useful for calibrating imprecise length measurements. Standard length and width of flukes are closely correlated ($r^2 = 0.90$), except in the case of a few large males with fluke widths exceeding 100 cm (Fig. 8). In a sample of West Greenland white whales taken in the 1920s, unspecified measurements of body length and fluke width were made for 184 whales (Fig. 8; Degerbøl & Nielsen 1930). However, that sample is not directly comparable with ours because 41 body lengths exceeded the largest obtained in the present study (468 cm), and Degerbøl & Nielsen did not measure fluke widths of animals less than 300 cm long. Despite the apparently close correlation, the large animals evidently add to the variability and should be excluded when comparing the two samples. If whales with body lengths of

Table 7. Changes in size of fresh and formalin-fixed testes, epididymides, uteri and ovaries of immature and lactating white whales. Left and right organs were not distinguished and instead the letters A and B were assigned to each set of organs (testes + epididymides, uterine horn + ovary). Levels of significance for one-tailed paired t-tests are given as NS = not significant, * = significant at $0.01 < P < 0.05$, ** = significant at $0.001 < P < 0.01$, and *** = significant at $P < 0.001$.

Organ	Immature males		Organ	Immature females		Lactating females	
	Change %	Significance		Change %	Significance	Change %	Significance
Testes			*Uterus*				
Mass A	−11	*	Mass	−3	***	0	NS
Mass B	−11	NS	Length A	−6	***	−7	***
Length A	−12	***	Length B	−7	***	−8	**
Length B	−10	***	Diameter	−10	***	−8	***
Large diameter A	−4	**	Wall thickness	+46	***	+68	***
Large diameter B	−4	**					
Small diameter A	+36	**	*Uterine horn*				
Small diameter B	+25	**	Diameter A	−10	***	−14	***
			Diameter B	−11	***	−12	***
Epididymides			Wall thickness A	+50	***	+73	***
Mass A	−10	***	Wall thickness B	+65	***	+86	***
Mass B	−2	***					
Length A	−9	***	*Ovaries*				
Length B	−8	***	Mass A	−16	***	−6	**
Large diameter A	−7	NS	Mass B	−19	***	−4	*
Large diameter B	+4	NS	Length A	−15	***	−15	***
Small diameter A	+50	***	Length B	−16	***	−15	***
Small diameter B	+43	***					

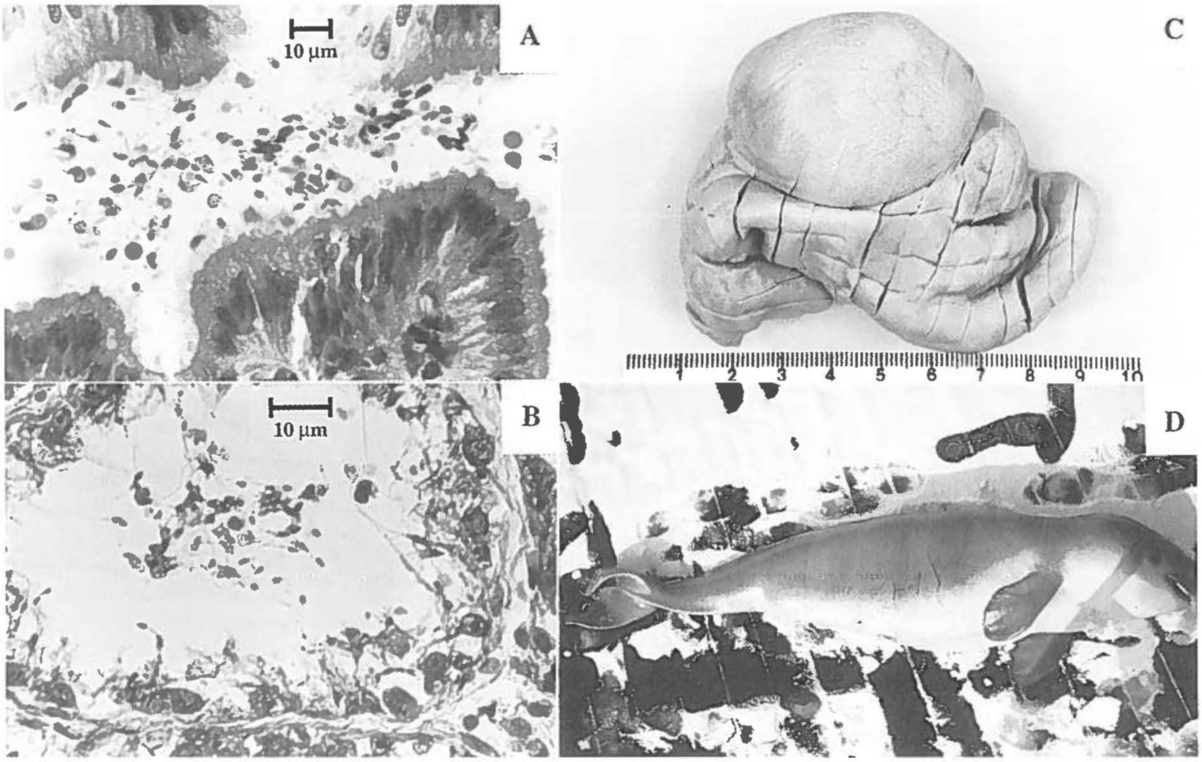


Fig. 9. Micrographs of haematoxylin- and eosin-stained sections of a) testis (x800) and b) epididymis with spermatozoa from white whales taken in May 1992. c) Ovary with corpus luteum and accessory corpora lutea from Upernavik 2 October 1989. d) Foetus (SL = 140 cm) of white whale from Qeqertarsuaq (Godhavn) 9 May 1992.

300–468 cm are compared for the two samples, the slopes and intercepts of the regressions are identical ($P > 0.2$), but the larger sample from Degerbøl & Nielsen (1930) shows a much greater variability, perhaps because the animals were measured less carefully.

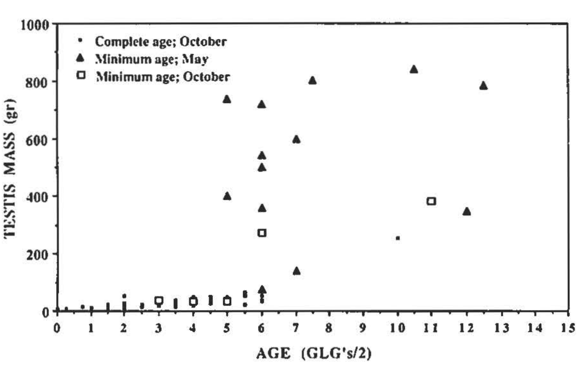


Fig. 10. Testis mass as a function of age.

Reproduction

Male reproduction

No difference in tubule diameter or presence of spermatozoa could be detected between peripheral and core samples of testes, hence peripheral sections from the plane adjacent to the epididymides were chosen for comparisons (Table 6).

Paired comparison of external measurements (mass and length) of testes and epididymides from immature whales shows that both organs shrink considerably during formalin fixation and that most measurements vary significantly between fresh and formalin-fixed tissue (Table 7). Also, the shape of both organs changes as the large diameters tend to decrease and the small diameters tend to increase. The comparison of testis size was done with formalin-preserved samples. Gonads from mature males taken in autumn and spring were significantly larger ($P < 0.05$) in all respects than those from immature whales (Table 6). Any external measurement of testis can therefore be taken as diagnostic for sexual maturity.

In spring (April-May), testes (and epididymides) taken from mature males were significantly larger ($P < 0.05$) in

Table 8. Comparison of uterus and ovary measurements from immature, lactating/resting and pregnant white whales from October. Right and left organs were mixed together and all measurements were taken on formalin-fixed tissue.

	Immature whales			Lactating or resting whales			Pregnant whales		
	Mean	95% CI	n	Mean	95% CI	n	Mean	95% CI	n
Uterus									
Mass (g)	190	158–221	82	1045	869–1222	26	3502	3043–3961	9
Length A (cm)	27	25–28	82	44	41–48	26	64	54–74	9
Length B (cm)	28	26–29	79	46	42–49	26	66	50–83	8
Diameter (cm)	4.7	4.4–5.1	83	10.0	8.9–11.1	26	23	18–28	8
Wall thickness (mm)	5.5	5.0–6.0	83	9.7	8.2–11.1	26	7.4	5.5–9.3	9
Diameter of horn A (cm)	4.0	3.7–4.3	83	8.6	7.8–9.4	26	31	21–42	6
Diameter of horn B (cm)	4.1	3.8–4.3	83	9.0	8.1–10.0	26	34	20–48	5
Thickness of horn A (mm)	4.2	3.8–4.4	81	7.8	6.6–9.0	26	4.7	2.5–6.9	9
Thickness of horn B (mm)	4.4	4.0–4.8	82	7.8	6.6–9.0	26	5.3	3.4–7.2	8
Ovaries									
Mass A (g)	14	12–15	82	40	35–46	25	79	64–95	9
Mass B (g)	14	13–15	81	43	38–48	24	57	38–76	10
Length A (cm)	6.5	6.3–6.8	83	8.5	7.9–9.2	26	9.5	8.0–11.0	8
Length B (cm)	6.7	6.5–7.0	78	8.9	8.3–9.6	24	8.8	7.9–9.6	10

length and mass than those sampled in autumn (September-October) (Fig. 10). Spermatozoa could be detected in samples from both October and May, but they were subjectively assessed to be more abundant in samples from May (Fig. 9). The autumn samples of testes with spermatozoa had no spermatozoa in the epididymides (n = 2).

All mature males, except one, had worn teeth with no neonatal line. As a result, age at sexual maturity is underestimated. Males younger than 6 years were all sexually immature. Two animals which were at least 6 years old were sexually mature. Seven of eight and three of four immature whales of 5 and 6 years, respectively, had no tooth wear (complete age; Fig. 10). Males probably reach sexual maturity at an age of 6–7 years.

No males shorter than 380 cm were sexually mature and all longer than 400 cm were mature.

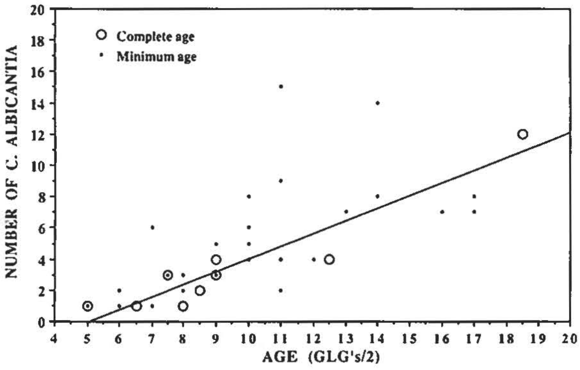


Fig. 11. Relationship between the total number of corpora albicantia and the age of 34 white whales.

Female reproduction

The uterus and ovaries show deformations during formalin fixation similar to those described for male sex organs. Generally the organs shrink during fixation, except that the thickness of the uterine walls increases significantly (Table 7).

The majority of females were collected during the autumn, a time when mature females either carry a foetus, have a suckling calf, are resting or have recently aborted. All females classified as sexually mature carried either a CL or a CA or were lactating.

One CL from a pregnant female taken in March had a diameter of 48 mm, and the mean of the diameters of 10 CLs from pregnant white whales taken in October was 41 mm (95% CI 39–44 mm). Three of the latter had accessory CLs on the same ovary, but these were considerably smaller than the primary corpora. One lactating white whale without a foetus taken in October had a small, but characteristic CL (14 mm), well below the mean size of CLs in October. This female may have aborted an earlier pregnancy.

The mean of the diameters of the largest CAs measured from 23 lactating white whales in October was 14 mm (95% CI 13–15). This value was not statistically different from the diameters of the largest CAs in five pregnant whales (mean = 14.95% CI 10–18) or from those in three lactating and pregnant whales (mean = 13.95% CI 5–21). The largest number of CAs in one ovary was 8; in both ovaries combined the largest number was 15. Regression of the number of CAs on age of whales with complete age suggests an age at first parturition of 5 years and an accumulation of 0.8 CAs per year ($r^2 = 0.89$; Fig. 11). The annual accumulation of CAs exceeds the pregnancy rate (see below), probably because accessory CLs or lutei-

Table 9. Reproductive status in relation to age for female white whales from West Greenland. All except two lactating females (8 and 12 years old) were taken in October. Parentheses indicate the subset of whales where the indicated age is minimum age because no neonatal line was detected in tooth sections (see Heide-Jørgensen *et al.* 1994).

Age (GLGs/2)	Number of animals in different reproductive categories Immature	Mature	Pregnant	Lactating	Pregnant & lactating	Resting	Sum
1–2	9						9
2–3	32						32
3–4	21						21
4–5	14(1)	1					15
5–6	6	2(1)		1		1(1)	8
6–7	2	5(4)	1(1)	4(3)			7
7–8	1(1)	9(6)	2(2)	5(3)	1(1)	1	10
8–9		4(2)	2(1)	2(1)			4
9–10		5(4)		5(4)			5
10–11		5(3)	1	2(2)	2(1)		5
11–12		5(5)	1(1)	4(4)			5
12–13		4(1)		4(1)			4
13–14		1(1)		1(1)			1
14–15		3(1)		1(1)	1(1)	1(1)	3
+15		6(4)		5(4)	1(1)		6
Sum	85	50	7	34	5	3	135

nized follicles sometimes give rise to several CAs (see Brodie 1971, Sergeant 1973).

The largest follicles in ovaries from 31 mature white whales taken in October had a mean diameter of 4.3 mm (95% CI 3.3–5.7 mm), whereas four whales taken in March-May had follicles with a mean of 7.5 mm (95% CI 2.7–12.3 mm). Examination of females in October showed that the mean length of nipples was about 2.0 cm (95% CI 1.9–2.2 cm) for 17 lactating whales, and less than 0.5 cm for four non-lactating.

The oldest immature female had a minimum age of 7 years. Most other immature whales had neonatal lines and their ages can be considered complete (Table 9). One pregnant female of 6 years or more had no CAs and therefore is assumed to have been pregnant for the first time. Another pregnant female with a complete age of 8

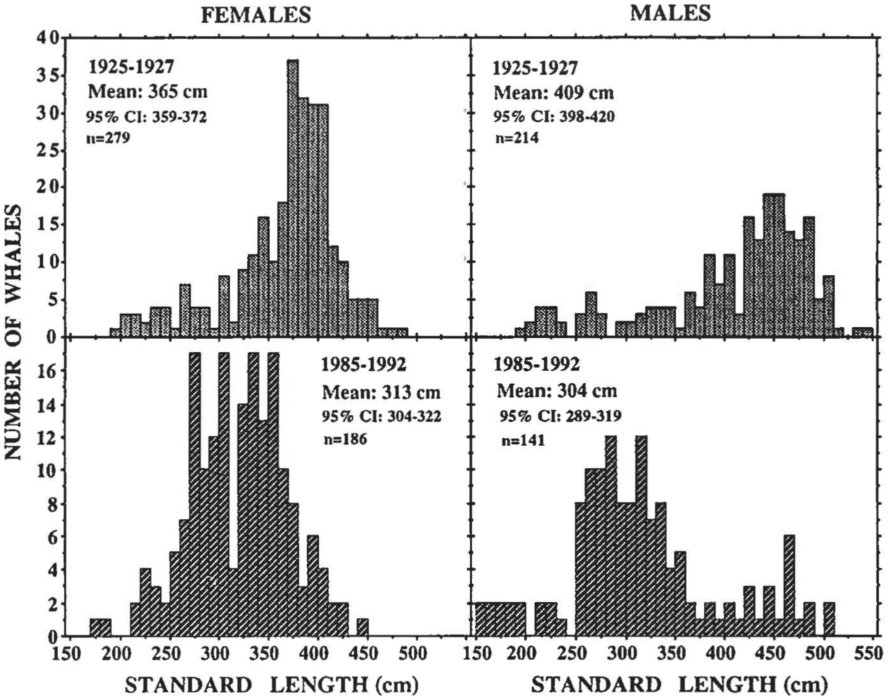


Fig. 12. Length distribution of landed white whales in two samples from West Greenland. The uppermost figures show the measurements from the 1920s presented by Degerbøl & Nielsen (1930) from southwestern Greenland. The lower figures show measurements from 1985–1992 from Disko Bugt and Upernavik.

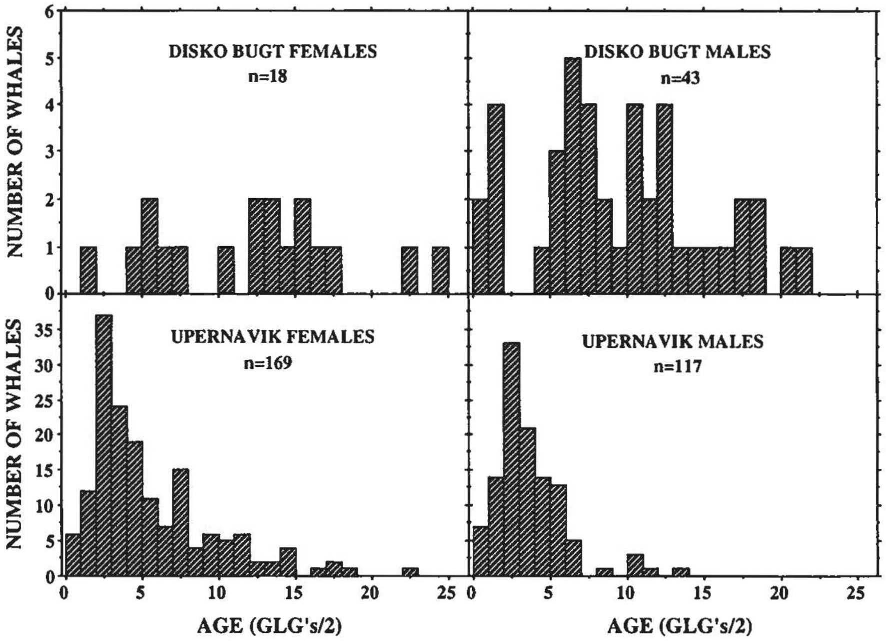


Fig. 13. Age distribution of male and female white whales caught in the drive fishery in Upernavik 1985, 1989–1991 and in Disko Bugt 1990–1992.

years had 1 CA. She would at the earliest have become pregnant for the first time at 5 years if birth intervals of 3 years are assumed. Two lactating females of complete ages of 5 and 6 years each had 1 CA, suggesting that they had become pregnant for the first time at ages of 4 and 5 years, respectively, or possibly 3 and 4 years if lactation lasts two years. However, other whales with complete ages had numbers of CAs that would, on the assumption of a three-year birth interval, give widely varying estimates of age at first pregnancy (Fig. 11). Despite the difficulties of estimating the age at first ovulation or first pregnancy, most first pregnancies apparently occur at ages of 4–7.

The two longest immature females were 340 and 348 cm in SL (6 and 3 years old, respectively). The shortest pregnant female was 327 cm (7 years) and the shortest lactating female was 325 cm (5 years). The length at which 50% of the females were mature was 345 cm.

Not all whales were checked for both lactation and pregnancy. However, among 25 lactating whales found to be non-pregnant, at least one pregnant whale was not lactating, and four whales were both pregnant and lactating. The pregnancy rate of 0.31 is calculated as the ratio between the number of pregnant whales (n = 11; Table 9) and the total number of mature whales examined for pregnancy (n = 36; Table 11, later).

Age, length and sex distributions in catches

Degerbøl & Nielsen (1930) could not estimate ages for their sample of white whales taken in 1925–1927, so comparisons with the present sample must be made on the basis of length distributions (Fig. 12). It is obvious that there was some size and sex selectivity in the drive-net fishery in the 1920s, as there has been in the recent harvesting. Young whales were obviously under-represented in the catch in the 1920s or they were not measured as consistently by Degerbøl & Nielsen as in this study (Fig. 12). We attempted to measure all landed whales but our sample, for unknown reasons, also shows a deficiency in length classes shorter than 250 cm (Fig. 12). Nevertheless, the whales from the 1925–27 sample were significantly ($P < 0.05$) longer for both sexes, even when both samples are truncated at 300 cm to avoid the bias caused by under-representation of young whales. Although the whales landed in the 1920s were generally longer than those harvested in recent years, they were not unrealistically long compared to recent measurements. The longest female and male from 1925–27 were 482 and 545 cm, respectively, compared with 444 and 500 cm for the present study.

The age and length distributions show clear differences between the autumn samples from the municipality of Upernavik and the spring samples from Disko Bugt (Fig. 13). Only seven males from Upernavik exceeded the minimum length (SL = 380 cm) at sexual maturity, whereas 48 females exceeded the minimum length at sexual maturity (SL = 345). For the spring samples from

Table 10. Prey items of white whales from West Greenland waters illustrated by presence of otoliths and squid beaks (divided by two) and other hard remains retrieved from subsamples (ss) of stomach contents or entire stomachs (es), range given in brackets. + indicates presence of squid beaks.

Area and year sample/ (GLGs/2)	*A. glacialis* or *B. saida*	*S. marinus*	Lantern-fish	Hali-but	Squid	Crustacean
Upernavik 1985, 1989						
Mean number in 9 es (0.75–10)	211 (45–730)	0	9 (0–20)	0.1 (0–1)	+ (1–27)	*Pasiphaeidae* sp., *Hypenidae* sp., *Pandalus* sp.
Mean number in 21 ss (1–10)	71 (12–285)	0	2 (0–10)	0	+ in 30%	*P. borealis*, *Pasiphaeidae* sp. *Pandalus* sp.
Qeqertarsuaq 1989–90, 1992						
Mean number in 4 es (7.5–12.5)	0.3 (0–1)	8 (1–25)	0	0.3 (0–1)	+ (> 200 in all)	*P. borealis*
Mean number in 2 ss (6–7.5)	0.5 (0–1)	4 (2–5)	0	0	+ in 50%	*Pandalus* sp.

Disko Bugt, 18 males and 6 females exceeded the minimum length at sexual maturity.

The samples from Disko Bugt represent a longer period of the year (February-May) and a wider array of hunting situations (ice edge, ice entrapment, open water) than do the samples from the municipality of Upernavik. The latter are all from the drive fishery in October. The sample size is too small for Disko Bugt samples to be considered representative of the variety of hunting situations involved. The samples nevertheless show that there is sex and age segregation of white whales in the two areas. Few mature males were taken in the municipality of Upernavik, and the herds exploited there clearly consisted of mainly mature and immature females and immature males (Fig. 13). Mature males are, however, found in the samples from Disko Bugt.

Feeding habits

One whale taken in late September with zero GLGs and a SL of 155 cm had nothing but milk in its stomach. This animal presumably was a calf of the year. Two other whales taken at the same season had one (SL = 219 cm) and two (SL = 215 cm) GLGs and are assumed to have been born in the previous year. Both had a mixture of milk, fish remains and squid eyes in their stomachs. Several whales with 2–4 GLGs had remains from fish and squid in their stomachs.

Due to decomposition of samples of stomach contents, it was generally impossible to distinguish between polar cod (*Boreogadus saida*) and arctic cod (*Arctogadus glacialis*). However, among those otoliths that could be identified *B. saida* was by far the most numerous of the two species. Although estimation of their relative quantitative importance was not attempted, the two cod species clearly contributed more to the white whale diet than any other prey item in the Upernavik area. Squid beaks were also numerous in white whale stomachs from both Upernavik and Disko Bugt. Redfish (*Sebastes marinus*), dominated in the samples from Disko Bugt. Halibut (*Reinhardtius hippoglossoides*) and shrimp (*Pandalus borealis*) were found infrequently in stomachs from both Upernavik and Disko Bugt, but lanternfish (Myctophidae) were found only in stomachs from Upernavik (Table 10).

Discussion

Body growth

Complete age can only be derived for age classes younger than 14 GLGs for males and younger than 20 GLGs for females (Heide-Jørgensen *et al.* 1994). This limitation adds to the uncertainty of estimates of age at sexual maturity, age-specific mortality and growth increment in relation to age. Growth curves in particular will be biased to the left because of truncation due to the incomplete age determinations. Hence the overall growth is accelerated when using minimum ages, *i.e.* underestimating age, and the theoretical age at physical maturity may therefore be attained earlier than in reality. This bias is especially pronounced in males where the neonatal line becomes worn away (at approximately 14 GLGs) earlier than in females (at approximately 20 GLGs) (Heide-Jørgensen *et al.* 1994).

However, for comparative purposes it can be assumed that this uncertainty is uniformly distributed across populations and that, for instance, asymptotic growth has similar errors from incomplete ages in different populations.

The sexual dimorphism described for other white whale stocks (see Doidge 1990a; Stewart 1994) is also evident for West Greenland white whales with respect to length. Body mass is subject to seasonal variations which remain to be quantitatively assessed for West Greenland white whales. However, Degerbøl & Nielsen (1930) mentioned that the white whales had thin blubber layers when they arrived in southwestern Greenland in November and were fatter in April when they left the wintering grounds.

The maximum length of white whales taken in the drive-net fishery in southwestern Greenland during the 1920s exceeded the maximum length of white whales measured in any other North Atlantic population, including the one that is currently exploited in West Greenland. Vladykov (1943) and Doidge (1990a) suggested that the exceptional lengths reported by Degerbøl & Nielsen were curvilinear rather than SLs. Curvilinear length exceeds SL by less than 5%; thus not all of the difference can be explained as an artifact of different measuring procedures. The width of the tail flukes is a less ambiguous measurement than SL, and the 1920s fluke measurements are greater than recent Greenland measurements.

If measurement error is ruled out as the explanation for the exceptionally large whales in Degerbøl & Nielsen's sample, two alternative hypotheses could explain the disparity between current and previous length distributions of white whales from West Greenland:

1. As a consequence of heavy exploitation in West Greenland throughout this century, the age structure has changed and old, large white whales are either rare or absent in the population.
2. Better (*e.g.* more abundant, more nutritious) prey may have been available to white whales in the 1920s than now. This would account for the larger size at physical maturity of the animals from southwestern Greenland.

These two hypotheses are not mutually exclusive. For example, a change in prey resources could in conjunction with exploitation have affected the age distribution. The increase in sea temperature in southwestern Greenland in the 1920s, and the concomitant increase in abundance of Atlantic cod (*Gadus morhua*) and other potential prey items (see below), may have enhanced growth potential of individual whales.

It seems unlikely that a large, genetically discrete white whale population would have occurred earlier in this century a few hundred kilometers south of the centre of the current distribution in West Greenland, and that the whales in such a population would have had a longer asymptotic SL than those in the current population. A possible connection between the southwestern Greenland, southeastern Baffin Island and northern Labrador populations, as suggested by Heide-Jørgensen (1994), would not explain the larger body size of white whales in southwestern Greenland, because these adjacent stocks off eastern Canada consist of whales that are significantly smaller than Greenland white whales (Brodie 1971, Doidge 1990a, Stewart 1994).

Reproduction

Sergeant (1973) found that sperm production began at a testis mass greater than 200 g, corresponding to a body length of 290–330 cm and an age of 7–9 years for western Hudson Bay white whales. West Greenland white whales also begin sperm production at a testis mass of 200 g or more, but such a testis size is attained at a greater body length (332–412) and an earlier age (6–7 years).

In Alaska Burns & Seaman (1986) found few or no spermatozoa in the testes and epididymides of mature males taken in April-May, whereas two males taken in mid-June had moderate numbers of sperm. They concluded that some "males may remain in breeding condition through June" but that most are in the retrogression phase by late April-May. Matings have not been reported from Greenland, but the abundance of spermatozoa detected in May samples suggests that matings occur in spring.

The lengths of three white whale foetuses from the White and Kara seas from October (45.6 cm) and December (85 and 90 cm) were identical to those of similar-aged foetuses from West Greenland (Ognetov 1985). Thus it seems reasonable to include data on growth of embryos and early foetuses from the White and Kara seas when predicting foetal development of West Greenland white whales. Measurements of foetuses from the White and Kara seas and West Greenland suggest implantation in May-June and parturition in April-May.

Parturition has been observed twice in West Greenland in April (1919 and 1923). One of the neonates reportedly was only 116 cm long. However, on this occasion the birth may have been provoked by the method of hunting the whales. Three free-swimming white whales 120, 147 and 165 cm long were measured in the last half of March 1926; judging from their lengths they must have been neonates (Degerbøl & Nielsen 1930). Heide-Jørgensen *et al.* (1993) observed neonatal white whales during aerial surveys off West Greenland in late March and early April. These authors were convinced from the size and colour of the calves, compared with those of accompanying adults, that the calves had been born in March of the same year. If this supposition was correct, then the period of parturition extends at least from March until May. Sergeant (1973) noted the difficulty of trying to specify the exact period of births despite the clear growth pattern of small foetuses. This difficulty was also noted by Burns & Seaman (1986) for white whales in Alaska where they estimated the birth period to extend "from April through July and perhaps later". The decline in foetal growth in

Table 11. Comparison of life history parameters from different populations of white whales. Pregnancy rate is calculated as the ratio of pregnant females to all mature females.

Parameter/Area Reference	West Greenland a)	Northern Quebec b)	Cumberland Sound c)	Hudson Bay d)	Alaska e)	White & Kara Sea f)	Sea of Okhotsk g)
Length at birth (cm)	150–160	–	160	151	155	160	170
Length of gestation (days)	330	390	441	425	441	330	345
Period of implantation	May	early May	May	mid April	mid April	May-June	April-May
Period of births	April-May	late May	August	early August	April-July	June-July	March-July
Length at sexual maturity							
Females (cm)	345	290	285	270	310	350	379
Males (cm)	390	–	384	310	–	–	415
Length at physical maturity							
Females (cm)	386	330	362	328	359	375	390
Males (cm)	483	349	427	377	427	434	–
Age at sexual maturity							
Females (GLGs/2)	4–7	6	5	4–6	4–7	2–9	–
Males (GLGs/2)	6–7	–	8	8–9	–	–	–
Pregnancy rate	0.31	0.26–0.41	–	0.47	0.34	0.36	0.33
Sample size	36	76	–	62	179	246	42

a) This study, b) Doidge 1990b and 1990c, c) Brodie 1971, d) Sergeant 1973 and Doidge 1990b, e) Burns & Seaman 1986, f) Ognetov 1981, Ognetov 1985 and this study, g) Kleinenberg *et al.* 1969.

the last trimester of pregnancy probably explains this extended parturition period in Alaska (Burns & Seaman 1986: fig. 14). However, few white whales are seen or caught in West Greenland between mid-May and September and we were therefore unable to describe the late phase of pregnancy in white whales.

West Greenland white whales are assumed to summer mainly in the Lancaster Sound region. Despite numerous field studies of white whales in the Lancaster Sound region during July-August, no births have been reported. White whales and narwhals classified as neonates were frequently observed on aerial surveys in Lancaster Sound in late May and early June, respectively (Cosens & Dueck 1990).

The frequency of accessory CLs for pregnant white whales from West Greenland (25%, n = 12) was higher than what has been reported from Alaska in a much larger sample (21%, n = 110, Burns & Seaman 1986), from Hudson Bay (12%, n = 44, Sergeant 1973) and from Cumberland Sound (13%, n = 39, Brodie 1971) as well as for narwhals *Monodon monoceros* (12%, n = 43, Hay 1984). However, the frequency of accessory CLs may be influenced by the time of sampling and the age composition of the sample. They may regress during pregnancy, and primiparous whales may carry accessory CLs relatively frequently as has been described for narwhals (Hay 1984).

Feeding habits

Young white whales begin feeding on fish and invertebrates after the first year, but their stomachs may contain both milk and solid food remains during the second year of life (Brodie 1971, Sergeant 1973, Burns & Seaman 1986).

The stomach contents of white whales taken in the municipality of Upernavik confirm that these whales consume pelagic gadids (*B. saida* and *A. glacialis*) which are also the key prey of several other species of marine mammal that summer in the high arctic, *e.g.* narwhals, ringed seals (*Phoca hispida*) and harp seals (*Phoca groenlandica*) (Finley & Gibb 1982, Bradstreet & Finley 1983, Finley *et al.* 1990, Siegstad 1988). On their wintering grounds in Disko Bugt, white whales consume several demersal and bathypelagic fish species of Atlantic origin (e.g. *Sebastes* sp. and *Reinhardtius hippoglossoides*). Redfish (*Sebastes* sp.) are also an important prey for ringed seals in Disko Bugt (Siegstad 1988). Capelin (*Mallotus villosus*), which are important prey of Hudson Bay and White Sea white whales (Sergeant 1973, Ognetov 1990), have not been found in the samples from Disko Bugt where capelin occur in large shoals during summer (Sørensen 1985). Capelin are rare north of the municipality of Uummannaq (Sørensen 1985) and it is not surprising that they were not found in white whales from the Upernavik area.

Degerbøl & Nielsen (1930) reported after examining "several hundred stomachs" that white whales in southwestern Greenland preyed exclusively on Atlantic cod, redfish, halibut and small catfish (*Anarhichas* sp.).

Comparison with other populations

For several reasons, detailed statistical comparisons of life-history values among different white whale populations are difficult. The variability of results reported by various authors is likely due to the difficulties of tooth wear, accessory corpora and complicated field conditions that impede consistent data collection (*e.g.* detection of both pregnancy and lactation or detection of milk in stomachs). Also, the populations are subjected to different harvesting regimes, and the studies used for comparisons have been conducted over a long time span.

The population of white whales off West Greenland resembles other white whale populations in several ways. Sexual maturity, defined as first ovulation, is attained at about 85% of length at physical maturity in all white whale populations. This conforms with Laws' rule that female sexual maturity is attained at about 87% of the length at physical maturity (Laws 1956). Also, this length is attained at about the same age (6 GLGs) by females in all populations (Table 11). The pregnancy rate of West Greenland white whales indicates that about a third of all mature females are pregnant at any given instant as also found in other white whale populations (references in Table 11) and in the narwhal (Hay 1984). Hence a three-year calving interval is suggested for white whales in all areas studied (except possibly Hudson Bay).

White whales off West Greenland differ from those in other areas by their larger size at physical maturity and their apparently faster foetal growth (Fig. 6 and Table 11). All evidence suggests that white whales off West Greenland have a gestation period of less than a year, which implies that they have a more rapid foetal development than that described for white whales from Canada and Alaska (Table 11) and for narwhals (467 days, Hay 1984). However, foetal growth deserves closer examination in all white whale populations.

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A note on the diet of narwhals (*Monodon monoceros*) in Inglefield Bredning (NW Greenland)

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Heide-Jørgensen, M. P., Dietz, R. & Leatherwood, S. 1994. A note on the diet of narwhals (*Monodon monoceros*) in Inglefield Bredning (NW Greenland) – Meddr Grønland, Biosci. 39: 213–216. Copenhagen 1994-04-22.

The contents of 35 narwhal (*Monodon monoceros*) stomachs were obtained from the Inuit hunt in Inglefield Bredning (NW Greenland) in the open-water seasons of 1984 and 1985. Questions concerning narwhal feeding habits were addressed by relating lengths of otoliths and invertebrate remains to the known lengths and weights of fishes and invertebrate species prior to digestion, and by assessing the number and volume of each prey species represented by the stomach contents. The 48 kg (wet weight) of stomach contents examined consisted of 64% arctic cod (*Arctogadus glacialis*), 15% polar cod (*Boreogadus saida*), 19% unidentified gadids and 2% invertebrates.

Key words:
Narwhal, *Monodon monoceros*, feeding habits, Greenland.

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Introduction

The narwhal (*Monodon monoceros*) is profoundly important to Inuit in the municipality of Avanersuaq (NW Greenland), especially to those people living in settlements along Inglefield Bredning. Narwhals congregate in this fjord, especially near its eastern end, during the open-water season from July through September (Born *et al.* 1994). Hunters in Avanersuaq catch an estimated 150–200 narwhals per year, and this represents more than 10% of the annual harvest of edible hunting products in the municipality (Born 1987, Heide-Jørgensen 1994).

Despite its importance to Inuit communities the narwhal's feeding habits have not been assessed quantitatively in Greenland. Vibe (1950) described some of the major prey items of narwhals in Avanersuaq. Meldgaard & Kapel (1981) examined the stomach contents of one narwhal caught in Melville Bugt. Dietz *et al.* (1994) summarized information on narwhal feeding in East Greenland waters. Finley & Gibb (1982) presented quantitative descriptions of narwhal feeding during June-September in and near Pond Inlet, eastern Canadian Arctic.

We used narwhals taken by Inuit in Inglefield Bredning to study narwhal feeding during the brief open-water seasons of 1984 and 1985.

Materials and methods

Standard material

Otoliths and fish measurements used in this study were obtained from trawl surveys by r/v *Adolf Jensen* in Inglefield Bredning (77°30'N, 70°00'W) and Melville Bugt (76°00'N, 62°00'W) during August 1987. The lengths and weights of the fish were measured before their otoliths were removed in the laboratory. Lengths of otoliths were measured with a micrometer.

Stomach samples

Stomach contents or whole stomachs (usually with data on length and sex of the whale) were collected by biologists or hunters from 35 narwhals (6 in 1984, 29 in 1985) killed between 23 July and 8 September in the open-water hunt in Inglefield Bredning. Samples were kept frozen until examination in the laboratory.

Sagittal otoliths, cephalopod beaks and skeletal parts of invertebrates were retrieved by washing and sieving the thawed stomach samples through fine-mesh (0.45

Table 1. Standard equations for fish length and weight on otolith length.

Species	Otolith length vs. fish length	Otolith length vs. fish weight
Arctic cod *Arctogadus glacialis* Melville Bugt	$FL = -52.19 + 31.81 * OL$ $R^2 = 0.97$, $N = 178$ range: 2.5–8 mm	$FW = 0.0089454 * OL^{4.2543}$ $R^2 = 0.96$, $N = 178$ range: 2.5–8 mm
Polar cod *Boreogadus saida* Inglefield Bredning	$FL = 5.46 + 23.75 * OL$ $R^2 = 0.91$, $N = 184$ range: 5.5–12 mm	$FW = 0.1475 * OL^{2.7320}$ $R^2 = 0.90$, $N = 192$ range: 5.5–12 mm

mm) netting. When possible, otoliths were identified to species and their lengths measured under a dissecting microscope or with a micrometer. These measurements were used to calculate fish weights and lengths, following Härkönen (1986). Weight was calculated in order to determine the proportional contribution (by wet weight) of each identified species. As teleost fishes contain two sagittal otoliths, the number of otoliths was divided by two.

Otoliths shorter than 5 mm generally could not be identified to species. As almost all of those that could be identified were from polar cod (*Boreogadus saida*), we used the standard equations for polar cod (Table 1) for all otoliths less than 5 mm long. The few otoliths of Liparidae could not be identified to species and were not used to estimate fish weight or length.

Most otoliths had been affected by gastric juices and had thus been shortened. However we assumed that otoliths from all species had been reduced in size by the same fraction and therefore that the food remains represented the relative importance of the various species in the narwhals' diet.

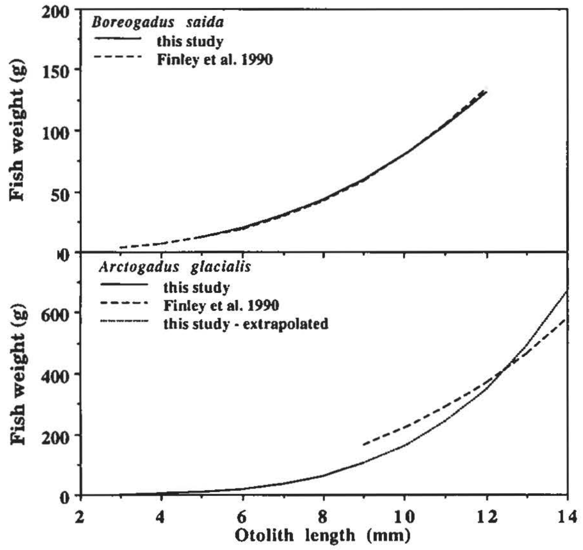

Fig. 1. Above: Regression of fish weight on otolith length for polar cod from Avanersuaq (see Table 1) and the Canadian High Arctic (Finley *et al.* 1990). Below: Regression of fish weight on otolith length for arctic cod from Melville Bugt (see Table 1) and from the Canadian High Arctic (Finley *et al.* 1990).

Whenever possible, squid beaks were identified to species and their lower crest lengths were used to estimate whole-animal weights (see Clarke 1986). Most invertebrates were heavily digested and impossible to identify to species. For a few of the invertebrate remains, weight was estimated by comparing samples of similar size and known weight.

Results

Standard material

Ninety-two arctic cod (*Arctogadus glacialis*) and 96 polar cod were obtained from the trawls. (The species that we call arctic cod is called polar cod in North America, and vice-versa). Fish length and fish weight were regressed on otolith length using linear and multiple regression, respectively (Table 1). The correlations for both species were highly significant (Table 1; Fig. 1). For polar cod there was a striking similarity between the standard equation characterising our sample and the equations characterising samples from the Canadian High Arctic (Fig. 1; Finley *et al.* 1990). For arctic cod the Canadian samples covered a larger range than the Greenland samples (Fig. 1; Finley *et al.* 1990), so we used our own equation for arctic cod otoliths between 5 and 9 mm and the Canadian equation for otoliths larger than 9 mm.

Inferences from stomach contents

The 1984 sample was too small to compare with the 1985 sample. Seventy-three percent of all the samples from both years were from August, the remainder from the end of July or the beginning of September. It was considered appropriate to pool all of the samples for our analysis.

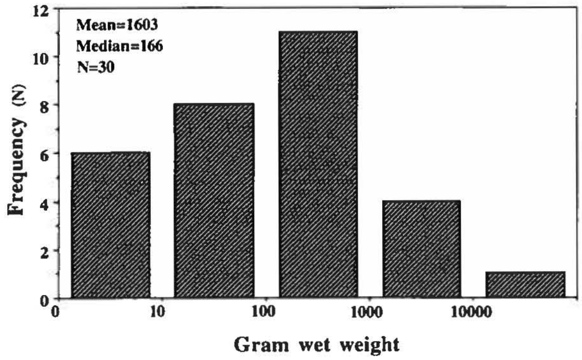

Fig. 2. Frequency distribution of weight of stomach samples.

We are uncertain how representative our sample of stomach contents may be for the narwhals feeding in Inglefield Bredning in 1984 and 1985. Empty stomachs were not always collected, and proportions of stomach contents sampled varied. Hence the findings from five empty stomachs are not included in this analysis, and the volume of stomach contents for a given individual must be considered a minimum estimate.

The 30 stomach-content samples contained a total of 3871 otoliths, approximately 2000 eye lenses, 24 cephalopod beaks and some 614 pieces of crustacean. Fourteen of the samples contained less than 100 g of prey items (Fig. 2). However, one of these contained approximately 1200 and another 75 eye lenses, indicating that these whales had fed recently on large numbers of fish or cephalopods.

Arctic cod and polar cod were clearly the dominant prey species for narwhals in Inglefield Bredning in 1984 and 1985 (Table 2). Although otoliths smaller than 5 mm could not always be identified to species, they all came from gadids; most were probably from polar cod since *Boreogadus* tended to be smaller than *Arctogadus* in our sample of narwhal stomach contents (see Fig. 3) and since nearly all of the otoliths <5 mm that were identifiable came from polar cod. We found no obvious difference in the food habits of male and female narwhals, at least with respect to amount and composition of food remains in the stomachs.

Because many of the otoliths were shortened by digestion, the distribution of estimated fish lengths has a negative bias. One stomach contained a large proportion of almost unaffected otoliths, together with some partly digested otoliths similar to those found in the other stomachs.

The length distributions of both polar cod and arctic cod (Fig. 3) are biased by the lack of positively identifiable otoliths smaller than 5 mm. This bias may explain why the mean lengths of both species are larger in this study than they were in the study at Pond Inlet by Finley & Gibb (1982).

Food intake has been underestimated in this study because of reduced otolith lengths or complete disappearance of otoliths due to digestion. Only one of the stomachs from which contents were sampled – that of a 4.3 m male taken on 3 August 1984 – contained a substantial amount of food remains (32 kg).

Table 2. Composition of narwhal diet in Inglefield Bredning during the summers of 1984–85.

Species	% occurrence in stomachs (N = 30)	% frequency of food items (N = 4359)	% wet weight (47862 g)
Arctogadus glacialis	20	14	64
Boreogadus saida	47	13	15
Gadidae sp.	87	60	19
Liparis sp.	7	<1	–
Gonatus fabricii	23	<1	1
Bathypolypus sp.	10	<1	<1
Crustaceans	27	13	<1

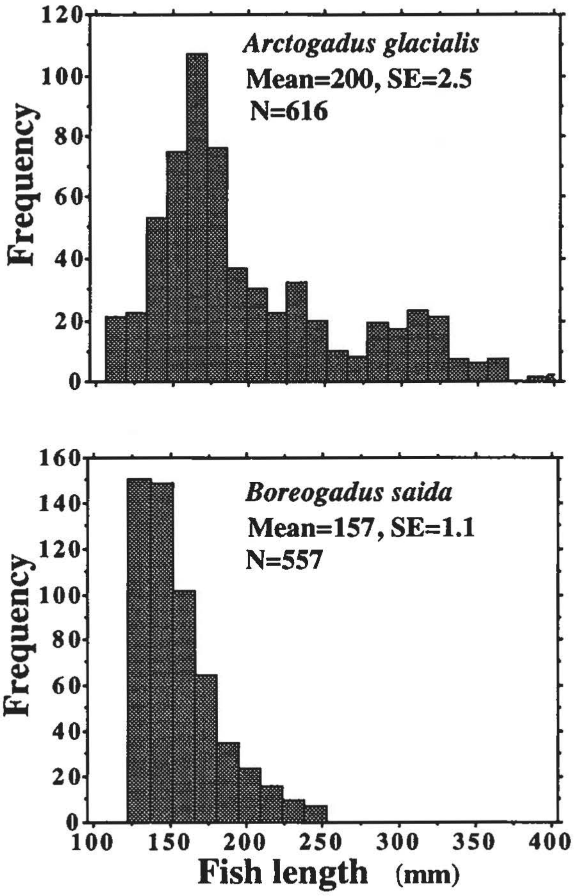

Fig. 3. Length distribution of polar cod (*Boreogadus saida*) and arctic cod (*Arctogadus glacialis*) calculated from otoliths retrieved from stomach samples of narwhals from Inglefield Bredning.

Discussion

Vibe (1950) stated that narwhals in some parts of the municipality of Avanersuaq fed equally often on polar cod and Greenland halibut (*Reinhardtius hippoglossoides*) and that crustaceans were important in the diet as well. Meldgaard & Kapel (1981) found polar cod and *Gonatus fabricii* in an adult male narwhal from Melville Bugt.

The dominant food species (64%) in our sample was arctic cod. This species constituted a smaller percentage (ice edge: 1.4%, ice cracks: 23.6%, open water: 3.3%) of the narwhal diet in Pond Inlet, northern Baffin Island (Finley & Gibb 1982). The other identified gadid species, polar cod, constituted 15% in Inglefield Bredning, compared with 55.1%, 15.3% and 94.5% in the three respective habitats of Pond Inlet (Finley & Gibb 1982).

Halibut was not found at all in our study, which was also the case for the open-water samples in Pond Inlet (Finley & Gibb 1982). However stomachs from animals caught at the ice edge and in ice cracks contained 31.8% and 55.0% wet weight of halibut, respectively, in the Pond Inlet area (*Ibid.*). Bruemmer (1971) observed halibut in the stomachs of narwhals taken in Inglefield Bredning in 1971 and reported evidence that halibut were abundant in the area at the time of his visit. Many hunters have recently told us that narwhals eat halibut, and halibut are caught on longlines in Inglefield Bredning during the winter (Kaj Søby, pers. comm. 1988). In a recent investigation of local knowledge in Northwest Greenland 30 out of 32 hunters interviewed in Avanersuaq municipality stated that they had found halibut remains in the stomachs of narwhals (Thomsen 1993). Halibut otoliths are considered less susceptible to digestion than are otoliths of the smaller cods, so halibut otoliths should remain in narwhal stomachs for longer periods than otoliths from polar and arctic cod (*cf.* Finley & Gibb 1982). Inglefield Bredning is the northern limit of the range of the Greenland halibut (Muus 1981), and thus recruitment of this species into Inglefield Bredning could be highly variable from year to year.

Gonatus fabricii constituted approximately 1% of the diet of narwhals in Inglefield Bredning. This was less than found in the Pond Inlet area where this cephalopod constituted 16% on average for the three habitats (see above) examined by Finley & Gibb (1982). The cephalopods of the genus *Bathypolypus* could not be identified to species but were probably *Bathypolypus arcticus*, a bottom-dwelling octopus. If this supposition is correct, then we can conclude that narwhals in Inglefield Bredning dive to depths of at least 350 m, which is the minimum depth in the middle of Inglefield Bredning.

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Size-at-age relationships as discriminators of white whale (*Delphinapterus leucas*) stocks in the eastern Canadian Arctic

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Stewart, R. E. A. 1994. Size-at-age relationships as discriminators of white whale (*Delphinapterus leucas*) stocks in the eastern Canadian Arctic. – Meddr Grønland, Biosci. 39: 217–225. Copenhagen 1994-04-22.

White whales harvested by Inuit at Arviat on western Hudson Bay, Pangnirtung on Cumberland Sound and Grise Fiord on the north side of Jones Sound were sampled for analysis of size and age in 1984–87. The sampling sites are thought to represent western Hudson Bay, Southeast Baffin and High Arctic stocks of white whales, respectively. Males were longer than females at all locations. White whales from western Hudson Bay were significantly shorter as adults than white whales from the other two locations. Analysis of published data showed that eastern Hudson Bay white whales are also significantly smaller than Cumberland Sound whales. Differences in asymptotic length between whales from Cumberland Sound and Jones Sound, and between whales from eastern and western Hudson Bay, were not significant.

Key words:
White whale, beluga, *Delphinapterus leucas*, stocks, growth.

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Introduction

Somatic growth is a fundamental characteristic of living things. It represents a significant energy requirement and is a key correlate of a variety of lifehistory traits (Calder 1982). Examination of growth rates can provide insights into ecological interactions, such as food availability (Innes *et al.* 1981). Moreover, because growth represents the interplay between the environment and genotype, it may be useful in identifying management stocks or populations. Klumov (1937, cited in Sergeant & Brodie 1969a), Sergeant & Brodie (1969a), Finley *et al.* (1982), Stewart & Walker (1987) and Doidge (1990a) examined white whales (*Delphinapterus leucas*) from different areas to assess the usefulness of size-at-age to distinguish among putative stocks. These studies disagreed on the degree to which size-at-age can separate individuals from different stocks.

Sergeant & Brodie (1969a) reported differences in the lengths of adult male white whales between western Hudson Bay (~350 cm) and Cumberland Sound (~450 cm). Finley *et al.* (1982) were unable to distinguish among whales sampled in eastern Hudson Bay, Ungava Bay and Hudson Strait using body length. Stewart & Walker (1987), in a preliminary analysis, concluded that whales from western Hudson Bay could be separated from whales from Cumberland and Jones sounds on the basis of growth curves. Doidge (1990a) found that while white whales from Hudson Bay tended to be shorter than others examined, differences were too slight to classify individuals on the basis of size. Here I describe growth and examine size-atage for white whales in the eastern Canadian Arctic to distinguish among putative stocks.

Materials and methods

White whales harvested by Inuit hunters were sampled at Arviat (known then as Eskimo Point 61°05'N, 94°06'W) on western Hudson Bay, Pangnirtung (66°07'N, 65°43'W) on Cumberland Sound and Grise Fiord (76°25'N, 82°52'W) on Jones Sound, Northwest Territories (N.W.T.), Canada (Fig. 1) from 1984 to 1987 (to 1986 in Pangnirtung). These sampling sites represent the pre-

Fig. 1. Sampling locations.

sumed western Hudson Bay, Southeast Baffin and High Arctic stocks respectively (Clarke *et al.* 1989, Cosens *et al.* 1990, Richard *et al.* 1990, Bodaly *et al.* 1992). Sampling effort was concentrated on the peak hunting periods at each location: July, August and September, respectively. Whales were usually shot although hunters at Arviat also used nets.

Body mass was determined by weighing intact whales suspended from a tripod. Mass was recorded to the nearest 5 kg, uncorrected for blood loss. Linear measurements, which were made to the nearest centimeter with a steel tape measure, followed American Society of Mammalogists Committee on Marine Mammals (1961) guidelines and included: standard length and girths at the eye, axilla, navel, anus and caudal peduncle at the base of the flukes.

Both jaws were collected to provide material for age estimation. Teeth were removed after gentle boiling. Longitudinal sections, 0.3 to 0.4 mm thick, were prepared (Wainwright & Walker 1988) and stored in a mixture of equal parts of glycerine, ethanol and water (Pueck & Lowe 1975). Age estimates were obtained by counting dentinal annuli in the second or fifth mandibular tooth, viewed wet with oblique reflected light using a variablepower dissecting microscope. Each section was read three to five times. Three identical readings were accepted as the final growth layer group (GLG) count. If there were not three identical readings, the mean and the maximum normed residual (MNR, Snedecor & Cochran 1980) was calculated for all five readings and any outliers were deleted. The final GLG count was the median of the remaining values (Stewart & Lavigne 1979). Ages were estimated by assuming that two GLGs were deposited each year (Sergeant 1973, Goren *et al.* 1987). Ages are therefore reported with half-year precision, indicating whether the last GLG formed was an odd or an even number. Absence of a neonatal line was used to determine if GLGs had been lost to tooth wear.

Gompertz growth curves for standard length and mass were fitted to the data using the non-linear curve fitting program in SAS (SAS Institute Inc. 1985). The growth curves were of the form:

$$\text{Size} = A(e^{(-e^{-k*\text{age}+k*t_0})})$$

where Size is length (cm) or mass (kg), A is the asymptote (cm or kg), k and t_0 are fitted constants, e is the base of natural logarithms (approximately 2.7183) and age is the estimated age of the whale (yrs). Preliminary analysis which included von Bertalanffy growth curves indicated that the Gompertz equation fit more of the data sets and produced higher F values.

The small sample sizes and the age distributions of whales from Pangnirtung and Grise Fiord precluded comprehensive comparison of the growth curves. Differences were assessed by comparing asymptotic size and by ex-

Table 1. Descriptive statistics of length (cm), mass (kg) and age (yr) for white whales sampled at three locations in the eastern Canadian Arctic.

Sex	Parameter	Location		
		Arviat	Pangnirtung	Grise Fiord
Female	length ($\bar{x}$±1 SE)	283.5±7.8	337.6±22.2	321.3±15.3
	N	51	7	12
	range	129–385	241–395	254–424
	mass ($\bar{x}$±1 SE)	363.7±20.1	575.7±62.7	525.5±73.9
	N	51	7	11
	range	45–685	320–840	300–1200
	age ($\bar{x}$±1 SE)	8.3±0.9	8.5±2.2	5.6±1.6
	N	52	7	12
	range	0.0–26.0	2.5–17.0	1.5–21.0
Male	length ($\bar{x}$±1 SE)	333.1±7.7	368.7±9.8	345.2±15.9
	N	68	25	18
	range	183–419	272–445	231–481
	mass ($\bar{x}$±1 SE)	528.3±25.8	812.4±56.2	665.3±76.8
	N	68	25	18
	range	145–1005	385–1300	250–1630
	age ($\bar{x}$±1 SE)	11.5±0.8	7.0±0.6	5.2±0.6
	N	70	25	18
	range	0.0–24.5	3.0–16.0	1.0–13.5

amining the distribution of the individual deviations around one growth curve. Asymptotes were compared using a t-test for unequal sample sizes and unequal variances (Snedecor & Cochran 1967) for sex differences at a site ($P < 0.05$) and between sites for each sex ($P < 0.01$). Asymptotes for whales from Hudson Bay (Doidge 1990a) and Alaska (Burns & Seaman 1985) were compared similarly.

Growth curves fitted to the Arviat data were used to predict size for whales from the other sites. This predicted value was subtracted from the observed value and the resulting deviations compared to the residuals of the Arviat growth curve. These data were analysed using a Kruskal-Wallis oneway ANOVA followed by Dunn's test for unequal sample sizes (Kuo *et al.* 1992) using SigmaStat™ (Bagdasian *et al.* 1992).

Mass-length relationships were examined using log-transformed data. Differences in sampling dates among locations may have caused the mass-length relationships to vary and data were analysed separately, by sex, for each location. Mass was also examined as a function of length plus the girths at the eye, axilla, navel, anus or caudal peduncle using stepwise regressions (SAS 1985, MAXR procedure). Length was forced as the first variable and each girth was added to the stepwise regression only if it had a partial $P < 0.01$. The girths at the eye, anus and tail never achieved this limit so the equations are of the form:

Table 2. Parameters (±1 SE) for the Gompertz equation $A(e^{(-e^{-k^{*}age+k^{*}})}$ for length and mass of white whales from three locations in the eastern Canadian Arctic. R^2 is corrected for the mean (1-(error SS/corrected total)).

Location	Sex	Length (cm)				Mass (kg)			
		A	k (yr^{-1})	t_0 (yr)	R^2	A	k	t_0	R^2
Arviat	F	330.9	0.31	−0.96	0.89	537.3	0.21	1.88	0.84
		±5.2	±0.04	±0.28		±24.4	±0.03	±0.38	
	M	388.4	0.21	−0.84	0.91	782.9	0.17	3.75	0.86
		±5.4	±0.02	±0.35		±38.0	±0.03	±0.46	
Pangnirtung	F	397.9	0.30	0.06	0.96	791.1	0.21	1.22	0.88
		±12.7	±0.08	±0.79		±99.6	±0.12	±1.26	
	M	450.0	0.28	0.47	0.87	1455.1	0.23	4.23	0.90
		±15.3	±0.06	±0.61		±127.2	±0.05	±0.38	
Grise Fiord	F	432.4	0.17	−2.30	0.91	did not converge (N = 12)			
		±24.0	±0.05	±1.29					
	M	545.0	0.15	−0.31	0.72	3897.1	0.09	11.96	0.79
		±117.7	±0.08	±1.11		±4180.9	±0.07	±12.06	

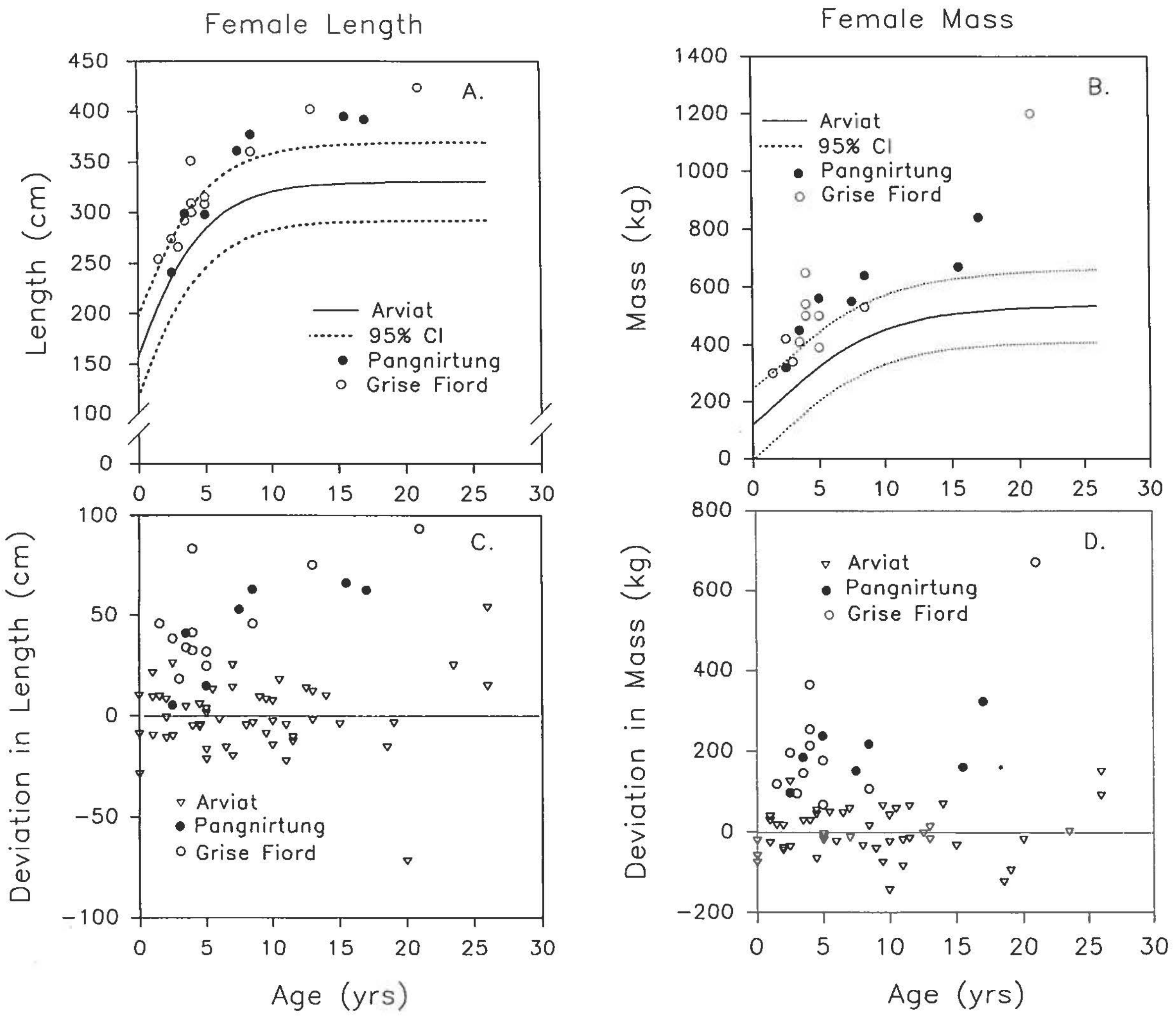

Fig. 2. Gompertz growth curves for length (A) and mass (B) of female white whales (*Delphinapterus leucas*) sampled at Arviat and deviations of length (C) and mass (D) data from that curve for whales sampled at Arviat, Pangnirtung and Grise Fiord. Gompertz growth curve is plotted with the 95% confidence interval of the population.

$$\log \text{mass} = a + b_l{*}\log \text{length} + b_{ag}{*}\log \text{axilla girth} + b_{ng}d{*}\log \text{navel girth} + \epsilon$$

where mass is total mass (kg), length is standard length (cm), a is the intercept, b_l, b_{ag} and b_{ng} are the coefficients associated with length, axillary and navel girth, respectively, and ϵ is the residual error.

Results

One hundred twenty-eight, 34 and 30 white whales were examined at Arviat, Pangnirtung and Grise Fiord, respectively. Due to missing data, sample sizes in various analyses are sometimes less than the number of whales sampled.

The sample from Arviat was the only one to include young of the year (Table 1). The largest female and the largest male were both sampled at Grise Fiord. The oldest whales were from Arviat.

The Gompertz model converged for all data sets (sex by locations) except for mass of females sampled at Grise Fiord (Table 2). Also, for male white whales from Grise Fiord, the Gompertz model estimated an asymptote which was associated with a large standard deviation (CV = 23%) and the asymptote was 13% greater than the maximum length observed.

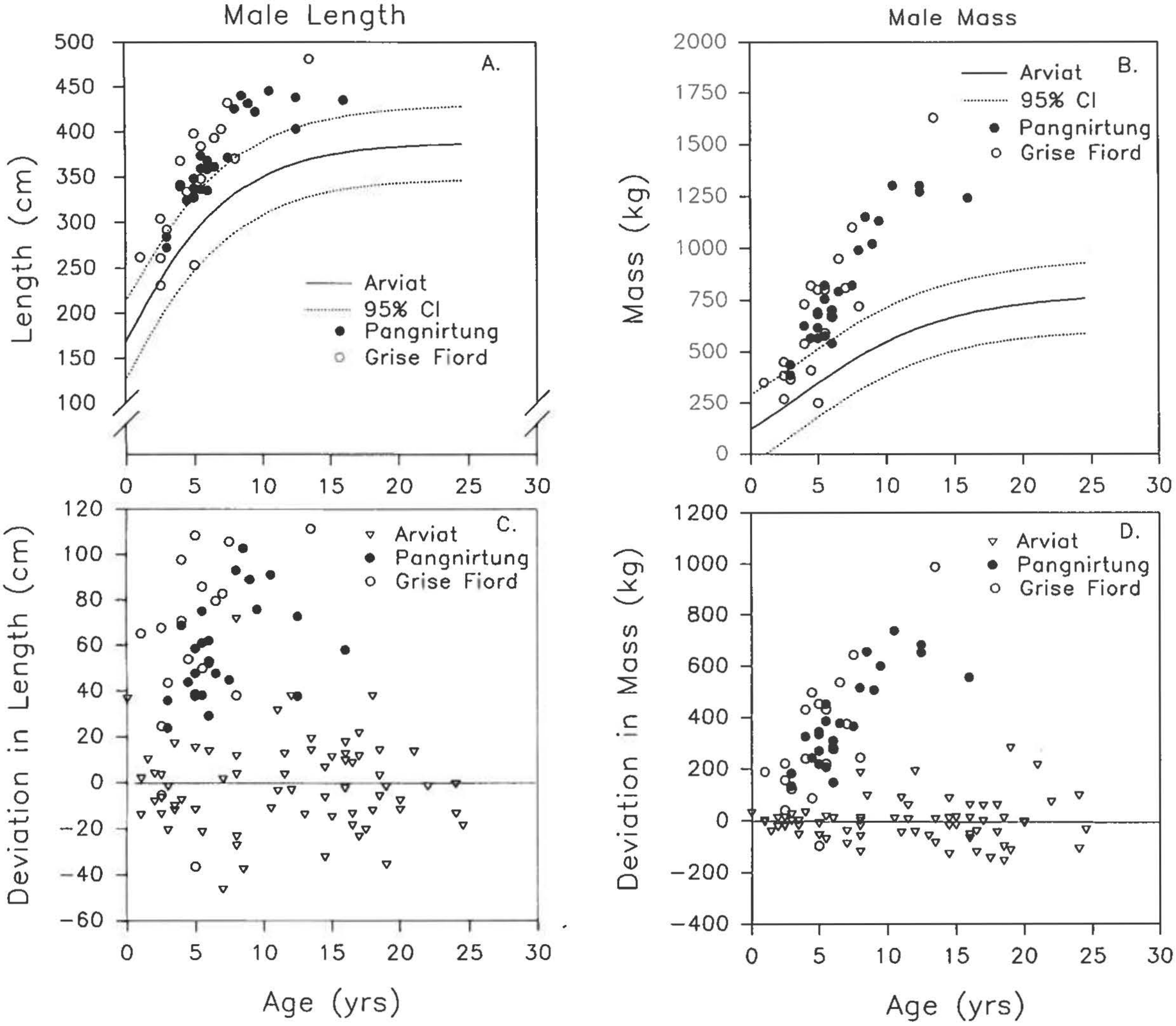

Fig. 3. Gompertz growth curves for length (A) and mass (B) of male white whales (*Delphinapterus leucas*) sampled at Arviat and deviations of length (C) and mass (D) data from that curve for whales sampled at Arviat, Pangnirtung and Grise Fiord. Gompertz growth curve is plotted with the 95% confidence interval of the population.

Sexual dimorphism

At all locations, maximum observed size was larger for males than for females. Asymptotic lengths of males were significantly greater than those of females at Arviat ($P<0.01$) and Pangnirtung ($P<0.05$). No significant differences in asymptotic length of males and females were detected at Grise Fiord ($P>0.05$) where the oldest male sampled was only 13.5 years old.

Asymptotic mass (Table 2) of females and males at both Arviat and Pangnirtung were significantly different ($P<0.01$). Males grew to a greater mass than did females. Growth-curve models did not produce testable asymptotes for females or males at Grise Fiord.

Stock differences

The asymptotic length from the Gompertz growth equation was significantly greater for whales from Pangnirtung ($P<0.01$) and Grise Fiord ($P<0.01$) than at Arviat for both females and males. Asymptotic mass was significantly greater at Pangnirtung for both males and females than at Arviat ($P<0.01$). Asymptotes for Grise Fiord whales were not compared due to the poor fit (Table 2). Observed lengths and masses of both males and females from Pangnirtung and Grise Fiord were outside the 95% confidence interval of the Arviat population after age ~5–7 years (Figs 2 and 3).

For both length and mass there were significant differences between sites in the distribution of deviations about

Table 3. White whale body mass (kg) as a function of length (cm) in the form log mass = a + b*log length where a is the intercept and b is the slope. Parameter estimates are ±1 SE. All lines were significant at $P<0.01$. ns indicates individual parameter estimates which were not significantly different from 0 (t-test, $P>0.05$).

Location	Sex	a	b	R^2	F_{df}
Arviat	F	−3.05 ±0.22	2.27 ±0.09	0.92	$614_{1.52}$
	M	−2.98 ±0.19	2.25 ±0.07	0.93	$936_{1.66}$
Pangnirtung	F	−1.13 ±0.74$_{ns}$	1.53 ±0.29	0.84	$27_{1.5}$
	M	−3.38 ±0.39	2.44 ±0.15	0.91	$257_{1.24}$
Grise Fiord	F	−3.13 ±0.77	2.33 ±0.31	0.87	$58_{1.9}$
	M	−3.10 ±0.53	2.33 ±0.21	0.88	$125_{1.17}$

the Arviat growth curve (Figs 2 and 3) (females: $\chi^2=33.78$, $DF=2$, $P<0.001$, males: $\chi^2=66.04$, $DF=2$, $P<0.001$). The Dunn's test of all pairwise comparisons indicated that the deviations were significantly greater at Pangnirtung and Grise Fiord than at Arviat ($P<0.05$) but that they were not different between Pangnirtung and Grise Fiord ($P>0.05$). All deviations at the latter two sites were greater than zero and increased with age (Figs 2 and 3).

Mass-length relationships

Length explained at least 85% of the variation in mass in the six sex-location analyses (Table 3). Improvements on these fits could be obtained by the addition of girth measurements, but the most useful girth varied among sex-location combinations and did not significantly improve the fit for males from Pangnirtung or for either females or males from Grise Fiord.

Overall, there were significant location effects ($F_{2.180}=28$, $P<0.01$) but not sex effects ($F_{1.180}=1.7$, $P=0.20$). Analysis of variance for sex differences at each location suggested that there was a difference between females and males at Pangnirtung ($F_{1.30}=4.77$, $P=0.04$), but this was not supported by t-tests ($P>0.05$). Similarly, significant differences among locations indicated by ANOVA ($P<0.01$) were not confirmed by t-tests ($P>0.05$). A single expression relating mass (kg) to length (cm) for all the data was:

$$\text{Log}_{10}\text{ mass} = -3.29 + 2.38*\log_{10}\text{ length},\ R^2=0.92,$$
$$F_{1.183}=2027$$
$$\text{or}$$
$$\text{mass} = 0.0005*\text{length}^{2.38}.$$

This equation tends to underestimate the mass of long white whales sampled at Grise Fiord in the fall.

Discussion

The statistical comparison of non-linear growth curves such as those derived from the Gompertz model is not simple (*e.g.* Cerrato 1990), partly because of correlations among the estimated parameters. In this study, comparisons were limited to tests of differences in asymptotes and of deviations from the growth curves for Arviat to avoid problems of parameter correlation. The latter test also reduces the impact of different age distributions for the three collection sites by allowing age-specific comparison.

Comparison of mass measurements is confounded by seasonal effects due to changes in feeding and reproductive status (Brodie 1989, Stewart & Stewart 1989). For

Table 4. Asymptotic (±1 SE) body lengths (cm) of white whales from five sites: Churchill (CH), northern Quebec (NQ), and Northwest Alaska (AK) (Doidge 1990a) and Arviat (AV) and Pangnirtung (PG) (present study). Grise Fiord data were excluded due to the high variation associated with the asymptotes. Sites which were not significantly different from each other ($P>0.01$) are underlined. Significant differences between sexes is indicated by: ns ($P>0.05$), * ($P<0.05$) or ** ($P<0.01$).

Location	CH	AV	NQ	AK	PG	Location Differences
Females						
Asymptotic length (cm)	328	331	330	359	398	CH NQ AV AK PG
SE	±6	±5	±6	±4	±13	
N	77	51	55	51	7	
Males						
Asymptotic length (cm)	377	389	349	427	450	NQ CH AV AK PG
SE	±14	±5	±10	±8	±15	
N	65	68	44	56	25	
Sex Differences	**	**	ns	**	*	

example, the mass-length relationships reported here, which are similar to those previously reported (Doidge 1990a), tended to underestimate the mass of longer males in the fall. Further discussion is limited to comparisons of standard length.

Sexual dimorphism

Although male white whales are widely known to be larger than females (Stewart & Stewart 1989), the degree of dimorphism reported varies among studies and stocks. Sergeant & Brodie (1969a: Fig 8) reported mean lengths for females and males of approximately 305 and 360 cm, respectively (males were 18% longer), in western Hudson Bay, 350 and 405 cm (males 16% longer) in Cumberland Sound, and 365 and 450 cm (males 23% longer) in Jones Sound. Average lengths of adult female and male white whales sampled in Cumberland Sound by Brodie (1971) were 362 and 427 cm, respectively; males were 18% longer. Mean lengths of adult, white-coloured whales from northwestern Alaska were 350.7 cm (females) and 402.9 cm (males 15% longer than females) (Burns & Seaman 1985).

Doidge (1990a) reanalysed the earlier data from western Hudson Bay (Sergeant & Brodie 1969a, Sergeant 1973) and northwestern Alaska (Burns & Seaman 1985) with his own data from northern Quebec. He did so in sufficient detail that statistical comparisons can be made with the current data (Table 4). There were significant sex differences in all but the northern Quebec sample (Table 4). Differences ranged from 6% in the northern Quebec to 18% and 19% in the Arviat and Alaska samples, respectively. Thus my analysis agrees with Doidge's conclusion that there was sexual dimorphism in size at some locations, but not that it was slight.

The degree of sexual dimorphism in size was substantial for all samples except the one from northern Quebec (Doidge 1990a). Male white whales from northern Quebec were also significantly shorter than males in a sample taken at Arviat in the same years (Table 4) (Doidge 1990a). If the male population segregates by size (Sergeant 1973, Burns & Seaman 1985) in northern Quebec, the sample may be biased toward smaller males. However it is not known if such segregation occurs at the Nastapoka River where the northern Quebec whales were caught (Doidge 1990b). Females at Arviat and in northern Quebec, collected in the same period, were virtually identical in asymptotic length (328 and 331 cm). The Arviat sample was a mix of shot and netted whales, although there may still be unknown sampling bias.

The mating system of white whales is poorly understood, and selection factors favouring dimorphism in size cannot be assessed. Such an analysis would have to consider the interaction of stock and sex differences. Moreover, relative stock size may influence the degree of apparent dimorphism if previous hunting pressure has selectively removed larger males from, for example, the northern Quebec population.

Stock differences

Several other studies examined the body size of white whales from the same locations used in this study. Sergeant & Brodie (1969a: Fig 8) concluded that white whales from different stocks could be distinguished on the basis of size-at-age. In their study, mean lengths of females were approximately 18% shorter in western Hudson Bay (305 cm) than in Cumberland Sound (350 cm), where they were less than 5% shorter than in Jones Sound (365 cm). Males showed a similar pattern: western Hudson Bay males (360 cm) were 13% shorter than Cumberland Sound males (405 cm) which were 14% shorter than Jones Sound males (450 cm). Brodie (1971) reported average lengths of 362 and 427 cm for females and males, respectively, in Cumberland Sound. Estimates from both previous studies are smaller than estimates of asymptotic length obtained in the current study for the same regions, although detailed comparisons are not possible. Superficial comparisons suggest the same pattern, however, with the difference in size-at-age between Hudson Bay whales and Cumberland Sound whales greater than between Cumberland Sound and Jones Sound whales.

Doidge (1990a) reanalysed the original data from Sergeant & Brodie (1969a) and Burns & Seaman (1985). His asymptotes for western Hudson Bay whales are not significantly different than the present estimates for Arviat (Table 4, $P > 0.05$). Thus, although there appear to be differences between the data of the present study and those collected previously in the same areas (Sergeant & Brodie 1969a, Brodie 1971), the only data set which can be compared statistically (western Hudson Bay, Doidge 1990a) was not significantly different.

Deviations from the Arviat curve support the conclusion drawn from the comparison of asymptotes. All the deviations from Pangnirtung and Grise Fiord were positive, suggesting that size differences may occur at early ages. However, it was not until they had matured at about 7 years of age (Stewart & Stewart 1989, Høier & Heide-Jørgensen 1994, Stewart 1994) that individual white whales from these locations exceeded the 95% CI for the Arviat population. Larger asymptotic size apparently results from faster growth rates as indicated by the steady increase in the deviations from the Arviat curve (Figs 2 and 3).

White whales from Hudson Bay appear to belong to a different stock (or stocks) than those in Cumberland Sound. The similar adult body length of females from the three locations in Hudson Bay (Arviat, Churchill and Nastapoka River) does not mean that they are from a common stock. It is highly unlikely, however, that the whales sampled at Churchill belong to a different stock than those sampled at Arviat, 250 km north along the presumed migration route (Sergeant 1973, Sergeant & Brodie 1969b).

The present analysis supports Doidge's (1990a) conclusion that Alaskan whales are longer than Hudson Bay whales, but not his assessment that this difference is small and limited in its application for stock identification. The comparison of asymptotic length indicates significant differences. Tests of deviations from the Arviat curve show significant differences. Also, for mature whales, individuals from Pangnirtung and Grise Fiord generally fall outside the 95% CI for the population at Arviat. They would be properly classified, therefore, as not belonging to the western Hudson Bay stock 95% of the time.

Such certainty does not exist for all comparisons of course. Recent studies in western Greenland (Heide-Jørgensen & Teilmann 1994) indicate a smaller asymptotic length for both males and females than I found at Grise Fiord. For males, the asymptotic length at Grise Fiord is suspect and larger males there were within the 95% CI of the estimate for western Greenland. For females, the confidence interval for asymptotic lengths of whales from western Greenland does not include the asymptotic length or maximum size of Grise Fiord females. Therefore the evidence of a shared stock between the Canadian high Arctic and western Greenland remains equivocal using size-at-age analysis.

The differences revealed by size-at-age comparisons are in good agreement with recent genetic studies. On the basis of size-at-age, white whales in western Hudson Bay are different from those in Cumberland Sound, Jones Sound and eastern Baffin Bay (off western Greenland), but they are not different from whales in eastern Hudson Bay. Cumberland Sound and Jones Sound whales could not be distinguished from each other and the separation of Jones Sound and western Greenland whales was uncertain. A study using restriction fragment length polymorphisms of mitochondrial DNA (mtDNA) indicated that eastern and western Hudson Bay whales belong to different stocks from whales in Cumberland Sound and Jones Sound (Helbig *et al.* 1989). This finding has been supported by more recent studies using mtDNA sequencing (Brown & Clayton 1993). Moreover, both genetic studies revealed stock differences where none was found in size-at-age analysis. Genetic analysis directly addresses the question of stock relationships and has greater potential to identify stocks. With developing techniques for nuclear DNA analysis, genetic studies also have the potential to provide information on stock status (*e.g.* Patenaude *et al.* 1992).

Body-size differences associated with some stocks of white whales are still of biological interest despite their waning importance to stock-identity questions. The hypothesis relating marine productivity to white whale body size (Sergeant & Brodie 1969a) has not been tested and few alternatives have been proposed. Within a species, larger body size may offer an advantage in environments with shorter productivity pulses, hence longer periods of poor food availability (Geist 1987, but see also Dunbrack & Ramsay 1993), regardless of total productivity. Whatever the forces at work, they appear to operate differently for males and females. The relationship between variation in differing body size and life-history traits of white whales remains unknown.

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Steroid hormones and prolactin in white whales (*Delphinapterus leucas*) from West Greenland

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Testosterone, progesterone, oestrogen and prolactin concentrations were determined in serum and urine samples collected from white whales (*Delphinapterus leucas*) taken by Greenlanders in the autumn of 1989–1991 and during May 1992. Hormone levels following long vs short intervals between hunting and isolation of serum samples were compared, and a significant difference was seen in the oestrogen concentrations. In male white whales the testosterone levels were significantly higher in sexually mature animals as compared to immature animals, 4.14 vs 0.96 nmol/l in serum samples and 0.62 vs 0.11 creatinine index in urine samples, respectively. Hormone levels of immature, pregnant, lactating and resting female white whales were compared, and the pregnant animals had higher levels of progesterone than the nonpregnant animals, 29.1 vs 1.76 nmol/l in blood and 22.1 vs 0.54 creatinine index in urine, respectively. The oestrogen level was higher in urine from pregnant females, 2.43 vs 0.37 creatinine index, but concentrations in serum were not significantly elevated. Lactating females had higher serum prolactin concentrations than nonlactating females, 4.35 vs 1.97 µg/l, respectively. In sexually mature males oestrogen concentrations were higher and progesterone concentrations were lower in May than in autumn. The reproductive states were indicated by both serum and urine concentrations of steroid hormones, but the two sample types did not show proportionality in hormone concentrations when taken from the same animal. Based on between-group variations in hormone content, models for diagnosis of sexual maturity in males and pregnancy in females are suggested.

Key words:
White whale, beluga, *Delphinapterus leucas*, testosterone, progesterone, oestrogen, prolactin.

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Introduction

The reproductive biology of the white whale (*Delphinapterus leucas*) has been incompletely characterized. Most literature describes general characteristics such as occurrence, growth, maturation, diets and pregnancy rates (see Sergeant & Brodie 1975, Stewart & Stewart 1989 for reviews). Few reports present details of the characteristics of the reproductive organs (Sergeant 1973, Heide-Jørgensen & Teilmann 1994). Recently Stewart (1994) reported the progesterone levels in female white whales from the eastern Canadian Arctic, but no reports are available on white whale sex hormones from elsewhere. Endocrine parameters have been described for some other cetaceans such as the fin whales (*Balaenoptera physalus*, Kjeld *et al.* 1992), the minke whale (*Balaenoptera acutorostrata*, Yoshioka *et al.* 1990, Yoshioka & Fujise 1992), various small delphinids (*Tursiops truncatus*, *Stenella longirostris* and *Delphinus delphis*, Sawyer-Steffan *et al.* 1983, Kirby 1984, Kirby & Ridgway 1984, Wells 1984, Ozharovskaya 1990, Schroeder 1990), the killer whale (*Orcinus orca*, Walker *et al.* 1988) and Dall's porpoise (*Phocoenoides dalli*, Temte 1991). The main purpose of most endocrinological studies of cetaceans has been to use hormonal parameters as diagnostic markers of pregnancy and male maturation, thus providing methods for predicting the dynamics of populations.

The literature on reproductive endocrinology of the odontocetes confirms the synthesis of progesterone from corpus luteum. The role of this hormone in luteal maintenance during pregnancy has been established for several terrestial species and one might extrapolate the mechanisms to marine animals. Thus the findings by Stewart (1994) confirm that pregnant white whales have high concentrations of progesterone in the blood. In killer whales oestrogens, *i.e.* oestradiol-17β and oestrone, peak in the pre-ovulatory phase of the oestrous cycle (Walker *et al.* 1988). However the elevated concentrations seen in most species during pregnancy have not been fully documented, although increased levels were reported for pregnant dolphins by Kirby & Ridgway (1984). Testosterone, the dominant androgen steroid, has been measured in elevated concentrations in sexually mature male Dall's porpoise (Subramanian *et al.* 1987, Temte 1991) and in the dolphins *Stenella longirostris* (Wells 1984) and *Tursiops truncatus* (Schroeder & Keller 1989). The presence and distribution of gonadotropins within reproductive groups have not yet been described in the literature, although early studies have indicated the existence of follicle stimulating, luteinizing and growth hormones, together with prolactin, as judged from isolation of the hormones from (unspecified) whale pituitaries followed by characterization in biological assays (Wallace & Ferguson 1964). Furthermore, prolactin as well as growth hormone producing cells have been identified immunocytochemically in pituitaries from several odontocetes (*Stenella plagiodon (=frontalis)*, *Feresa attenuata* and *Orcinus orca*, Schneyer & Odell 1984).

The present investigation was based on serum and urine samples collected from the Inuit catch of white whales in West Greenland during 1989–1992. Among the purposes were to analyse the variation in concentrations of steroid hormones in peripheral blood and in excreted urine between groups of female white whales representing different reproductive states, and between groups of male white whales to judge whether maturation and/or influence from the mating season could be detected. Also, the content of the peptide hormone prolactin in the blood was used to identify hormonal correlates to lactation in female white whales. Finally, the measured hormone levels were used in diagnostic models to predict pregnancy and lactation in females and sexual maturation in males.

It was also possible to evaluate the influence of procedural changes on the subsequent hormone analyses, since our procedures for collecting and processing samples improved during the sampling period. Sampling methods were compared with a view to defining convenient methods for collection of serum from cetaceans and other marine vertebrates under extreme field conditions.

Materials and methods

Collection of samples

Over a four-year period (1989–92) blood and urine samples were taken from white whales in various age, sex and reproductive states off West Greenland. The white whales had been killed in the Inuit hunt as described elsewhere (Heide-Jørgensen & Teilmann 1994). Blood samples were obtained from 75 females and 52 males, urine samples from 32 females and 20 males, all from a total of 131 animals (four animals were represented solely by urine samples). All samples were taken from whales caught during the autumn (September–October), with the exceptions that three serum samples and one urine sample came from sexually mature males and one serum sample from a lactating female killed in May. The reproductive states – immature, resting mature, pregnant and lactating in females; immature and sexually mature in males – were judged by examining the reproductive organs (see Heide-Jørgensen & Teilmann 1994). Fifty-three blood samples came from immature females, four from pregnant animals, 15 from lactating females and one from a resting female; in addition, two females were simultaneously lactating and pregnant. Forty-six males were immature and six were mature. For the urine samples the distribution was 24, 2, and 6 for immature, pregnant and lactating females, and 18 and 2 for immature and mature males, respectively. The following sampling procedures were carried out:

The samples in 1989–90 were taken by puncturing a large vein usually several hours or even days *post mortem*, and isolating the serum by passive coagulation for 24 hours (treatment 1). This collection comprised 28 blood samples, all of which appeared brownish-black due to extreme hemolysis and partial degradation. In 1991–92 the animals were brought to the research vessel *Adolf Jensen* within a few hours after being killed. The blood samples (N = 99) were isolated by cardiac puncture, and serum was harvested by centrifugation immediately after collection (treatment 2). When the latter sampling method had been used, serum samples were only weakly hemolysed. Serum samples were aliquotted and stored at –28°C. Urine samples were taken from the bladder into 50 ml plastic tubes and stored at –28°C.

Hormone analyses

All common reagents for construction and performance of hormone analyses were of at least analytical grade. Progesterone and oestrone for preparation of calibrator series were dilutions of reference standards from Sigma® (Sigma Chemical Compagny, St. Louis, Mo., USA), which also delivered the horseradish peroxidase, type VI for synthesis of enzyme conjugates. Steroid derivatives for coupling to horseradish peroxidase came from Steraloids® (Steraloids Inc., London, UK).

Serum and urine samples were subjected to steroid hormone analyses after appropriate processing. The measured concentrations of steroid hormones are reported in SI units, *i.e.* nmol/l.

Initially hormone levels in urine were indexed against the protein content. However due to occasional contamination of the urine with other body fluids unrealistic protein concentrations were indicated, and creatinine was used instead for indexing. Creatinine was measured by a kinetic picrate method without deproteinization according to Jaffé (Creatinine UNI-KIT II, Roche®, Switzerland), and the index was calculated as the concentration of the hormone in pmol/l divided by the creatinine content in µmol/l (Creatinine index = 10^6* molecular ratio). Creatinine content was not measured for six female and four male urine samples that had been collected more than six months before the time of analysis because this molecule is too unstable. To estimate steroid hormone levels from these samples a standard value for creatinine content was derived from the remaining samples (4343 and 4799 µmol/l for males and females, respectively). The group means were used in order to avoid introduction of bias in the statistical treatment of missing observations (Weisberg 1985).

Acid hydrolysis of urine samples

Urine samples were subjected to hydrolysis of conjugated steroids prior to steroid extraction: Urine was diluted with hydrochloric acid to a final concentration on 2 mol/l, and samples were then placed in a boiling water bath for 15 min. After cooling, hydrolysates were neutralized with NaOH until a pH of 6–8 was achieved.

Steroid extraction procedures

For the purpose of isolation of the steroid hormones, serum samples and urinary hydrolysates were subjected to organic solvent extraction as previously described (Rice *et al.* 1993). Briefly, sodium chloride was added to all samples prior to extraction to a final concentration of 0.5 mol/l. The extraction was executed twice, each time with four volumes of freshly opened diethyl ether. Ether phases were evaporated, and the extracts were resuspended in assay buffer in a volume so that the response was within 20–80% of displacement in the assays. The recovery of radiolabelled controls averaged >90% for progesterone and >95% for oestrone, oestradiol-17β and testosterone.

Progesterone analysis

Progesterone was quantified using an enzyme-linked immunosorbent assay (ELISA) as described by Rice *et al.* (1993). The antiserum was raised against 11α-hydroxyprogesterone-11-hemisuccinate: BSA, and the conjugate was progesterone3-O-(carboxymethyl)oxime: horseradish peroxidase. The antibody showed the following cross-reactivities at 50% of displacement (CR): progesterone 100%; 11α-hydroxyprogesterone 5%; pregnandione 0.4%; other steroids tested < 0.05%. Each sample was assayed in duplicate. The limit of detection (LDC) defined as 2* standard deviation of zero binding value was < 0.2 nmol/l. The inter- and intraassay coefficients of variation (CV) were < 10 and 8%, respectively.

Oestrogen analysis

The ELISA method described by Rice *et al.* (1993) was used to determine the oestrogen content in the sample extracts. The conjugate was 17β-oestradiol-3-hemisuccinate coupled to horseradish peroxidase, and the antibody (Dr. B. Svenstrup, States Serum Institute of Denmark) was raised in a rabbit against oestradiol-17β-6-O-(carboxymethyl)oxime: BSA. The antibody was previously characterized in radioimmunoassay (Callesen *et al.* 1986). In ELISA the major CRs were: oestradiol-17β 100%; oestrone 17%; oestriol 0.3%. The ELISA was characterized with respect to assay variation, inter- and intraassay CV 12 and 10%, respectively, and sensitivity as LDC was 4–10 pmol/l. There was parallelism between dilutions of controls and the dose response curve. However, when assaying white whale samples the requirement for parallelism between dilutions of sample extracts and the measured concentrations could not be met. The displacement curves for dilutions of extracts had slopes which were more similar to the displacement curve for oestrone than to the one for oestradiol-17β. This indicates that oestrone is present in high concentrations relative to oestradiol-17β in the white whale extracts, as has been reported for killer whales (Walker *et al.* 1988). Consequently oestrone was used for calibration of the oestrogen analysis, although a possible presence of oestradiol-17β might lead to overestimation of oestrogen concentrations.

Testosterone analysis

Testosterone concentrations were measured using a commercially available radioimmunoassay kit from DPC® (Diagnostic Products Corporation, Los Angeles, California), developed for use on extracts of blood and urine. LDC was 0.2–0.5 nmol/l, and inter- and intraassay CV was < 10%. The antiserum displayed the following CR's, taking testosterone as 100%: Dihydrotestosterone 34%; 5βandrostan-3α,17β-diol 3.8%; 11-hydroxytestosterone 3.3%; 5α-androstan-3α,17βdiol 2.9%; 5α-androstan-3β,17β-diol 2.7%; androsterone 2.1%; and other steroids tested (*e.g.* 11-deoxycortisol, 11-keto-testosterone and androstenediol) below 1%; all according to the manufacturer.

Prolactin analysis

A commercial kit, Prolactin Serozyme® (Serono Diagnostics, Switzerland), designed for the determination of prolactin in human blood samples, was used to quantify prolactin in white whale serum samples. The antibody of the kit had previously shown a recognition of essential structures of the hormone by reaction with prolactin from the antarctic fur seal (*Arctocephalus gazella*) by Boyd (1991). Data on cross-reactivity were only available for human gonadotropins: Luteinizing, follicle stimulating and thyroid stimulating hormones and placental lactogen did not show any interference in the analysis; the human growth hormone showed a slight cross-reactivity in the assay corresponding to 0.35 µg/l for each IU/l of 1st IRP 66/217.

In order to increase the sensitivity and ease the processing, we modified our method slightly with respect to volumes of samples and reagents, and with respect to temperature and time of incubations: Fifty µl of sample or standard in duplicates was mixed with 100 µl of anti-prolactin reagent and incubated for 60 min at room temperature. Following this, 100 µl of the separation reagent was added, and the incubation continued for 20 min. The next steps were magnetic separation and a single washing with 500 µl of wash solution, ending with enzyme reaction for 40 min at room temperature. The colour development of the enzyme assay was monitored at two wavelengths, 492 and 550 nm, so that a wide-range calibration curve was obtained, as suggested by the manufacturer. The assay characteristics stated by the manufacturer were not altered, as judged from control determinations: Interassay CV 5–6%, intraassay CV 2–4% and LDC 0.2 µg/l. The reference preparation 2nd IRP 83/562 was used for calibration in µg/l.

The specific recognition of white whale prolactin in the kit was investigated by analysis of partially purified prolactin. The prolactin was isolated from the pituitary of a lactating female which had given birth shortly before her death; this pituitary was expected to contain high amounts of prolactin. The preparation followed the diethyl aminoethyl ion exchange chromatography described by Wallace & Ferguson (1964). Growth hormone and luteinizing hormone did not bind to the ion exchanger, while prolactin did bind and was eluted from the column by a change in pH of the elution buffer. Subsequently, pH of the effluent was adjusted to 5.1, and a precipitation with 40% (V/V) of ethanol was performed (Hartree 1966). In this step of purification the follicle stimulating and luteinizing hormones remained unprecipitated whereas prolactin could be isolated by centrifugation. The resulting precipitate was dried under vacuo, resuspended in the kit's serum diluent and used for characterization of the assay.

Statistical methods

Calculations of calibration curves for the hormone analyses were assisted by regression analysis of the log/logit transformation of the response versus the calibrator dose.

Routine descriptive statistical methods as described by Box *et al.* (1978) were used. Nonbalanced analysis of variance and comparison between group means was performed in SAS® (SAS Institute Inc. 1987) using the general linear models (GLM) procedure. Group mean comparisons were made with the Hochberg's GT2 method, which was reported to be suitable for unequal group sizes (SAS Institute Inc. 1987). Linear regression analyses were performed via the GLM procedure in SAS® (SAS Institute Inc. 1987). Regression analysis of logarithmically transformed observations was introduced in order to achieve homogeneity of the variance (Weisberg 1985). The logarithmic regression analysis has an additional advantage in an expression of proportionality, since $\ln Y = \ln(a*X) = \ln a + \ln X$, giving the slope equal to 1, when proportionality exists.

Models for predicting state of reproduction according to hormone levels were computed with the assistance of the categorical data modeling procedure in SAS® (SAS Institute Inc. 1987). Briefly, an iterative procedure of parameter estimation was performed in conjunction with an estimation of the likelihood ratio, and the probability of model fitting and the significance of the individual parameters were used to judge statistical significance (see Shott 1991 and Jensen & Høier 1993 for reviews).

Results

Evaluation of the prolactin analysis

A white whale pituitary preparation, enriched with respect to prolactin, was tested for response in the analysis at various dilutions. The recovery of white whale prolactin (in arbitrary units: mU/l) measured in the kit as human prolactin is shown in Fig. 1. The regression equation was, (X, Y) = (added mU/l, recovered µg hPRL/l), $Y = -1.64 + 2.34*X$, where the intercept did not differ from 0 ($P = 0.63$). The logarithmic regression analysis gave $\ln Y = 0.83 + 0.97*\ln X$, and the slope was not different from unity ($P = 0.34$). Fig. 1 also depicts the determination of a white whale serum sample in different dilutions with the kit's serum diluent. The resulting regression analysis gave a straight line correlation, (X, Y) = (dilution, measured prolactin): $Y = -0.10 + 0.16*X$, $R = 0.98$, intercept not different from 0 ($P = 0.93$), and the logarithmic regression equation was: $\ln Y = -2.59 + 1.18*\ln X$, the slope was not different from unity ($P = 0.32$). Thus, proportionality apparently exists between the kit's human

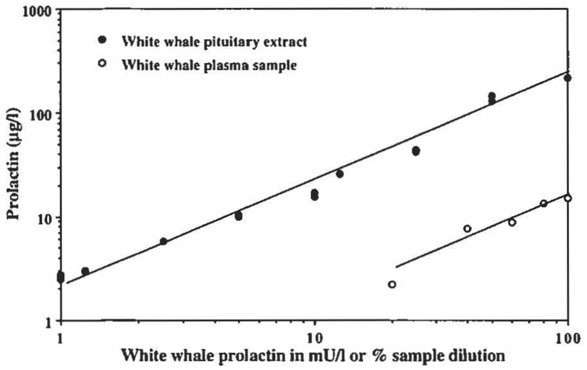

Fig. 1. Determination of prolactin content (µg/l) in dilutions of white whale pituitary extract and of a white whale plasma sample. White whale pituitary extract as mU/l, sample dilutions as percent dilution.

calibrators and the response from white whale prolactin assayed as a prolactin-enriched pituitary preparation as well as from white whale serum samples.

Effect of changes in sampling technique

In order to see whether the difference in sampling technique, treatment 1 and 2, influenced the analyses of hormone contents in the serum samples, the concentrations measured with the two types of treatment were compared within the various groups of reproductive activity by unbalanced analysis of variance. A general tendency towards elevated steroid concentrations was seen for treatment 1 as compared with treatment 2, but only the oestrogen determinations showed a significant difference (Table 1). No between-treatment difference could be discerned for the prolactin measurements.

Correlation between plasma and urine samples

Urine samples less than 6 months of age at the time of analysis were checked for creatinine content. The analysis resulted in: mean – standard error of the mean ± SE (range), 4343 ± 314 (2980 – 7719) µmol/l for males and 4799 ± 291 (1843 – 8089) µmol/l for females; means of the two groups were not different (P = 0.14).

Material from animals subjected to both blood and urine sampling was used to investigate the relationship between the levels of unconjugated steroid hormones in the blood and the amount of a given hormone secreted into the urine, the latter being a measure of the total metabolism of that hormone when indexed against creatinine. Linear regression analyses showed a significant influence of the measured concentrations in serum samples on the corresponding steroid concentrations in urine, whereas only the analysis of progesterone observations gave a significant correlation between serum and urine concentrations in the logarithmic regressions (Table 2). Moreover all slopes in logarithmic regressions were sig-

Table 1. Mean concentrations of progesterone, oestrogen, testosterone and prolactin in serum from various reproductive classes of white whale using different isolation procedures. preg&lact: lactating pregnant females. nd: not determined. P(treat) = Probability for identical results from the two treatments in unbalanced analyses of variance.

	Male white whales		Female white whales				
	immature	mature	immature	pregnant	lactating	preg&lact	P(treat)
Number of observations:							
Treatment-1	15	1	16	3	3	1	
Treatment-2	31	5	37	1	12	1	
Progesterone (nmol/l):							
Treatment-1	2.06	1.91	2.39	29.1	2.00	24.1	
Treatment-2	1.08	0.60	1.28	24.0	2.40	38.9	
Difference	−0.99	−1.33	−1.11	−5.08	0.40	14.7	0.12
Oestrogen (nmol/l):							
Treatment-1	6.27	3.36	7.22	9.48	7.58	4.15	
Treatment-2	2.40	8.22	2.42	5.91	2.82	0	
Difference	−3.87	4.87	−4.81	−3.57	−4.76	−4.15	<0.001
Testosterone (nmol/l):							
Treatment-1	1.35	5.95	nd	nd	nd	nd	
Treatment-2	0.77	3.78	nd	nd	nd	nd	
Difference	−0.58	−2.17	nd	nd	nd	nd	0.08
Prolactin (µg/l):							
Treatment-1	3.38	2.07	3.19	1.49	1.15	2.40	
Treatment-2	2.73	1.64	1.73	2.83	4.56	13.3	
Difference	−0.68	−0.57	−1.46	1.34	3.41	10.9	0.95

Table 2. Statistical parameters for comparison between serum and urine levels of steroid hormones in white whales. R = coefficient of correlation for the regression model. P(model) = probability for the regression model in analysis of variance. $P(\beta_0 = 0)$ = probability for Y-axis scission = 0. $P(\beta_1 = 1)$ = probability for slope = 1. Serum-P4, -OEST, -TES = Serum concentrations of progesterone, oestrogen and testosterone in nmol/l. Urine-P4, -OEST, -TES = urine concentrations of the steroids as creatinine index.

Linear regression, $Y = \beta_0 + \beta_1 * X$:					
Y	X	N	R	$P(\beta_0 = 0)$	P(model)
Serum-P4	Urine-P4	48	0.844	0.0040	0.0001
Serum-OEST	Urine-OEST	47	0.296	0.0029	0.0435
Serum-TES	Urine-TES	15	0.812	0.0098	0.0002
Logarithmic regression, $\ln Y = \beta_0 + \beta_1 * X$:					
Y	X	N	R	$P(\beta_1 = 1)$	P(model)
Serum-P4	Urine-P4	48	0.618	0.0059	0.0001
Serum-OEST	Urine-OEST	47	0.088	0.0001	0.56
Serum-TES	Urine-TES	15	0.397	0.0001	0.1434

nificantly different from 1; therefore a direct proportionality between serum and urine steroid levels could not be confirmed.

Hormone levels in male white whales

Testosterone, progesterone and oestrogen were measured in serum and urine samples from immature and mature male white whales, and prolactin was measured in the serum samples (Table 3). Group mean comparisons in analysis of variance indicated that the testosterone levels were unevenly distributed: 0.96 and 4.14 nmol/l in serum (P = 0.001) and 0.11 and 0.61 creatinine index in urine (P = 0.01) from immature and mature animals, respectively. Oestrogen levels changed insignificantly in serum from 3.66 nmol/l in immature to 7.41 nmol/l in mature animals, while the urine creatinine index increased from 0.47 in immature to 1.33 in mature animals (P = 0.01). Progesterone did not vary significantly between the groups, although a trend towards elevated levels was observed in serum from immature males (P = 0.07). Prolactin concentrations had a very high individual variation, as can be seen from the measured ranges, and no between-group difference was observed.

The samples from male white whales offered the possibility of investigating the influence of hunting season on hormone concentrations. A thorough statistical analysis of the combined effects of seasonality and maturity could not be performed because we had insufficient material, but the data from sexually mature males could be compared between spring (N = 3) and autumn (N = 3) seasons of collection. Testosterone and prolactin did not differ

Table 3. Concentrations of testosterone (TES, nmol/l), progesterone (P4, nmol/l), oestrogen (OEST, nmol/l) and prolactin (PRL, µg/l) in male white whale serum and urine (as creatinine index) according to sexual-maturity status. N = number of observations, mean = mean concentration, SE = standard error of the mean, range = minimum and maximum concentration measured, P(diff) = probability for difference between groups in analysis of variance.

Serum hormones:															
	TES				P4				OEST				PRL		
N	mean	SE	range	N	mean	SE	range	N	mean	SE	range	N	mean	SE	range
Immature males															
46	0.96	0.13	0–4.72	46	1.40	0.11	0.57–3.88	46	3.66	0.79	0–32.7	36	2.82	0.95	0.22–34.7
Mature males															
6	4.14	1.33	0.69–8.53	6	0.80	0.28	0.22–1.91	6	7.41	2.26	3.36–17.8	6	1.72	0.20	1.04–2.22
P(diff)		0.0001				0.07				0.11				0.64	

Urine hormones:											
	TES				P4				OEST		
N	mean	SE	range	N	mean	SE	range	N	mean	SE	range
Immature males											
14	0.11	0.03	0.004–0.39	18	0.64	0.04	0.40–1.00	18	0.47	0.06	0–1.13
Mature males											
2	0.61	0.52	0.09–1.13	2	0.66	0.26	0.40–0.92	2	1.33	0.99	0.34–2.32
P(diff)		0.01				0.92				0.01	

Table 4. Concentrations of progesterone (P4, nmol/l), oestrogen (OEST, nmol/l), and prolactin (PRL, µg/l) in serum from female belugas at different reproductive states. N, mean, SE, and range as in Table 3, all pregnant = pool of pregnant plus lactating, pregnant animals; all lactating = lactating plus pregnant lactating animals. Columns having different superscripts of the mean concentrations are significantly different ($\alpha = 0.05$).

Reproductive states	N	P4 mean	SE	range	N	OEST mean	SE	range	N	PRL mean	SE	range
Immature	53	^{b}1.61	0.19	0.54–9.86	53	3.87	0.69	0.15–25.2	44	2.00	0.26	0–12.8
Pregnant	4	^{a}27.9	4.52	22.4–41.4	4	8.39	2.81	2.99–16.1	4	1.82	0.35	1.23–2.83
Lactating	15	^{b}2.32	1.02	0.73–16.5	15	3.77	1.28	0–18.5	15	3.88	1.34	0.15–20.9
Resting	1	^{b}1.08	–	–	1	1.33	–	–	1	1.54	–	–
Pregn. lactating	2	^{a}31.5	7.39	24.1–38.9	2	2.09	2.06	0–4.15	2	7.87	5.47	2.40–13.3
all pregnant	6	^{a}29.1	3.52	22.4–41.4	6	6.42	2.31	0–16.1	6	3.84	1.91	1.28–13.3
all nonpregnant	69	^{b}1.76	0.26	0.54–16.5	69	3.81	0.60	0–25.2	60	2.46	0.40	0–20.9
all lactating	17	5.76	2.60	0.73–38.9	17	3.57	1.15	0–18.5	17	^{a}4.35	1.31	0.2–20.9
all nonlactating	58	3.41	0.94	0.54–41.4	58	4.15	0.67	0–25.5	49	^{b}1.97	0.26	0–12.8

between seasons, whereas progesterone concentrations decreased significantly ($P < 0.05$) from autumn to spring: 1.34 ± SE 0.31 nmol/l for autumn samples and 0.26 ± SE 0.02 nmol/l for spring samples (Fig. 2). Oestrogen also appeared to differ between the seasons: 4.22 ± SE 0.76 nmol/l in autumn and 10.6 ± SE 3.82 nmol/l in spring ($P = 0.05$).

Hormone levels in female white whales

Serum progesterone levels were high in pregnant females (mean = 27.9 nmol/l) and in females that were simultaneously lactating and pregnant (mean = 31.5 nmol/l) (Table 4). All nonpregnant females had low serum progesterone concentrations (mean progesterone = 1.76 nmol/l), except one animal killed in May that had a high concentration (16.5 nmol/l). She was lactating and had probably calved less than 14 days prior to catch. Concentrations of oestrogen and prolactin did not differ significantly between the reproductive states, although pregnant females had a higher mean value for oestrogen. Progesterone and oestrogen were significantly elevated ($P < 0.05$) in the urine from pregnant animals compared with that of lactating or immature animals (Table 5). When serum levels of all pregnant animals were compared with those of all nonpregnant animals, progesterone concentrations were significantly higher ($P < 0.05$) in the former than the latter (Table 4). Furthermore, a comparison of all lactating with all nonlactating females showed that prolactin levels in serum were significantly higher ($P < 0.05$) in the former than the latter (Table 4).

Diagnosis of reproductive state following hormone determinations

The between-group comparisons with respect to hormone content of serum and urine indicated differences between whales in the various reproductive classes. In order to clarify whether these differences could be used to diagnose the reproductive states of individuals, hormone concentrations were correlated to group specificity by using a categorical model (Table 6). The male serum samples collected in May were excluded from this investigation due to an effect from the time of sampling (Fig. 2), and no analysis was made on male urine samples owing to the low number of observations (Table 3). As an illustration of the model fitting, Table 6 shows the numbers of correct

Table 5. Concentrations of progesterone (P4) and oestrogen (OEST) in urine from female belugas in different reproductive states. Concentrations are given as the creatinine index. N, mean, SE, and range as in Table 3. Columns having different superscripts of the mean concentrations are significantly different ($\alpha = 0.05$) according to group mean comparison following unbalanced analysis of variance.

Reproductive states	N	P4 mean	SE	range	N	OEST mean	SE	range
Immature	24	^{b}0.55	0.03	0.28–0.88	23	^{b}0.34	0.05	0.11–1.04
Pregnant	2	^{a}22.1	11.8	10.2–33.8	2	^{a}2.43	1.92	0.68–4.17
Lactating	6	^{b}0.53	0.05	0.38–0.67	6	^{b}0.40	0.08	0.26–0.76

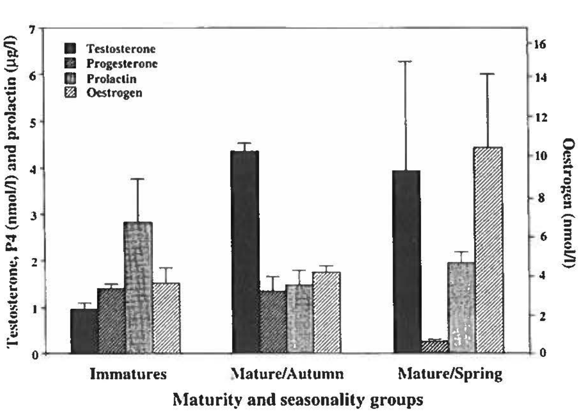

Fig. 2. Mean concentrations of testosterone, progesterone, oestrogen (nmol/l) and prolactin (µg/l) in immature and mature male white whales sampled in autumn and spring.

and incorrect predictions when using the models on the set of observations and taking the cut-off value to be a probability of 0.50. Serum (threshold = 19.5 nmol/l) and urine (6.19 creatinine index) progesterone levels are found to be powerful indicators of pregnancy, and serum testosterone level (3.30 nmol/l) can be used to diagnose male sexual maturity.

Discussion

Evaluation of prolactin analysis

White whale serum samples responded in the analysis, which had been originally designed for the determination of human prolactin levels, and sample dilutions reacted proportionally to the calibration curve. Serum components other than prolactin might have reacted with the antibody of the kit. There is, for example, a close structural relationship between prolactin and growth hormone in several species (Posner 1977). Also, Nicoll *et al.* (1977) have described the binding of serum components from hypophysectomized pigeons to an antibody raised against mammalian prolactin. It is therefore essential to investigate whether the kit actually measured prolactin and not another substance in the serum samples, and for this purpose a white whale pituitary extract was prepared. It was enriched with respect to the content of prolactin using techniques which deselected other gonadotropins. The result confirmed that dilutions of the preparation reacted proportionally to the calibration curve, and this allowed us to conclude that the molecule recognized by the kit's antibody was of pituitary origin. Moreover, since growth, luteinizing and follicle stimulating hormones were preferentially removed by the methods used to prepare the extract, according to data on whale gonadotropin migration in the chromatographic method used (Wallace & Ferguson 1964), it is likely that the kit measures white whale prolactin specifically. It can therefore be concluded that the method does measure white whale prolactin in a way which depicts proportionality between white whale prolactin and the calibration curve, although the absolute concentrations cannot be determined.

Effect of changes in sampling technique

A comparison between the two sampling techniques (treatments 1 and 2) within the reproductive groups of both sexes indicated a trend towards overestimating concentrations of oestrogen and testosterone in treatment 1

Table 6. Logistic regression models for the diagnosis of male maturity and of pregnancy and lactation in females based on the concentrations of progesterone (P4), oestrogen (OEST), testosterone (TES) and prolactin (PRL) in serum samples, and indexed concentrations of P4, OEST and TES in urine samples. Serum concentrations in nmol/l (PRL in µg/l), urine concentrations as creatinine index. The regression equations represent the significant model (P = 0.05). Response in test: correct(+) or incorrect(−) result in analysis using odds ratio equal to 0.50 as the threshold value. Threshold values are the concentrations corresponding to P(odds ratio) = 0.5.

Male sexual maturity:			Response in test			
	Estimated	threshold	immature		mature	
	regression equation (E)		+	−	+	−
Serum	−4.0821+1.2385*(TES)	3.30	46	0	5	1
Female pregnancy:			nonpregnant		pregnant	
			+	−	+	−
Serum	−59.58+3.064*(P4)	19.5	60	0	6	0
Urine	−12.94+2.091*(P4)	6.19	29	0	2	0
Urine	−5.684+4.7094*(OEST)	1.21	29	0	1	1

P(odds ratio) = exp(E)/(1 + exp(E)), where E is the expression derived from logistic regression.

relative to treatment 2. This trend was observed despite the use of methods designed for extracted material which should have eliminated any effects from steroid-binding globulins and other nonspecific effects from the blood matrix. The reasons for the discrepancy are most likely related to metabolic changes in the steroids, *e.g.* from hydratization of conjugated steroids or from oxidation of the steroids. Whether such changes occur during hunting, sample collection or the subsequent storage period (up to 2 years in a freezer) cannot be determined. However hemolysis reportedly affects the results of progesterone analysis, possibly by releasing enzymes that modulate the molecule so that it cannot be recognized by the antibody used in the analysis (*e.g.* Reimers *et al.* 1983, Vahdat *et al.* 1984, Inns & Cecchini 1989, Yoshioka & Fujise 1992). Also, Van der Molen & Groen (1968) have described the 20α-hydroxysteroid-dehydrogenase-dependent interconversion between progesterone and 20α-dihydroprogesterone and between androstenedione and testosterone in hemolyzed blood.

Based on the probable presence of hydrolytic enzymes and oxidoreductases in hemolysed blood, we conclude that treatment 1 possibly results in elevated steroid concentrations. Thus the more laborious treatment 2 must be recommended for the collection of blood samples. Nevertheless the difference between the two treatment groups is not unambiguous, and some of the difference might be explained by factors other than the treatment procedures. For instance there might be some individual variation within the groups owing to changes in hormone concentrations, *e.g.* in the period immediately prior to the onset of maturity in the male and female immature groups, when steroid release could be expected. Also, the group of pregnant females might be nonhomogeneous, since the secretion of oestrogen, for example, probably varies during gestation. It is important to bear in mind that the number of observations per group is small, especially when the groups are further divided into two treatment categories.

Prolactin determinations apparently were not influenced by the difference in sampling technique. The antigenic structures of prolactin seem to have been maintained even under extreme hemolysis. However another possible explanation is that the prolactin measurements reflect a large individual variation within the reproductive groups. For instance the largest measured concentration of prolactin was found in an immature male. The finding of high concentrations of the hormone in nonlactating females and in males emphasizes the complexity of prolactin action, since its secretion is regulated by many factors. In addition to the direct influence of hormone-regulating mechanisms, factors such as time of day, photoperiod and temperature affect prolactin secretion (see McNeilly 1980 for a review). Also, physiological stress might be an essential factor for the secretion of prolactin from the pituitary, and the animals sampled in this study may have been hunted for several hours before being killed.

Correlation between serum and urine samples

A comparison between serum steroid concentrations and the amounts of the same steroid excreted into the urine confirmed a covariation, although proportionality between the two types of steroid determination could not be confirmed by logarithmic regression analysis.

The unconjugated steroids in the blood reflect the amounts active in regulation of reproductive events at the time of sampling. The concentrations are not constant, since they change following episodic secretions leading to diurnal and long-term variations. The urinary steroids, in contrast, characterize the hormonal turnover integrated over a longer period and thus reflect prolonged processes, *e.g.* luteal maintenance or placental activity. Thus the two types of sample depict different expressions of hormonal activity, and the lack of proportionality might be expected. We suggest that the urinary steroids are better indicators of hormonal activity owing to their low sensitivity to short-term variations. On the other hand, when hormones were used to describe different reproductive classes both sample types proved equally useful, except that serum oestrogen did not vary significantly between pregnant and nonpregnant females.

Hormones in male white whales

In male white whales the group comparisons were confounded by the presence of three samples from mature animals collected in May; all other samples were obtained in autumn.

The most obvious features that distinguished sexually mature males were the elevated testosterone concentrations in serum and urine samples, regardless of the time of catch. Our results showed a four-fold increment in testosterone concentration between sexually immature and mature males. Male white whales have not been previously characterized with respect to testosterone content in immature and mature animals, so the only available data for comparison are from the investigations of other cetaceans: Testosterone concentrations of sexually mature Dall's porpoises averaged 10.46 ± SE 1.20 ng/ml (36.2 ± 4.2 nmol/l), while those of immature animals averaged 1.00 ± SE 0.52 ng/ml (3.5 ± 1.8 nmol/l) (Temte 1991). Comparable results were obtained when following a male Dall's porpoise throughout one year (Subramanian *et al.* 1987). Testosterone was measured in a few male delphinids (Wells 1984, Schroeder & Keller 1989), indicating summer levels of 50–200 nmol/l, in contrast to winter levels of 0–20 nmol/l. Similar seasonal variation in testosterone secretion has also been documented in mysticete cetaceans (fin whales and minke whales, Kjeld *et al.* 1992, Yoshioka & Fujise 1992) with high concentrations measured during summer vs low winter levels.

Thus care must be taken in interpreting hormone levels in species that have seasonal mating.

The progesterone content of serum and urine from male white whales varied according to the time of hunting and sampling rather than the state of maturity. The measured levels were comparable to the progesterone content in serum and urine from nonpregnant females, and this possibly reflects the release of progesterone from cortex of the adrenal glands. Further investigation is needed, but the seasonal variation might be explained by the fact that secretion of progesterone and other corticosteroids increases in autumn, and possibly winter, owing to an overall change in metabolic activity. Another possible explanation is that the growth of testes which occurs in May (Heide-Jørgensen & Teilmann 1994) affects the levels of progesterone and other steroid hormones.

The oestrogen content of male serum and urine samples did not differ between immature and mature animals. Comparisons between May and autumn samples from mature animals indicated that oestrogen is possibly found in higher concentrations in May, coinciding with the growth of testes in males (Heide-Jørgensen & Teilmann 1994) and the onset of oestrous in females (Stewart & Stewart 1989).

The prolactin content of serum from males apparently was unaffected by either sexual maturity or the time of capture. The dominant feature of the prolactin analysis was the very high variation between individuals. When all white whale samples were compared the highest prolactin concentration was measured in serum from an immature male. This animal's sexual-maturity state should not have affected the result because the most common function of the hormone is to induce milk-producing tissue (McNeilly 1980). The more generalized effects of prolactin, such as those related to responsiveness to changes in photoperiod, might be invoked to explain the finding of a maximum concentration in an immature male killed in autumn.

Hormones in female white whales

The main variation in hormone levels of female white whales was seen for progesterone in pregnant vs nonpregnant animals. Progesterone concentrations varied significantly and specifically between the total group of pregnant females and the group of nonpregnant females, and this was seen whether the pregnant animal was lactating or nonlactating. The mean concentrations were 29 nmol/l for pregnant and 1.8 nmol/l for nonpregnant animals, the latter being near to the concentrations seen in males, thereby indicating a lack of luteal activity. The only exception was a lactating female that had a serum progesterone concentration between the two group means (16.5 nmol/l). Stewart (1994) reported the mean progesterone level in pregnant white whales caught in the eastern Canadian Arctic to be 9.26 ng/ml (29.4 nmol/l), with a range between 1.48 and 16.20 ng/ml (4.7–51.5 nmol/l). Immature and nonpregnant females in his study had mean concentrations of 1.37 ng/ml (4.4 nmol/l), ranging from 0.50 to 5.40 ng/ml (1.6–17.2 nmol/l). Thus there is a good agreement between our results and those of Stewart (1994) with respect to progesterone concentrations in pregnant white whales. However nonpregnant females in our study had lower progesterone concentrations than those described for nonpregnant females by Stewart (1994). This difference may be explained by the use of different analytical procedures. Also, one cannot exclude the possibility of a population difference between the white whales in West Greenland and the Canadian Arctic.

Stewart (1994) reported one lactating female in his sample of nonpregnant white whales to have had a high serum progesterone concentration (5.40 ng/ml = 17.2 nmol/l). It was suggested that she had recently calved, and this would agree with our observation of high progesterone levels shortly after parturition. The reason for this phenomenon is not clear, but an explanation could be that the progesterone which maintains pregnancy in white whales is of placental origin.

The high individual variation in serum prolactin levels which characterized males was also observed in females. When comparing all female reproductive groups no particular one could be identified by the prolactin concentration alone, although both nonpregnant and pregnant lactating animals had higher mean prolactin levels. When the data were pooled, lactating animals showed a significantly higher prolactin level than nonlactating animals. This would appear to indicate that prolactin concentrations are higher in lactating than in nonlactating females. However, due to the high individual variation within the different reproductive groups it is difficult to make a clear distinction between prolactin concentrations in lactating and nonlactating females.

The oestrogen content in samples from females was not affected by either pregnancy or lactational amenorrhea as one would expect it to be, although the measurements did show tendencies towards elevated and lowered concentrations, respectively. Our inability to separate mean concentrations of oestrogen with respect to reproductive group might be explained by the small number of observations in each group, combined with a high variability within the groups. The latter effect could have been at least in part due to the between-treatment difference, which was significant for oestrogen.

Diagnosis of reproductive state following hormone determinations

Concentrations of progesterone in female serum or urine and of urine oestrogen can be used to diagnose pregnancy. Serum testosterone can be used to diagnose sexual maturity in males. The models can be used for calculating threshold values between pregnancy and nonpregnancy in females, and sexual maturity and immaturity in males (Table 6). The overall oestrogen content in serum was not found to be useful for specifying female reproductive classes. Prolactin concentration exhibited too much individual variation to be a reliable predictor of lactation in female white whales.

We compared our model for diagnosing pregnancy by reference to a threshold value of 19.5 nmol/l progesterone in white whale serum with the corresponding threshold value of 3 ng/ml equal to 9.5 nmol/l proposed by Stewart (1994). Our logistic regression model clearly suggests a higher cut-off value. We did not observe any false predictions of pregnancy in our investigation, whereas Stewart (1994) found that in two cases out of 12, pregnant white whales were judged to be nonpregnant. The discrepancy could be due to the low number of observations in our study (4 pregnant white whales), or to the variability in methods employed for sample treatment and progesterone analysis in both studies.

Conclusions

This study reports the concentrations of progesterone, testosterone, oestrogen and prolactin found in serum and urine of white whales hunted off West Greenland. Our results reflect the hormonal parameters of animals which have been subjected to stress during hunting for up to several hours. The time span between killing and sample collection may have influenced the hormone levels in the blood and urine samples. We also cannot exclude the possibility of an effect from the sample treatment performed under extreme field conditions. This study will therefore be most instructive for samples collected under the same conditions. Care should be taken if our results are used, for example, in a comparison with white whales living in captivity. The quality of blood samples from relatively unstressed, living animals is much different from the quality of the blood samples used in this study.

Progesterone appears to be suitable for predicting pregnancy in female white whales when measured in serum or urine, and testosterone in both serum and urine could be used for determining the maturity status of male white whales. Urine oestrogen might be used for detecting pregnancy in females. The concentrations of steroid hormones in urine are probably more reliable for characterizing reproductive state than are the corresponding serum concentrations.

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Progesterone levels and reproductive status of white whales (*Delphinapterus leucas*) from the Canadian Arctic

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Stewart, R. E. A. 1994. Progesterone levels and reproductive status of white whales (*Delphinapterus leucas*) from the Canadian Arctic. Meddr Grønland, Biosci. 39: 239–243. Copenhagen 1994-04-22.

Serum progesterone levels were compared to the presence and size of ovaries, corpora lutea and fetuses in white whales sampled at three sites in the eastern Canadian Arctic. Generally, a progesterone level greater than 3.00 ng/ml indicated a pregnancy although there was some overlap in the range of values with mature, nonpregnant whales. This overlap may be an artifact of sample management or may indicate failed or failing pregnancies. Data are not available to test these hypothesis. Progesterone concentration was not significantly correlated with ovarian mass, corpus luteum mass or fetus mass. Ovaries of immature whales were significantly smaller than those of mature-but-not-pregnant and pregnant whales.

Key words:
White whale, beluga, *Delphinapterus leucas*, Monodontidae, Odontoceti, progesterone, reproduction.

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Introduction

Understanding the nature of reproductive cycles is basic to understanding the ecology of organisms and populations (Smith 1976). Although assessing the reproductive status of wild white whales (*Delphinapterus leucas*) has relied on examination of ovarian structures from harvested whales (*e.g.* Kleinenberg *et al.* 1969, Sergeant 1973, Burns & Seaman 1984), live whales handled for tagging, captures for aquaria and other purposes could provide information on reproduction. For some small stocks it may be useful to capture white whales alive specifically to determine reproductive status if a nonlethal method for doing so is available and the need warrants. Here I report on an initial effort to relate circulating levels of progesterone to the ovarian structures, hence reproductive status, of white whales.

Materials and methods

Reproductive tracts, blood samples and lower jaws were obtained from white whales landed by Inuit hunters during their subsistence hunts near Arviat (formerly Eskimo Point, 61°05'N, 94°06'W), Pangnirtung (66°07'N, 65°43'W) and Grise Fiord (76°25'N, 82°52'W) N.W.T., Canada, from July through September 1984–1987. Data collected included the date and approximate time of death, the presence and nature of mammary secretions and the presence of term fetuses. At Arviat, where some whales were taken in nets, associations of newborn white whales with adults in the net were recorded to help assess female status. This method was quickly discredited when newborn calves were also found with only males.

Blood was drawn 0.5 to 48 h after death by chest puncture using a 50 cc syringe and delivered into untreated blood tubes. Most blood samples were centrifuged within 2 h after collection and the serum was drawn off and frozen separately. Some blood samples were frozen whole until they were thawed and separated just prior to being analysed. Information was not available to assess the effect of this difference in treatment but the treatment was independent of reproductive class. Reproductive tracts were frozen or stored in 10% neutral buffered formalin until examined later. There was possibly some change in mass associated with the different preservation methods for ovaries (Heide-Jørgensen & Teilmann 1994) but tracts were frozen or fixed irrespective of reproductive class.

In the laboratory the ovaries were removed from the reproductive tract and weighed individually to the nearest 0.01 g. If a large corpus luteum was visible externally, it was removed intact from the ovary, weighed to the nearest 0.01 g and measured to the nearest 0.1 mm across three orthogonal diameters. Here the overall diameter of the corpus luteum for each white whale is defined as the mean and the maximum diameter is defined as the largest of these three measurements. Ovaries were then sectioned serially with a scalpel at 5 mm intervals and the presence of other corpora lutea, corpora albicantia and follicles recorded. The uterus was subjectively graded by size (small, medium, large) (Burns & Seaman 1984). The horns and body of the uterus were opened and examined for signs of pregnancy, such as increased vascularization, smoothing of the internal walls and the presence of a fetus. Fetuses were removed and weighed to the nearest 0.1 g.

Females were categorized as immature, mature but not pregnant and pregnant. Immature whales had no corpora lutea or corpora albicantia, were not lactating, were not pregnant, and had small uteri. Mature-but-not-pregnant white whales displayed some of the following features: presence of corpora albicantia or regressing corpora lutea (Kirby 1990), evidence of lactation, and a medium-sized, empty uterus with sharp ridges on the internal walls, with little evidence of vascularization (Burns & Seaman 1984). Initially, pregnant white whales were defined by the presence of a large corpus luteum lacking obvious connective tissue or by the presence of a fetus. However no large corpora were found without a fetus and the presence of a fetus became the sole criterion. Fetus size was used as an index of the time the female had been pregnant.

The concentration of progesterone in serum was determined by radioimmunoassay (RIA) following Yuthasastrakosol *et al.* (1974). Briefly, extraction was accomplished by combining 250 µl of serum with 750 µl of phosphate-buffered saline (PBS, pH 7.2) and 5.5 ml of ethyl ether. The mixture was vortexed for 4 min, equilibrated for 15 min and lyophilized on dry ice/ethanol (-43°C). The decanted supernatant was dried under a stream of nitrogen gas in an oscillating water bath (37°C), then reconstituted with 1.250 ml PBS. For the RIA the P4 antisera developed in rabbits (A18, N. Rawlings, University of Saskatchewan, Saskatoon, SK) was used at 1:2500 initial dilution in PBS. Labeled P4[1,2-^{3}H(N)] (New England Nuclear, Boston, MA) was diluted in PBS to ~10 000 cpm/100 µl. The scintillation cocktail was Ecolume (ICN Biomedicals Inc., Irvine, CA). Typical ranges for inter- and intra-assay coefficients of variation in this lab are 6–12% and 4–9%, respectively. The mean sensitivity of the assay at 95% binding is 12 pg per tube.

Jaws were kept frozen until the teeth were extracted. Longitudinal thin sections (approximately 0.3 mm) of teeth were prepared (Wainwright & Walker 1988) and used to estimate ages (see Stewart 1994 for details). The sections were viewed using reflected light with a variable-power dissecting microscope. Ages, in years, were based on the formation of two growth layer groups per year (Goren *et al.* 1987, Brodie *et al.* 1990).

All data were tested for normality (Kolmogorov-Smirnov with Lilliefors' correction) and equal variances (Levene medial test) (Kuo *et al.* 1992) at $P > 0.05$. All data sets failed at least one of these tests and were subsequently analysed using Kruskal-Wallis ANOVA on ranks and Dunn's multiple comparisons (Kuo *et al.* 1992). Within a category, correlations were examined between progesterone level and maximum ovarian mass, and, among pregnant whales, corpus luteum and fetal mass using Spearman rank order correlations (Kuo *et al.* 1992). For statistical analysis the ovaries of each female were identified as large-ovary and small-ovary rather than as left or right to group those with a corpus luteum together. Average age of maturity was calculated following DeMaster (1978). SigmaStat™ software was used for all other analyses (Kuo *et al.* 1992). Means are presented ± 1 SD.

Results

Reproductive status was determined for 63 female white whales (52 from Arviat, 5 from Pangnirtung, 6 from Grise Fiord) which provided data on two or more of progesterone level, age, ovary mass and ovarian structures. Differences in sample sizes for some analyses resulted from missing data. The data from the three locations have been combined.

The mean ages of the females in the three reproductive classes were significantly different (Table 1, Kruskal-Wallis ANOVA on ranks, $P < 0.001$). Immature females were significantly younger than either mature-but-not-pregnant or pregnant females (Dunn's multiple comparison, $P < 0.05$) but ages of mature, nonpregnant females and mature, pregnant females were not significantly different ($P > 0.05$). The oldest immature whale was 6.5 years old. The youngest mature, nonpregnant whale was 5 years old and had a single corpus albicans. The youngest pregnant whale was 4 years old and had one corpus luteum and a small fetus. The average age of maturation was 6.43±0.11 ($N = 59$).

The estimated time from the whale's death to sample collection was recorded infrequently. The average time was 8.9±12.9 hours (range 0.5 to 48 h, $N = 19$). The correlation between this time and progesterone level was not significant ($P = 0.64$) for immature ($R = -0.17$, $N = 9$) or for mature-but-not-pregnant whales ($R = -0.50$, $P = 0.23$, $N = 7$). Time-to-sampling was available for only three pregnant females. They were 1.5, 1.5 and 6.5 h associated with progesterone levels of 11.42, 14.10 and 6.50 ng/ml, respectively.

Mean progesterone levels varied significantly among the three classes of females (Table 1, $P < 0.001$). Progesterone levels in immature and mature-but-not-pregnant females were significantly lower than in pregnant ones (P

Table 1. Mean progesterone concentrations in the serum, ages, mass of the large-ovary, mass of the small-ovary, and mass of the fetus in white whales (*Delphinapterus leucas*) according to reproductive status. Subscripts indicate means in a column which were not significantly different (Kruskal-Wallis ANOVA at $P < 0.001$, and Dunn's multiple comparison at $P < 0.05$).

Class	Progesterone (ng/ml)	Age (yr) (g)	Large-ovary Mass (g)	Small-ovary Mass (g)	Fetus Mass (g)
IMMATURE					
$\bar{x}$	1.18_a	3.1	9.53	8.03	
SD	0.56	1.8	5.08	4.11	
Range	0.50–2.60	0–6.5	1.43–19.88	1.24–15.30	
N	24	24	22	22	
MATURE, NOT PREGNANT					
$\bar{x}$	1.59_a	13.2_b	38.78_c	29.93_d	
SD	1.07	6.2	18.28	14.47	
Range	0.50–5.40	5–26	12.31–85.36	10.30–68.59	
N	21	22	20	20	
MATURE, PREGNANT					
$\bar{x}$	9.26	10.4_b	60.65_c	22.64_d	379.2
SD	5.09	4.1	21.03	6.13	239.9
Range	1.48–16.20	4–18.5	36.44–118.79	8.32–32.90	76.0–923.3
N	12	13	14	14	13

< 0.05). The level in the one newborn whale sampled was 2.00 ng/ml, slightly greater than 1 SD (0.56) above the mean for immature whales (1.18 ng/ml). The mean for immature and mature-but-not-pregnant whales was 1.37±0.86 ng/ml (N = 45).

The mass of the large-ovary varied among classes (Table 1, $P < 0.001$). Changes in ovary mass due to formalin fixation (Heide-Jørgensen & Teilmann 1994) are insufficient to account for the differences found among reproductive classes. The large-ovary was lighter in immature whales than in mature-but-not-pregnant and pregnant whales (Dunn's multiple comparison, $P < 0.05$). Large-ovaries of mature, nonpregnant and pregnant whales were not significantly different ($P > 0.05$). The average difference in large-ovary mass between mature, nonpregnant whales and mature, pregnant whales (approximately 22 g) was similar to the mass of the corpus luteum in pregnant whales (23.64±10.27 g, N = 13).

The average of maximum diameters of corpora lutea was 40.60±5.35 mm and the average of the overall diameters was 34.40±4.76 mm (N = 14). Corpus luteum mass was best predicted by using all three diameters (mass = $0.0005 * D_1 * D_2 * D_3 + 2.62$, $R^2 = 0.93$, $F_{1,12} = 127.9$, $P < 0.01$). Overall and maximum diameters explained less of the variation in mass ($R^2 = 0.69$ and 0.87, respectively).

The mass of the small-ovary also varied with reproductive class of the females (Table 1, $P < 0.001$) due to lighter ovaries in the immature whales ($P < 0.05$). The small ovaries of mature-but-not-pregnant and pregnant whales were not significantly different ($P > 0.05$).

Progesterone level and large-ovary mass were not correlated in immature (Spearman rank order: $R = -0.13$, $P = 0.58$, $N = 20$) or mature-but-not-pregnant whales ($R = 0.41$, $P = 0.09$, $N = 18$). Among pregnant whales, progesterone level did not correlate with large-ovary mass ($R = -0.12$, $P = 0.72$, $N = 12$) with the mass of the corpus luteum ($R = -0.08$, $P = 0.78$, $N = 12$), or with the mass of the fetus ($R = 0.19$, $P = 0.58$, $N = 11$). Fetus mass did not correlate with corpus luteum mass ($R = -0.36$, $P = 0.24$, $N = 12$) or large-ovary mass ($R = -0.10$, $P = 0.74$, $N = 13$).

Discussion

Assessing hormonal dynamics in wild whales has several limitations not present with captive animals (Høier & Heide-Jørgensen 1994). Post-mortem changes before and after sampling are difficult to control. The inability to centrifuge blood in some field situations introduces another variable. However in this study these variables were distributed among samples without regard to reproductive class of the females. With small sample sizes there was no relationship between the lag in sampling and progesterone levels. Also the serum levels of progesterone in this sample of white whales were within the ranges reported for other whales.

Kirby (1990) summarized data on circulating progesterone levels for many odontocetes. Typically, baseline values were less than 1 ng/ml; levels at ovulation were over 1 ng/ml, but only for short periods; and levels during pregnancy were over 3 ng/ml. All values for pregnant whales except one killer whale (*Orcinus orca*, 3.8 ng/ml) exceeded 5 ng/ml up to 13 days before giving birth (Kirby 1990) when progesterone levels may decline (Temte & Spielvogel 1985). Other studies on odontocetes also reported nonpregnant progesterone levels of 0.5 to 1.5 ng/ml (Joseph *et al.* 1987) and values for pregnant whales over 5 ng/ml (Temte & Spielvogel 1985, Joseph *et al.* 1987).

Diagnostically values above 3.00 ng/ml over an extended period were used to indicate pregnancy in the bottlenose dolphin (*Tursiops truncatus*); baseline was less than 1.00 ng/ml (Sawyer-Steffan *et al.* 1983). Schroeder (1990) recommended the following progesterone levels for clinical assessment: anestrous or non-pregnant, < 1 ng/ml; ovulation = 1 ng/ml; pregnancy = 3 to 52 ng/ml in three separate tests at two-week intervals. He reported 100% accuracy in predicting pregnancy using this method for 28 pregnancies and four species.

Baseline progesterone levels for the white whales examined here are represented by the progesterone concentrations in immature and nonpregnant whales. The average (1.37 ng/ml) was inflated slightly by one nonpregnant whale with a value of 5.40 ng/ml. This whale had a relatively large (9.88 mm) regressing corpus luteum and was lactating. She was sampled on 24 July 1986 at Arviat and may have calved so recently (Sergeant 1973, Brodie 1989) that progesterone levels had not yet returned to baseline levels. Repeated assays from recently parturient females (Schroeder 1990) would be required to test this interpretation. Excluding this animal, the baseline progesterone level was 1.28 ± 0.60 ng/ml (N = 44) with a range of 0.50 to 2.94 ng/ml. Thus a serum concentration of 3.0 ng/ml progesterone might be used to indicate pregnancy in white whales, as in bottlenose dolphins (Sawyer-Steffan *et al.* 1983, Kirby 1990, Schroeder 1990). All but two pregnant white whales in the present study had progesterone levels greater than 5 ng/ml.

Høier & Heide-Jørgensen (1994) reported the only other data on progesterone levels in wild white whales. Their values, converted to ng/ml, were 0.55 and 9.91 ng/ml for immature plus nonpregnant and pregnant classes, respectively. For pregnant white whales their values are nearly identical to those found in this study (9.26 ng/ml). Although their value for the combined immature and mature-but-not-pregnant whales appeared lower than the pooled mean in this study (1.37 ng/ml), it was within 1 SD (0.86 ng/ml).

The predictive reliability of progesterone levels to determine pregnancy is challenged by the two pregnant whales in my study which had progesterone levels lower than 3 ng/ml (EP85–12: 1.48 ng/ml with a 370.0 g fetus and PG86–13: 1.60 ng/ml with a 76.0 g fetus). Levels for the other 10 pregnant whales ranged from 5.70 to 16.20 ng/ml. Reasons for the two seemingly low values are unclear. Speculation that female (PG86–13) was in an early stage of luteal development and fetal growth (Boyd 1991) is not supported by the size of the corpus luteum, which was the heaviest examined. Moreover another female with a 78.5 g fetus had a progesterone level of 5.70 ng/ml. PG86–13 was sampled up to 10 h after death, as were other whales which had progesterone levels consistent with their reproductive class. Female EP85–12 drowned in a net during a three-day storm so the time of death is uncertain and there could have been a significant delay before she was sampled. However a mature, nonpregnant whale caught in the same net had a progesterone level of 1.48 ng/ml, almost exactly equal to the mean of her reproductive class (1.49 ng/ml). EP85–12, had the smallest corpus luteum weighed. Sample management may have been a factor in these two low values, or both pregnancies may have been failing. In this case, progesterone level might be a more predictive measure of pregnancy than the presence of a fetus, but there are no data with which to test this hypotheses.

The lack of correlation between progesterone level and ovary mass in immature and mature-but-not-pregnant whales and the marginal correlation in pregnant ones differs from the curvilinear relationship between progesterone level and ovary mass in Dall's porpoises (*Phocoenoides dalli*) (Temte & Spielvogel 1985). Temte & Spielvogel's regression, however, included both pregnant and nonpregnant whales and was of a form requiring a zero-intercept, outside the range of their data. These authors demonstrated a significant difference in mean progesterone levels between the two groups, and pooling of such data in a regression masks the threshold concept (Sawyer-Steffan *et al.* 1983) relating progesterone to pregnancy. For white whales ovarian mass was useful in distinguishing between immature and mature-but-not-pregnant whales, although there was some overlap in ranges.

As in the present study, the relationship between progesterone level and fetus size was not significant in the Dall's porpoise (Temte & Spielvogel 1985) although a general hormone model for pinnipeds (Boyd 1991) indicates a correlation between fetus size and progesterone level. My sample of white whales represents a limited and short segment (30 days) of a long gestation (330–435 days, Brodie 1989, Heide-Jørgensen & Teilmann 1994). A greater range of gestational ages is required to test the hypothesis that hormonal patterns in white whales are fundamentally different than in pinnipeds.

In summary, serum progesterone levels ≥3.00 ng/ml appear to be reliable indicators of pregnancy in white whales and could be used with live whales. While the results of this study appear robust in spite of variable field conditions, it will be necessary in the future to test the effects of delays in sampling and different sample handling procedures. The effects of the latter might best be tested with captive whales. Females reached maturity at 4 to 7 years of age, with a mean of 6.43, consistent with other studies (Braham 1984, Heide-Jørgensen & Teilmann 1994).

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PCB's and other organochlorine contaminants in white whales (*Delphinapterus leucas*) from West Greenland: variations with age and sex

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Stern, G. A., Muir, C. G., Segstro, M. D., Dietz, R. & Heide-Jørgensen, M. P. 1994. PCB's and other organochlorine contaminants in white whales (*Delphinapterus leucas*) from West Greenland: variations with age and sex. Meddr Grønland, Biosci. 39: 245–259. Copenhagen 1994-04-22.

Blubber samples from 138 white whales from two locations in West Greenland (the Nuussuaq area, ca. 74°N, 58°W, and the Disko Bugt area, ca. 69°N, 53°W and skin and kidney samples from 20 white whales from Nuussuaq were analysed for PCB congeners and related organochlorines (hexachlorohexanes (ΣHCH), chlorinated bornanes (ΣCHB), chlordane (ΣCHLORD), DDT-related compounds (ΣDDT), dieldrin and mirex). The large sample size permitted a detailed assessment of the variation of contaminant levels with age and sex. Mean concentrations of all major organochlorine (OC) groups (ΣPCB, ΣDDT, ΣCHLORD, ΣCHB) were not significantly different between the Nuussuaq and Disko Bugt groups. After an age of 5.5 years, a consistent decline in concentration levels of all four major OC's was observed in females. In contrast, only marginal differences in ΣPCB, ΣCHB and ΣCHLORD concentrations and a substantial increase in ΣDDT were observed in males. The observed decline in females occured near the age of attainment of sexual maturity and preceding commencement of lactation. Residue levels in sexually immature animals (male and female) and male-female differences in mean concentrations of ΣPCB and p,p'-DDE in adult animals are consistent with a lactation period of less than one year. Young animals could be distinguished from adults, using principal component analysis, by higher proportions of lower chlorinated PCB's and more watersoluble OC's such as p,p'-DDE which are preferentially transferred during lactation.

Key words:
White whale, beluga, *Delphinapterus leucas*, Greenland, age, sex, lactation, parturition, organochlorine, PCB, DDT.

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Introduction

Previous studies of white whales (*Delphinapterus leucas*) from Canadian and Alaskan waters indicated that organochlorine chemicals such as polychlorinated biphenyls (PCB's) and other organochlorines (OC's) were present at low parts per million (μg/g) concentrations in blubber samples of all stocks (Muir *et al.* 1990, Becker *et al.* 1992). The presence of these contaminants, which are associated with reproductive failure in other marine mammals and birds (*e.g.* Peakall 1975, Reijnders1986), is of concern from the point of view of the long-term health of the white whale populations (Martineau *et al.* 1987, Muir *et al.* 1990). The white whale is important to the Inuit population in arctic coastal communities of Greenland, Canada and Alaska, since marine mammals constitute an important part of their traditional diets. Knowledge of levels of the contaminants in the whale tissues is useful for assessing the extent of dietary exposure (Kinloch *et al.* 1992).

In the studies by Muir *et al.* (1990) and Becker *et al.*

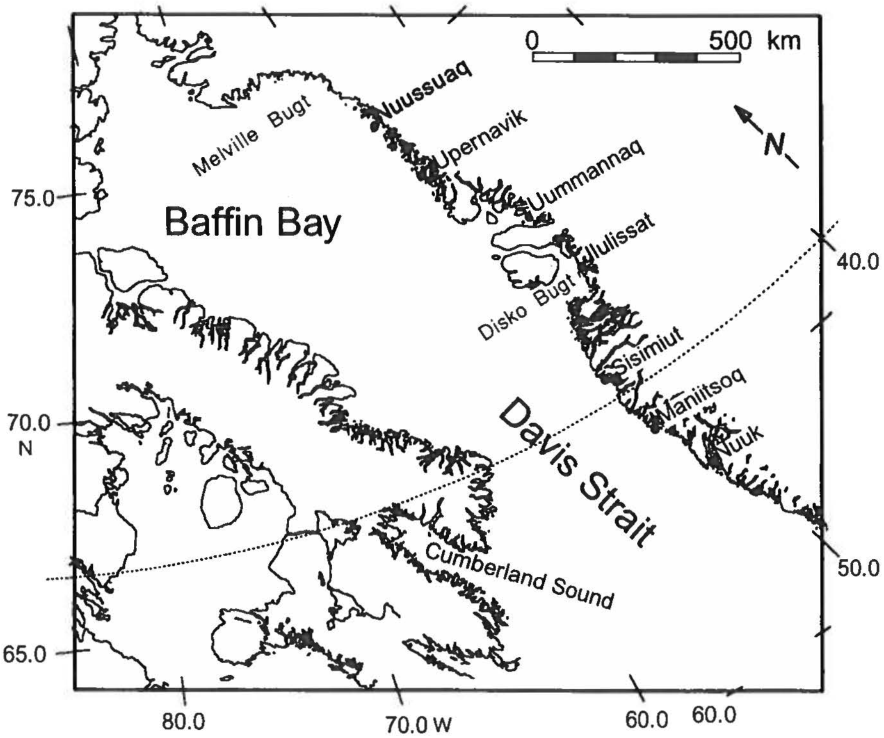


Fig. 1. Map showing Nuussuaq and Disko Bugt regions of West Greenland where white whale samples were collected.

(1992) comparisons of contamination levels between stocks were carried out on a limited number of sex and age classes. The main objective of the present study, was to examine the level and the influence of sex and age on concentrations of major contaminants in white whales sampled in western Greenland. This knowledge should enable better design of future monitoring studies of white whales and other small toothed cetaceans. A second objective was to provide information on levels of contaminants in skin (mattak) and kidney for which figures have not previously been reported.

Materials and methods

Samples

A total of 174 white whale blubber, 113 skin and 110 kidney samples from the Nuussuaq (ca. 74°N, 58°W) and Disko Bugt (ca. 69°N, 53°W) areas of West Greenland (Fig. 1) were received from the Greenland Environmental and Fisheries Research Institutes during 1989 and 1990. Details of the collection procedure were given by Hansen *et al.* (1990) and Heide-Jørgensen & Teilmann (1994). Samples were shipped frozen in styrofoam insulated containers and were stored upon receipt at −40°C. Animals were classified by sampling location, standard length and sex. Age was estimated as described by Heide-Jørgensen *et al.* (1994). From the 174 blubber samples, 138 were selected for analysis to cover a range of ages with approximately equal numbers of males and females. Analysis was performed on 20 skin and kidney samples selected from animals containing the highest contaminant levels in blubber. All were age 5 years and younger.

Organochlorine Analysis

Determinations of PCB's and organochlorine pesticides in blubber tissues followed the procedures described by Muir *et al.* (1990). Briefly, samples of blubber (2.2 g) were mixed with anhydrous sodium sulfate (pretreated by heating at 600°C for 6 hours) and ball-milled (30 minutes) with hexane. The extract was centrifuged and a portion (1/11) removed for lipid determination. Internal standards of aldrin and octachloronaphthalene (OCN) were added to a 0.5 ml aliquot of the extract which was then fractioned on Florisil® (1.2% (v/w) deactivated with water) into three eluates; hexane (F1), hexane: DCM (85:15) (F2) and hexane DCM (1:1) (F3) (Norstrom & Won 1985). The chromatography on Florisil separated PCB's, chlorobenzenes, p,p'-DDE and mirex in F1 from most toxaphene components, chlordane-related compounds and p,p'-DDT in F2. F3 contained heptachlor epoxide and dieldrin. Florisil eluates were evaporated to about 2 ml, transferred to vials and made up to 2.5 ml in isooctane for gas chromatographic (GC) analysis.

Skin and kidney samples, because of their lower lipid

Table 1. Age groups and numbers for male and female white whales used in statistical comparisons.

Group	Age (years)	Sex	N
1	NB – 1.0	M	8
		F	6
2	1.5 – 2.5	M	19
		F	11
3	3.0 – 4.0	M	11
		F	13
4	4.5 – 7.5	M	20
		F	19
5	8.0 – 15.0	M	9
		F	14
6	> 15.0*	M	4
		F	4

* Oldest male and female animals were 22.0 and 18.5 years, respectively.

content, were analysed as above with some minor modifications: 5.0 g samples were homogenized by blending with dry ice. The dry ice was allowed to sublime and the homogenate was mixed with anhydrous sodium sulfate (pretreated by heating at 600°C for 6 hours) and ball-milled (30 minutes) with hexane. Internal standards of aldrin and OCN were added and an aliquot of the extract equivalent to about 0.1 g of lipid was then fractionated on Florisil as above.

Florisil eluates were analysed by capillary GC with (^{63}Ni) electron capture detection. Samples were injected (splitless mode) on a 60 m × 0.25 mm i.d. DB-5 column (film thickness 0.25 μm) with H_2 carrier gas (Muir *et al.* 1988). PCB's and organochlorine pesticides were identified and quantified as described previously (Muir *et al.* 1988). Total PCB (ΣPCB) was the sum of all congeners. Total chlordane (ΣCHLORD) was the sum of all chlordane-related compounds including heptachlor epoxide while total DDT (ΣDDT) was the sum of p,p'-DDE, -DDD, -DDT and o,p'-DDT. Chlorinated bornanes (CHBs) were quantified after first obtaining response factors for individual CHB peaks from the weight percent of each peak in the total ion chromatogram (electron ionization GC-mass spectrometry) of a toxaphene standard. Total CHBs (ΣCHB) was the sum of the areas of 19 peaks (8 major peaks were generally observed) (Muir *et al.* 1990).

Internal standard recoveries were determined in all samples. Recoveries of aldrin and OCN were uniformly greater than 90%. A cod liver standard reference material (SRM-1588) from the National Institute of Standards and Technology (Gaithersburg, Va) was employed for major organochlorine pesticides and PCB congeners.

Statistical Analysis

Correlation analysis was used to measure the relationship between concentrations of major contaminants and ratios of selected compounds with age and length. The general linear models procedure of SAS (SAS *Institute* 1992) with an analysis of covariance was then used to test the hypothesis that mean concentrations of major contaminants and ratios of selected compounds did not vary with age group. To compare whales at varying stages of growth, blubber samples from both males and females were assigned to one of six different age groups (Table 1). Where there were significant effects ($P < 0.05$), the mean square error from the ANCOVA was used with Tukey's test to identify the age groups which differed in mean concentrations (wet weight). Principal component analysis (PCA) was conducted using the statistical software program SIRIUS (Karstang & Kralheim 1990) to examine pattern similarities and differences between mean concentrations of individual PCB and organochlorine contaminants in blubber samples with age group and sex. Mean concentrations for each age group were normalized (expressed as a fraction of the combined sum of the concentrations of all residues) to avoid the influence of absolute concentrations. Autoscaling to unit variance was used to minimize any statistical bias associated with the order-of-magnitude differences in chemical concentration. The number of statistically significant principal components was determined using cross validation (Sharaf *et al.* 1985). Contaminants with the highest contributions to the differences observed between the individual age groups and clusters will be located furthest from the origin of the axis. The greater the distance along an individual principal component axis, the more an individual contaminant contributes to the variation accounted for along that axis. A negative or positive position along the axis indicates whether a certain contaminant is negatively or positively correlated with the principal component. An age group or cluster positioned along a positive principal component axis will contain low concentrations of contaminants with negative loadings and higher concentrations of contaminants with positive loadings. An age group or cluster positioned along a negative principal component axis contains the opposite relationship. As a result, the position of an age group or cluster on a principal component axis relative to other age groups or clusters indicates differences in contaminant profiles.

Results

Age and sex differences

Mean concentrations (arithmetic) of major organochlorine groups (ΣPCB, ΣDDT, ΣCHB, ΣCHLORD) and p,p'-DDE in male and female blubber samples were calculated for animals of the same age (Tables 2 and 3, respectively). The relationships between age and the resulting mean concentrations of ΣPCB, ΣDDT, ΣCHB and ΣCHLORD and the ratios p,p'DDE/ΣDDT and ΣDDT/ΣPCB of males and females are described in Figs.

Table 2. Arithmetic mean concentrations of major contaminants with age in male white whale blubber from West Greenland (μg/g wet weight).

AGE	N	ΣPCB	ΣDDT	ΣCHB	ΣCHLORD	p,p'-DDE
0.0	2	6.75	5.28	4.82	2.94	3.20
0.25	1	10.87	8.10	6.22	4.86	5.80
0.75	1	1.84	1.01	2.36	1.04	0.52
1.0	4	6.48	3.92	4.49	2.51	2.33
1.5	6	5.59	3.61	4.06	2.65	2.06
2.0	6	4.83	3.59	4.43	2.64	1.78
2.5	7	6.51	5.22	5.08	3.47	3.28
3.0	8	5.44	4.00	3.50	2.48	2.42
3.5	1	3.56	1.90	2.47	1.63	0.91
4.0	2	4.84	2.31	2.38	1.82	1.25
4.5	2	4.54	2.79	3.57	2.12	1.49
5.0	8	5.17	3.98	3.31	2.21	2.26
5.5	2	3.58	2.88	2.73	2.06	1.60
6.0	6	5.52	4.18	2.74	2.05	2.53
7.0	2	5.32	3.13	3.15	1.84	1.84
8.0	1	7.37	5.44	4.46	2.96	2.83
10.0	1	3.36	2.14	2.68	1.28	1.12
11.0	1	5.53	4.94	4.46	2.69	2.95
12.0	3	3.68	2.54	2.54	1.48	1.48
13.0	3	4.90	5.03	3.39	2.05	2.87
16.0	1	6.05	6.85	4.13	2.35	3.35
17.0	1	5.62	7.02	3.65	2.33	3.52
21.0	1	5.79	5.61	2.72	2.07	3.25
22.0	1	4.42	5.38	2.74	1.77	2.89

2, 3 and 4 (preliminary statistical analysis indicated that geometric means calculated from $\log_{10}$ transformed data were generally only slightly lower than the corresponding arithmetic means. Arithmetic means were therefore used in Tables 2 and 3 and Figs. 2, 3 and 4).

With the exception of mirex and ΣOCTA (octachlor-

Table 3. Arithmetic mean concentrations of major contaminants with age in female white whale blubber from West Greenland (μg/g wet weight).

AGE	N	ΣPCB	ΣDDT	ΣCHB	ΣCHLORD	p,p'-DDE
0.25	1	7.16	5.36	5.38	3.52	3.07
0.50	1	3.86	2.41	5.43	2.12	1.24
0.75	1	2.84	1.73	3.65	1.65	0.86
1.0	3	5.10	4.53	5.66	3.35	2.16
1.5	1	2.43	1.35	3.33	1.46	0.62
2.0	6	5.34	3.40	4.55	2.67	1.78
2.5	4	5.48	4.17	4.23	2.66	2.51
3.0	4	5.62	3.49	4.73	2.71	1.80
3.5	6	5.10	3.61	3.31	2.15	2.17
4.0	3	4.91	2.93	2.94	1.93	1.76
4.5	1	6.97	4.80	2.65	2.52	2.81
5.0	3	4.50	3.80	3.35	2.22	2.18
5.5	2	5.29	4.38	3.65	2.68	2.54
6.0	2	2.89	2.06	2.73	1.38	1.04
7.0	8	3.68	2.76	2.31	1.64	1.63
7.5	3	2.53	1.57	2.04	1.20	0.86
8.0	1	0.84	0.35	0.55	0.33	0.18
9.0	3	2.63	2.79	1.75	1.13	1.42
10.0	3	0.91	0.44	1.31	0.41	0.20
11.0	1	1.00	0.45	1.23	0.49	0.23
12.0	1	1.10	0.56	1.55	0.50	0.23
13.0	2	1.45	1.40	1.44	0.66	0.66
14.0	2	1.17	0.67	1.65	0.56	0.32
15.0	1	0.61	0.30	1.00	0.30	0.14
17.0	3	0.93	0.77	1.24	0.50	0.32
18.5	1	0.94	0.50	1.40	0.43	0.26

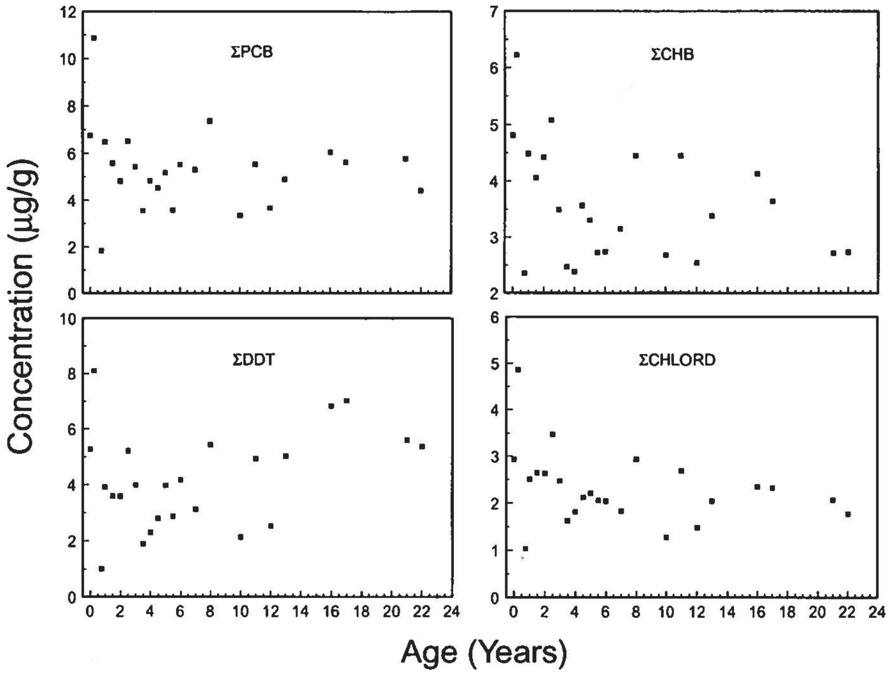


Fig. 2. Relationships between age and the arithmetic mean concentrations (for animals of the same age) of ΣPCB, ΣDDT, ΣCHB and ΣCHLORD in blubber samples of male white whales from West Greenland.

inated biphenyls), significant ($P < 0.01$) negative correlations were observed for both age and length in female blubber samples (Table 4). In male blubber samples, dieldrin, ΣHCH and ΣTRI (trichlorinated biphenyls) were significantly negatively correlated and mirex and ΣOCTA significantly positively correlated with age and length. The p,p'-DDE/ΣDDT concentration ratio was significantly negatively correlated with age in females and the ΣDDT/ΣPCB concentration ratio significantly positively correlated with both age and length in males. In kidney samples, age was significantly ($P < 0.05$) negatively correlated with ΣCBz and ΣTRI concentrations in females and dieldrin, ΣHEXA and ΣHEPTA concentrations in males (Table 5). In contrast to what was observed

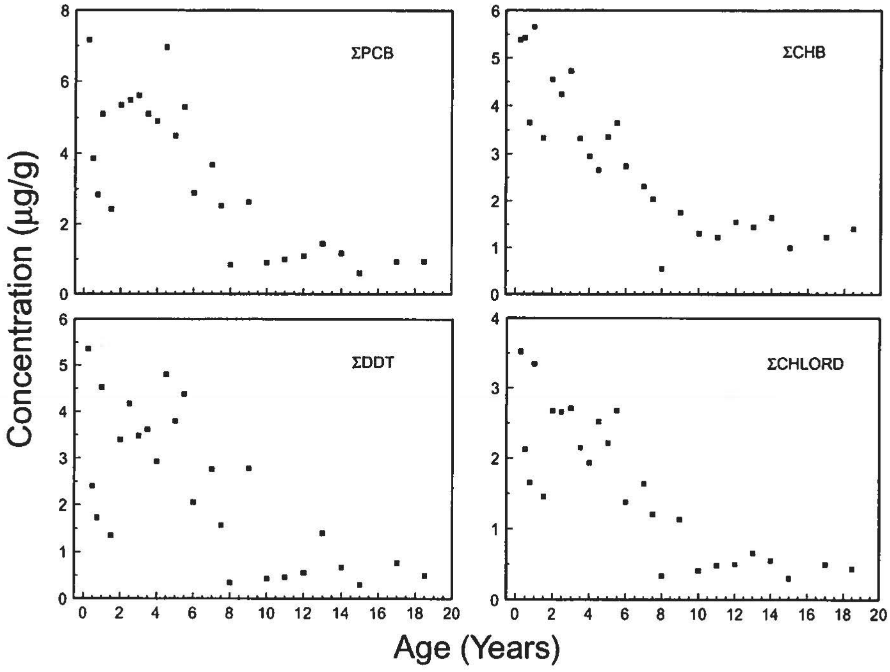


Fig. 3. Relationships between age and the arithmetic mean concentrations (for animals of the same age) of ΣPCB, ΣDDT, ΣCHB and ΣCHLORD in blubber samples of female white whales from West Greenland.

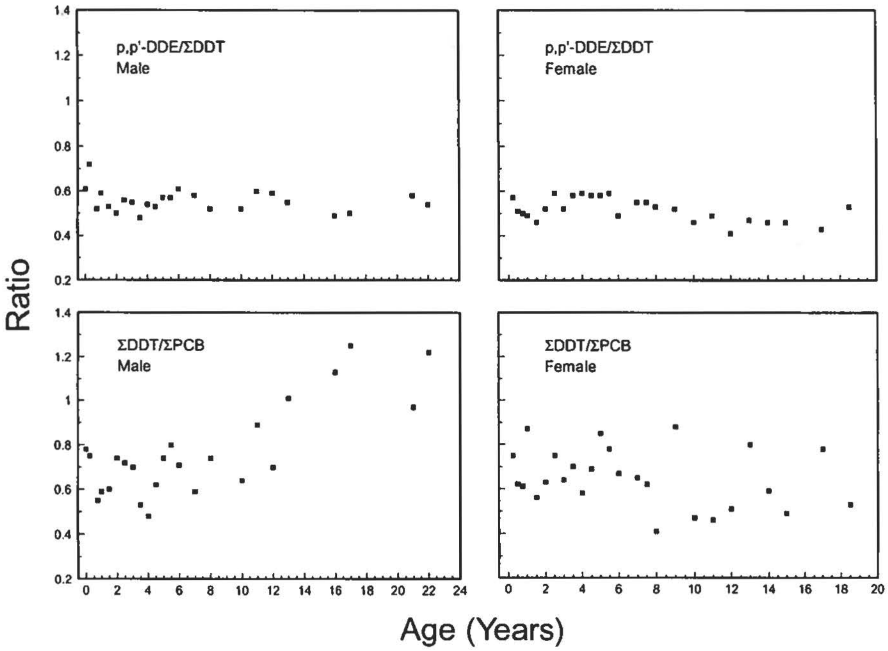


Fig. 4. Relationships between age and p,p'-DDE/ΣDDT and ΣDDT/ΣPCB in blubber samples of male and female white whales from West Greenland.

in blubber, the p,p'-DDE/ΣDDT and ΣDDT/ΣPCB concentration ratios were strongly positively and moderately negatively correlated, respectively, with age in females. No significant correlations were observed with skin samples.

Results from ANCOVA and Tukey's test, used to compare mean concentrations of selected organochlorine contaminants in female and male blubber samples with age group, are shown in Tables 6 and 7, respectively. Generally, mean concentrations in females 8 years and older (groups 5 and 6) were significantly ($P < 0.05$) lower than those in most younger animals. In addition, mean concentrations in females aged 4.5 to 7.5 years (group 4) were significantly lower ($P < 0.05$) than those observed in animals 2.5 years and younger (groups 1 and 2). For γ-HCH, ΣHCH, ΣCBz and ΣCHB, females aged 3.0 to 4.0 years (group 3) had significantly lower mean concentrations than did those which were 1 year of age and younger (group 1). In males, few contaminants showed any significant differences in mean concentration with age group. When observed, however, differences between the youngest and oldest animals predominated.

Pattern similarities and differences between the mean concentrations of 91 individual PCB and organochlorine contaminants in blubber samples with age group (Table 1) and sex were examined using PCA. Using cross vali-

Table 4. Correlations of organochlorine concentrations (wet weight) with age and length in white whale blubber samples from West Greenland.

Sex	N	Factor	DIELD	MIREX	ΣCHB	ΣDDT	ΣCHLORD	ΣHCH	ΣCBz	ΣPCB
M	71	Age	−0.325*	0.461*	−0.272	0.108	−0.254	−0.473*	−0.213	−0.136
	60	Length	−0.358*	0.485*	−0.221	0.105	−0.217	−0.544*	−0.252	−0.122
F	67	Age	−0.699*	−0.118	−0.720*	−0.545*	−0.703*	−0.716*	−0.666*	−0.658*
	64	Length	−0.613*	−0.208	−0.606*	−0.490*	−0.586*	−0.596*	−0.589*	−0.525*

Sex	N	Factor	ΣTRI	ΣTETRA	ΣPENTA	ΣHEXA	ΣHEPTA	ΣOCTA	DDE/ΣDDT	ΣDDT/ΣPCB
M	71	Age	−0.419*	−0.093	0.259	0.008	0.198	0.602*	−0.008	0.528*
	60	Length	−0.439*	−0.100	0.281	0.030	0.269	0.579*	−0.036	0.454*
F	67	Age	−0.625*	−0.663*	−0.651*	−0.601*	−0.517*	−0.183	−0.417*	−0.099
	64	Length	−0.582*	−0.545*	−0.484*	−0.485*	−0.414*	−0.160	−0.295	−0.204

* Correlation coefficient significant at $P < 0.01$

Table 5. Correlations of organochlorine concentrations (wet weight) with age (newborn to 5 years) in white whale kidney and skin samples from West Greenland.

Sample	Sex	N	DIELD	ΣCHB	ΣDDT	ΣCHLORD	ΣHCH	ΣCBz	ΣPCB	ΣTRI
Skin	M	10	−0.156	−0.179	−0.117	−0.161	−0.214	−0.222	−0.387	−0.110
	F	9	−0.079	0.075	−0.015	−0.083	−0.473	−0.426	−0.095	−0.653
Kidney	M	10	−0.743*	−0.379	−0.686	−0.595	−0.575	−0.573	−0.651	−0.151
	F	10	−0.485	−0.604	−0.591	−0.523	−0.621	−0.760*	−0.524	−0.678*

Sample	Sex	N	ΣTETRA	ΣPENTA	ΣHEXA	ΣHEPTA	ΣOCTA	DDE/ΣDDT	ΣDDT/ΣPCB
Skin	M	10	−0.439	−0.442	−0.335	−0.029	0.143	−0.481	0.361
	F	9	−0.223	−0.112	0.073	0.052	0.441	0.274	0.047
Kidney	M	10	−0.601	−0.627	−0.662*	−0.719*	−0.596	−0.039	−0.009
	F	10	−0.567	−0.567	−0.424	−0.424	−0.417	0.717*	−0.560

* Correlation coefficient significant at $P < 0.05$

dation, it was determined that the first and second principal components accounted for 38.7 and 27.4%, respectively, of the total variability in the data set. The most notable feature in the resulting score plot (Fig. 5A) is the alignment of the female and male age groups along the first and second principal component axis, respectively. Two distinct clusters are apparent. The first consists of males aged 4 years and younger (groups 1–3) and females aged 1.5 to 4 years (groups 2 and 3). The second cluster consists of males and females aged 4.5 to 7.5 years (group 4). For animals 8 years of age and older (groups 5 and 6) different contaminant profiles are evident in each age group as well as with sex. These results correspond well with those presented earlier (Tukey's test). The importance of individual contaminants in determining the positions of age groups and clusters of age groups along the principal component axes is partially explained by the principal component loading plots (Fig. 5B-D). The loading plot depicting individual OC's only (Fig. 5B) shows that males 8 years and older (groups 5 and 6) are characterized by higher proportions of DDT related compounds, some chlordane-related compounds and mirex. In fe-

Table 6. Comparison between mean concentrations of selected organochlorine contaminants in female blubber samples with age group[†] (comparison significant at $P < 0.05$).

Residue	F Value	R^2	Significantly different age groups
α-HCH	6.20	0.44	GR5<2; GR1>6,5,4,3
β-HCH	9.39	0.54	GR6<4,3,2,1; GR5<4,3,2,1; GR4<2
γ-HCH	10.42	0.57	GR6<3,1; GR5<3,2,1; GR4<2,1; GR3<1
OXYCHLORD	7.90	0.50	GR6<3,2,1; GR5<4,3,2,1; GR4<1
t-CHLORD	3.39	0.30	GR5<2,1; GR4<1
c-CHLORD	4.47	0.37	GR1>6,5,4,3,2
t-NONA	9.12	0.53	GR6<4,3,2,1; GR5<3,2,1
c-NONA	15.62	0.66	GR6<3,2,1; GR5<4,3,2,1; GR4<3,2,1
DIELD	10.84	0.58	GR6<3,2,1; GR5<4,3,2,1; GR4<2,1
p,p'-DDE	4.86	0.38	GR6<3,2; GR5<4,3,2,1
ΣCHLORD	10.49	0.57	GR6<3,2,1; GR5<4,3,2,1; GR4<1
ΣHCH	11.62	0.59	GR6<3,2,1; GR5<4,3,2,1; GR4<2,1; GR3<1
ΣCBz	12.60	0.61	GR6<3,2,1; GR5<3,2,1; GR4<2,1; GR3<1
ΣCHB	13.16	0.62	GR6<3,2,1; GR5<4,3,2,1; GR4<2,1; GR3<1
ΣDDT	5.43	0.40	GR6<3,2,1; GR5<4,3,2,1
ΣPCB	9.16	0.53	GR6<4,3,2,1; GR5<4,3,2,1
ΣTRI	8.16	0.51	GR6<2,1; GR5<3,2,1; GR4<2,1
ΣTETRA	7.53	0.49	GR6<3,2,1; GR5<4,3,2,1
ΣPENTA	9.78	0.55	GR6<3,2,1; GR5<4,3,2,1; GR4<3
ΣHEXA	7.60	0.49	GR6<4,3,2,1; GR5<4,3,2,1
ΣHEPTA	5.55	0.41	GR6<3,2; GR5<4,3,2
ΣOCTA	2.46	0.23	GR5<3
DDE/ΣDDT	4.34	0.35	GR6<4,3; GR5<4,3

[†] For group definition see Table 1.

Table 7. Comparison between mean concentrations of selected organochlorine contaminants in male blubber samples with age group[†] (comparison significant at $P < 0.05$).

Residue	F Value	R^2	Significantly different age groups
β-HCH	4.95	0.40	GR6<2,1; GR5<2,1; GR4<1
γ-HCH	4.87	0.40	GR5<2,1; GR4<2,1
c-CHLORD	2.63	0.26	GR6>4,3,2
c-NONA	5.70	0.43	GR5<1; GR2>6,5,4
p,p'-DDT	3.42	0.32	GR6>5,4,3,2,1
MIREX	3.78	0.34	GR6>4,3,2,1
ΣHCH	4.15	0.36	GR5<2,1; GR4<1
ΣTRI	3.40	0.31	GR1>6,5,4
ΣOCTA	5.93	0.44	GR6>4,3,2,1; GR5>1
ΣDDT/ΣPCB	4.34	0.37	GR6>4,3,2,1

[†] For group definition see Table 1.

males o,p'-DDT, p,p'-DDT, p,p'-DDD and mirex are predominant in the older animals while higher proportions of p,p'-DDE are found in animals aged 7.5 years and younger (group 1–4). Females 8 years and older (groups 5 and 6) are distinguished from younger females and older males (> 4 years) by greater loadings of higher chlorinated OC's (ΣCHB, *cis–* and *trans*-chlordane and OCS) as well as 1,2,3,4- and 1,2,4,5-T_4CBz, P_5CBz and α-HCH. In males and females OC's such as *cis–* and *trans*-nonachlor, β- and γ-HCH, HCBz and dieldrin are most predominant in animals younger than 7.5 years (groups 14).

Five distinct clusters of PCB's are observed in the loading plots in Figs. 5C and 5D. Moving clockwise,

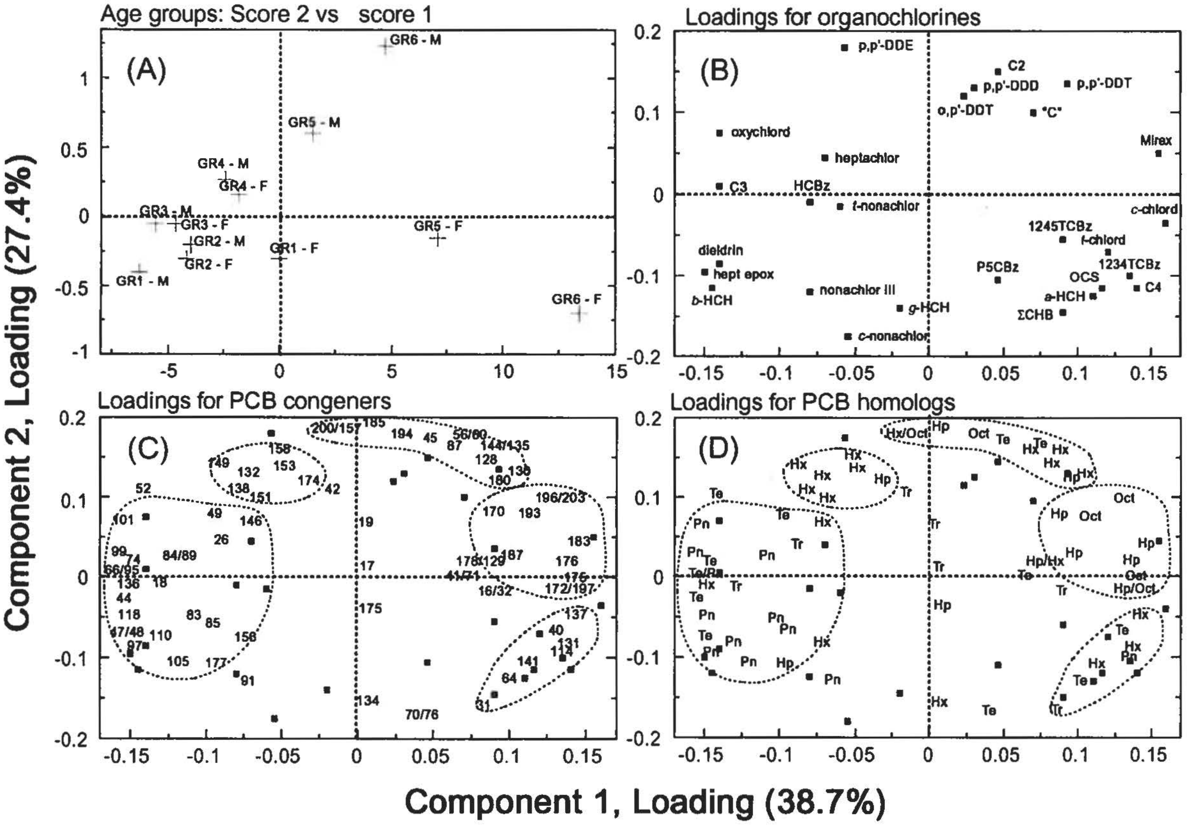


Fig. 5. (A) Score plot of principal components 1 and 2 for 91 individual OC's and PCB contaminants in the blubber of white whales from West Greenland showing similarities and differences between age group and sex. Loading plots for data in (A) showing (B) OC's (C) PCB congeners and (D) PCB homologs. Generally, the higher chlorinated OC's and PCB's are more predominant in male and female animals above the age of 15 years (group 6).

Table 8. Concentrations (mean ± standard deviations) of major organochlorines in blubber from Greenland and Canadian waters (µg/g wet weight).

Location	Sex	Age (years)	N	ΣPCB	ΣDDT	ΣCHB	ΣCHLORD
Nuussuaq/	M	5.2±4.7	71	5.38±2.27	4.06±2.50	3.69±1.46	2.41±1.08
Disko Bugt*	F	6.3±4.6	67	3.74±2.31	2.69±1.94	3.01±1.62	1.79±1.11
Jones Sound	M	4.4±2.2	8	2.53±0.57	1.96±3.20	4.25±1.02	1.87±0.44
	F	4.6±2.9	7	2.46±1.98	2.19±1.69	3.74±2.12	1.84±1.13
Cumberland	M	7.3±6.5	6	4.91±0.25	6.83±1.89	5.78±5.39	2.38±0.40
Sound	F	8.1±7.3	6	1.15±0.41	0.93±0.55	1.77±1.76	0.62±0.15
West Hudson	M	13.0±4.8	4	3.12±0.34	3.13±0.20	5.10±0.42	2.33±0.26
Bay	F	10.3±4.1	4	0.96±1.00	0.85±0.96	1.77±0.41	0.85±0.80
East Hudson	M	12.0±9.5	8	2.77±0.51	2.27±0.68	4.13±0.82	1.86±0.35
Bay	F	11.9±6.4	8	1.23±0.84	0.98±0.73	1.99±1.10	0.87±0.58

* Preliminary statistical results indicated that the mean concentrations of all major organochlorine groups were not significantly different between Nuussuaq and Disko groups for males or females (using the Student t-test at $P < 0.05$). Results from both regions were therefore combined.

cluster 1 consists primarily of tetra and pentachlorobiphenyl congeners which are predominant in males less than 7.5 years of age (groups 1–4) and in females 1.5 to 7.5 years old (groups 2–4). Cluster 2 consists almost exclusively of hexachlorobiphenyl congeners which are most significant in males 4.5 to 15 years old (groups 4 and 5) and in females 7.5 years old and younger (groups 1–4). Cluster 3 is comprised of a mixture of tetra- through to octachlorinated PCB congeners which are predominant in males older than 15 years (group 6) and in females 1 year and younger (group 1) and 8 years and older (groups 5 and 6). Cluster 4 consists of hepta- and octachlorinated PCB congeners which are predominant in older females (groups 5 and 6) and in males aged 1.5 to 15 years (groups 2–5). Finally, cluster 5 consists of a mixture of tri- through to hexachlorinated PCB's. This group of congeners is most significant in females 8 years of age and older (groups 5 and 6) and in males 2.5 years old and younger (groups 1 and 2).

Discussion

Geographical variation in element concentrations

The major organochlorine contaminants in all white whale blubber samples were ΣPCB ΣCHB, ΣDDT (mainly p,p'-DDE) and ΣCHLORD (mainly *trans*nonachlor and oxychlordane). ΣHCH, chlorobenzenes (ΣCBz; tetra-, penta- and hexachlorobenzene) and dieldrin were present at lower concentrations than the four major groups. The results (mean ± standard deviation) for ΣCHLORD, ΣDDT, ΣPCB and ΣCHB are presented in Table 8 along with published results from other locations (Muir *et al.* 1990). Mean concentrations of ΣPCB and ΣDDT in males from Nuussuaq and Disko Bugt were significantly higher than those in males from Jones Sound and East and West Hudson Bay (Student's t-test at $P < 0.01$) but were not statistically different from levels in Cumberland Sound animals. This may be partly attributed to differences in dietary exposure to organochlorines between whales inhabiting the Davis Strait/Baffin Bay area and those inhabiting the generally shallower waters of Hudson Bay and Hudson Strait. Greenland halibut (*Reinhardtius hippoglossoides*), for example, which are important prey for white whales in West Greenland (Degerbøl & Nielsen 1930, Kleinenberg *et al.* 1969), are widely distributed from the Gulf of St. Lawrence to Baffin Bay but are not found in the shallower waters of Hudson Strait. In females significantly higher levels ($P < 0.01$) of ΣPCB, ΣDDT and ΣCHLORD were observed in animals from Nuussuaq and Disko Bugt compared to those from Cumberland Sound and Hudson Bay. Although dietary exposure may account for some of the variation among stocks, decreasing levels of contamination with age, due to lactational transfer to offspring, is most likely the major contributing factor. Animals from Cumberland Sound and Hudson Bay were older, on average, than those from Nuussuaq and Disko Bugt.

Transference of contaminants to offspring

With the exception of animals from Jones Sound (which were all juveniles), mean concentrations of ΣDDT and ΣPCB were significantly lower in females than in males (t-test at $P < 0.01$). This difference in tissue burden is the result primarily of lactational transfer of persistent organochlorines to offspring and, secondarily of placental transport from female lipid tissue to foetus (Addison & Brodie 1977, Duinker & Hildebrand 1979, Reijnders

Table 9. Mean, ranges and male-female differences in the concentrations (µg/g wet weight) of ΣPCB and p,p'-DDE in marine mammals.

Species	Sex	N	Concentration† (µg/g wet weight)		Male-Female differences‡		Lactation period (months)
			ΣPCB	p,p'-DDE	ΣPCB	p,p'-DDE	
Baird's beaked whale*	M	13	3.6	14			
Berardius bairdii			[2.0–5.1]	[9.5–19]			
	F	7	2.0	7.8	55	52	< 6
			[1.5–2.8]	[4.1–17]			
Minke whale*	M	10	0.02	0.09			
Balaenoptera acutorostrata			[0.01–0.03]	[0.08–0.14]			
	F	11	0.008	0.04	40	43	3–6
			[0.003–0.02]	[0.01–0.08]			
White whale	M	30	5.0	2.4			
Delphinapterus leucas			[1.5–8.7]	[0.72–6.0]			
	F	36	2.3	0.96	46	40	< (12)§
			[0.47–8.5]	[0.01–4.2]			
Dall's porpoise*	M	14	12	12			
Phocoenoides dalli			[7.1–16]	[6.6–15]			
	F	13	2.8	4.1	23	34	8–18
			[1.0–4.0]	[1.3–7.2]			
Striped dolphin*	M	21	32	39			
Stenella coeruleoalba			[15–56]	[21–60]			
	F	3	4.7	4.0	15	11	18
			[1.5–6.7]	[0.79–5.8]			

* Subramanian *et al.* (1987).
† Mean/[range]. Values include those of adult specimens only.
‡ Percentage of ΣPCB and p,p'-DDE concentrations in females to those of males.
§ Calculated lactation period from the relationship between male-female difference and lactation period.

1980, Wagemann & Muir 1984, Subramanian *et al.* 1988, Boon *et al.* 1992). Previous studies have shown that the differences in ΣPCB and p,p'-DDE levels between adult males and adult females can vary widely among species of cetacean and that the male-female differences are negatively correlated with the length of lactation periods (Subramanian *et al.* 1987). For example the lactation period for every parturition is relatively short (3–6 months) in the minke whale (*Balaenoptera acutorostrata*) (Stewart & Leatherwood 1985). The ΣPCB and p,p'-DDE levels in females of this species were 40 and 43%, respectively, of those in males of corresponding ages (Subramanian *et al.* 1987). In comparison the lactation period of female striped dolphins (*Stenella coeruleoalba*) is 18 months (Miyazaki 1981) and the male-female differences in ΣPCB and p,p'-DDE levels were only 15 and 11%, respectively (Subramanian *et al.* 1987). Comparing the male-female percentages of ΣPCB and p,p'-DDE in white whales (46 and 40%, respectively) with four other cetaceans, a lactation period of less than 1 year could be inferred (Table 9). This estimate is in agreement with that of Vladykov (1944) and Kleinenberg *et al.* (1969), but is much shorter than the more recently suggested 2 year period (Brodie 1971, Sergeant 1973, Burns & Seaman 1985, Heide-Jørgensen & Teilmann 1994).

A lactation period, with the main transferance within a year or less is also implied by the relationships between age and the arithmetic mean concentrations (for animals of the same age) of ΣPCB, ΣDDT, ΣCHB and ΣCHLORD (Figs. 2 and 3). Highest residue levels were observed in 3-month old males and females. Dramatically lower levels were observed in animals 6 and 9 months of age. These results suggest that the diet of calves consists solely of milk during the first 3 months and that milk is possibly supplemented by easily captured prey during the next few months. The young whales would become nutritionally independent from their mothers at about 9 months of age. The observed drop in residue levels might also be attributed partially to the rapid growth (and subsequent dilution of contaminant levels) that occurs during the first year of age (Brodie 1971, Heide-Jørgensen & Teilmann 1994). Residue levels had returned to pre-nursing levels in animals aged 1 to 2 years. After age 5.5 a sharp decrease in the levels of all four major contaminant groups was observed in females compared to only marginal differences in ΣPCB, ΣCHB and ΣCHLORD concentrations and a substantial increase in –DDT in males. This result is consistent with the age of attainment of sexual maturity in females and commencement of lactation (Brodie 1971, Heide-Jørgensen & Teilmann 1994). If one looks closely at the ΣPCB, ΣDDT and ΣCHLORD contaminant levels in females 6 years and older, mean concentrations seem to peak at 7, 9, 13 and 17 years, suggesting somehow synchronously parturition at two-year intervals in the early years of an animal's reproduc-

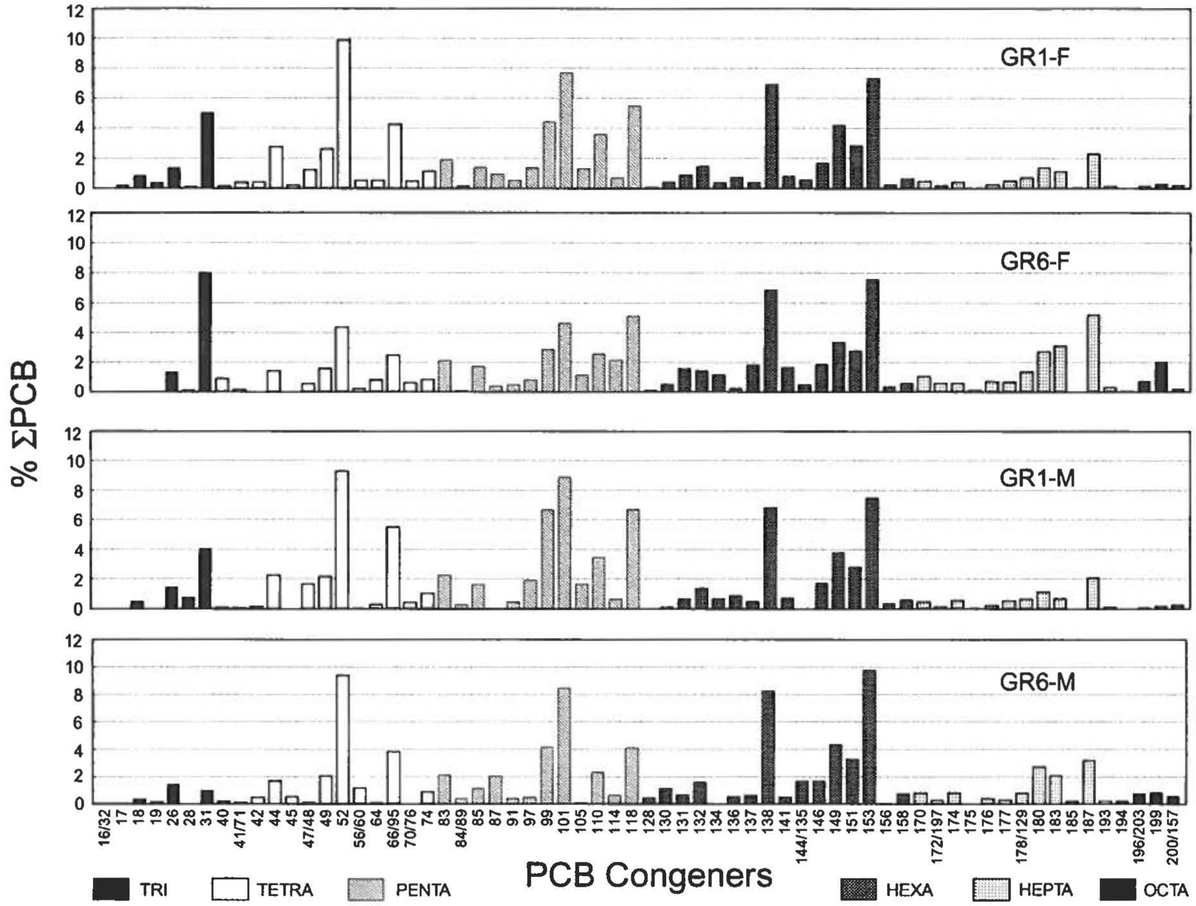


Fig. 6. PCB congeners expressed as a percent of ΣPCB in blubber samples of male and female white whales 1 year old and younger (Group 1) and 15 years and older (Group 6).

tive life and a lengthening resting period between parturitions to 4 years as the animal gets older (for an average parturition frequency overall of approximately 3 years). Evidence supporting this observation is very weak, however, since no significant differences were observed (t-test at $P < 0.05$) between mean concentration levels at

Table 10. Comparison of ratios of blubber to skin and of blubber to kidney organochlorine concentrations in male white whales from West Greenland, as measured on a wet and lipid weight basis.

	Wet weight basis				Lipid weight basis			
	Blubber/Skin		Blubber/Kidney		Blubber/Skin		Blubber/Kidney	
Age	ΣPCB	ΣDDT	ΣPCB	ΣDDT	ΣPCB	ΣDDT	ΣPCB	ΣDDT
0.0	10.68	8.29	53.53	58.19	1.24	0.96	1.43	1.56
1.0	15.18	8.38	50.21	51.60	1.11	0.61	2.13	2.19
1.5	30.67	24.07	120.39	66.45	1.45	1.14	3.58	1.98
2.0	12.80	8.19	38.46	39.79	1.06	0.67	0.81	0.83
2.0	6.36	4.46	82.00	88.08	0.86	0.61	1.55	1.67
2.0	9.68	4.24	137.97	106.54	2.42	1.06	4.55	3.51
2.5	14.67	9.71	64.45	54.78	2.07	1.37	2.01	1.71
3.0	12.17	7.31	64.90	58.87	1.55	0.93	2.02	1.83
3.0	12.21	8.70	53.74	43.68	0.94	0.67	2.34	1.90
4.5	11.47	5.14	101.16	93.98	1.27	0.57	1.70	1.58
Mean	13.59	8.85	76.68	66.20	1.40	0.86	2.21	1.88

Table 11. Comparison of ratios of blubber to skin and of blubber to kidney organochlorine concentrations in female white whales from West Greenland, as measured on a wet and lipid weight basis.

	Wet weight basis				Lipid weight basis			
	Blubber/Skin		Blubber/Kidney		Blubber/Skin		Blubber/Kidney	
Age	ΣPCB	ΣDDT	ΣPCB	ΣDDT	ΣPCB	ΣDDT	ΣPCB	ΣDDT
0.25	8.11	5.82	28.79	21.29	0.98	0.70	0.90	0.67
0.50	16.34	8.59	15.18	11.95	1.26	0.66	1.13	0.89
0.75	10.08	4.76	12.29	8.28	1.18	0.56	0.78	0.53
1.0	10.63	8.51	32.92	29.64	1.11	0.77	1.16	1.04
1.5	8.10	3.92	19.14	12.74	1.33	0.65	1.26	0.84
2.0	25.25	24.04	45.80	47.09	1.51	1.44	1.32	1.35
2.5	6.85	4.39	21.78	19.05	0.96	0.61	0.96	0.84
3.0	–	–	26.95	26.57	–	–	0.92	0.91
3.0	13.50	8.42	50.00	33.27	1.83	1.15	1.96	1.31
3.5	8.15	3.87	19.40	16.21	1.25	0.59	1.14	0.95
Mean	11.89	8.04	27.23	22.61	1.27	0.79	1.27	0.93

yearly intervals (*i.e.* between 6 and 7, 7 and 8 year olds etc.) due to limited numbers of identical year classes.

Contaminant ratios

The mean p,p'-DDE/ΣDDT ratios determined from the blubber of males and females were 0.56–0.05 and 0.52–0.05, respectively. These ratios were comparable to those from Hudson Bay and Jones Sound, but were significantly lower than those from the St. Lawrence River and higher than those from the Beaufort Sea (Muir *et al.* 1990). Ratios for the kidney of males and females are, respectively, 0.60–0.03 and 0.56–0.05. p,p'-DDE/ΣDDT ratios approaching 0.6 imply that no recent significant input of DDT has occurred in Baffin Bay/Davis Strait waters (Aguilar 1984). In young white whales of both sexes (Fig. 4) the p,p'-DDE/ΣDDT ratio is highest when they begin to be suckled as newborn calves, drops off at the beginning of the weaning period and increases once again when they are nutritionally independent from their mothers. The higher ratio in suckling calves suggests that proportionally more p,p'-DDE is transfered to offspring during lactation. Similar results were observed in a study of fur seals (Kurtz & Kim 1976) where it was found that blubber of nursed pups had a higher p,p'-DDE/ΣDDT ratio (90%) than blubber of mothers with yearlings (60%)

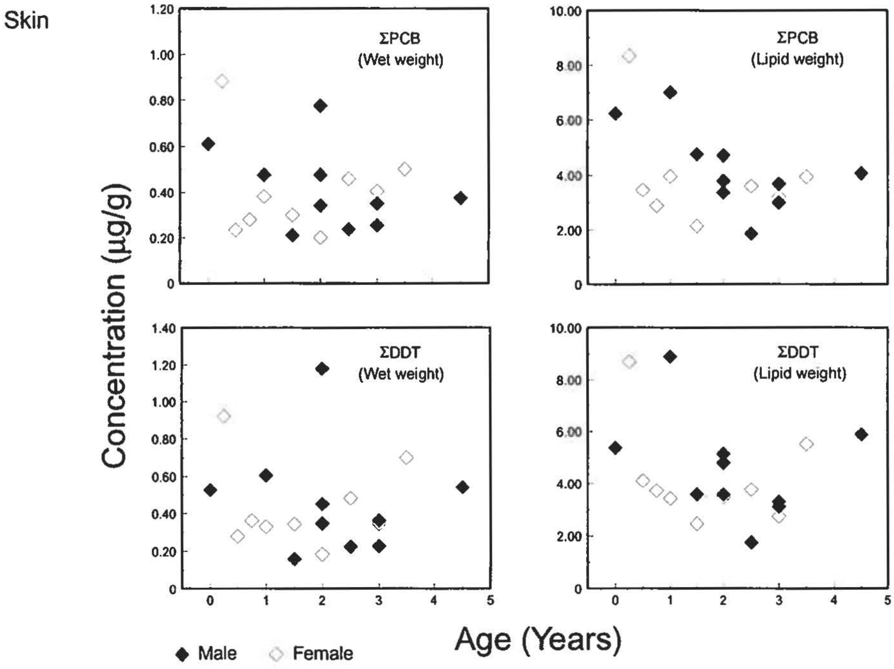
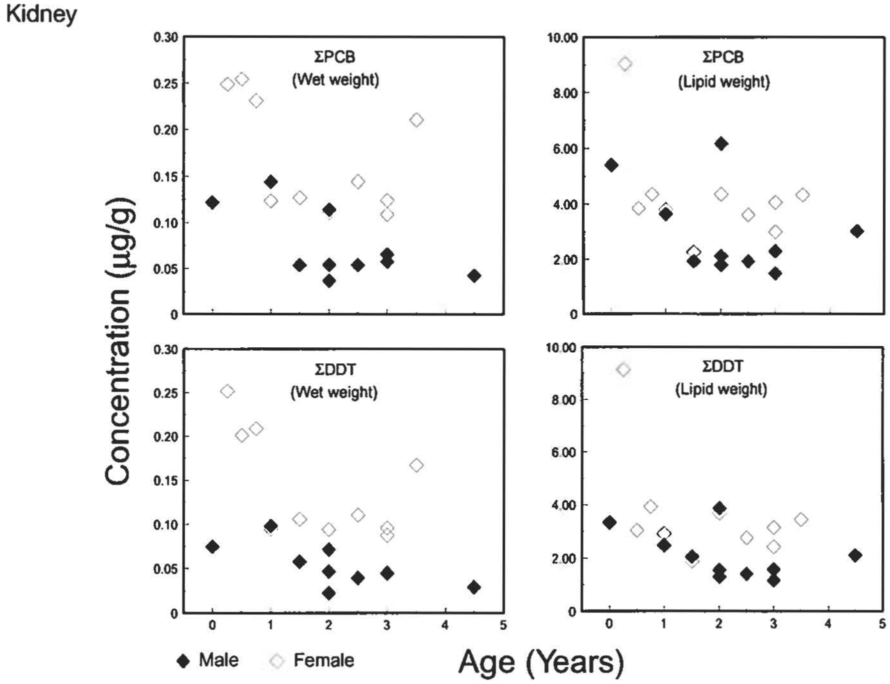


Fig. 7. Relationships between concentrations (wet and lipid weight) of ΣPCB and ΣDDT with age (5 years and younger) in skin samples from male and female white whales from Nuussuaq.

Fig. 8. Relationships between concentrations (wet and lipid weight) of ΣPCB and ΣDDT with age (5 years and younger) in kidney samples from male and female white whales from Nuussuaq.



of the same population. Lower water solubility and higher lipophilicity (octanol-water partition coefficient) of a compound should reduce the reproductive-transfer rate to offspring. The above results, therefore, are not surprising since the water solubility of p,p'DDE is approximately 10 times that of p,p'-DDT (Suntio *et al.* 1988). As young white whales become nutritionally independent and continue to mature, their diet progresses from easily captured prey such as molluscs, annelids and crustacea to larger items higher in the food chain such as squid and various fish species (Kleinenberg *et al.* 1969, Brodie 1971, Heide-Jørgensen & Teilmann 1994). Relative proportions of p,p'-DDE to ΣDDT have been shown to increase from lower to higher trophic levels (Jensen *et al.* 1969, Tanabe *et al.* 1984), suggesting, that the observed rise in levels of p,p'-DDE relative to ΣDDT beginning at the end of the weaning period might in part be due to a change in diet. Consistent with the previous findings of p,p'-DDE/ΣDDT variation in the blubber of fin (*Balaenoptera physalus*) and sei whales (*Balaenoptera borealis*) (Borrell & Aguilar 1987, Aguilar & Borrell 1988) and of St. Lawrence white whales (Martineau *et al.* 1987), an increasing p,p'DDE/ΣDDT ratio might also be attributed to the corresponding rise in organochlorine levels. Higher tissue pollutant levels induce enzymatic activity and result in proportionally higher abundances of metabolized forms. Once females reach sexual maturity, a gradual decrease in the p,p'-DDE/ΣDDT ratio with age is observed due to preferential excretion of p,p'-DDE during lactation. In males the proportions of p,p'-DDE and ΣDDT remain fairly constant, suggesting a trend toward equilibrium between the rate of pollutant intake and subsequent degradation of DDT to p,p'-DDE.

The ΣDDT/ΣPCB ratio shows a substantial increasing trend with age (and with pollutant burdens) in males and only a marginal change in females, resulting in higher overall ratios in adult males than in adult females (Fig. 4). As with p,p'-DDE/ΣDDT, this ratio is similar in immature whales of both sexes but differs in adults. As shown earlier in Fig. 3, both ΣDDT and ΣPCB levels decrease substantially with age in sexually mature females. The drop in ΣDDT levels is due primarily to preferential unloading of p,p'-DDE while the decrease in ΣPCB is attributed to preferential elimination of the tri, tetra and pentachlorinated congeners (Tanabe *et al.* 1982, Subramanian *et al.* 1988). While the ΣPCB levels seem to change only marginally with increasing age in adult males, a substantial increase in ΣDDT is observed and is thus accountable for the observed increasing trend in the ΣDDT/ΣPCB ratio.

Among the 64 PCB congeners routinely detected in white whale blubber (Fig. 6) (coeluting congeners are considered as a single component here), the relative proportions of the normally recalcitrant hexa, hepta and octochlorobiphenyls (*i.e.* those having either no adjacent unsubstituted positions or those with unsubstituted *ortho-meta* (*o,m*) positions with more than one *ortho*-chlorine substituent), as well as those which are unsubstituted at the *meta-para* (*m,p*) positions (the above two categories account for all the hexa, hepta and octachlorobiphenyls detected with the exception of PCB 156) were generally either higher or remained unchanged in animals (male and female) 15 years and older (group 6) compared to that of the corresponding congeners in animals 1 year old and younger (group 1). The reduced capability for biotransformation in the latter category of PCB's is thought to be due to the relatively low activity of cytochrome P450 monooxygenase enzymes which are responsible for CYP2B-type metabolism (Boon *et al.* 1989, Boon *et al.* 1992, Norstrom *et al.* 1992). A different trend is observed for the lower chlorinated congeners (*i.e.* tri, tetra and pentachlorobiphenyls). In this case, especially in females, greater relative proportions are generally observed in the younger animals. In females this is attributed to the preferential elimination of these PCB's during lactation and to the fact that a larger proportion of lesser chlorinated PCB's possess vicinal hydrogens in the *metapara* position in combination with only one *ortho*-chlorine substituent (*i.e.* they are more easily metabolized). In males only the latter explanation is relevant thus accounting for the reduction in observed relative differences compared to the females.

In agreement with our results, ΣPCB, ΣDDT and ΣCHLORD concentrations in the blubber of white whales from the Hudson Bay region were found to be negatively correlated with age and length in females (Muir *et al.* 1990). In contrast to our results however, the levels of these contaminants in the blubber of female white whales from the St. Lawrence estuary were found to be strongly positively correlated with age (Martineau *et al.* 1987, Muir *et al.* 1990). A positive correlation with age in sexually mature females suggests that contaminant intake exceeds contaminant loss during reduced or non-occuring lactation. This result is consistent with the much higher level of exposure of St. Lawrence white whales to PCB's and other pollutants compared to that of arctic white whales (Muir *et al.* 1990) and to possible reproductive dysfunction (Martineau *et al.* 1987, Addison 1989).

Tissue comparisons

On a wet-weight basis ΣPCB and ΣDDT levels were 4 to 140 times higher in blubber than in skin and kidney. However when expressed on a lipid weight basis the distribution of these contaminants approached proportionality with tissue fat content (Tables 10 and 11). As was also observed in St. Lawrence white whales (Martineau *et al.* 1987) ΣPCB and ΣDDT concentration in males were approximately two times lower in the kidney than in the blubber. Figs. 7 and 8 demonstrate the relationship between age and concentration of ΣPCB and ΣDDT in skin and kidney, respectively, on a wet- and lipid-weight basis for both males and females. The highest contaminant levels observed in kidney and skin of females occurred at approximately 3 months of age. Unfortunately kidney and skin samples from the male of the same age were not analysed. However since ΣPCB and ΣDDT levels were highest in blubber of the same animal and a certain proportionality has been shown to exist between contaminant levels in blubber and skin and kidney, it is not unreasonable to expect that correspondingly high levels would have been observed in this individual.

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