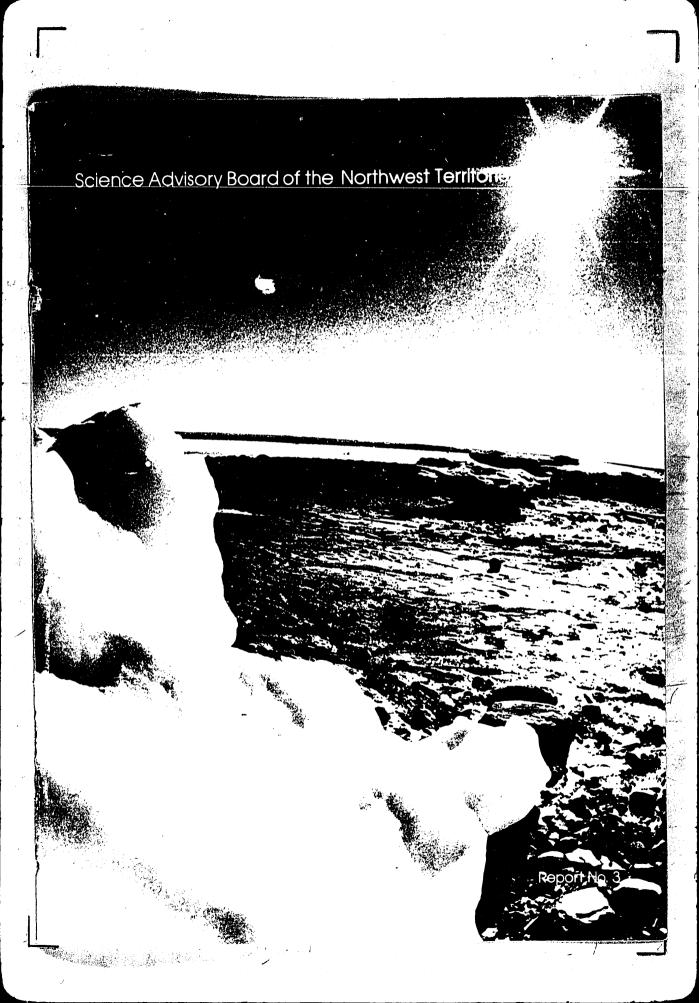
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THE PRESENT STATUS AND FUTURE MANAGEMENT OF ARCTIC MARINE MAMMALS IN CANADA

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FOREWORD

The exploitation of marine mammals has been a dominant human activity in the coastal Northwest Territories during the entire period of human settlement here. Although the archaeological record is not definitive; it may have been the pursuit of marine mammals that was responsible for three distinct waves of immigration from Alaska. The Thule from which the present Inuit are descendent arrived approximately 1,000 years ago in pursuit of large whales. It was these same large whales that introduced the European culture to the coastal inuit in both the Eastern and Western Arctic. Although the quest for the Northwest Passage first brought the two cultures into contact it was undoubtedly the whalers that introduced the greatest changes to the coastal inuit before the expansion of the Hudson's Bay Company to most coastal regions of the Northwest Territories under human settlement. Although the Hudson's Bay Company was primarily interested in furs, they operated a whaling station at Pangnirtung until 1958.

Although commercial whaling similar to that of the late 19th century is no longer practised in the Northwest Territories by southern or foreign interests, whaling remains a significant practise in many coastal communities. Seals on the other hand seem to have replaced whales as the prime source of income for many Inuit. The sale of seal pelts brought more revenue to the Northwest Territories than any other fur bearing species in 8 of 16 consecutive years ending in 1977. The current interest in promoting inter-settlement trade of edible marine mammal products should promote the return to complete utilization of seal and whale carcasses as in former times.

This paper is intended to familiarize the reader with the ecological relationship between arctic marine mammal resources and their environment. The authors were encouraged to comment on the scientific and administrative status of current marine mammal management efforts. While this paper reflects the views of the authors, The Science Advisory Board is pleased to publish and distribute this work in order to promote a better understanding of these valuable northern resources.

Ben A. Hubert Executive Secretary Science Advisory Board of the Northwest Territories Yellowknife, Northwest Territories January, 1980

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INTRODUCTION

The principal aim of this report is to review the available information on marine mammals in the Canadian Arctic with respect to the future management of these species. Implicit in this report is the realization that the inuit population is increasing and, despite social changes, there will be pressure for increased harvests of marine mammals. In order to evaluate the potential for increased harvests, it is necessary to assess the state of current knowledge and management practices. With this information, data gaps can be identified and recommendations for filling these gaps can be made.

An imprecise but nevertheless important distinction needs to be made between the historic and future roles of management in the Arctic. Up to the present, management has been based on protecting the resource while providing a sustainable annual harvest during a period when, generally, the level of harvesting activity has been declining. Management at this level can be successful with relatively unsophisticated and imprecise information. However, given the probable increases in demand for marine mammals, it is necessary to estimate what the possible and optimum yield levels are for each species and how these harvests should be distributed geographically. This requires that management philosophy be changed from reacting to local overharvesting and halting the consequent population declines to a more forward-looking philosophy based on ecological knowledge. An objective of this approach should be to estimate ultimate optimum yield levels (recognizing that these are difficult to define) and to manage the populations in ways consistent with these estimates. Population and ecological modelling techniques need to be applied in order to provide information needed for social planning by the harvesters.

The tone of the report that follows is generally negative. Our purpose is to identify information gaps of importance for future management and we tend to downplay those areas where knowledge is sufficient for present management.

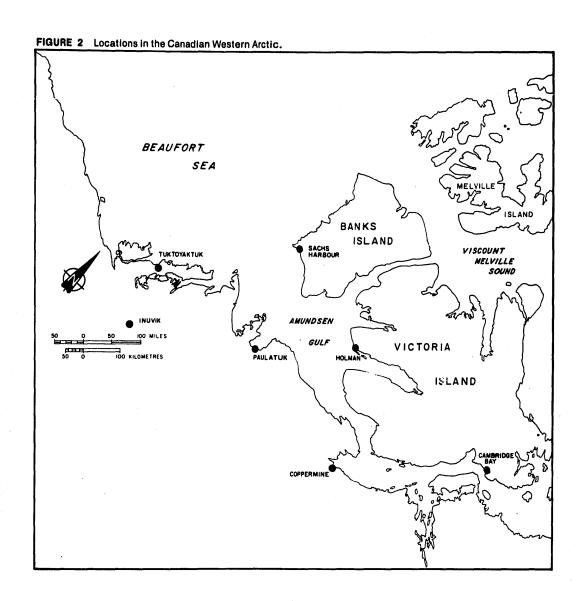
We begin this report with an overview of current knowledge of primary and secondary production processes in arctic marine systems. We then discuss available knowledge of the diets of arctic marine mammals and the major food chains that have been identified. The main body of the report consists of a review of the types of information required for management of marine mammal populations and an assessment of the adequacy of this information for each of the principal marine mammal species in the Canadian Arctic. This section of the report is fairly detailed since in several instances we question the adequacy of the data and/or disagree with the interpretation that has been applied to the data. In some cases, the interpretations that we question have been accepted as bases for management strategies and we feel that it is important that we present the reasons for our disagreement so that others can evaluate each side of the case.

The final sections of the report include a discussion of the concept of maximum sustained yield, the reasons why it might be a dangerous management goal for arctic marine mammals, and a summary of the important gaps in the information required for management. These sections are followed by a series of conclusions and recommendations for research required to provide a predictive capability for future management at optimum or increased levels of harvest.

Although this report is dated 1979, the literature review is current only to the fall of 1978. Very few more recent references have been added.

Figures 1 and 2 show the locations that are frequently mentioned in this report.

FIGURE 1 Locations in the Canadian Eastern Arctic. HUDSON



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The conclusions and interpretations in this report are those of the authors. The following acknowledgements of assistance from various scientists should not be construed to indicate that these scientists agree with our conclusions. We thank D. Dowler and B. Wong of Fisheries and Marine Service, Yellowknife; N. Simmons and T. Chowns of N.W.T. Fish and Wildlife Service; R. Riewe of University of Manitoba; K. Hay, H. Silverman and G. Wenzel of McGill University; B. Kemper and N. Snow of Dept. of Indian and Northern Affairs; G. Finney of Canadian Wildlife Service; J. P. Prevett and H. G. Lumsden of Ontario Ministry of Natural Resources; and M. Fraker of F. F. Slaney and Company and LGL Ltd. for providing unpublished material and/or for discussions of some of the questions discussed in the report. We also thank A. W. Mansfield, D. E. Sergeant and T. G. Smith of the Arctic Biological Station for many educational discussions of the biology of arctic marine mammals.

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PRIMARY PRODUCTION PROCESSES

INTRODUCTION

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The primary production of living material in the biosphere is accomplished by plants and a few microorganisms such as bacteria. Plants utilize the energy in light to convert carbon dioxide and water, through the following generalized reaction, to organic (carbon) compounds suitable as constituents of living material:

$$CO_2 + H_2O + light > CH_2O + O_2$$
 (1)

This type of reaction is mediated by chlorophyll pigments and requires other substances such as nitrate, phosphate, trace metals and sometimes vitamins. These substances are termed nutrients and are essential for plant growth.

The total amount of organic material produced by a plant is termed gross production. Some of this material is lost during respiration (the use of organic material to obtain energy needed by the plant for maintenance). What remains is termed net production, which is available for cropping by herbivorous animals. in the case of marine plants some additional organic material is lost as dissolved organic matter.

In the sea, most primary production is by microscopic unicellular plants called phytoplankton. Measuring the productivity of these tiny plants in a three-dimensional, turbulent, fluid medium that covers three quarters of the globe is a formidable task. Common approaches have been to measure the amount of

Photosynthesis, and thus primary production, can be limited by one or more of many factors. The availability of certain nutrients is often a limiting factor in the sea. Measurements of nutrient concentrations in the water give an indication of an area's potential for productivity. Sunlight is rapidly absorbed by sea-water, by ice and by living and non-living particles. It is generally accepted that photosynthesis can take place to a depth where usable light intensity has decreased to one per cent of surface intensity (Lorenzen 1976). The layer of water with sufficient light to support photosynthesis is termed the euphotic zone. Figure 3 summarizes some of the main features of primary pro-

duction in arctic seas, and the following sections

oxygen liberated by the reactions of equation (1), the

change in pH resulting from the absorption of CO2 by

the plants, or the change in standing stock of

phytoplankton. The amount of chlorophyll present per

unit volume is commonly taken as an index of standing stock, but this index is not very precise. The accepted

technique at present is to add radioactive carbon (C14)

to an enclosed volume of sea-water and measure the

amount incorporated into plant tissue, with the result

expressed as carbon fixed per unit tissue per unit time, or carbon fixed per unit volume (or surface area) of

water per unit time.

describe these processes.

PRIMARY PRODUCTION PROCESSES IN ARCTIC SEAS

LIGHT

Although lack of light limits plant growth during the arctic winter, sufficient light to permit photosynthesis is available from at least March to October. During the latter period, the depth of the euphotic layer depends on ice cover and on the amount of suspended sediment and living material in the water. Rapidly varying factors such as angle of incidence of sunlight, cloud cover and wave conditions also affect the depth of the euphotic layer.

Under ice, the euphotic layer is shallow, primarily because of the attenuation of light by ice. During winter photosynthesis ceases altogether in the absence of light. Furthermore, the water column under ice is often unstable, so phytoplankton may sink below the euphotic layer at a rate fast enough to prevent rapid development of large populations even when light is available. Hence, there is low productivity and standing stock of phytoplankton under the ice in early spring (March-April) (Thomson et al. 1975; Buchanan et al. 1977; Horner 1977).

The depth of the euphotic zone is reduced where river discharge causes high sediment concentrations. Off the Mackenzie delta, Grainger (1975) found the euphotic zone to be less than one metre thick. Further offshore, where there was much less suspended sediment, light penetration reached 60 m. In Lancaster Sound, Sekerak et al. (1976b) found that the euphotic zone varied from about 24 to 40 m in thickness. In Hudson Bay, Bursa (1961a) implied that the euphotic zone reached 50 m in some places.

TEMPERATURE AND SALINITY

Low water temperature in itself does not preclude high productivity (Dunbar 1968). Fluctuations in salinity caused by ice-melt and freshwater runoff also do not necessarily affect the total productivity of the community, but are important in determining its species composition. Production rates can vary among species, so salinity-induced changes in species composition have the potential to affect total productivity.

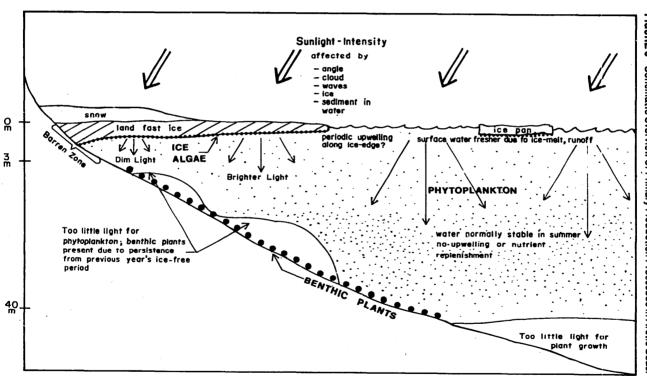


TABLE 1

Nitrate, Phosphate and Silicate Concentrations at Assistance Bay, Cornwallis Island, in August 1975 (from Sekerak et al. 1976a).

Sampling Depth m	Reactive Nitrate mg-at N/m³	Reactive Phosphate mg-at P/m ³	Reactive Silicate mg-at Si/m³	Temp. °C	Salinity
0	⋖ 0.05	0.78	0.70	0.4	28.4
10	0.14	0.49	0.68	0.3	29.5
20	0.20	0.64	1.54	0.1	31.0
30	0.54	0.93	1.29	-0.1	32.2
40	2.40	1.00	3.05	∙0.3	32.2

The temperature and salinity regime has pronounced effects on the stability of the water column, and thus on nutrient concentrations. Nutrient concentrations are extremely important in determining the productivity of an area.

NUTRIENTS

The inorganic nutrient salts of phosphate, nitrate and silicate are major requirements for growth of phytoplankton. In addition, diatoms require silicates for the formation of frustules. The lack of replenishment of these nutrients in the surface waters of arctic seas during late spring, summer and early fall is the basic reason for their low productivity (Dunbar 1968), in early spring, the sea water is isothermal and isohaline1, with high nutrient concentrations at all depths. With the coming of summer, ice-melt and increased insolation warm and freshen surface waters, which lowers their density and causes stratification. Therefore, once nutrients have been exhausted in the upper layers, they cannot be replenished from nutrient-rich deep water. Table 1 illustrates this condition of temperature decrease and salinity and nutrient increase with depth in the Canadian Arctic Archipelago. This density stratification is also a feature of Hudson Bay, where it results from massive freshwater runoff.

Nitrate is generally considered to be the limiting nutrient in the sea (Ryther and Dunstan 1971). Exhaustion of nitrate before exhaustion of phosphate and silicate has been noted in Frobisher Bay (Grainger 1971), the Beaufort Sea (Grainger 1974) and various locations in the Arctic Archipelago (Sekerak et al. 1976a; Buchanan et al. 1977; Thomson et al. 1978).

ICE BIOTA

A universal feature of springtime sea ice appears to be a bloom of algae in the lower surface of the ice. This ice-algal bloom has been recorded at many locations in Arctic and Antarctic seas (e.g., Buchana et al. 1977; Horner 1977; Thomson et al. 1978) and in some areas it may be a major contributor to total primary productivity (McRoy and Goering 1974). This adaptation of algae

to the presence of ice allows the cells to receive adequate sunlight and nutrients to carry on photosynthetic activity. The productivity of the ice-algal layer has been measured in several areas, but not successfully in the Canadian Arctic. Figure 4 summarizes current knowledge of the seasonal cycle of the ice-algae (epontic) community.

PHYTOPLANKTON

The seasonal cycle of phytoplankton in the Canadian Arctic is summarized in Figure 4. During the winter. small numbers of phytoplankton survive by forming resting stages and some survive heterotrophically (Allen 1971). The algal community in the undersurface of the ice begins to develop in early spring and reaches maximum development in May (Figure 4). During this time, planktonic populations of 'shade-adapted' pennate diatoms of the genera Navicula, Nitzschia and Fragilaria are beginning to develop (Bursa 1961b). In June, this epontic community begins to disintegrate and the pennate diatoms reach population maxima (Bursa 1961b; Bain et al. 1977). Many ice-algal cells are presumably released into the water column at this time, but it is unknown how much they contribute to the spring plankton bloom. Some species are found in both the epontic and the planktonic communities.

The planktonic pennate diatoms decline in abundance during ice break-up and are replaced by 'sun'-adapted centric diatoms, chiefly of the genus *Chaetoceros* (Bursa 1981b; Sekerak *et al.* 1976b). The timing of the preceding events may vary according to year and location.

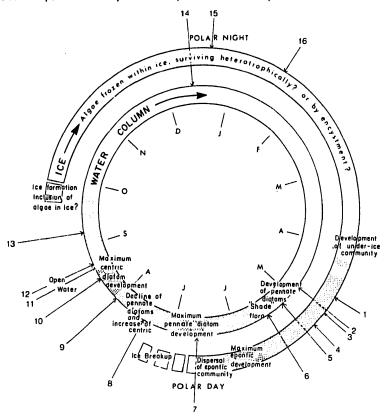
BENTHIC PLANTS

Benthic plants include the macrophytic algae (i.e. kelps), unicellular microphytic algae (e.g., diatoms) and the aquatic angiosperms (e.g., eelgrass). The productivity of benthic plant communities can be very high. Like other plants, benthic algae require light and nutrients. The large species such as the Laminariales (kelps) normally require a rock substrate for attachment.

^{&#}x27;i.e. Uniform temperature and salinity, and thus density, over a wide range of water depths.

i.e. Using pre-existing organic compounds rather than manufacturing them by photosynthesis.

FIGURE 4 Annual Cycle of Phytopiankton and Epontic Algal Development in Arctic Waters. Timing of events is only approximate and some relationships are not clearly understood (from Bain et al. 1977).



Epontic community on under surface of ice, Resolute Passage (M. Foy, pers. obs.).

 First appearance of Achnenthes-Fragilaria community in plankton beneath ice, igloolik, Foxe Basin (Buras 1961b).

A ...

 Late April First appearance of eponitic community, Pt. Barrow, Chukchi Sea (Horner 1977).

Early May Considerable chlorophyll a concentrations in bottom of ice, Jones Sound (Apollonio 1965).

5.7 May

Low concentrations of Nitzschia delicalissima in water column. Epontic community dominated by Nitzschia trigge, well developed, West Barrow Strait (Thomson et al. 1975).

6. 14 May
Low concentrations of Nitzschia trigida, Stauroneis guadripedis in water column. Eponitic community dominated by Nitzschia trigida, well developed, Austin Channel (Thomson et al. 1975).

7. 12-23 June Maximum development of pennate diatom 'shade' flora (dominated by *Nilzschia grunowi)*, Wellington Channel (Bain *et al.* 1977).

8. 15 July Maximum development of pennate diatom 'shade' flora (dominated by Achnanthes teenlate), Igloolik, Foxe Basin (Bursa 1961b).

9. 3 August Plankton dominated by Nitschia seriata, Creawell Bay, Somerset Island (Sekerak et al. 1978a).

10. 11 August Maximum development of centric diatom flora (dominated by Cheetoceros socialis), Igloolik, Foxe Basin (Bursa 1861b). 11. 19 August Plankton de

Plankton dominated by Chastoceros socialis, Assistance Bay (Sekerak et al. 1976a).

12. 22 August

Maximum development of centric diatom flora (dominated by Chaetoceros socialis), Froblaher Bay (Bursa 1971).

13. Early De September at

Decline in phytoplankton abundance, especially in the dominat Chaeloceros socialis, evident in Lancaster Sound (Sekerak et al. 1976b).

14. 10 December No living phytoplankton cells in water column, Frobisher Bay (Bursa 1971).

15. December, January

A few liking dilatons and flagellates throughout ice (Horner 1977).

4

The intertidal zone, which in temperate latitudes supports a luxuriant growth of algae, is for the most part barren in the Arctic (Ellis 1955; Lee 1973; LGL Ltd. unpubl. data). Below the intertidal is a barren zone extending to depths of two or three metres. Extensive tidal flats are likewise barren. The presence of fast ice throughout most of the year, the continual abrasion by pan ice during the open water period and fluctuations in temperature and salinity are responsible for the sparse vegetation in these habitats. These areas may support more vegetation in Hudson Bay than in more northerly areas (Bursa 1968). In general, however, very little primary production occurs in the Arctic in the shallow and intertidal areas that, in tropical and

temperate latitudes, support diverse and abundant plant life.

Where conditions permit, generally at depths below the above-described barren zone, luxuriant stands of kelp are found in the waters of the Arctic Archipelago and Hudson Bay. Much of the material (fronds, stipes, etc.) produced by macrophytes enters the food web as detritus and dissolved organic matter.

The productivity of benthic plants has not been studied in Arctic Canada. Studies of the microalgae off northern Alaska indicate that this group may be very productive in the Arctic (Matheke and Horner 1974).

CIRCUMSTANCES RESULTING IN INCREASED PRODUCTIVITY

HYDROGRAPHIC PHENOMENA

Mechanisms that bring nutrient-rich deep water to the surface result in higher productivity. In the Antarctic, prevailing winds cause surface water to move away from the continent; this results in continuous large-scale upwelling and high primary productivity. Other regions where permanent upwelling causes high productivity are generally found off the west coasts of continents at locations where the prevailing winds drive surface waters offshore.

Localized periodic upwellings such as one found in the Gulf of St. Lawrence by Greisman and Ingram (1977) may also occur. Synoptic oceanographic observations are required to detect this phenomenon but work of this type has not been performed in the Canadian Arctic.

The meeting of two currents may also cause deep water to come to the surface. The rich fisheries resources of the Grand Banks of Newfoundland are the result of such an interaction between currents. Currents flowing over a sill may also enrich surface waters.

One or all of the above hydrographic phenomena may take place in the Canadian Arctic, but observations to date have been insufficient to document them.

ICF

McRoy and Goering (1974) suggest that the presence of ice and its associated flora increases the primary productivity of the Bering Sea. The presence of ice for part of the year in the Canadian Arctic may also increase total annual productivity since nutrients used by the ice flora in spring, when the water column is unstable, would be at least partially replenished. Thus development of the ice flora would not substantially reduce subsequent planktonic production.

ICE-EDGES

Various species of seabirds and marine mammals

sometimes concentrate at the edge of landfast ice (Burns 1970; Fay 1974; Bradstreet 1977; Bradstreet and Finley 1977). These congregations may be due to higher productivity or greater availability of food near ice-edges. McRoy and Goering (1974) found that in the Bering Sea the highest open water primary productivity occurred at the ice-edge, but it was not clearly shown that the ice-edge per se was the cause. Bain et al. (1977) found high standing stocks of phytoplankton and zooplankton at the Wellington Channel ice-edge. but no comparable data from areas away from the iceedge were obtained. Recently, Clarke (1978) has shown theoretically how wind-driven upwelling could occur at fast ice-edges, and there is field evidence that upwelling does in fact occur at fast ice-edges (Bain et al. 1977) and pack ice-edges (Buckley et al. 1979). Thus there are indications that ice-edges are areas of high primary productivity, but the evidence is equivocal.

OTHER CIRCUMSTANCES

Steven (1974) believes that seabird excretion may be responsible for high nutrient concentrations and high standing crops of phytoplankton near breeding sites in the Gulf of St. Lawrence. Tuck (1960) had earlier speculated that this phenomenon also occurs in the Arctic. This could locally enrich stable surface waters near major seabird colonies in the Arctic, but to date this has not been documented.

Polynias and leads in ice may support higher productivity than water under ice, but this circumstance has not been adequately documented. Factors involved include the higher light intensity in open water and the fact that polynias are often areas where there are strong currents (and thus the likelihood of mixing). On the other hand, such areas lack the ice-algal community.

Waters near glacier fronts have been reported to have unusually high concentrations of certain nutrients. The responsible mechanisms have been the subject of some debate (Apollonio 1873; Dunbar 1973).

PRODUCTIVITY OF ARCTIC WATERS IN RELATION TO WORLD OCEANS

Total primary production in the world's oceans is about one third that of the land (Table 2). There are considerable differences in the productivity of different oceanic areas (Table 3); in general, arctic seas are comparatively unproductive. The Arctic Ocean is only slightly smaller than the Antarctic Ocean but its total annual productivity is more than an order of magnitude smaller. It should be borne in mind that there are few published data on the productivity of the Arctic and that values for the Arctic in Tables 2 and 3 are imprecise. Nonetheless, the low productivity of Arctic seas is well established, and is primarily a result of the fact that the water column is normally stable during the summer in the Arctic. Nutrients are not replenished from deeper waters.

The few measurements of primary productivity made in the Canadian Arctic are summarized in Table 4. Table 5 gives a rough estimate of total primary productivity of the Canadian Arctic, based on our extrapolations from available literature. Table 5 includes the Canadian part of the Beaufort Sea but excludes any other part of the Arctic Ocean. We estimate that annual net primary productivity (benthic productivity excluded) in Canadian arctic seas is, very roughly, 110 x 10° t C/yr (110 x 10° kg C/yr).

It is emphasized that there have been extremely few measurements of net primary productivity of phytoplankton, benthic microalgae, macrophytes or iceedges in the Canadian Arctic. Data from arctic waters

TABLE 2

Total Annual Primary Production of the Earth's Terrestrial and Marine Systems (from Rodin et al. 1975 and Platt and Subba Rao 1975).

Area		10° t dry wt/yr*
Land	Polar	1.33
	Boreal	15.17
	Subboreal	17.97
	Subtropical	34.55
	Tropical	102.53
	Total	171.54
Lakes and	rivers	1.0
Ocean		
	Indian	12.72
	Atlantic	18.84
	Pacific	22.02
	Antarctic	6.36
	Arctic	0.24
	Total	60.18
Global Tota	al	232.72

^{*1} metric tonne (t) = 1000 kg

TABLE 3
Comparative Annual Primary Production in Various Marine Waters.

Area		g C/m ² •yr* Reference	
Open Ocean	Long Island Sound	470.0	Crisp 1975;
	Sargasso Sea	134.0	Platt and Subba Rao 1975
	Gulf of Mexico	175.2	
	Bedford Basin	219.0	
	Off Barbados	105.8	
	Antarctic Ocean	5475.0	
	Off Peru	3650.0	
	Indian Ocean	73-182	
	Arctic Ocean**	1	English 1959
	Resolute Bay	32	Welch and Kaiff 1975
	Off Barrow, Alaska —		Horner 1977
	Epontic Community	5	
Nearshore Benthic	Fucus Beds, Woods Hole.	7300	Kanwisher 1966
	Mass.	, , , ,	
	Laminaria, Nova Scotia	1750	Mann 1972
	Coral Reef	4200	Odum and Odum 1955

^{*}units are grams of carbon fixed by photosynthesis per m2 each year.

^{**}English (1959) worked from a drifting ice-island in the central arctic basin.

outside Canada are also very limited. Thus it is not possible to provide a precise estimate of total net primary productivity in Canadian arctic waters, or to provide any reliable information about geographic or habitat related differences in productivity.

Regional variability is important because marine mammals and other consumers are concentrated in certain areas and habitats; it is the productivity in these specific areas, coupled with any large-scale transfer processes that may exist, that is important in any discussion of food availability.

TABLE 4
Summary of Primary Production Measurements in the Canadian Arctic.

Location	No. of Stations	Date	Productivity	Reference
Southern Beaufort Sea	9	5 July-9 Aug.	0.10-1.19 g C/m ² •day	Hsiao <i>et al</i> . (1977)
Resolute Bay, N.W.T.	9	July-Oct.	32 g C/m²•yr 0.45 g C/m²•day (max.)	Welch and Kalff (1975)
Frobisher Bay, N.W.T.	30	1967-1976	42 g C/m²•yr (ave.) (◀0.001-1.545 g C/m²• day)	Grainger (1971) computed by Welch & Kalff (1975)
Alert, N.W.T.	11	10 July-12 Aug. 1957	9 g C/m²•yr 0.550 g C/m²•day (max.)	Apollonio (1976a)
Jones Sound, N.W.T.	11	July-Aug. 1961	35-40 g C/m ² •yr 1.97 g C/m ² •day (max.)	Apollonio (1976b)
	8	June-July 1963	20 g C/m ² •yr 1.16 g C/m ² •day (max.)	

TABLE 5
Primary Productivity of Canadian Arctic Marine Waters.

	Area (km²)	Productivity		
		g C/m²•yr*	10 ⁶ t C/yr*1	
Planktonic				
Channels among Arctic Islands N of 78°	120,000	9	1.1	
Channels among Arctic Islands S of 78°	790,000	30	23.7	
Hudson Bay and Str., Foxe Basin, Ungava Bay	1,000,000	40	40.0	
Beaufort Sea (Canadian)	280,000	40	11.2	
Baffin Bay (Canadian), Davis Str.	500,000	40	20.0	
Epontic	2,690,000	5	13.5	
Total			109.5	

^{*}Based on sources cited in Tables 3 and 4.

^{**1} metric tonne (t) = 1000 kg.

LIMITS TO SECONDARY PRODUCTION

Plant tissue is converted into animal tissue by herbivorous animals, which are in turn eaten by carnivorous animals and so on up the food chain. This transfer from one consumer level to another involves a loss of approximately 70 to 90% of the energy per transfer at lower trophic levels (Ryther 1969), and over 99% in the final transfer to marine mammals. In this sense the shortest food chains are the most efficient. However, many marine food chains are long; for example, the transfer from diatoms through copepods, arctic cod and seals to polar bears (Figure 5) involves four energy transfers. Over the long term, most of the primary pro-

duction in the sea is eventually utilized by other organisms and often recycled several times; however, much of the production may be routed through food chains that do not lead to vertebrate groups (marine mammals, seabirds, fish).

For convenience, pelagic and benthic food chains are treated separately in the following sections. However, there is a transfer of energy between these two food chains. Ice biota are considered to be part of the pelagic food web in the following sections.

PELAGIC FOOD CHAINS

MAJOR PELAGIC GROUPS

The main components of pelagic food chains in the Arctic are as follows:

Primary Producers
Diatoms
Dinoflagellates

Dinoflagellates Microflagellates Other phytoplankton **Primary Consumers**

Copepods
Thecosomatous pteropods
Larvaceans
Benthic larvae
Mysids
Euphausiids

Primary Carnivores

Chaetognaths
Hyperlid amphipods
Gymnosomatous pteropods
Pelagic cnidarians
Ctenophores
Cod
Capelin

Figure 6 shows representatives of some of these groups diagrammatically.

Copepods are the primary consumers of phytoplankton in most of the oceanic regions of the world. In the Arctic, copepods of the genera Calanus and Pseudocalanus are dominant. They are efficient filter feeders with mouth parts adapted to gnawing the hard frustules of diatoms (Anraku and Omori 1963). Much effort has been expended in attempting to quantify the productivity of copepods by measuring rates of feeding. respiration, assimilation, reproduction and growth, and by studying life histories and population dynamics of natural populations. In spite of the voluminous literature on copepods, some important aspects are still poorly known. For example, it has only recently been shown that copepods can survive on detritus alone (Roman 1977) and often feed on it extensively in nature (Poulet 1976).

In temperate waters, an accepted figure for zooplankton production is about 20% of phytoplankton production (Mullin 1969). However, this figure may be too high for arctic waters (McLaren 1969). As an adaptation to arctic conditions, arctic zooplankters reach a large size and have longer life cycles than their temperate counterparts. Averaged over the year, arctic zooplankters use proportionately more energy for maintenance and less for growth than related temperate groups. However, during periods of food availability, energy conversion efficiencies must be quite high. Lee (1974) has shown that Calanus hyperboreus stores lipids during summer for utilization during the winter. Conover (1962) found that C. hyperboreus had high growth efficiency (52 to 90%) while growth was taking place and that it was adapted to take advantage of periods of food abundance that occupied less than 20% of its life span. During the short period of phytoplankton abundance during summer, zooplankton productivity must be very high and, during the rest of the year, very low.

Energy passes from herbivorous zooplankton to vertebrates both directly and through intermediate groups. Mysids, euphauslids, pteropods and large *Calanus* spp. are eaten by vertebrates. Mysids are eaten by ringed seals at some places and times, and herbivorous zooplankton of various kinds are eaten by bowhead whales. However, energy must usually pass through at least one more consumer level before being passed on to marine mammals. The main vectors for this transfer are the hyperiid amphipods, especially *Parathemisto libellula* (Dunbar 1957), arctic cod (Bain

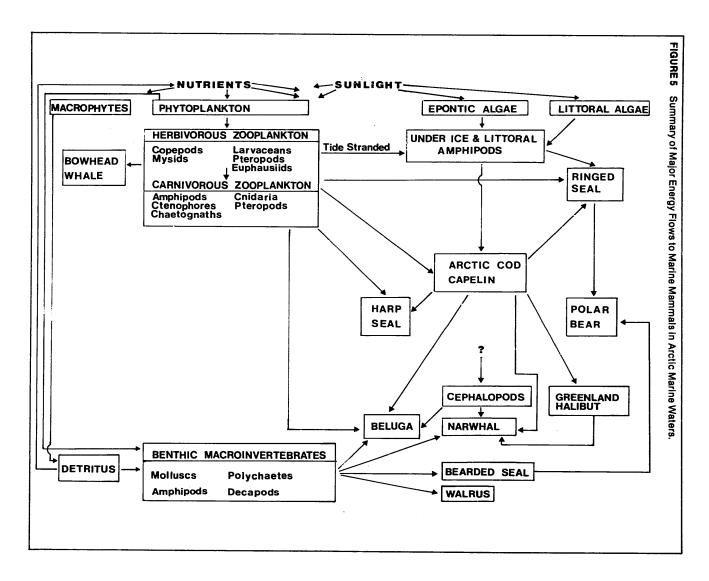
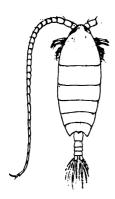
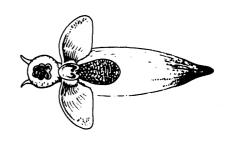


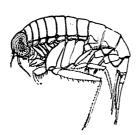
FIGURE 6 Some Animals Important in Arctic Marine Food Chains.
Sizes quoted are lengths of individuals typically eaten by vertebrates (adapted from Bradstreet 1976).



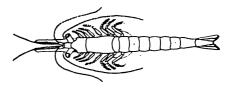
Calanus hyperboreus (Copepod) 3-8 mm



Clione limacina (Pteropod) 5-10 mm



Parathemisto libellula (Amphipod) 15-35 mm



Mysis oculata (Mysid) 12-30 mm



Arctic Cod 50-175 mm

and Sekerak 1978) and capelin (Lalli et al. 1973). P. libellula is a pelagic amphipod that consumes copepods and, to a lesser degree, chaetognaths, fish larvae, euphauslids, other crustaceans, polychaetes and phytoplankton (Dunbar 1957; Wing 1976). Available data from a wide variety of arctic areas indicate that post-larval arctic cod feed in a variety of habitats including benthic, nearshore and under-ice areas, and consume mainly amphipods, copepods, mysids and decapods (reviewed by Bain and Sekerak 1978; see also Craig and Griffiths 1978; Frost et al. 1978). In the Canadian Arctic, capelin are common only in the southeastern part and Hudson Bay (Templeman 1968); they feed primarily on copepods, euphauslids and to a lesser degree amphipods (Corlett 1968; Prokhorov 1968).

Some pelagic invertebrates that consume herbivorous zooplankton do not appear to be important, either directly or indirectly, to marine mammals. Ctenophores and pelagic cnidaria are voracious predators and often deplete the standing stocks of herbivorous zooplankton (Fraser 1962), but are not known to be important foods for marine mammals. Similarly, chaetognaths are also major predators of copepods, but are not a major source of food for vertebrates. Most energy flowing through ctenophores, cnidaria and chaetognaths does not appear to reach marine mammals.

AMOUNT OF FOOD AVAILABLE TO MARINE MAMMALS

The amount of food available to pelagic-feeding marine mammals might be estimated either by direct measurement of standing stocks and turnover rates of organisms known to be consumed, or by tracing the route of the previously estimated total pelagic primary production of the Canadian Arctic through the food web. Unfortunately, knowledge of the structure of the food web and of the various rates, efficiencies and losses is inadequate to permit meaningful estimates from either approach. As an indication of the difficulties, we list below some of the uncertainties involved in a calculation of food availability from net primary production.

- —How accurate is the estimate of 110 x 10⁹ kg C/yr net primary production, which is based on a very few measurements (Tables 4, 5)?
- —How much primary production becomes detritus? More generally, what are the nature and magnitude of exchanges between the benthic and pelagic food webs?
- —What is the efficiency of energy transfer to herbivores? from herbivores to subsequent trophic levels?
- —What fraction of the herbivore production is diverted to groups unimportant to marine mammals (ctenophores, chidaria, chaetognaths)?
- -What fraction of the herbivore production is con-

- sumed directly by marine mammals? by organisms that are consumed by mammals?
- —More generally, what is the allocation of energy among short, efficient pathways and long pathways that are often less efficient?
 - e.g. Herbivore ➤ Mammal
 Herbivore ➤ Arctic cod ➤ Mammal
 Herbivore ➤ Parathemisto ➤ Mammal
 Herbivore ➤ Parathemisto ➤ Arctic cod ➤
 Mammal
- —How much overlap is there in use of food by marine mammals, seabirds, and fish and invertebrate predators?

In addition to these uncertainties about the functioning of the pelagic food web, two other data gaps prevent any precise evaluation of the degree to which marine mammal populations of the Canadian Arctic are limited by food.

 We do not know what proportion of the theoretical secondary productivity is actually accessible to marine mammals (see 'Availability of Food' section, below). We do not have accurate information about food requirements of the existing mammalian populations, since population sizes and individual energy requirements are both imprecisely known for most species.

BENTHIC FOOD CHAINS

The benthic animals of the Canadian Arctic Archipelago have received relatively little scientific attention. Most of the work that has been conducted concerns only taxonomy and distribution, not ecological relationships. As yet no comprehensive treatment of the polychaetes and amphipods, two of the most important groups, exists for the vast marine area between Ungava and Alaska.

MAJOR BENTHIC GROUPS

In the Arctic, the most diverse and richest benthos is found in shallow waters below the 'barren zone' but less than 50 m deep (Ellis 1960; Thomson et al. 1975; Sekerak et al. 1976a; Buchanan et al. 1977). Benthic animals in such relatively shallow areas are the primary food source for walruses and bearded seals, and are also taken by whales. The benthic animals that are most important as food for walruses, bearded seals and belugas are the clam Mya truncata, the cockle Serripes groenlandicus, and decapod crustaceans. In addition to these, benthic fish, sea urchins, polychaete worms, other bivalves, amphipods and isopods are also taken. Other benthic animals common in the Arctic include various cnidarians (hydroids, anemones) and several additional groups of crustaceans and echinoderms.

Feeding Mode Major Groups Scrapers of Algal Films Filter Feeders Sediment Feeders Scavengers Carnivores Herbivores on Macrophytes Major Groups Chitons, Gastropods, Amphipods Serpulid and Sabellid Polychaetes, Bivalves Polychaetes, Bivalves, Ophiuroids Amphipods, Decapods Errant Polychaetes, Fish Sea Urchins

Because of ice scour and fluctuations in temperature and salinity, benthic areas less than two or three metres deep and the intertidal zone are essentially barren of sedentary infauna and epifauna (Ellis 1960; Lee 1973). Mobile epibenthic amphipods, myslds and isopods do move into these areas when conditions permit. Mysids sometimes form dense shoals along the shoreline in shallow water and are also abundant in deeper water under the fronds of kelp (Griffiths and Craig 1978; Thomson et al. 1978). Mysids are an important food for ringed seals (McLaren 1958a), Mysids are also eaten by arctic cod (Bain and Sekeral 1978; Craio and Griffiths 1978), which are in turn important to vertebrates. The littoral amphipods do not appear to be a major food source for marine mammals, but they too are eaten by arctic cod (Bain and Sekerak 1978) and thus enter vertebrate food chains.

FOOD OF BENTHIC ORGANISMS

Benthic animals have diverse habits and habitats and derive their food from many different sources (Table 6).

Much of the benthos derives its food from detritus and organic matter in the sediments. Most of the bivalves (Lubinsky 1972) and decapods (Squires 1968) are sediment or detritus feeders, and most of the arctic polychaetes (maldanids, terebellids, capitellids, ampharetids) are sediment feeders. Many of the benthic filter feeders apparently ingest material of benthic rather than pelagic origin (Marshall 1970). The foods of these macrobenthic organisms are the microbial heterotrophs that live in the sediment and decompose the organic matter (Wildish 1977).

The ultimate source of food for benthic organisms is the primary productivity of the phytoplankton and benthic plants, and organic matter of terrestrial origin. Most of the productivity of benthic macrophytes may enter the benthic food web. Although all of the available phytoplankton may initially enter the pelagic food web, the majority is recycled as faeces, excreta, ecdysal waste and food killed but not eaten. Most of this eventually makes its way into benthic food chains.

PRODUCTIVITY OF THE BENTHOS

Insufficient data exist at this time to make an estimate of benthic productivity in the Canadian Arctic. The standing crop of benthic animals is certainly quite

high. In the Arctic Islands and Foxe Basin, benthic biomass is about 100 to 400 g wet wt/m² (Ellis 1960; Buchanan et al. 1977). Values are lower in the western Beaufort Sea (Carey et al. 1974).

Studies of life cycles and growth rates of benthic animals as well as zooplankton indicate that arctic populations exhibit slower average growth rates than their temperate counterparts (Dunbar 1968). Andrews (1972) found, for example, that the growth rates of three species of arctic bivalves were about three to five mm/year and that growth was faster in the subarctic. Curtis (1977) has recently shown that west Greenland polychaetes have slow growth rates. Slow growth rates imply that the arctic benthos has a low productivity to blomass ratio.

AVAILABILITY OF FOOD TO MARINE MAMMALS

Our ability to calculate the numbers of marine mammals that theoretically could be supported by production processes in the Canadian Arctic is limited not only by uncertainties about production rates, but also by uncertainties about the proportion of this production that is available to marine mammals. Competition with other consumer groups is presumably a factor, but so are physical factors, especially ice and water depth, that limit accessibility to food resources. Much of the secondary productivity of the Arctic is inaccessible to marine mammals for much or even all of the year.

COMPETITION

Large pelagic fish are absent in polar seas, possibly because their niches have been filled by marine mammals (Dunbar 1959). Thus, the ultimate predators in pelagic food chains of the Arctic are the marine mammals and seabirds. There appears to be considerable overlap in the feeding areas and diets of seabirds and marine mammals feeding pelagically and especially along ice-edges; arctic cod and *Parathemisto*, for example, are important to both birds and mammals.

Benthic-feeding mammals probably do not compete with benthic-feeding fish and seabirds since most of

the latter are too small to take advantage of the main food resources of benthic-feeding mammals (e.g., large burrowing bivalves).

FAST ICE

Most channels in the High Arctic and nearshore areas throughout the Arctic are covered by landfast ice for seven to 12 months of the year. Several species of amphipods have been reported to be associated with the ice-algal community during spring (Barnard 1959; Thomson et al. 1975, 1978; Buchanan et al. 1977). These animals apparently graze on the ice algae (Apollonio 1961; Alexander et al. 1974; Horner 1977). The arctic cod, which is a major link in the transfer of energy to vertebrates (Figure 5), apparently also concentrates under ice at certain times and locations. The ecology of arctic cod has been reviewed by Bain and Sekerak (1978), but is as yet not well known. Planktonic and benthic invertebrates also occur under fast ice as well as in open water.

The ringed seal is the only species of arctic marine mammal that is well adapted to utilize food resources under extensive areas of fast ice. Amphipods (iceassociated and planktonic) and arctic cod are taken under the ice (Finley 1978). However, the distribution and density of ringed seals are apparently limited in most circumstances by ice type (McLaren 1958a). Where ice type is a limiting factor, under-ice food resources may not be utilizable even by this ice-adapted species. Other species of marine mammals are generally unable to reach under-ice food resources except near ice-edges and polynlas. An unknown fraction of the secondary production under fast ice may become accessible later when it is carried to open water by currents or after the ice melts. Nonetheless, the presence of ice clearly reduces the proportion of this secondary productivity that marine mammals can consume.

WATER DEPTH

Walruses and bearded seals feed on benthic animals. These pinnipeds are believed to feed only in relatively shallow water (to 80 m in the case of the walrus — Vibe 1950), so benthic productivity in deeper areas is inaccessible. Some deep-water regions of the Arctic support substantial populations of benthic animals (e.g., Carey and Ruff 1977). Some of this deep-water production is used by deeper-diving species (e.g., nar-whal), but deep-diving species do not occur in all arctic waters, and even where they do occur they apparently consume only some of the types of benthic animals present (e.g., Vibe 1950: 85). Thus some of the available benthic production is not utilized by marine mammals.

Shallow-water nearshore areas tend to remain covered by fast ice for more of the year than deeper areas, further restricting locations and times when benthic animals are accessible. Walrus distribution may also be ilmited by the availability of suitable ice pans or terrestrial sites for haul-out; benthic animals occuring in shallow-water areas far from suitable walrus haul-out sites would not be exploitable.

It is uncertain what proportion of the zooplankton that marine mammals consume occurs close enough to the surface to be utilized. The planktonic amphipod Parathemisto is an important food of ringed seals, which are reported to be shallow-water feeders (to about 90 m — Mansfield 1967a). High densities of Parathemisto, especially P. abyssorum, can occur below 100 m (e.g., Sekerak et al. 1976b). Some of this production may become accessible when Parathemisto move upward toward the surface, which they do in late summer (Dunbar 1946). Also, the maximum depths attainable by arctic marine mammals are not well known, and for some species may be greater than has been assumed. However, some zooplankton as well as benthos is likely to remain inaccessible because of water depth.

GEOGRAPHIC VARIATION

Too few intensive studies have been conducted in the Canadian Arctic to document the amount of geographic variation in secondary productivity, but available measurements of standing crop suggest that the range is considerable (for reviews, see Bain et al. 1977; Buchanan et al. 1977). This further complicates any attempt to calculate food availability, since the individual characteristics of each accessible area must be taken into account in order to obtain a precise overall estimate.

CONCLUSIONS

Available data are inadequate to permit meaningful calculation of the amount of secondary production in the Canadian Arctic or to permit comparisons of food availability with food requirements of existing marine mammal populations. In general, secondary productivity in arctic seas can be expected to be low relative to other oceans because of the low primary productivity of arctic marine waters. However, in favourable conditions the short-term production rate can be substantial. Standing crops, particularly of benthic animals, can also be large; this is a reflection of the slow growth rates and high biomass to production ratios that are characteristics of cold arctic waters.

In addition to the rate of secondary production, accessibility is a major factor affecting the amount of food available to marine mammals. Most importantly, the exclusion of most species from large parts of the Arctic by ice during most of the year limits the proportion of the secondary production that can be utilized by marine mammals.

IMPORTANT FOOD CHAINS INVOLVING MARINE MAMMALS

In this section we first summarize the available literature concerning the diets of the marine mammal specles discussed in this report, and then outline what is known about the feeding dependencies of some of the key food species.

Specific information about the proportion of energy obtained from the various food organisms is not available for any of the marine mammals discussed. For some species there is information about the relative volumes or weights of various foods found in mammal stomachs, but these data are imprecise because of differences among food taxa in digestion rate and energy content. For example, fish are often represented only by their otoliths, and sould only by their beaks. In such cases it is invariably unclear how long the otoliths or beaks had been accumulating, and how much the food organisms had weighed when they were incested. In many reports of food habits, the only information given is a list of species or groups present or, only slightly better, the proportion of the stomachs in which each food taxon was found. Because of these inadequacies in the available data, food habits of marine mammals from the Canadian Arctic cannot be defined quantitatively at present.

BELUGA (WHITE WHALE)

The beluga feeds on a wide variety of fish and invertebrates of benthic and pelagic origin (Kleinenberg et al. 1964). In arctic waters, arctic cod (Boreogadus saida) appear to be very important to belugas (Vibe 1950: Kleinenberg et al. 1964; Medvedev 1971; Finlev 1976). Vibe also lists the Greenland halibut (Reinhardtlus hippoglossoides) as an important food. In Hudson Bay. capelin (Mallotus villosus) and other fish are apparently important (Doan and Douglas 1953; Sergeant 1973a). Decapod crustaceans and squid are also taken over much of the range (Kleinenberg et al. 1964; Sergeant 1973a; Finley 1976). However, quantitative data on the food habits of belugas in the Canadian Arctic are lacking. Results from elsewhere indicate that diet varies with age and season, but there are few corroborative data from the Canadian Arctic. M. Fraker (personal communication) found that most belugas taken in the Mackenzie estuary had empty stomachs, which indicates that they may fast for the three to four week period when they are in that area. Sergeant (1969) estimated that captive belugas eating fish consume an average of about five per cent of their body weight each day.

NARWHAL

Qualitative assessments of the diet of narwhal indicate that arctic cod, squid, decapod crustaceans and the Greenland halibut are taken. There is considerable qualitative evidence that arctic cod are significant in the diet of narwhals. In Eclinse Sound, northern Baffin Island, Degerbøl and Freuchen (1935) noted that narwhal fed voraciously on 'small tom cod' (presumably arctic cod). Mansfield et al. (1975a) found remains of arctic cod and squid in 10 narwhals taken in the same area. Vibe (1950) suggested that arctic cod are the principal food in west Greenland waters, and attempted to relate the distribution and movements of narwhal to the distribution of arctic cod. K. Hay (Arctic Biological Station), H. Silverman (McGill University) and K. J. Finley (LGL Ltd.) have examined the diet of narwhals taken from 1974 to 1978 in the vicinity of Pond Inlet (personal communication). Preliminary evidence confirms the importance of arctic cod in the diet; varying amounts of decapod crustaceans, squid and Greenland halibut are also eaten. Work in Russian waters indicates that narwhals feed on a wide variety of foods but primarily take cephalopod molluscs: fish and crustaceans were of secondary Importance (Tomilin

There is no information on the diet of narwhals in Canadian waters for the months of October through May. Thus, foods taken during migration and in winter are not known.

BOWHEAD

The bowhead is a skimming-type baleen whale, and thus is adapted to feed by straining small animals from large volumes of water (Nemoto 1970)1. Brown (1868) reported that zooplankton, mainly copepods and to a lesser degree pteropods, were important components of the diet in the Davis Strait and Baffin Bay area. Mitchell (1975c) states that bowheads consume mysids, amphipods and various small to medium size zooplankton. In the western Arctic, bowheads consume euphausiids (90.3% of subsample volume in two specimens), gammarid amphipods, the hyperiid amphipod Parathemisto libellula, copepods, and occasional small sculpins (Durham, cited by Marquette 1977; Lowry et al. 1978). The presence of gammarid amphipods and sculpins, plus a report of polychaetes, gastropods, echinoideans, reptantian decapods, sand and gravel in one bowhead from the Chukchi Sea (Johnson et al. 1966), suggest that bowheads sometimes feed near or on the bottom, at least in nearshore waters.

When struck by a harpoon, the bowhead is capable of diving to depths of 500 to 600 m. However, it spends most of its time feeding close to the surface with dives of five to 10 minutes duration (Scoresby 1820; Scammon 1874).

¹ See also Pivorunas (Amer. Sci. 67: 432-440, 1979).

WALRUS

The walrus is a bottom feeder that concentrates on bivalve molluscs. Vibe (1950) found that in shallow waters (◄40 m) off northwest Greenland, walruses fed preferentially on the feet of cockles. In deeper waters, siphons of the smaller bivalves Mya and Saxicava dominated the diet; these two species were more abundant in the deeper waters. Other bivalves (Macoma, Astarte), cephalopods, priapulids and holothuroideans comprised, on a biomass basis, only a small part of the diet, Mansfield (1958) obtained similar results in the Hudson Bay, Foxe Basin and Frobisher Bay regions; cockles and the bivalves Mya and Saxi cava were the most frequent foods. However, gastropods were also common, and holothuroideans, squid, priapulids, decapods, isopods, polychaetes and fish otoliths were present in a minority of the stomachs. Alaskan and Soviet studies have provided similar results (Buckley 1958; Krylov 1971), Mansfield (1958) suggested that walruses feed on groups other than molluscs when migrating through areas where molluscs are not accessible.

In the most comprehensive quantitative study of walrus diets, Fay et al. (1977) found that over 60 genera of benthic organisms were taken by Pacific walruses in the Bering Sea but that a few kinds of bivalve molluscs (Mya, Spisula, Serripes, Clinocardium and Hiatella) formed the bulk of the diet. Fay et al. found that walruses fed selectively on these bivalves but in winter took other organisms in areas where bivalves were uncommon.

Fish are occasionally taken (Dunbar 1949). Mansfield (1958) found fish otoliths in one of 19 walrus stomachs, and he and Krylov (1971) cite two records of walruses from Soviet waters that contained largely arctic cod.

Fragments of skin and blubber of several species of pinnipeds (most commonly the ringed seal) and cetaceans have often been found in walrus stomachs (for review, see Fay 1960; also Dunbar 1949; Loughrey 1959). Some is taken from carrion, but walruses are believed to attack living ringed seals. Vibe (1950) suggested that walruses take seals during the long migrations across the sea or along ice-edges where there are no suitable foraging grounds. Walruses are believed to forage only to depths of about 80 to 90 m (Vibe 1950; Buckley 1958). Occasional rogue male walruses may adopt a seal-feeding habit even when other food is accessible (Fay 1960).

HARBOUR SEAL

The food habits of this species have not been studied in the Canadian Arctic, where it is one of the less common seal species. Elsewhere, harbour seals commonly eat a wide variety of fish species, squid and octopus; less frequent food items include crustaceans and, rarely, seabirds (Dunbar 1949; Spalding 1964; Kenyon 1965; Mansfield 1967a; Kosygin and Gol'tsev 1971; Lowry et al. 1977).

HARP SEAL

Food habits of harp seals while they are in the Canadian Arctic during summer are poorly known. Sergeant (1973b) reported the frequency of occurrence of various food items in a total of 16 harp seals collected there; in descending order of frequency, important food taxa were arctic cod, mysids, amphipods (primarily Parathemisto Ilbellula) and euphauslids. Templeman and Hunter (in Blacker 1968; 137) and Anders et al. (1967) mention that the arctic cod is an important food of harp seals in Davis Strait and Cumberland Sound. Halibut, squid and occasionally lumpfish were found in specimens from Smith Sound (Degerbøl and Freuchen 1935). Off west Greenland, arctic cod and euphausiids are also taken, but capelin are believed to be especially important (Dunbar 1949; Sergeant 1973b). None of the studies to date has taken account of the differences in size of the various prey items. If this were done, fish would probably assume even greater prominence in the diet.

In the northwest Atlantic, harp seals eat pelagic fish (especially capelin) and pelagic and benthic crustaceans (euphausiids, mysids, amphipods, decapods), with smaller quantities of benthic fish and cephalopods (Sergeant 1973b). Adult harp seals may be able to dive to as much as 250 m.

HOODED SEAL

The food habits of this species have not been studied in the Canadian Arctic, or in west Greenland, and are poorly known in the Atlantic Ocean. Stomachs of hooded seals killed while they are hauled out in the whelping and moulting areas are usually empty. Redfish (Sebastes marinus), Greenland halibut and squid have been found in stomachs (Mansfield 1967a; Sergeant 1976a). The hooded seal is believed to feed at greater depths than the other seal species discussed below.

RINGED SEAL

The ringed seal is able to maintain breathing holes through the ice throughout the winter, and thus can overwinter in much of the Arctic that is inaccessible to other marine mammals except in summer. The diet of the ringed seal has been studied off southern Baffin Island and Igloolik and near Bathurst Island as we'l as in Soviet, Alaskan and Greenland arctic waters.

Ringed seals usually eat primarily crustaceans, fish, or both. Off eastern Baffin Island in late summer, Dunbar (1941) found crustaceans, particularly the pelagic amphipod Parathemisto (= Themisto) libaliula and the mysid Mysis oculata, to predominate, but one seal had eaten mainly the pteropod Limacina helicina. Dunbar (1949) mentions that Hildebrand found that ringed seals of Ungava Bay ate mainly Mysis and euphauslids (Thysanoessa). Off southern Baffin Island, McLaren (1958a) found that Parathemisto, Mysis and arctic cod were the most common foods. Mysids, fish and decapods predominated in shallow waters, but Parathemisto was more important in offshore deeper waters. Similarly, Finley (1978) found that at Freemans Cove, Bathurst island, during June, ringed seals consumed mainly mysids, amphipods (Parathemisto and Onisimus) and arctic cod, with occasional sculpins, gastropods and decapods, whereas in offshore areas of Barrow Strait during mid-winter they fed heavily on Parathemisto libellula.

In contrast to the results of McLaren (1958a) and Finley (1978), Vibe (1950) reported (without details) that in west Greenland the arctic cod is the principal food in places where the ringed seal forages at great depths, while amphipods and decapods are the principal foods near the coasts. Mysids, amphipods, arctic cod and also squid are taken off east Greenland (Johansen in Dunbar 1949).

Results from shallow coastal waters off western Alaska indicate that fish, mainly arctic cod with some sculpins, dominate the diet in winter (November to February) whereas invertebrates, mainly shrimp, crabs and amphipods, dominate in spring. Kumlien (1879) reported that in Cumberland Sound ringed seals subsisted mainly on fish (cod, sculpins, seasnalls) during winter, and Smith (1973c) stated (without details) that their diet consisted mostly of fish, particularly arctic cod, during winter and early spring. However, fish do not invariably dominate the winter diet (cf. Finley 1978).

Since ringed seals collected from the ice during the period of haul-out and moult in spring usually have empty stomachs, it has been suggested that they fast at this time (McLaren 1958a; Smith 1973a). However, seals that have been hauled out for long periods are easier to collect than those that have recently hauled out (Vibe 1950), and the apparent absence of food may reflect the high gastrointestinal clearance rate (generally five to nine hours — Parsons 1977) rather

than long-term fasting. Pikharev (1946, cited by Lowry et al. 1977) found that during the moult period the only seals that contained food were those in the water or that had just hauled out. Similarly, Shustov (1970) found that stomach contents became either well digested or undetectable within one hour after ringed seals hauled out. Finley (1978) found that faecal samples taken from the Ice during the haul-out period contained typical food items. This evidence shows that at least some ringed seals do eat during the haulout period, but loss of weight and other changes at this time (McLaren 1958a) suggest that less food is consumed then than at other times.

Lowry et al. (1977, 1978) have reviewed the Alaskan and Soviet literature on diet of the ringed seal. The chief components are gammarid and hyperilid amphipods, mysids, euphauslids, shrimp and fish (often including arctic cod). Proportions of these taxa vary markedly. Lowry et al. (1978) conclude that 'it appears that food consumed by Ringed Seals at any given place and time will consist of the most abundant and available suitable species . . .'. Suitable species throughout the range apparently include various pelagic and benthonic fish and crustaceans found within 100 m (McLaren 1958a) of the surface. The arctic cod and Parathemisto libellula are often major components of the diet.

BEARDED SEAL

The bearded seal is primarily a benthic feeder with a very diverse diet that apparently varies with location and time of year (for reviews, see Chapskil 1938; Kosygin 1971; Lowry et al. 1977). Food habits have been studied extensively in the Soviet Arctic and western Alaska, but there is very little information from Canada (cf. Dunbar 1941; Beaubier et al. 1970; Finley 1976).

Major invertebrate foods can include various gastropod (especially *Buccinum*), bivalve and cephalopod molluscs, crabs and shrimps. Other invertebrate foods include amphipods, isopods, holothuroideans, echiurids, sponges, priapulids and polychaetes (Chapskil 1938; Vibe 1950; Johnson *et al.* 1966; Burns 1967; Beaubler *et al.* 1970; Kosygin 1971; Finley 1976; Lowry *et al.* 1977).

Arctic cod and various benthic fish form a variable portion of the diet. Chapskil (1938), citing studies from several parts of the Soviet Arctic, concludes that arctic cod play a major role in the life of this species. Burns (1967) found that arctic cod assumed greater importance in the diets of the more northerly-collected animals, but that sculpins were, overall, the most commonly taken fish. Near Thule, Greenland, Vibe (1950) reported that bearded seals are normally omnivorous benthic feeders, but sometimes eat exclusively arctic

cod when water depths exceed 100 m. In these circumstances the seals were presumably unable to reach the bottom. Where bearded seals can reach the bottom, they have been found to take sculpins and other demersal fish such as halibut, eelpouts, lump-suckers and seasnalls (Dunbar 1941; Vibe 1950; Johnson et al. 1966; Burns 1967; Kosygin 1971; Finley 1976; Lowry et al. 1977).

There has been no attempt to determine the proportion of total energy input contributed by the various food items taken by bearded seals.

MAJOR FOOD GROUPS

On the basis of the available literature, certain major food groups for arctic marine mammals can be identified. The precise significance of each group remains uncertain, however, because of the scarcity of quantitative data, particularly from most of the Canadian Arctic, and the paucity of data about seasonal and geographic differences in diet. With these limitations, Figure 7 summarizes the probable major feeding dependencies of marine mammals in the Canadian Arctic, and the following sections discuss the trophic relationships of the major food taxa.

ARCTIC COD

This fish (Figure 6) is often the main food for belugas, narwhals, ringed seals and harp seals, and it is occasionally an important food for bearded seals and, less frequently, walruses. It is also a major food source for several of the abundant seabird species in the Canadian Arctic (Bradstreet 1976, 1977; see Figure 8). Of the marine mammals discussed here, the hooded seal and bowhead are the only species not known to consume arctic cod. The seasonal distribution of the arctic cod is poorly understood (Bain and Sekerak 1978), and may have a major influence on the distribution and success of the marine mammal species for which it is a major food (Vibe 1950).

Food items of arctic cod from the Russian Arctic include copepods, small bottom crustaceans (shrimp, amphipods, larvaceans, fish eggs, and young-of-the-year fish (Andiyashev 1954; Hognestad 1968; Kleinenberg et al. 1964). Ponomarenko (1967) found that cod larvae and fry, as they grew, fed successively on copepod eggs, nauplii and copepodites.

Few studies of the food habits of arctic cod have been performed in the Canadian Arctic. Young-of-the-year (13) from Wellington Channel had eaten diatoms and copepod nauplii (Bain et al. 1977). Arctic cod (83) from the nearshore bottom of Strathcona Sound were eating mostly copepods, amphipods and decapods (Bohn and McElroy 1976). Bain and Sekerak (1978) quantitatively examined the summer diet of 252 arctic cod collected in shallow nearshore waters of Cornwallis Island; nearshore crustaceans — Onisimus littoralis (60% of wet

weight), Gammarus sciosus (5%) and Mysis spp. (5%) — were particularly important.

Off northern Alaska, Craig and Griffiths (1978) also noted that in nearshore waters arctic cod fed primarily on crustaceans, mainly mysids (over 71% of dietary wet weight). Frost et al. (1978) collected 157 arctic cod from Alaskan offshore waters, many from the bottom in waters near the edge of the polar pack ice. The most important food items were zooplankton: the copepods Calanus hyperboreus, C. glacialis and Pareuchaeta glacialis, and the amphipods Apherusa glacialis and Parathemisto libeliula.

In summary, available data indicate that larval cod feed on diatoms and the early (small) stages of copepods, whereas larger cod feed primarily on copepods and a variety of larger crustaceans including amphipods, mysids and decapods. The arctic cod is a major link in the transfer of food energy from lower trophic levels to marine mammals and seabirds (Figure 4). Available evidence suggests that this energy can come from invertebrates inhabiting the benthonic, pelagic and epontic communities, since arctic cod can be found, at one time or another, in each of these habitats.

CAPELIN

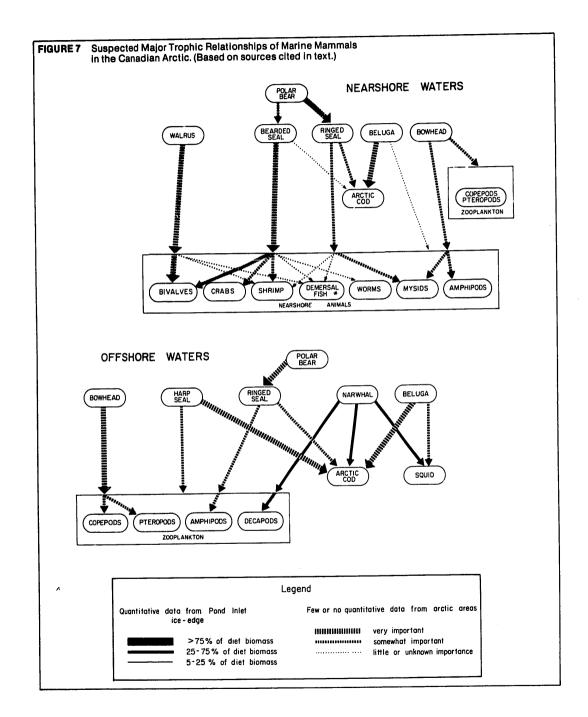
This fish species is common in the southeastern part of the Canadian Arctic, including parts of Hudson Bay, and is known to be important to belugas and harp seals. Capelin feed primarily on copepods, euphausiids and to a lesser degree amphipods (Corlett 1968; Prokhorov 1968).

BENTHONIC FISH

Bottom-dwelling fish are taken at least occasionally by all of the marine mammals discussed, but none of the mammals seem to depend primarily on these fish. Even the bowhead has been found to consume sculpins, although it is uncertain that they were taken from the bottom. Quantitative data are scarce, but epibenthic crustaceans (amphipods, mysids, isopods) appear to be the main food source for sculpins (Sekerak et al. 1976a; Craig and Griffiths 1978).

PARATHEMISTO LIBELLULA

This pelagic hyperiid amphipod (Figure 6) is a major food for ringed seals, and is also taken by harp seals, bowheads and perhaps other mammals as well as by various seabirds (Bradstreet 1976, 1977). P. libellula feeds mainly on herbivorous zooplankton, and Dunbar (1957) considered it to be very important in the transfer of food energy from lower trophic levels to vertebrates (see Figure 8). Copepods were the most commonly found food items in the guts of P. libellula collected off Baffin Island (Dunbar 1946). Wing's (1976) detailed study of the feeding habits of this species in Alaska indicates that copepods were the dominant food items but chaetognaths, fish larvae, euphausiids, other crustaceans, polychaetes and phytoplankton were also eaten.



OTHER CRUSTACEANS

Other benthic and pelagic crustaceans important to marine mammals include

decapods

 probably taken at least occasionally by all species discussed (in the case of the hooded seal, specific evidence seems to be lacking);

mysids

- important to ringed seals; also taken by harp seals and bowheads;

euphausiids - important to bowheads; also taken by harp and ringed seals:

amphipods - ringed and bearded seals, bowheads.

Arctic decapods appear to be primarily detritus eaters; they may also eat other crustaceans and foraminifera (Sauires 1967).

Mysids feed while swimming and collect food particles on their finely spaced setae. The feeding habits of arctic species have not been studied but mysids are known to feed on phytoplankton and suspended detritus in other regions.

Euphausiids are pelagic shrimp-like crustaceans. Most are filter feeders.

Several species of amphipods are closely associated with the undersurface of the ice, and most of these apparently graze on ice-algae (Apollonio 1961; Alexander et al. 1974; Horner 1977; Welch and Kalff 1975). When ice cover is absent, some of these species occur planktonically, whereas others assume a benthic habitat.

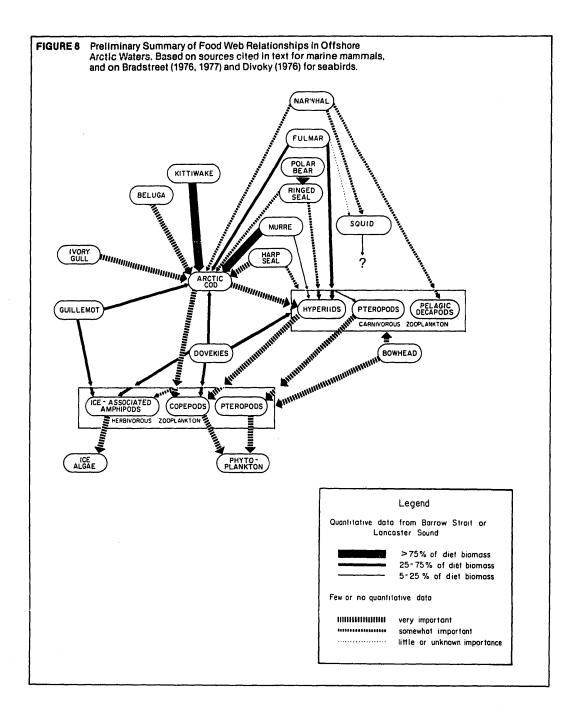
The major 'benthic' amphipods are Onisimus littoralis. Anonyx spp. and Gammarus setosus, each of which sometimes closely associates with the undersurface of ice in nearshore areas. At such times they apparently graze on ice-algae (Buchanan et al. 1977). In ice-free periods, O. Ilttoralis and Anonyx nugax are usually benthic scavengers (Dunbar 1954a; MacGinitie 1955; Steele 1961; Green and Steele 1975) and Gammarus setosus may be a grazer of algae films (Steele 1961).

MOLLUSCS

Bivalve molluscs are the primary food of the walrus; bivalves and gastropods are important foods for the bearded seal. Lubinsky (1972) noted that in arctic Canada 86% of the bivalve fauna are sedimentation (deposit) feeders (i.e. ingest the substrate). However, some bivalves are filter feeders, and may utilize material of benthic (e.g., bacteria, phytobenthos) rather than of pelagic (e.g., phytoplankton) origin. Among the common filter-feeding molluscs are members of the genera Astarte, Clinocardium, Mya, Mytllus, Serripes and Thirasira; common deposit feeders are members of the genera Macoma, Nucula, Nuculana, Portlandia and Yoldia (Ockelmann 1958).

CONCLUSIONS

The marine mammals of the Canadian Arctic eat many types of foods, but a few groups are of special significance (Figure 8). The arctic cod is important not only to several species of marine mammals, but also to numerous seabirds. Parathemisto is directly important to ringed seals and probably harp seals, but is also important because it is a food source for arctic cod. Iceassociated amphipods do not seem to be of major direct significance to mammals, with the possible exception of the ringed seal, but they too are a food source for arctic cod. Molluscs are major food sources for walruses and bearded seals; accessibility to mollusc beds in shallow, nearshore waters is probably critical to these species.

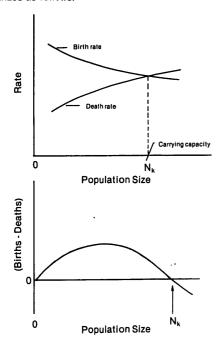


INFORMATION REQUIRED FOR MANAGEMENT

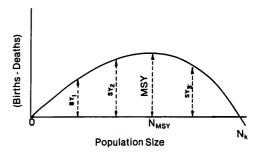
GENERAL CONCEPTS

A central objective of wildlife management is to devise and implement policies that allow wildlife resources to be used while at the same time ensuring their continued existence in a state that will permit ongoing use. This is the concept of 'sustained yield'. Sustained yield is possible because of the manner in which most wildlife populations are limited. Low density populations increase in size because the birth rate exceeds the total death rate.* However, the increase does not continue indefinitely. Instead, most populations ultimately 'level off' at a population size determined by one or more limiting factors (e.g., available food supply, suitable space). In a population of constant size, the average birth and death rates over a period of time must be the same. According to this concept, if the population size somehow exceeds the carrying capacity of the environment, the death rate will exceed the birth rate until the population size is reduced to the carrying capacity.

The relationships mentioned above can be summarized as follows:



In an unexploited and stable population whose size is determined by the carrying capacity of the environment, births are balanced by natural deaths. Any increase in deaths, such as by hunting, will cause the total death rate to exceed the birth rate, and the population size will decline. However, at a lower population size the natural death rate is less than the birth rate. At any particular population size below the carrying capacity, the annual number of births exceeds the annual number of natural deaths by (in theory) a specific amount.** If the annual number of deaths caused by hunting is adjusted to equal that excess, and if other factors remain constant, the population size will stabilize and the take by hunters can be sustained from year to year (sustained yield) without further changes in population size. If the sustained population size is that at which annual births exceed natural deaths by the maximum possible amount, the allowable kill by hunters is the maximum sustainable yield (MSY). Thus, according to this simple model there is a sustainable yield for each population size up to the carrying capacity



but there is only one population size at which MSY is attainable. These concepts and their limitations are discussed in detail in Eberhardt (1969), Emlen (1973), Ricker (1975) and Gulland (1977).

^{*}In this context, birth and death rates are the numbers of individuals born and dying each year divided by the population size.

It is possible that if the population is reduced to an extremely low density, birth rate may not exceed death rate, since reproduction
may be impaired by rarity of encounters among individuals or perhaps lack of social facilitation.

COMPLICATIONS

If the shape and parameters of the curve shown above were known and stable, then the sustainable yield for each population size would be known, and quotas could be set based on present population size and a management strategy (i.e. is the population size to be increased, held constant or reduced). However, the details of the curve are rarely known, since such knowledge would require one to know birth rate (b) and natural death rate (d) as functions of population size (N). This can only be done if these parameters can be measured accurately at a wide variety of population sizes (rarely possible) or if the density-dependent mechanisms controlling b and d can be studied experimentally (also rarely possible). Density-dependent processes associated with reduced population size might include (Allen and Chapman 1977; Eberhardt 1977)

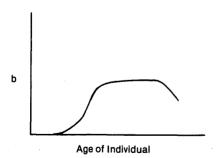
- -lowered age of sexual maturity;
- -increased growth rate:
- Increased rate of ovulation and/or successful pregnancies;
- -lower death rate among immatures and/or adults.

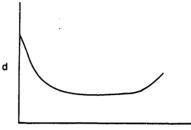
Besides the difficulties inherent In defining any of these relationships, the resultant knowledge can only be applied if present population size, age structure and sex ratios are known.

A simpler strategy is to attempt to maintain the present population size, even if it is uncertain whether this is above or below MSY. This simpler strategy requires knowledge of present birth rate (b), natural death rate (d) and population size (N). Assuming that bbd, süstainable yield is SY = (b-d) N.

Even this strategy can be difficult to implement, since all three of the required parameters are usually difficult to estimate. Some of the common complications are that

 b and d depend on the age of the animals, often in the following manner.





Age of Individual

Thus, overall b and d must be estimated taking into account the age and sex structure of the population.

- Age and sex structure are usually difficult to estimate because age and sex related differences in catchability and hunting mortality result in biased samples.
- Most methods for estimating b and d from sex and age structure data assume that population size has been stable over many years. This is rarely tested and often untrue. Year-to-year fluctuations in environmental conditions and hunting pressure affect population size.
- 4. Hunting is likely to affect some age and sex categories more than others. If only the older animals are hunted, the recruitment rate into the huntable population (rather than birth rate) should be balanced by total mortality of the huntable population.
- The age and sex structure of the population may be biased by year-to-year differences in hunting pressure.
- Because of (4) and (5), density-dependent variations in b and d are likely to occur even when the 'simpler' strategy of maintaining present population size is in use.

In recent years attempts have been made to construct population models that allow for as many as possible of the above complications. Basic principles of population dynamics are used to define the nature of relationships. All available data about population size, harvest, age and sex structure, age-specific reproductive rates, age-specific and sex-specific mortality rates, and density-dependent functions are used to quantify the relationships. Williams (1977) points out that the validity of such increasingly sophisticated analytical techniques depends on the quality of the basic data. Some of these data are usually unavailable. In these cases the model is clearly an incomplete description of population processes, and cannot be expected to

reliably predict sustainable yield or other parameters for more than a brief period or in circumstances different from those in which the data were collected. Information about density-dependent functions is especially hard to obtain, and in its absence predictions about MSY are very questionable (Eberhardt and Siniff 1977; Lett and Benjaminsen 1977). However, in cases where historical data are available about population trends when harvests of known sizes were taken from populations of known sizes, estimates of sustainable yield or even maximum sustainable yield may be possible (Guiland 1971).

An additional complication common to all management strategies is that populations or 'stocks' to be managed must be defined; all parameters discussed above refer to a particular population. Populations are often not readily defined. A small amount of intermixing may occur between stocks that are usually separate. In some species, stocks are separate at one time of year (which may or may not include the breeding season) and mixed at other times of year. In most situations the animals and the hunting pressure are both unevenly distributed over the range of the stock; hunting mortality in certain local areas (e.g., near settlements) may markedly exceed that elsewhere, and the local response of the animals will depend on their site tenacity, social structure and population genetics. In some species there is pronounced segregation of sex and/or age classes at certain times of year. As a result, hunting mortality for different age and sex classes can vary markedly among areas.

The above discussion has dealt with a single species in isolation. However, changes in the population size of one species are likely to affect the populations of its food organisms, competitors and predators. These direct effects could lead to indirect effects elsewhere in the trophic web. Thus, achievement of MSY of one species may have undesirable biological effects, and may ultimately affect the sustainable yield of the species in question or of other species valuable to man. The 'optimal' sustainable yield in an ecosystem sense may differ from the maximum sustainable yield. The optimal sustainable yield is difficult to define or determine (Roedel 1975; Larkin 1977; Eberhardt 1977), but the following general principles have recently been formulated by an inter-agency workshop concerning management and conservation of living resources (Holt and Talbot 1978:14):

- The ecosystem should be maintained in a desirable state such that
 - a. consumptive and nonconsumptive values could be maximized on a continuing basis,
 - b. present and future options are ensured, and
 - risk of irreversible change or long-term adverse effects as a result of use is minimized.
- Management decisions should include a safety factor to allow for the facts that knowledge is limited and institutions are imperfect.
- 3. Measures to conserve a wild living resource

- should be formulated and applied so as to avoid wasteful use of other resources.
- 4. Survey or monitoring, analysis, and assessment should precede planned use and accompany actual use of wild living resources. The results should be made available promptly for critical public review.'

INFORMATION REQUIRED

Data required for management depend on the goal of management and the characteristics of the species. In general, so ne of the necessary data are unavailable or biased, and general principles, incomplete data and indirect evidence must often be used instead. Thus, the list of parameters that may be useful is longer than the minimum number that, if accurately known, would suffice. The following sections summarize the data that are required or that often prove to be useful.

DISTRIBUTION

The seasonal distribution of each separate stock should be known, at least in a general way, so that the locations and times when it is subject to high natural mortality and hunting can be evaluated. Information about the circumstances and degree of exchange among partially distinct stocks is important in order to assess the effects of localized harvests.

STATUS AND SIZE OF POPULATIONS

'Status' here refers to trends in population size. Is it declining, stable or increasing? Is the trend accelerating or is the population stabilizing? Is the trend similar throughout the range of the stock? Information about status can indicate whether present management policies (if any) are having the desired effect on population size; e.g., has sustained yield been achieved. Status is often easier to measure than population size, since trends can be identified by incomplete surveys or index methods as long as the fraction of the stock counted either is known or remains constant.

Population size is an essential parameter for any form of management other than 'trial and error' reaction to historical trends. In general, a 'trial and error' system for setting quotas or hunting regulations is suitable only if exploitation is at a low and relatively stable rate, and even then trends must be monitored. Any more sophisticated management strategy requires an estimate of population size. Analytical methods may permit calculation of an allowable harvest as a percentage of population size, but this can only be translated into a quota if population size is known.

^{&#}x27; See May et al. (Science 205: 267-277, 1979) for a recent discussion.

POPULATION STRUCTURE AND DYNAMICS

Analysis of population structure and dynamics is severely limited unless a reliable method for determining the age of a specimen is available. All species of arctic marine mammals breed and give birth at known species-specific times of year. Thus the problem is to determine the age in whole years. Seals can generally be aged by counting annual layers in the canine teeth, and baleen whales can be aged by layers in the ear plug. Toothed whales have layers in their teeth, but the number of layers deposited annually is sometimes uncertain. Most ageing methods that do exist are of recent origin (since 1950), and older studies often did not provide age-specific data.

Relevant data about reproductive biology include the type of mating system, age at first breeding (for males and females separately), proportion of the mature females ovulating and giving birth each year, agespecific rates of ovulation and giving birth, frequency of multiple births and duration of lactation. The type of mating system is important in determining the relative effects of harvesting males and females; if a few males have harems and others do not reproduce, it is probable that the latter group can sustain high mortality with little effect on the reproductive potential of the population. All parameters listed above are involved in calculations of recruitment. Some of them can be density dependent. Information about this density dependence is not necessarily important if the management goal is to maintain the present population size, but it is of critical importance when the goal is maximum or 'optimum' sustainable yield.

The mortality rate is an essential parameter in any calculation concerning population dynamics. In most cases it is important to know the mortality rates for juvenile, immature and adult animals separately, since these rates are usually different. The relationships between mortality rates and population density are needed in order to calculate maximum sustainable yield. Information about the causes of natural mortality and about factors limiting population size is valuable for interpreting or predicting temporal changes, responses to changed conditions and interspecific effects.

HARVEST AND UTILIZATION

Accurate information about current and historical harvest levels (including hunting loss) is essential for any active management program. This information is needed to determine harvest level relative to sustained yield or any quotas that may exist. The mortality due to harvesting, together with natural mortality, is a key component of any calculation concerning population dynamics. The age and sex structure of the animals killed is important, since this affects the composition of the remaining population.

Numbers of animals killed but not retrieved must be included in hunting mortality figures. Unretrieved animals include those that sink before they can be re-

trieved, and those that are wounded and die later because of their wounds. Unretrieved animals are not normally reported or recorded at present. The few correction factors for non-retrieval that have been derived are generally based on small samples and may not apply in altered circumstances. The percentage non-retrieval often depends on the type of hunt (e.g., from fast ice or from boat? rifle or harpoon? were animals driven into shallow water before being shot?) and on the time of year. Information about these factors is needed in order to estimate non-retrieval.

The geographic distribution of the harvest should be known. Hunting pressure is likely to be concentrated near settlements, and the harvest mortality rates in those areas will exceed the rate elsewhere in the Arctic. Effects of this uneven harvest pattern on a population will depend on the degree of exchange of animals among local areas. This factor is of particular concern in the case of species that are non-migratory. However, it could be important even in the case of a migratory species, since different age and sex classes sometimes have different migration routes or seasonal distribution patterns; a localized harvest might thus take an unrepresentative fraction of the total number of some particular age or sex class.

Long-term trends in harvest level are often the only available data concerning previous population size, and are an important tool for monitoring current trends in population size. Trends in harvest level are much more valuable as indicators of trends in population size if information about hunting effort is also available. Fisheries biologists have developed numerous analytical methods based on 'catch per unit effort' data (Ricker 1975; Gulland 1977). These methods could be applied to marine mammals if catch, non-retrieval and effort were known.

The manner in which each species of marine mammal is utilized by the inuit is relevant in assessing the importance of the species to inuit and in predicting future trends in hunting level. Utilization of some species has changed considerably since southern materials were introduced to the Arctic, and since motorized toboggans began to reduce the need for dog food. Thus information about utilization is likely to be inaccurate if it was obtained more than a few years ago.

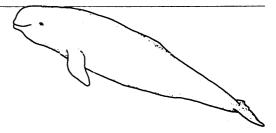
BELUGA OR WHITE WHALE

DISTRIBUTION

Belugas occupy a discontinuous circumpolar range in arctic and subarctic waters. At least five separate populations are thought to exist in the Canadian Arctic (Sergeant and Brodie 1975) although the evidence is weak. In summer, these populations occur in the Beaufort Sea, Lancaster Sound, Cumberland Sound, Ungava Bay and Hudson Bay areas. Most knowledge of these populations has come from studies conducted during the short summer period (generally July and August) when belugas frequent coastal areas (Doan and Douglas 1953; Sergeant and Brodie 1969; Brodie 1971; Sergeant and Hoek 1974; Finley 1976; Fraker 1977a). Knowledge of the winter distribution and habits of the beluga is meager.

Belugas usually begin to arrive at the summering areas during May and June. Certain specific coastal areas within the general summering areas are traditionally occupied during mid-summer, generally from late July or early August to late August (Sergeant 1973a; Finley 1976; Fraker 1979). By the end of September, as freeze-up occurs, most belugas have vacated their summering grounds (Sergeant and Hoek 1974; Johnson et al. 1974; Finley and Johnston 1977).

Belugas that summer in the Beaufort Sea make long migrations to the Bering Sea (Fraker 1979), where they winter in and along the front of the seasonal ice pack and perhaps in persistent natural open-water areas farther north (Kleinenberg et al. 1964). However, from October to May there are few observations of belugas. Occasionally they are trapped by the ice and attempt to maintain breathing holes (Kumlien 1879; Porsild 1918; Vibe 1967; Freeman 1968; Finley and Johnston 1977; Kapel 1977). At least some belugas from western Hudson Bay apparently overwinter in the northwest part of the bay (Sergeant 1973a) but details and numbers are unknown. Several belugas were observed in extensive leads in the ice between Lake Harbour and Coral Harbour in January 1975 (Stephansson 1975), It has been suggested that belugas from Lancaster Sound make local migrations and overwinter in Lancaster Sound or the 'North Water' of Baffin Bay (Sergeant and Hoek 1974; Sergeant and Brodie 1975). However, only the easternmost part of Lancaster Sound is free of landfast ice in certain years (Lindsay 1975; LGL Ltd. unpublished data), and recent late winter surveys there and in the North Water (LGL Ltd. unpublished data) revealed only small numbers of belugas. It is probable that most of the belugas from Lancaster Sound and also Cumberland Sound overwinter along the edge of the pack ice in Davis Strait and in the Disko Bay region of west Greenland (Kapel 1975a). Belugas from northeastern Hudson Bay and Ungava Bay are also thought to overwinter in the Davis Strait area (JBNQNHRC 1976) and off northern Labrador (Degerbøl and Freuchen 1935). Aerial surveys in March 1978 found about 400 belugas in eastern Davis Strait



and 75 In Frobisher Bay (McLaren-Marex Inc. 1979). Thus, populations of belugas that summer separately in the eastern Arctic and Hudson Bay may mingle during winter.

Current knowledge of the distribution of belugas in the Canadian Arctic is summarized in Figures 9 and 10.

STATUS AND SIZE OF POPULATIONS

Because belugas concentrate in large numbers in traditional coastal areas during part of the summer, aerial censuses are greatly facilitated. The main limitation is that water turbidity may impair visibility in certain areas such as the Mackenzie and Churchill River estuaries. Roughly 24,000 to 28,000 belugas are known to summer in the Canadian Arctic, based on a few surveys of the known summer concentration areas (Table 7). In addition belugas are known to occur in James Bay and eastern Hudson Bay (Jonkel 1969) and in the St. Lawrence River (about 500 — Sergeant and Brodie 1975).

Sergeant and Brodie (1969, 1975) suggest that belugas in the Canadian Arctic form discrete populations. Their evidence is based on differences in body lengths of belugas from different areas and also on the supposed geographic isolation of populations. While the belugas of the Beaufort Sea are isolated from those in the eastern Arctic, the discreteness of populations in the eastern Arctic is not well substantiated. Sergeant and Brodie (1969) combine statistics from belugas captured at Somerset and Ellesmere Islands and suggest that this population is isolated from populations in west Greenland and Cumberland Sound. The Lancaster Sound population was estimated at 10,000 animals by Sergeant and Brodie (1975).

Brodie (1971) provided evidence that the belugas of Cumberland Sound had declined due to overexploitation from commercial and non-commercial hunting, which took approximately 10% of the population annually during the 1950's. Sergeant and Brodie (1975) note that this population has steadily diminished over a long period. A kill of 177 belugas in 1977 represented 22% of the population of 810 estimated to be present

FIGURE 9 Distribution and Migration Routes of Belugas in the Canadian Eastern Arctic. (Based on sources cited in text.)

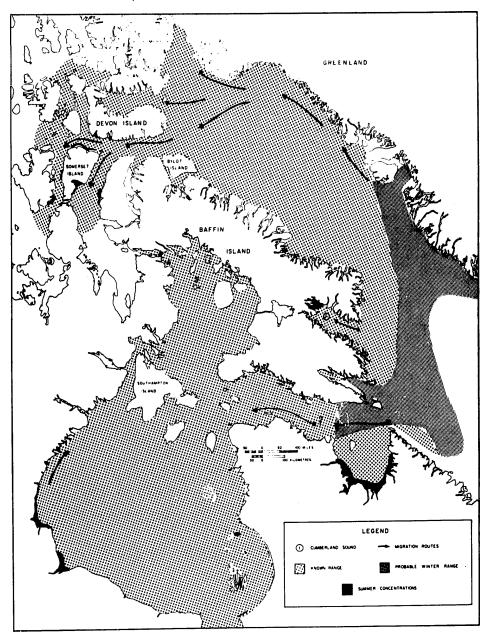


TABLE 7

Maximum Numbers of Belugas Observed at Various Locations in the Canadian Arctic¹.

Area	Estimated Number	Source
Western Hudson Bay	10,000	Sergeant (1973a)
Ungava Bay (northeastern Hudson Bay)	1.000	Sergeant and Brodie (1975)
Beaufort Sea (Mackenzie River delta)	4,000-6,000	Fraker (1977b), Sergeant and Hoek (1974)
Lancaster Sound and adjacent channels	8,000-10,000	Sergeant and Brodie (1975), Finley (1976)
Cumberland Sound	750	Brodie (1971)
Total	24,000-28,000	

^{&#}x27;Table adapted largely from Sergeant and Brodie (1975), with the addition of more recent estimates.

(Imperial Oil Ltd. et al. 1978). The beluga population of Cumberland Sound could be considered in jeopardy given the excessive kill, especially if there is little or no recruitment from other populations as suggested by Sergeant and Brodie (1975). The population was estimated to number about 500 animals in 1978 (B. Kemper, personal communication).

Sergeant and Brodie (1975:1052) state that long term catches of 500 belugas per annum at Churchill 'had no effect on population over decades', but they also mention (p. 1052) that 'white whales of the Churchill River have already been reduced historically by trading, hunting and port development'. Sergeant and Brodie (1975) state that there is no evidence of any decline in the numbers of belugas in the Beaufort Sea.

There is no historical information on the size of the Lancaster Sound population of belugas. These animals were exploited by the whalers in Baffin Bay, Lancaster Sound and Prince Regent inlet. Lubbock (1937) records over 15,000 belugas taken in these areas from 1868 to 1910. Since Lubbock reports on the take of only a variable proportion of the whaling ships and since data are lacking for several years, it is probable that the total take was closer to 30,000 belugas. The Lancaster Sound population has been only lightly hunted in recent years and Sergeant and Brodie (1975) thought the population was probably stable at the current level of about 10,000 belugas.

POPULATION STRUCTURE AND DYNAMICS

The age structure of beluga populations has been deduced primarily from analyses of tooth layers. Two dentine layers and one mandibular layer are believed to be deposited annually (Brodie 1969; Sergeant 1973a) although direct proof is lacking. Sergeant (1973a) mentioned that layers were difficult to count because of their irregularity in many animals, their close spacing and convoluted shape in the older females, and wear in the older animals, especially males. In most collections there was the further problem that the capture method resulted in selectivity for size and sex. Fraker (1977a) found that there could be differences of at least 10 growth layers in different teeth from the same beluga, presumably due to differential rates of wear.

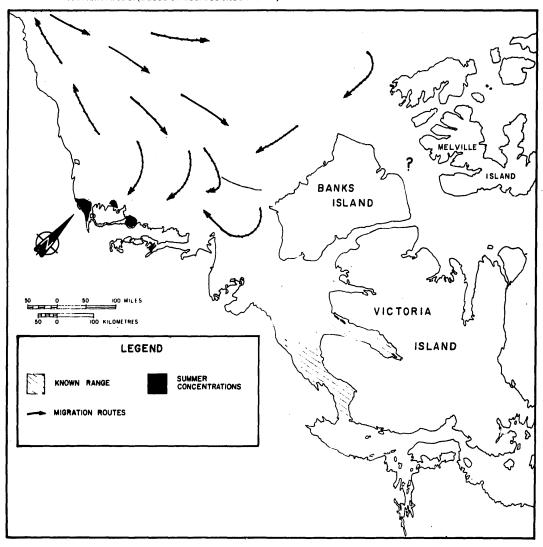
Obviously, the technique for ageing belugas needs to be verified and improved. Misinterpretations of age can lead to substantial errors in assessment of propulation structure and, ultimately, sustainable yields of beluga populations. For example, Fraker (1977a) suggested that a reasonable estimate of the maximum life span of belugas from the Beaufort Sea was about 50 years whereas Sergeant (1973a) suggested that maximum ages were 25 to 30 years.

REPRODUCTIVE BIOLOGY

Although there is no information on the mating behaviour of belugas, limited data from other toothed whales suggest that the beluga may be polygynous (i.e. one male breeds several females) (Kleinenberg et al. 1964).

Brodie (1971) found that sexual maturity of female belugas in Cumberland Sound was attained when nine to 10 tooth layers were present (believed to be five years). Males attained sexual maturity by eight years of age. Sergeant (1973a) found ages (based on tooth

FIGURE 10 Distribution and Migration Routes of Belugas in the Canadian Western Arctic. (Based on sources cited in text.)



layers) of sexual maturity to be similar for belugas from western Hudson Bay.

Conception occurs in early May, gestation lasts 14.5 months, and calving occurs in late July and early August at Cumberland Sound (Brodie 1971). Lactation lasts about two years and most females produce a single calf once in three years (Brodie 1971; Scrgcant 1973a). Sergeant (1973a) found that 41% of all mature females taken at Whale Cove were pregnant in late summer when conceptions had ceased. At this rate mature females become pregnant once in 2.4 years on average. The actual birth rate would be somewhat less than 0.41 per mature female per year and Brodie (1971) assumes it to be about 0.33 calves per female per year.

MORTALITY FACTORS

Apart from man, the beluga has few predators. Killer whales are known to kill belugas occasionally (Kleinenberg et al. 1964) and there are a few reports of polar bears killing belugas (Kleinenberg et al. 1964; Heyland and Hay 1976). The effects of these two predators appear to be insignificant to the beluga populations.

Herds of belugas are occasionally trapped in ice and can suffer high mortality (Porsild 1918; Vibe 1967; Freeman 1968; Finley and Johnston 1977).

The rates of natural mortality has not been quantified.

AGE AND SEX STRUCTURE

Sergeant (1973a) reviews the sex ratio of belugas sampled in a variety of ways from several areas. There is great variability in sex ratios among samples. This is due to sampling blases and to non-random distribution of size and sex among the herds. Sergeant (1973a) and Brodie (1971) conclude that the sex ratio at birth is 1:1 and this ratio continues through adulthood. However, Fraker (1977a) found that the annual harvest in the Mackenzie delta was about 80% males and he believed that the adult sex ratio was no inner 1:1.

Sergeant (1973a) constructed age-frequency distributions. Extreme ages were 25 to 30 years; 20 to 21 years was considered to be the age at last birth for females (Brodie 1971; Sergeant and Brodie 1975).

On the basis of a sample of 234 belugas from Churchill, Sergeant (1973a) suggested that mortality rates of adults were relatively uniform until the age of 15 to 20 years when mortality was rather high. This trend was not evident in a smaller sample (116) from the Mackenzle delta (Sergeant 1973a).

Because of the small sample sizes and biases in sampling techniques no reliable mortality rates have been calculated for belugas.

POPULATION DYNAMICS

Brodie (1971) and Sergeant (1973a:1065) state that mature female belugas produce a calf once in three years; a birth rate of 0.33. However, Sergeant (1973a: 1084) states that frequency of calving is once in three years for 75% of the females and once in two years for 25% of the females, resulting in a birth rate of 0.38. The pregnancy rate was 0.41 (Sergeant 1973a).

Sergeant (1973a) calculated the annual recruitment of calves to be 12% of the population. This figure is in agreement with observed frequencies of newborn calves at Somerset Island after calving was thought to be complete (Finley 1976). Brodie (1971) roughly calculated the recruitment rate of calves to the population to be 0.09 by using an age of first birth of six years, sex ratio of unity, one calf every three years, and an age of last birth assumed to be 21 years.

The mortality rate for calves and immature animals is unknown. These age classes were underrepresented in the samples reviewed by Sergeant (1973a). Sergeant (1973a) compared samples from Russia and Greenland and calculated that calf mortality was about 10% between the ages of two and eight months. However, there are no estimates of the rate of recruitment into the adult breeding population nor of annual variations in this rate.

Age-specific and sex-specific adult mortality rates have not been calculated.

The rate of recruitment of caives to the population (nine to 12%) should not be equated with the potential sustainable yield of the population. Natural mortality of caives and sub-adults occurs and the recruitment of belugas to the breeding population is undoubtedly less than nine to 12%.

HARVEST AND UTILIZATION

Because of their habit of gathering in large numbers in coastal areas, belugas have been subject to heavy exploitation by drive fisheries in the past. The potential for such exploitation was first realized by the Hudson's Bay Company in eastern Hudson Bay but as with many such fisheries the enterprise collapsed after a short period of heavy exploitation (Low 1908; Anderson 1934).

As the bowhead whale fishery declined toward the end of the 1800's, some whalers turned their attention toward belugas and large numbers were driven on shore in some of the traditional summering areas. In Elwin Bay on Somerset Island at least 3,300 belugas were killed between 1888 and 1895, with the largest catch of 1,424 in 1895 (Lubbock 1937). Large numbers of belugas were killed at Cape Sparbo in Jones Sound; in 1911, 750 were taken (Degerbøl and Freuchen 1935). In Cumberland Sound, large numbers of belugas were killed from 1923 to 1925; over 800 were killed in 1924 (Anderson 1934).

Commercial fisheries established in western Hudson Bay typically have operated for brief periods before they were shut down. A fishery at Churchill, Manitoba, took an average of 450 belugas per annum between 1950 and 1960. A local net fishery run by native people was established at Whale Cove in western Hudson Bay and who operational intermittently from 1961 to 1969 with an average of 200 belugas being taken annually (Smith and Taylor 1977).

ANNUAL HARVEST

アファイル・ラー・アイト かんきんしょう しょうしょう アイト・アイト

Harvest statistics for belugas are very incomplete for the 1970's (Smith and Taylor 1977). In 1973, the last year for which catch statistics are given by Sergeant and Brodie (1975), the catch for the entire Canadian Arctic was given as 538 belugas. This figure is certainly an underestimate since in Ungava Bay and north-eastern Hudson Bay, the total catch was estimated at nearly 800 belugas (JBNQNHRC 1976). The most complete statistics for recent years come from the Mackenzie delta where harvests have averaged about 150 belugas per annum from 1972 to 1976 (Brakel 1977; Fraker et al. 1978).

Kills of belugas in the high arctic islands are generally low and restricted primarily to the communities of Grise Fiord and Resolute (Bissett 1987a; Riewe 1977). Riewe (1977) estimated that 40 belugas were taken per year at Grise Fiord although the catch could be quite variable with none caught in bad ice years such as 1972 and as many as 118 caught in good years such as 1987.

Anders et al. (1987) estimated that the average kill in Cumberland Sound was 60 belugas. Smith and Taylor (1977) stated that Inuit at Pangnirtung have restricted their catch to a maximum of 40 whales following management recommendations by fisheries biologists. However, in 1977, the kill was 178 whales (Fisheries and Marine Service, Yellowknife), which is clearly higher than the sustainable yield for this small population.

Recent estimates of beluga harvests are presented in Table 8. These estimates were gathered by N.W.T. Game Officers and dederal Fisheries Officers and compiled by Fisheries and Marine Service in Yellowknife (data supplied by D. Dowler and B. Wong). It is not known what proportion of the actual harvest is represented in Table 8, but it is believed to be high. The harvest at Churchili, Manitoba, is not included in the table. The harvest by Quebec communities based on JBNQNHRC (1976) is included.

In addition to the Canadian catch, annual catches of 561 to 1,509 belugas (mean 937) were reported in west Greenland in 1966-74 with an additional 125 to 150 taken in Thule District (Kapel 1977). In Alaska, the total removal of belugas was 215 (plus 100 to 115 lost) in 1977 and 165 (plus 80 to 90 lost) in 1978 (G. Seaman, Alaska Dept. of Fish and Game, *in litt.* to M. Fraker, LGL Ltd.). It is not known what proportion of this kill is from the population that inhabits the Mackenzie estuary.

SEASONAL AVAILABILITY

Hunting of belugas in the Canadian Arctic is restricted primarily to the short summer period of June to September. In fact most of the hunting is restricted to a very brief interval in mid to late summer after the ice has cleared from the shore. Hunters at Resolute usually depend on a brief appearance of large numbers of belugas in late August or early September just before freeze-up. At Grise Fiord, belugas usually make a brief appearance just before freeze-up although in some years such as 1968, 1969 and 1972, heavy ice kept them away (Riewe 1977). In the Mackenzie delta, whaling usually reaches a peak in the first half of July and is intensive for a period typically of three weeks when belugas are concentrated in the estuaries (Fraker 1977a).

TABLE 8
Reported Harvest of Belugas In the Canadian Arctic.

Community	19761	1977'	1975'
Resolute Bay	11	17	
Grise Fiord	- 15	. 11	
Pangnirtung	120	178	
Frobisher Bay	10	3	
Lake Harbour	41	26	
Cape Dorset	10	7	
Hall Beach	10	18	
igloolik	22	15	
Sanikiluaq		14	
Coral Harbour	42	52	
Repulse Bay	34	40	
Chesterfield Inlet	20	18	
Rankin Inlet	25	12	
Whale Cove	5	30	
Eskimo Point	20	39	
Mackenzie Delta	154	148	
Great Whale River			26
ไทยผู้ผลดู			97
Akudivik			5
Sugluq			122
Wakeham Bay			162
Koartak			31
Payne Bay			43
Leaf Bay			7
Fort Chimo			53
George River			19
Port Burwell	*		8
Totals	539	625	573

Based on data from Fisheries and Marine Service, Yellowknife

^{*}Based on data from JBNQNHRC (1976) (excludes Povungnituk)

No harvest or harvest not reported.

HUNTING TECHNIQUES

In the Canadian Arctic, the most common present-day technique of hunting belugas is to force them into shallow water with a motor boat and then to shoot them with a medium-calibre rifle such as a .303 or .30/30. In the Mackenzie delta, belugas are pursued in the shallow estuaries with boats powered by outboard motors of 20 to 80 hp (Fraker et al. 1978). The animals usually are first wounded by gunshots; the objective is to permit close approach but, in order to prevent sinking in the turbid water, not to kill the animal outright. The belugas are then harpooned and finally dispatched with more shots. The harpoon is attached by a line to a 10 gallon fuel barrel - the replacement for the traditional sealskin buoy (aavituk). At Creswell Bay, Somerset Island, a successful hunt was observed in 1975: three hunters in a freighter canoe powered by a 20 hp outboard motor drove a herd of approximately 100 belugas close to shore and succeeded in killing 14 (LGL Ltd., unpublished data).

HUNTING LOSS

The number of belugas killed but not recovered is usually high. In the Mackenzie delta losses are variably estimated as one-third to one-half of the whales shot (Fraker et al. 1978; Smith and Taylor 1977), Hunt (1976) cited in Fraker et al. 1978) noted several factors that contributed to the high loss rate. Several belugas are sometimes wounded during indiscriminate shooting. Wounded animals are often lost in the confusion and turbidity, and animals that are mortally wounded may sink to the bottom before they are harpooned. Separation of the young from their mothers results in calf mortality. Some hunters are negligent about retrieving the whale after it is shot. Losses in other areas of the Arctic are variable. In western Hudson Bay the losses are thought to be insignificant because most animals are secured by harpoon, in Cumberland Sound the harpoon is less frequently used and losses may be higher (Smith and Taylor 1977).

Shooting of belugas is not widely practised in the U.S.S.R. since it is estimated that at least 50% of the animals are lost in this way. Instead net fisheries are the most common way of catching belugas (Kleinenberg et al. 1964).

Occasionally hunting is conducted opportunistically from the shore. For example, at Resolute in early September of 1976 belugas were seen close to the shore. About 10 or 12 people at the settlement were alerted and drove to the shore. Many shots were fired from the beach and at least five belugas were hit. None were retrieved because a boat was not immediately available (LGL Ltd. unpublished data).

Netting has proven to be a very effective method of catching belugas in the past (McLaren and Mansfield 1960; Sergeant 1968) but use of this method appears to have declined in recent years because the availability of outboard motors 'has greatly reduced the amount of patience and work required for whaling' (Fraker 1977a).

UTILIZATION

Mature belugas weigh from 540 to 765 kg and approximately 60% of this is considered potentially edible (Brakel 1977). However, muktuk (skin and thin layer of blubber), which comprises 18% of the body weight (Brakel 1977), is often the only product taken. In the Mackenzie delta, beluga meat is also taken and dried for use but it is not considered a prime food (Brakel 1977). In summarizing the socio-economic importance of belugas in the Mackenzie delta area, Brakel (1977) suggested that their current importance to the Inuit 'may be more a matter of preference than necessity'. However, Fraker (1977a) stressed the high cultural and social values of the hunt.

¹ Published as Hunt (Can. Fish. Mar. Serv. Tech. Rept. No. 769, 1979).

DISTRIBUTION

The narwhal is found primarily in eastern Canadian and Greenland arctic waters. It is a migratory species that vacates most of its Canadian range during the winter fast ice period. The winter range of the narwhal is poorly known but it is thought to include the south edge of the winter pack ice in Davis Strait as well as the Disko Bay area of west Greenland (Vibe 1967; Kapel 1975a, 1977). M'Clintock (1859) frequently observed narwhals migrating northward through the pack ice in late March of 1858 in the middle of Davis Strait (about 68°30'N). Mansfield et al. (1975a) thought that some narwhals probably wintered in the 'north water' at the north end of Baffin Bay; however, a recent survey (LGL Ltd. 1978; unpubl. data) did not confirm this.

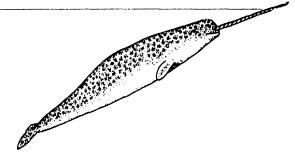
Most narwhals migrate north into Baffin Bay in spring but a small, undetermined number move through Hudson Strait into northern Hudson Bay and Foxe Basin (Banfield 1974; Mansfield et al. 1975a). The northward migration in Baffin Bay begins in March and most animals follow the receding ice up the west coast of Greenland to Melville Bay and the Thule area. Some animals continue north into Smith Sound but most turn west and southwest and enter Jones Sound and Lancaster Sound in June and July (Kapel 1975a; Mansfield et al. 1975a; Johnson et al. 1976). It is not known whether other northward routes through Baffin Bay are also used.

Large numbers of narwhals summer in Admiralty Inlet and Eclipse Sound. B. Kemper (in Milne and Smiley 1978) estimated 10,000 narwhals in Admiralty Inlet in 1975. Narwhals also move west into the Arctic Archipelago via Barrow Strait. Small numbers of these animals move north of Barrow Strait into McDougall Sound and Wellington Channel. However, substantial numbers move south into Peel Sound (over 1,000 animals — Finley and Johnston 1977) and presumably into Prince Regent Inlet and Guif of Boothia.

The autumn migration generally retraces the spring and summer movements in the archipelago. Southward migration in Baffin Bay is not well understood. Narwhals leave the Arctic Archipelago in September to October (Johnson et al. 1976; Finley and Johnston 1977). A southward movement has been observed along the east coast of Baffin Island during October and November (Anders et al. 1967; Freeman 1976). Vibe (1967) stated that southward migrating narwhals follow the border of the Canadian-Greenland current in Baffin Bay. The principal southward migration routes are not known.

Current knowledge of distribution of narwhals is summarized in Figure 11.

¹ Recent studies (1978-79) by LGL Ltd. for the Petro-Canada EAMES Project have clarified migration routes of narwhals in Baffin Bay (in prep.).



STATUS AND SIZE OF POPULATIONS

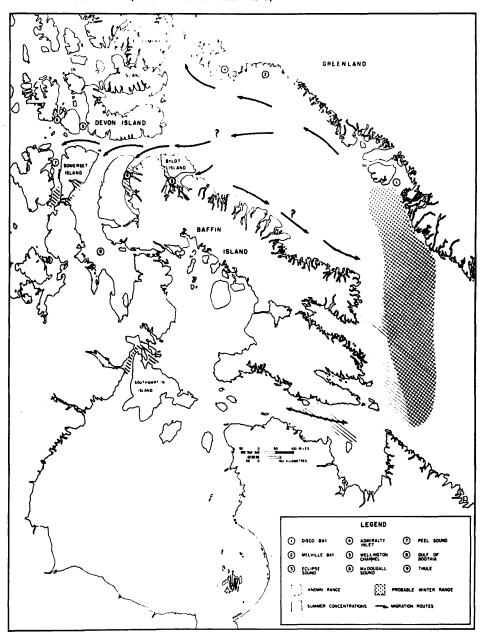
Estimates of numbers of offshore species such as the narwhal have, until recently, been based on observations from ships and coastal vantage points. Recent industrial activities in the north have greatly increased aerial survey coverage of offshore waters and not surprisingly the different techniques yield different results.

It has recently been estimated that between 20,000 and 30,000 narwhals entered Lancaster Sound in 1976 (Davis et al. 1978a). This estimate is based on a combination of shore-based observations (Greendale and Brousseau-Greendale 1976) and intensive aerial surveys designed for birds (Johnson et al. 1976) and involves a complex series of assumptions and extrapolations. The estimates need to be verified with surveys designed specifically for narwhals. It is important that increases in estimates of population sizes due to improved survey techniques not be interpreted as real increases in population sizes.

The narwhal also summers in Jones Sound (numbers unknown but thought to be low), in Thule District of northwest Greenland (about 2,500 animals — Bruemmer in Mansfield et al. 1975a) and in northern Hudson Bay and Foxe Basin (numbers unknown but thought to be low — Mansfield et al. 1975a). Clearly, available information on the size of the narwhal population is inadequate. The range (10,000) for the estimate for Lancaster Sound exceeds the numbers thought to be present in each of the other summering areas and perhaps all of them combined!

There is no information about the interrelationships among the various summering populations of narwhals. It is not known whether they represent semi-solated stocks with restricted genetic interchange or whether all of the animals belong to a single freely interbreeding population. Based on the meager available information on migration and wintering areas, it seems likely that the animals in Thule, Jones Sound

FIGURE 11 Distribution and Migration Routes of Narwhals in the Canadian Eastern Arctic. (Based on sources cited in text.)



and Lancaster Sound are, at least, potentially interbreeding. Too little is known about the movements of the Hudson Bay-Foxe Basin population to determine whether it is partially isolated from the Baffin Bay animals.

POPULATION STRUCTURE AND DYNAMICS

The population structure of the narwhal is very poorly understood. K. Hay of Arctic Biological Station and McGill University has recently (1974-1976) conducted a study of aspects of the reproductive biology of the narwhal but his data are not yet fully analyzed. Narwhal reproductive biology is assumed to be similar to that of the closely related beluga (Mansfield *et al.* 1975a) and current management is based on this unproven assumption.

REPRODUCTIVE BIOLOGY

Although there is no information on the breeding behaviour of the narwhal, Hay and Sergeant (1976) suggest that the species is polygamous. Polygyny is implied from features such as sexual dimorphism (males larger than females), later attainment of sexual maturity in the males than in the females, and the presence of a tusk on the male narwhal.

Breeding occurs about mid-April, gestation lasts about 14.5 months and calving occurs about mid-July (Best and Fisher 1974; Mansfield et al. 1975a). Assuming a lactation period of 20 months, as in the beluga (Sergeant 1973a), females may produce a calf every third year (Degerbøl and Freuchen 1935; Mansfield et al. 1975a) but the proportion that do is unknown. The age of sexual maturity in the narwhal is assumed to be similar to that in the beluga, which matures at five years (females) and eight to nine years (males) (Brodie 1971).

AGE STRUCTURE

The use of tooth and mandibular layering for evaluating the age structure of narwhal populations appears to be of limited value (K. Hay personal communication). As with belugas there are difficulties in interpreting the number of tooth layers in older animals and determining the number of layers laid down per year. There is no information on age-specific mortality, age-specific reproductive variability or reproductive longevity.

MORTALITY FACTORS

Apart from hunting (discussed later) there is little quantitative information about natural mortality.

Killer whales are known to take narwhals (Degerbøl and Freuchen 1935); however, killer whales are not numerous within the range of the narwhal and it is

doubtful whether they have a significant effect on narwhat populations.

There are several accounts of narwhals being trapped in the ice where they may suffer high mortality, particularly when found by inuit hunters (Brown 1868; Porsild 1918; Vibe 1950; Kapel 1977). In the winter of 1924, around 600 narwhals were trapped in the ice in Admiralty inlet and a total of 203 tusks were taken by the inuit (Degerbøl and Freuchen 1935).

POPULATION DYNAMICS

There are too few data on narwhals to make reliable statements about the population dynamics of the species. The available information on the closely related beluga was reviewed in the account of that species.

There is no information about the natural regulation mechanisms that act on narwhal populations and there is no information about the potential carrying capacity, for narwhals, of arctic marine areas.

HARVEST AND UTILIZATION

Historical records indicate that in the late 1800's and early 1900's either relatively few narwhals were taken or few were reported by whalers (Lubbock 1937). However, William Duval told Soper (1928) that the whalers had taken as many as 2,800 narwhals in one year from Eclipse Sound.

ANNUAL HARVEST

At present the killing of narwhals is restricted primarily to the eastern Canadian Arctic (particularly Baffin Island) and along the west coast of Greenland. Consistently high numbers of animals are taken by two north Baffin communities — Pond Inlet and Arctic Bay. The catch for these two communities was estimated as 300 annually from 1973-1975 (Smilth and Taylor 1977). Smaller numbers are taken regularly at Grise Fiord and Clyde River. Numbers taken by other communities are often quite variable from year to year and occasionally may be unusually high (e.g., 73 at Cape Dorset in 1966 — Higgins 1968; 90 at Pangnirtung in early 1960's — Smith and Taylor 1977).

Catch statistics are very incomplete. Mansfield et al. (1975a) estimated that the annual take may be 500 to 600 (including a Greenland catch of 100 to 135 narwhals) and that the annual maximum kill may be in the order of 1,150 when a roughly estimated loss of 50% is included. Kapel (1975a) estimated that the annual harvest of narwhals in west Greenland waters is actually about 500 animals, but his more recent figures (Kapel 1977) are slightly lower. About 125 to 250 are taken annually in Thule District in summer, and 107 to 474 (mean 221) were taken annually elsewhere along the west coast of Greenland in 1967-1974. Most of the narwhals taken in Greenland south of Thule District are

taken in fall, winter and spring, and probably include narwhals that enter Canadian waters in summer.

The Canadian harvest of narwhals is now regulated by a community quota system. The allowable harvest in each community with a quota is presented in Table 9. The regulations (established in 1976) prohibit the killing of calves and females accompanied by a calf.

TABLE 9

Annual Quota (1978) for Harvest of Narwhals in the Canadian Arctic.

Settlement Area	Quota
Resolute Bay	20
Creswell Bay	12
Grise Flord	20
Arctic Bay	100
Pond Inlet	100
Clyde River	50
Broughton Island	50
Pangnirtung	15
Frobisher Bay	10
Lake Harbour	10
Cape Dorset	10
Coral Harbour	10
Repulse Bay	15
Hall Beach	10
Igloolik	10
Pelly Bay	10
Spence Bay	10
Gjoa Haven	10
Total	472

HUNTING LOSS

Losses of narwhals due to sinking and wounding are very high. Mansfield et al. (1975a) estimate the loss at 50%. In west Greenland the loss at the ice-edge hunt is also estimated at up to 50% (Bruemmer cited by Mansfield et al. 1975a). Hay (1976) found sinking losses to be about 20% during late summer; however, he noted that losses at the ice-edge hunt, where most of the narwhals are taken, were higher but not quantifiable. Observations of the 1978 ice-edge hunt at Pond Inlet have not yet been tabulated, but cursory examination indicates that a 50% loss is an underestimate (LGL Ltd, unpublished data).

SEASONAL AVAILABILITY

The majority of the narwhals are taken during the brief summer period of late June to September. At Pond Inlet and Arctic Bay the Inuit depend on the presence of narwhals at the ice-edges of Pond Inlet and Admiralty Inlet in June and July. It is during this period, particularly late June to early July, when the hunting is most concentrated and large numbers of narwhals are taken.

Narwhals penetrate quickly into areas where ice is breaking up and in favourable years they have been known to penetrate far into the archipelago, accounting for the occasional hunt near settlements such as Spence Bay and Pelly Bay. For example, in the late summer of 1975, the people of Pelly Bay managed to kill seven of about 50 narwhals that appeared near the settlement; this was an unusual occurrence (D. Dowler, personal communication).

HUNTING TECHNIQUES

The ice-edge hunt is an important hunt in which many narwhals are taken by the Inuit of Pond Inlet and Arctic Bay. At Pond Inlet, a few tent camps are usually established along the ice-edge in early June and the ice-edge is often patrolled on snowmobiles until narwhals are spotted. Narwhals that approach the ice-edge within 50 m are shot at with .303 and .3006 rifles loaded with hard tip bullets. If the animal is killed and remains afloat it can be retrieved with a boat. The hunt retreats with the ice-edge and the hunters anxiously await the appearance of narwhals in the small holes and ice cracks as narwhals push into the disintegrating fast ice. Narwhals in ice cracks are fairly easy to pursue and kill.

Later in the summer narwhals are usually found in flords. These narwhals are driven by boats (equipped with 20 to 60 hp engines) into shallow water and are shot. A few experienced hunters may harpoon the whales as is routinely done in the Thule District of northwest Greenland. In 1977, this technique was employed successfully at Creswell Bay (LGL Ltd., unpublished data). The animal was usually harpooned after it had been shot once; a sealskin buoy (aavituk) and a drag device slowed the animal down until it was dispatched with more shots.

UTILIZATION

The narwhal has always been prized for its skin (muktuk), which, in the raw state, is reputed to be high in Vitamin C content. The whale meat has traditionally been used as dog food but the Importance of this has been declining with the decrease in the number of dogs (Mansfield et al. 1975a). Recently there has been concern that high prices paid for ivory may induce hunters to kill many more males for their tusks (Mansfield et al. 1975a). Inuit at Creswell Bay killed only large males in the hunts observed in 1976 and 1977. All meat was stored for use as dog food during the winter (LGL Ltd. unpublished data). Riewe (1977) stated that narwhal ivory sold for \$44 per kg (as much as \$300 per tusk) in 1972 at Grise Fiord. Long tusks (180 to 250 cm) are presently selling for about \$75 per kg (\$350 to \$450 per tusk) at Pond Inlet. Smaller tusks are in greater demand as souvenirs and are sold for about \$100 per kg.

¹ To be published as Finley et al. (Rept. Int. Whal. Commo 30, 1980). Loss rate at ice-edge hunt was 69%, based on a small sample. (N = 16).

KILLER WHALE

DISTRIBUTION

The killer whale is distributed throughout the world's oceans but is most abundant in the cooler temperate and arctic waters of both hemispheres.

In late summer, the killer whale may be found in the eastern Canadian Arctic in Baffin Bay, eastern Lancaster Sound, Davis Strait and at the entrance of Hudson Strait (Lubbock 1937; Miller 1955; Bissett 1967b; Imperial Oil et al. 1978). There are conflicting accounts regarding its occurrence in Hudson Bay (Degerbøl and Freuchen 1935; Loughrey 1959; Sergeant 1968), where it must be at most sporadic in its occurrence during the summer season. Similarly its occurrence in the western Canadian Arctic is not well documented.

The killer whale usually arrives in arctic waters during summer after the pack ice disperses. It appears to avoid areas of heavy ice and consequently it does not penetrate far into the Arctic Archipelago.

STATUS AND SIZE OF POPULATIONS

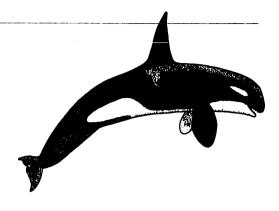
Nothing is known about discreteness of stocks although it appears that populations in the northern hemisphere are separated from those in the south.

Little is known about the numbers of killer whales. In the Atlantic, the largest numbers appear to occur in the northeastern sector, particularly along the coast of Norway (Jönsgard and Lyshoel 1970). In the eastern Canadian Arctic, killer whales are infrequently seen, and then only in small numbers (Degerbøl and Freuchen 1935; RRCS 1977; Imperial Oil et al. 1978).

POPULATION STRUCTURE AND DYNAMICS

Nothing is known of the population structure of killer whales.

The birth season has not been defined clearly although it appears that relatively more calves are born in late autumn and winter (Jönsgard and Lyshoel 1970; Mitchell 1975b). The gestation period is thought to be at least 12 months (Mitchell 1975a). Females and males seem to attain sexual maturity when about 16 and 19 feet (4.9 and 5.8 m) long, respectively (Jönsgard and Lyshoel 1970). Nothing is known of the age of sexual maturity or reproductive rate.



HARVEST AND UTILIZATION

Mitchell (1975b) has reviewed the international fishery for killer whales. Relatively small numbers are taken. The killer whale is not regularly taken by Canadian Inuit.

Fourteen killer whales were observed by biologists from MacLaren Atlantic Ltd. at the head of Cumberland Sound in mid-August 1977; the animals were sighted again in September when they were trapped in a small saltwater lake (Imperial Oil Ltd. et al. 1978). All 14 of these whales were shot by local residents (D. Dowler, Fisheries and Marine Service, Yellowknife, personal communication). No use was made of the dead animals. A local Game Officer was prohibited by the hunters from collecting biological samples from the dead animals (T. Chowns, personal communication).

There is an unsubstantiated report of two killer whales that appeared in Baker Lake in the late summer of 1978. Apparently both animals were killed by native hunters (Nunatsiag News, August 1978).

The killer whale is well known to many Inuit communities in the eastern Canadian Arctic. Until very recently there has been no attempt, as far as we know, to kill these animals. Numerous accounts mention the benefits gained by Inuit hunters when killer whales are in the vicinity; other species of marine mammals are reported to take shelter among the ice floes or in near-shore waters where they become easy prey for the Inuit (Brown 1868; Low 1906; Degerbøl and Freuchen 1935; Bissett 1967b; Higgins 1968).

BOWHEAD OR GREENLAND RIGHT WHALE

The bowhead is a medium-size baleen whale; it reaches lengths of over 20 m.

DISTRIBUTION

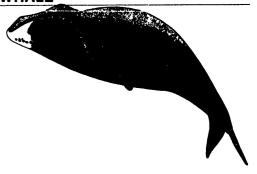
Bowheads occupy a discontinuous circumpolar range in arctic waters, primarily north of 60°N. Two isolated populations are found in the Canadian Arctic.

In the western Arctic, bowheads summer in the Amundsen Gulf area, which was an old whaling ground (Fraker 1979). Bowheads winter in the Bering Sea and migrate past Point Barrow, Alaska, into the Beaufort Sea in late April, May and early June; most individuals pass Point Barrow during the first half of May (Fiscus and Marquette 1975; Braham et al. 1977a; Marquette 1977). From Point Barrow most are thought to head northeast through the southern polar pack ice to reach the Banks Island region; they are then thought to move south off the west coast of Banks Island into Amundsen Gulf (Figure 12) (Fraker 1979). Late migrating individuals probably travel further south in the Beaufort Sea. Very little is known about the fall movements of bowheads out of the eastern Beaufort Sea (Fraker 1979).

In the eastern Arctic, much of our knowledge of the distribution and migrations of bowheads comes from historical accounts of the 19th century whalers who pursued the bowhead to the far reaches of its range and brought it to near extinction. Mansfield (1971) has summarized recent sightings of bowheads to show that they correspond to former whaling grounds. Ross (1974) has reconstructed the summer distribution of the bowhead in Hudson Bay based on logbooks and journals of whalers from 1860 to 1915. Ross discussed the possibility that the bowheads of northwestern Hudson Bay were a resident population separate from that in Davis Strait and Baffin Bay. Evidence of winter residence was inconclusive (Ross 1974); however, Low (1906) stated that bowheads entered Hudson Strait as early as April and late in the fall bowheads moved eastward through Hudson Strait. A few bowheads may overwinter in Hudson Bay (Low 1906; Degerbøl and Freuchen 1935).

In reference to the bowhead population of Davis Strait-Baffin Bay, Mansfield *et al.* (1975b:13) stated that the migrations 'are not well known, if indeed they occurred'. In fact there are numerous accounts of these migrations based on the whalers' intimate knowledge of this animal (Figure 13).

The first major whaling ground in Davis Strait, the 'South West Fishery', was located along the edge of the pack ice off Cumberland Sound (Brown 1868; Kumlien 1879; Lubbock 1937). This fishery was operational as early as March. Bowheads wintered along the edge of the pack ice in Davis Strait, off the mouths of Cumberland Sound and Hudson Strait, and all along the north coast of Labrador (Brown 1868; Low 1906).



Bowheads appeared along the west coast of Greenland in May in the vicinity of 65° to 70°N (Brown 1868). From here they moved north during early June along the west Greenland coast to Melville Bay where they crossed the northern edge of the 'middle pack' to northwest Baffin Bay (Low 1906). Brown (1868) stated that the bowheads crossed the 'middle pack' near latitude 71°30'N. The whalers were unable to penetrate the ice in Baffin Bay and continued their journey along the coast of Greenland until they reached Melville Bay during June. The whalers crossed the north end of Baffin Bay and again met with the bowhead in July on the last major whaling grounds in northwestern Baffin Bay, particularly around Lancaster Sound (Brown 1868; Lubbock 1937). Although many whales penetrated westward into Barrow Strait and Prince Regent Inlet. the largest numbers were found in the vicinity of Pond Inlet and Eclipse Sound (Brown 1868).

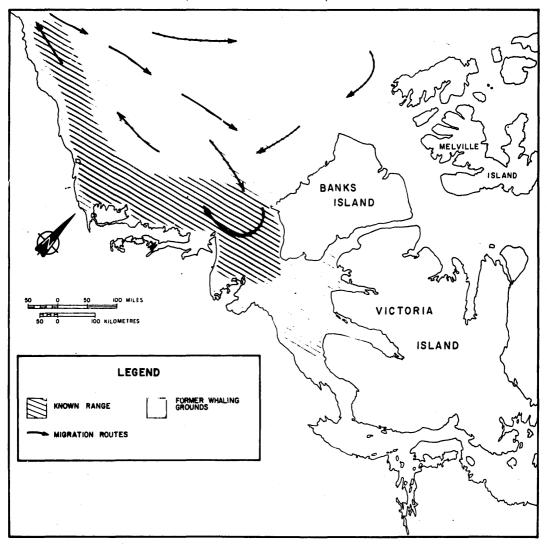
During September and October bowheads moved southward along the east coast of Baffin Island. Large numbers of bowheads entered Cumberland Sound in September and October and remained there until December.

STATUS AND SIZE OF POPULATIONS

Mitchell (1973) stated that 'any estimate of the status of bowhead whales is largely guesswork; it is presumed that in the eastern Arctic, at least, the population is very low'. The bowhead populations of the eastern Arctic had a much longer history of exploitation than those in the west and apparently show few signs of recovery after having been brought to near extinction at the beginning of this century (McVay 1973). Mansfield (1971), on the basis of recent sightings, suggested that the bowhead population of Canada is recovering well. It seems likely that the number of recent sightings is partly a function of increased activity in the north during the last decade and may not represent a significant increase in the population.

FIGURE 12 Distribution and Migration Routes of Bowhead Whales in the Canadian Western Arctic. (Besed on sources cited in text.)

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The population of bowheads that frequented northwest Hudson Bay was relatively small compared to the population in Davis Strait and Baffin Bay. Ross (1974) estimated that 688 bowheads were taken in northwest Hudson Bay during the whaling period from 1860 to 1915. There has been no similarly thorough review of the whaling records for Davis Strait and Baffin Bay.

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The useful but very incomplete records of Lubbock (1937) indicate that whaling intensity was much greater in Davis Strait and Baffin Bay. In 1823, 782 bowheads were taken by 29 whaling ships; over 41 ships were present but the catch by the others was not recorded by Lubbock. This was the best year for whaling in the area? but other large catches are also reported. In 1828, over 550 bowheads were taken by 30 of over 50 ships present. In 1830, 100 whaling ships were present in Baffin Bay (Lubbock 1937). The whale fishery in Davis Strait began in the early 1700's; penetration into the northwest Baffin Bay was first achieved by the whalers in 1817. Commercial whaling in Baffin Bay and Davis Strait had vitually ceased by 1915.

Fraker (1977b) cites Rice (1974) as estimating that the north Pacific populations of bowheads may have numbered between 4,000 and 5,000 animals prior to exploitation. It is not known what proportion of the population entered Canadian waters. The current population in the eastern Beaufort Sea was estimated to be in the 'low hundreds' (Sergeant and Hoek 1974). The current 'best estimate' of the number of bowheads passing the northwestern coast of Alaska is 2,264 (Braham et al. 1979).

POPULATION STRUCTURE AND DYNAMICS

Knowledge of the reproductive biology of bowheads is limited to historical accounts. Mating was thought to occur in summer and the young were born in March or April after a gestation of nine or ten months (Scoresby 1820; Brown 1868).

There are no data on the population dynamics of bowhead whales. Evidently, they are long-lived with a low reproductive rate. Estimates of the maximum sustainable yield of the pre-harvesting stocks of other large baleen whales are only two to four per cent of the stock (Allen and Chapman 1977).

HARVEST AND UTILIZATION

The native hunt of bowheads in the eastern Arctic continued until the 1940's, based primarily out of Pangnirtung (Mansfield et al. 1975b). Bowheads have not been taken in the Canadian portion of the Beaufort Sea in recent years, but they are hunted by inuit during the migrations near the Alaskan coast. The bowhead whale was declared an 'endangered species' by the U.S. government in 1970. In 1977, the international Whaling Commission moved to extend the ban on commercial hunting of bowhead whales to apply also to hunting by natives. This position was modified in 1978 and a small quota has been assigned to natives in Alaska³ in Canada, bowheads can be taken only by Inuit and only if a permit has been issued by the Minister of Environment. No permits were issued in 1978 and none were requested.

The last record of a bowhead being taken in the Canadian Arctic was an animal killed near Repulse Bay in 1975 (D. Dowler, personal communication).

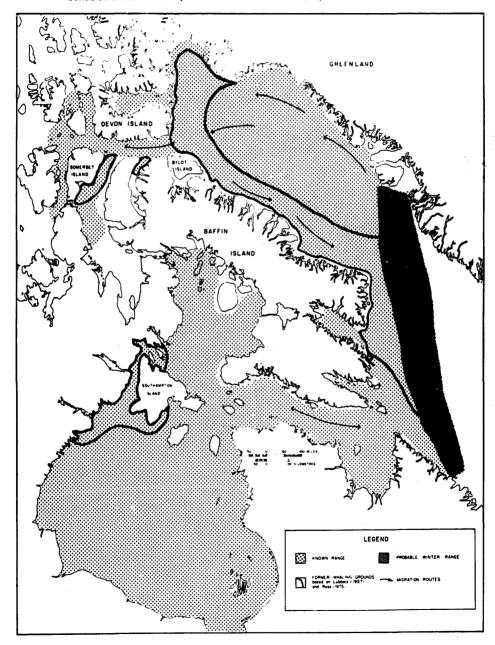
¹ Ross (Arctic 32: 91-121, 1979) has now published such a review. Over 28,000 bowheads were secured here between 1719 and 1911, and the total kill was considerably larger.

Ross (1979) lists four years when over 1,000 bowheads were secured in the Davis Strait/Baffin Bay area, including 1,632 bowheads in 1833.

³ Recent publications concerning bowheads off Alaska include Braham et al. (Rept. Int. Whal. Commn 29: 291-306, 1979) and Marquette (Rept. Int. Whal. Commn 29: 281-289, 1979).

Mating may occur in spring (Everitt and Krogman, Arctic 32: 277-280, 1979).

FIGURE 13 Distribution and Migration Routes of Bowhead Whales in the Canadian Eastern Arctic. (Based on sources cited in text.)



WALRUS

DISTRIBUTION

The walrus occupies a discontinuous circumpolar range, primarily north of 60°N latitude. The Pacific race of the walrus occurs in the Bering and Chukchi Seas and formerly the Beaufort Sea. Only occasional individuals have strayed into the Canadian sector of the Beaufort Sea and adjacent channels in recent times (Fay 1957; Buckley 1958; Youngman 1965; Harington 1966; Usher 1968).

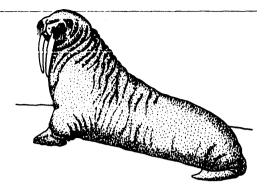
The Atlantic walrus occurs in the eastern Arctic, Foxe Basin and Hudson Bay (Mansfield 1967a) (Figure 14). In northern Foxe Basin, the presence of shallow water and year-round ice allows most of the walruses to remain there all year (Mansfield 1958). In spring as the ice recedes and breaks up, the walruses are found in the vicinity of the Spicer Islands in central Foxe Basin and along the coast of Melville Peninsula, south of Igloolik. In late summer of some years, walruses drift south on ice pans and reach southeastern Southampton Island and the Cape Dorset, Nottingham Island and Salisbury Island areas at the west end of Hudson Strait (Loughrey 1959). Thus, there is at least potential mixing with the animals of the Southampton Island area and with the walruses that migrate through Hudson Strait.

Walruses reside year-round in northwest Hudson Bay, principally in the waters along the south and west coasts of Southampton Island and the west shore of Hudson Bay south to Eskimo Point (Mansfield 1958). Most of the walruses in this population are thought to overwinter in the leads and open water areas found in northwest Hudson Bay. However, it is not known whether migrants from Hudson Strait reach the Southampton Island area in summer as suggested by Degerbøl and Freuchen (1935).

There is a regular westward movement of walruses along the south coast of Hudson Strait in the early summer. These animals stop at Akpatok Island in June and then proceed west northwest reaching Salisbury Island (females and calves) and Nottingham Island (buils) in August (Degerbøl and Freuchen 1935; Loughrey 1959). An eastward migration along the north shore and offshore waters of Hudson Strait occurs in autumn. Some walruses overwinter in Hudson Strait (e.g., Middle Savage Islands — Mansfield 1958) but the numbers and locations are poorly known.

A small population of walruses inhabits southeastern Hudson Bay around the Belcher, Sleeper and Ottawa Island groups. It is thought that these animals winter in the permanent leads near these islands (Loughrey 1959).

The eastward movement of walruses through Hudson Strait in October apparently splits up with some moving south down the northern Labrador coast and others following the Baffin coast north to the mouth of Frobisher Bay (Loughrey 1959). Walruses probably

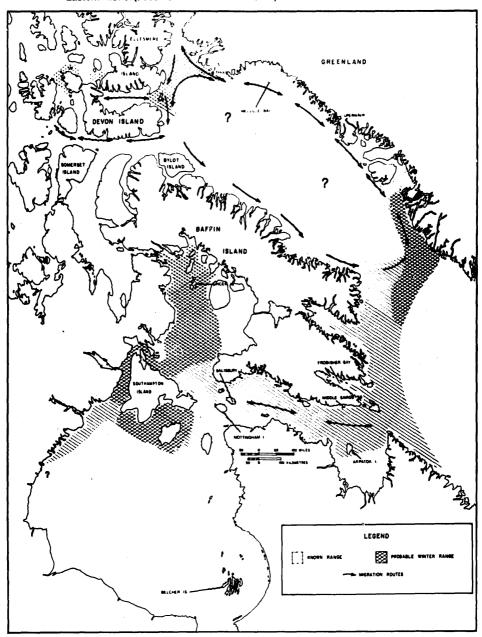


winter along the edge of the fast ice and in the pack ice off southeastern Baffin Island and along the southern margin of the pack ice across Davis Strait (Loughrey 1959; Vibe 1967). Hansen (no date) cited by Dunbar (1949) states that wairuses breed on the pack ice, over deep water, offshore in Davis Strait in May and June. It seems likely that Hansen was referring to calving rather than copulation. Loughrey (1959) notes that they calved there in spring of 1951.

The walrus population in Baffin Bay is difficult to assess since it has been highly exploited commercially and relatively small numbers remain. Major wintering grounds formerly occurred on the west coast of Greenland between 66° and 69° N (Freuchen 1921) and along the south margin of the Davis Strait pack ice (Loughrey 1959; Vibe 1967). Walruses moved north along the west Greenland coast in May and June and few occurred south of Upernavik (72°N) during the summer. The migrants pass Melville Bay and arrive in the Thule District of northwest Greenland, where they meet the substantial population that overwinters in this area (Vibe 1950). Some walruses penetrate north through Smith Sound and others cross to southern Ellesmere Island. In autumn a southward migration occurs along the Baffin Island coast. A northward spring migration along the Baffin coast has not been documented and may not be possible due to extensive fast ice and heavy pack ice normally present along this coast in spring and early summer. The evidence for this circular migration around the margins of Baffin Bay and northern Davis Strait is still circumstantial and is based on observations when there was a much larger population than is currently extant. Because of the long distances involved, Freuchen and Salomonsen (1958) and Vibe (1967) believed that the migration took more than one year. However, it should be noted that the Pacific walrus undertakes annual migrations that, in some cases, cover round-trip distances of at least 3,200 km (Burns 1965).

Walruses penetrate into the central Arctic Archipelago through Lancaster Sound and Jones Sound. A small population overwinters in the central high Arctic

FIGURE 14 Distribution and Migration Routes of Walruses in the Canadian Eastern Arctic. (Based on sources cited in text.)



(Figure 14) and comes in contact with the migrants entering from Baffin Bay (Davis et al. 1978b; Kiliaan and Stirling 1978).

Current knowledge of walrus distribution is unsystematic and has been pieced together from a variety of sources and from observations over a period of many years. Wintering areas, migration routes and interrelationships among geographic populations are not known with any certainty.

STATUS AND SIZE OF POPULATIONS

Information on the present size of the various eastern North American geographic populations of the wairus is basically lacking. Similarly, data on commercial pre-exploitation levels are unavailable; hence the potential carrying capacity of the eastern arctic marine environment cannot be estimated. Several lines of evidence suggest that most wairus populations have been depleted in the past few hundred years and present populations have not recovered these losses.

HISTORIC POPULATIONS

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The initial onslaught on walruses began as populations of the bowhead whale decreased and the whaling fleets began taking other marine mammal species. The Pacific walrus population was estimated at 200,000 animals during the period 1650 to 1860. The American Bering Sea whalers began taking walruses in about 1860 and took approximately 100,000 animals in the decade 1870 to 1880 (Fay 1957). Brooks (1954) and Fay (1957) estimated that the population was only 45,000 walruses during the period 1930 to 1950. These figures are not particularly accurate (Buckley 1958; Burns 1965) but they indicate the extent of the decline. The population has recovered and again numbers about 200,000 animals (Estes and Gol'tsev cited by Fay et al. 1977).

There are no estimates of the size of the eastern arctic walrus populations in the pre-whaling era. Whaling began in southern Davis Strait in the early 1700's and the whalers first penetrated into northern Baffin Bay in 1817 (Lubbock 1937). Whaling in northern Hudson Bay began in 1860 (Ross 1975). Most whaling had ceased in the eastern Arctic by 1910 to 1915 but commercial exploitation of walruses continued periodically until 1952 (Anderson 1934; Mansfield 1973). Kill statistics are very incomplete but a few examples will illustrate the extent of the kill. Burwash (cited by Anderson 1934:79) indicates that the largest terrestrial haul-out site in eastern Canadian Arctic occurred at Padlei south of Padloping Island, northeast of Cumberland Sound; at this site one company 'took over 4,000 [walrus] skins per year'. It is not known when this take occurred, for how long it occurred, or whether other 'companies' were involved. Ross (1975), on the basis of whaling records, states that whalers in northern Hudson Bay took 2,750 wairuses in the period 1900 to 1915. Burwash (cited by Anderson 1934) believed that these

whalers (primarily the Dundee steamer Active) retrieved only one of every four to five walruses killed and the Hudson Bay population was much reduced. Over 3,200 walruses were taken by the whalers in Davis Strait and Baffin Bay in the four year period 1907 to 1910 (Lubbock 1937).

Commercial exploitation of walruses in Canada was banned in 1928 (Mansfield 1973). The last commercial exploitation of walruses in the eastern Arctic occurred between 1949 and 1952, when Norwegian vessels took over 2,000 animals in Davis Strait. This hunt was banned in 1957 (Mansfield 1973).

In addition to commercial harvests, many authors beginning with Freuchen (1921) noted that the introduction of firearms and motorized boats led to increased inuit harvests (and hunting loss) of walruses to satisfy demands of European traders and to support increased numbers of dog teams needed for trapping of arctic foxes for the Hudson's Bay Company and other traders.

The above facts indicate that eastern arctic walrus populations were probably much reduced by a variety of human agents. The extent of the reduction is unknown but probably was most severe in Baffin Bay and Davis Strait and least severe in Foxe Basin where little exploitation occurred.

CURRENT POPULATIONS

The current sizes of walrus populations are virtually unknown. Loughrey (1959) and Mansfield (1986) calculated that a total population of about 23,000 to 25,000 walruses would be necessary to support the annual native kill of the mid-1950's in the eastern Arctic. This calculation assumed that the populations were stable and no convincing evidence was or is available on this question. Unfortunately, this estimate of 25,000 walruses has recently been considered by some authors to be a population estimate rather than a figure derived for discussion purposes only.

The walrus population in the Southampton Island area of northwest Hudson Bay was studied by Mansfield (1958) and Loughrey (1959). An aerial survey of the terrestrial haul-out sites in this area detected about 3,000 walruses at these sites. A repeat survey in 1961 found a similar number of animals and the population was thought to be 'undiminished' (Mansfield 1973:75).

The walrus population in Foxe Basin is apparently larger than that in the Southampton Island area (Mansfield 1973) but no surveys of Foxe Basin have been conducted. The population in southeast Hudson Bay (Belcher, Sleeper and Ottawa Islands) is not large (Loughrey 1959; Manning 1976) but again no systematic data are available. Loughrey (1959) cites C. H. D. Clarke as observing 1,000 walruses hauled out at Cape Henrietta Maria on the Ontario coast in 1955. In fact, Clarke (personal communication) was reporting an observation made by someone else. Since the 1980's, a small haul-out site has been occupied, in September, at Cape Henrietta Maria; this site contained about 300

animals in 1978 (J. P. Prevett and H. G. Lumsden, Ontario Ministry of Natural Resources, personal communication).

The number of walruses using Hudson Strait is unknown. Currie (1968) estimated that about 1,500 walruses used the Ungava Bay area in the late 1960's but it is not known what proportion of the Hudson Strait population regularly uses Ungava Bay.

There is no current quantitative information on the size and etatus of the walrus population in Baffin Bay and northern Davis Strait. Judging by the fragmentary information on the commercial harvest, this population was probably among the largest in the eastern Arctic. Vibe (1950, 1967) documents the movements and distribution of the overwintering population in Thule District of northwest Greenland but he gives no numbers.

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Recent studies in the central high Arctic found that 200 to 300 walruses overwintered at the west end of Jones Sound and in Penny Strait in 1976 to 1977 and that the summer population in the central archipelago numbers at least 1,000 animals (Davis et al. 1978b). This study was based on aerial surveys of terrestrial haul-out sites and of the intervening coastal waters; less than half of the animals recorded were actually using the haul-out sites. Continuous observations of a haul-out site on the east coast of Bathurst Island revealed that the numbers of walruses using the site throughout the season were highly and unsystematically variable (Salter 1978).1 Thus caution should be exercised in the interpretation of the results of single surveys of haul-out sites such as the surveys conducted near Southampton Island.

To summarize, the numbers of walruses in most parts of the eastern Arctic are not known.

Management of a species requires knowledge of stocks or sub-populations within the species. If semiisolated stocks exist, then each stock should be managed and harvest levels adapted to the size of the stock. Mansfield (1958) and Loughrey (1959) suggest that walruses in Foxe Basin and northwest Hudson Bay are at least semi-isolated from each other and observations from Loughrey (1959) and JBNQNHRC (1976) suggest that the walruses in southeast Hudson Bay are semi-isolated from other groups. The status of the Hudson Strait walruses is unclear; some may mix with animals from Southampton Island, Foxe Basin and Davis Strait (Anderson 1934; Degerbel and Freuchen 1935; Loughrey 1959). The status of groups of walruses that overwinter in areas (e.g., west end Jones Sound, Thule District, Hudson Strait) that are on migration routes for other segments of the population is unknown.

POPULATION STRUCTURE AND DYNAMICS

The reproductive biology of the Atlantic walrue was studied in northwest Hudson Bay and Foxe Basin by Mansfield (1958) and Loughrey (1959). These pioneering studies provide most of our knowledge of population structure and reproductive biology of the walrus in the eastern Arctic. More intension studies have been conducted on the Pacific race of the walrus (see Burns 1965) and this information is used where appropriate below.

Walruses can be relatively accurately aged by counting annual cementum layers of the teeth (Mansfield 1958; Burns 1965; Krylov 1965). Due to tooth wear, this method slightly underestimates the age of walruses, especially the older animals (Burns 1965).

REPRODUCTIVE BIOLOGY

The walrus is apparently polygamous (Brooks 1954; Loughrey 1959) with the male breeding several females. The breeding season of the Pacific walrus extends from December through early June (Brooks 1954) with a peak of activity during February and March; the breeding season in the eastern Arctic is probably similar. Implantation is delayed until May or June and the single calf is born in May or June of the following year (Mansfield 1958; Burns 1965). The calf is dependent on the female and lactation lasts for about 18 months to two years (Brooks 1954; Mansfield 1958; Burns 1965).

Most males become sexually mature and capable of breeding at six or seven years of age (Mansfield 1958) or six to eight years of age in the Pacific population (Burns 1965). Monsfield (1958) found that the age of first breeding in semale Atlantic walruses ranged from five to 11 years with an effective average (based on 15 specimens) of eight years, Burns (1965) found that age of first breeding in Pacific walruses ranged from four to 10 years with most breeding for the first time between their fifth and eighth year of life.

Based on a sample of 17 mature females from Southampton island, Mansfield (1958) calculated an annual birth rate of 0.35 or one calf every 2.9 years. In a larger sample (227 mature cows) of the Pacific walrus, Burns (1965) found that the average annual birth rate per mature female was 0.43 or one calf every 2.3 years. Burns (1965) suggested that 80% of mature cows calve every two years; 15% bear calves every third year and the remainder calve less frequently; the last group consists of older cows. Harbo (cited by Burns 1965) found that only 85% of the conceptions resulted in live births in the Pacific population.

It is not known whether the lower birth rate observed for the Atlantic walrus is real or whether it is an artifact of the small sample from the eastern Arctic.

¹ Published as Salter (Can. J. Zool. 57: 1169-1180, 1979).

AGE AND SEX STRUCTURE

Information on age and sex structure of walrus populations has been derived primarily from hunter-killed specimens. Many workers have commented on the potential for blases in such samples. Hunters do not select animals randomly and, in most cases, rarely take small calves. In many populations of walruses there is a marked sex and age segregation at certain times of the year and hunters from a particular community concentrate on certain classes of animals because they are the only ones accessible to them. Thus, great care must be exercised when interpreting the results from hunter-killed walruses.

The sex ratio of newborn calves is approximately 1:1. There is little information on the sex ratio of adult walruses in the eastern Arctic. In Alaska and Siberia, more females were taken by hunters in some areas. However, recent quotas on females have shifted hunting pressure to males. In a polygynous population, the under-representation of adult males is not considered to affect the production of the population and Alaskan hunting regulations are designed to reduce hunting pressure on adult females (Burns 1965).

Mansfield (1958) found walruses up to 28 years of age in northwest Hudson Bay and Burns (1965) found the oldest animals to be 33 years in the Alaskan samples. Few animals reached these maximum ages in either population. Samples from the eastern Arctic are too small to construct life tables or meaningful representations of the age structure of the population. Burns (1965) combined several samples (total of 1,651) of male walruses taken in Alaska and summarized the age composition. Burns (1965) stated that the female segment of the herd is subject to extremely biased sampling as a result of migration patterns, herding tendencies and hunting vulnerability; he concluded that the age composition of the female segment could not be reliably determined from hunter samples in Alaska. This is a potentially serious problem since it is the female segment that determines the reproductive rate in a polygynous species. It is implicitly assumed, but it has not been demonstrated, that the age composition of the females is similar to that of males.

MORTALITY FACTORS

Natural mortality to walruses has not been quantified but most workers assume it to be low. The only natural predators are polar bears and killer whales. Neither is thought to take large numbers of walruses regularly (Loughrey 1959). Accidents at terrestrial haul-out sites cause some mortality, usually to smaller animals (Loughrey 1959; Burns 1965). Severe winter conditions could freeze areas that usually retain open water, and thus force walruses into deep water areas where feeding would be difficult. Several instances of single walruses being trapped away from open water by ice have been recorded. Large scale mortality from this source has not been recorded but it could occur unnoticed in the northern wintering areas.

The principal source of walrus mortality is from hunting, which is discussed later.

POPULATION DYNAMICS

The annual birth rate per adult female was calculated at 0.43 for the Pacific race and 0.35 for the eastern Arctic population. Burns (1965) estimated (methods not stated) that 36% of the Pacific population was younger than six years and hence were non-breeders. Assuming a 1:1 sex ratio of adults, the annual increment of calves to the population was approximately 14%. Mansfield (1973) estimated the annual increment of calves for eastern Arctic walruses to be 11%. There are no quantitative estimates of mortality rates for calves and immature walruses. Mansfield (1958) assumed that calves had a high survival rate prior to weaning because of the constant parental care by the female.

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Estimates of mortality rates have been derived for adult walruses and then compared to the annual increment to determine the status of the population. Burns (1965) used the data on male walruses from Alaska to derive a 'catch-curve', from which he estimated that annual mortality for males aged 13 to 27 years was about 13%. This mortality includes both natural and hunting mortality. Because more males than females are taken by hunters, Burns (1965) believed that the mortality rate for females was somewhat lower. Application of the 13% mortality rate to all ages and sexes in the population and comparison of this rate to the annual increment of calves (14%) suggests that the population should be increasing slightly (Burns 1965).

The most serious gap in the above argument concerns the assumption that walrus calves and immatures have the same mortality rate as do full grown adult males. This assumption is unlikely to be true. In many species, adults have much higher survival rates than do young and sub-adults. On the other hand, the adult males were subjected to higher hunting mortality than were other segments of the population. The key parameters that need to be determined are the annual increment to the breeding population (rather than the annual increment of calves), and the mortality rate of adult females.

There are no direct estimates of mortality rates of calf and immature walruses for any population and there are no direct estimates of mortality of adult walruses for the eastern Arctic populations. It is not known whether the Alaskan estimates are applicable to Canadian populations. Similarly, it is not known what proportion of the Alaskan mortality is due to natural causes as opposed to hunting. The former are assumed to be insignificant.

It should be noted that Russian workers studying the Pacific walrus have arrived at a figure of 6.3% as the annual increment of calves into the population (Krylov 1965). Burns (1965) discussed the Russian data and points out several problems with their techniques.

Therefore, in the present report, we have used the data from the American studies.

LIMITING FACTORS

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erit.

There is no information about the natural population regulating mechanisms affecting walrus populations. Virtually all populations have been subjected to commercial and native exploitation and many populations are known or suspected to be smaller now than in historical times. The population of walruses in Foxe Basin was not heavily exploited by commercial hunters and may be close to its historical size.

in the absence of man, walrus populations probably depend on the following:

- The availability of large areas of shallow water (80 m or less) with a suitable bottom substrate to support a productive bivalve community.
- The presence of reliable open water over rich feeding areas, particularly in winter when access to many feeding areas is denied due to ice cover.
- The presence of haul-out areas in close proximity to feeding areas; haul-out platforms are usually lice-pans and ice-edges although terrestrial sites are used in the ice-free summer period.

The role of social behaviour in population regulation by walruses is not known and the effects of increased densities of walruses on age structure and reproductive rates are also not known. The capacity of the benthonic food resources to support increased walrus populations has only recently been studied. Pioneering quantitative comparisons of walrus diets and standing crops of bivaives were made by Vibe (1950) in Thule District, Greenland. Fay et al. (1977) have determined that the large Pacific walrus population is a significant predator of Bering Sea mollusc populations. They suggest that this predation is very close to the annual net production of molluscs and in some local areas may be exceeding it. No similar studies have been conducted in the Canadian Arctic.

To sum up, the carrying capacity for walruses of arctic marine waters can be estimated when information about food availability and habitat requirements is available. However, it is not currently possible to predict the number of walruses that can be supported by the marine system in arctic Canada.

CURRENT HARVEST AND UTILIZATION

The harvest of walruses in the eastern Arctic has fluctuated greatly. The heavy commercial exploitation that ended in 1952 was discussed previously. The native harvest of walruses is believed to have declined in the late 1960's due to the replacement of dog teams by snowmobiles. Recent harvest levels may be increasing due to the increased market for walrus tusks (Friesen 1975).

ANNUAL HARVEST

As with other marine mammal species, the available harvest data are extremely difficult to interpret. The following discussion ignores hunting losses. These are discussed later.

Loughrey (1959) estimated that the annual take of walruses in the Canadian Arctic was about 1,200 in the early 1950's; the take in Greenland was 550 to 750. Over half of the Canadian harvest was from the Foxe Basin and northwest Hudson Bay populations. The available evidence suggests that walruses taken in western Greenland are part of the Baffin Bay population that frequents Canadian waters.

Mansfield (1973) estimated that the average annual walrus kill in the 1960's was about 500 in eastern Canada, plus about 200 in western Greenland. Smith and Taylor (1977) present data taken from R.C.M.P. game reports for the years 1962 to 1971 which give an average annual take of 544 walruses excluding northern Quebec and Greenland. However, the accuracy of the figures for the 1960's is doubtful. Anders (1965) stated that the annual take in Foxe Basin alone was between 500 and 600 animals in 1965 and 700 in 1962. The R.C.M.P. game reports for this area give an average take of 103 with a maximum of 125 during the period 1962 to 1971 (Smith and Taylor 1977).

Reliable estimates of the annual walrus harvest in the 1970's are not available. Stephansson (personal communication, cited by Friesen 1975) suggested that the take in 1974 was over 400 animals. The most reliable recent information concerns the walrus take by northern Quebec communities. These communities took about 110 walruses per year in a two year period — 1973-74 and 1974-75 (JBNQNHRC 1976). The west Greenland take was about 200 to 250 animals in 1974 (Kapel in Reeves 1978).

Based on information in Friesen (1975), Usher (1975), Freeman (1976) and Smith and Taylor (1977), the following communities in N.W.T. still hunt walruses on a more or less regular basis: Igloolik, Hall Beach, Coral Harbour, Rankin Inlet, Belcher Islands, Cape Dorset, Lake Harbour, Frobisher Bay, Pangnirtung, Broughton Island, Clyde River, Pond Inlet, Grise Fiord and Resolute Bay.

Hunting loss

The problem of non-retrieval of killed and wounded walruses has been recognized for a long time and traces from the advent of the use of firearms to hunt walrus (Freuchen 1921; Dunbar 1954b). The loss rate varies with area, season and type of hunt, Loughrey (1959) arrived at an average loss rate of about one-third for the eastern Arctic. Thus, only 67% of the animals killed were retrieved. Freeman (1974/75) found that the retrieval rate was 70 to 80% for walruses taken during two open water hunts near Wairus Island, south of Southampton Island. These hunts were conducted from Peterhead boats in 1970 and the walruses were driven into shallow water before being killed. Smith and Taylor (1977) observed a retrieval rate of only 30 to 50% during a similar open water hunt (location not stated). In Alaska the retrieval rate is only about 50% (Buckley 1958; Burns 1965). Clearly, the loss rate is high and the harvest figures discussed in the preceding section need to be adjusted to account for these losses before the impact of hunting on walrus populations can be determined.

Another source of bias in the harvest figures presented above is the non-reporting of kills. Freeman (1969/70) found that calves taken in the Southampton island area were not reported even when they were retrieved. In the 1961 hunt, calves constituted 20% of the kill; thus the reported kill of 153 should have been 183 (Freeman 1969/70). Also, the death of a lactating female can result in the death of her calf even though the calf is not directly harmed (Burns 1965) although Eley (1978) documents a case of adoption of an apparently orphaned calf Pacific wairus.

HUNTING TECHNIQUES

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A variety of techniques was used for hunting wairuses. The key factor determining hunting methods is that wairuses sink when dead. Thus, the outright killing of a wairus in open water results in loss of the animal unless it has been harpooned or killed in shallow water where it can be retrieved off the bottom.

The technique of driving walruses into shallow water before killing is used during open water hunts from Peterheads in the Coats Island area (Freeman 1974/75). In other open water situations, walruses are wounded to slow them down and to allow a harpoon with a float to be attached to the animal before it is killed. Hunts of walruses on pan ice, floe-edges and newly-forming ice involve killing the animal instantly so that it cannot reach the water. Wounded animals can often be harpooned in the water if boats are present. The most successful hunts involve the use of fully-decked Peterhead boats to visit the waters near large terrestrial haul-out sites in late summer and early autumn (Mansfield 1973).

UTILIZATION

Apart from the social values accruing to successful wairus hunters, the historic principal use of the animal was as a source of high quality dog food. The lvory and the blubber and meat for human consumption were clearly of secondary importance (Freeman 1969/70). With the decline in use of dog teams, the demand for dog food has decreased although it is still important in some localities (e.g., Coral Harbour — Freeman 1974/75). Friesen (1975;92) notes that much hunting is now conducted for the tusks; each animal produces '6 to 10 lbs of ivory which can be sold for \$8-10 per pound'. Walrus ivory sold for \$12 to \$15 per pound in 1977 (D. Dowler, Fisheries and Marine Service, personal communication).

The average weight of adult male Atlantic walruses is 900 kg; adult females average 570 kg. By the end of the first year, calves weigh about 200 kg (Mansfield 1973). Adult weights were quite variable and the averages given above were not reached before 10 years of age (Mansfield 1958). Freeman (1969/70) gives an average adult weight of 512 kg (28 specimens) for walruses (both sexes included) taken at Southampton Island; averages were 305 kg for sub-adults and 103 kg for calves.

HARBOUR SEAL

DISTRIBUTION

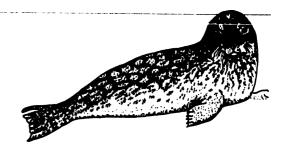
This widely distributed and relatively sedentary species occurs along the coasts of western Europe, eastern and western North America, and northeast Asia.

The subspecies in eastern North America, Phoca vitulina concolor, is often called the ranger seal. It occurs in small numbers north and west along the coasts of eastern Baffin Island, southwest Greenland, Ungava Bay, Hudson Strait, and Hudson and James Bays (Mansfield 1967b). It occasionally occurs in northern Foxe Basin (Anders 1965), around Pond Inlet (Tuck 1957; Bissett 1967b), and along eastern Ellesmere Island (Alexandra Fiord - Mansfield 1987b; Smith and Taylor 1977), and there is a questionable record from the Thule District of northwest Greenland (Vibe 1950). The harbour seal is believed to remain in these areas throughout the year, overwintering at locations where currents maintain open water through the winter (Mansfield 1967b). However, there are very few winter records, and the extent of movements is unknown.

Harbour seals often wander into rivers, and there are records from rivers and lakes (1) southwest of Ungava Bay, (2) east of Richmond Gulf (Hudson Bay), (3) along the Thlewiaza and other rivers west of Hudson Bay and (4) In Foxe Peninsula of Baffin Island (Mansfield 1967b; Beck et al. 1970; McLaren et al. 1977). The second of these groups has been described as a separate, isolated subspecies, P. v. mellonae. However, the degree and duration of isolation of all the freshwater groups from the marine concolor is uncertain.

Pacific harbour seals occur rarely in the southern Beaufort Sea (Mansfield 1967b; Abrahamson 1968). McLaren (1966a) suspected that these seals are members of the western North American subspecies, P. v. richardsi. However, they might also be the ice-inhabiting form P. v. largha (or P. largha) of northeast Asia and the Bering Sea; both forms occur off western Alaska (Fay 1974). Serological evidence suggests that the two forms are biochemically very similar (Shaughnessy 1975), but their behavioural and physiological differences suggest that largha is a separate species (McLaren 1966a; Shaughnessy and Fay 1977).

¹ Burns (pp. 192-205 in: D. Haley [ed.], Marine mammals of eastern North Pacific and arctic waters, Pacific Search Press, Seattle, 1978) gives more information about largha, which is commonly called the spotted seal.



STATUS AND SIZE OF POPULATIONS

The harbour seal is sparsely and locally distributed throughout its arctic range. No estimates of population sizes are available for the Canadian Arctic. Anders at al. (1967) report that it was formerly common in Cumberland Sound but is now 'only an occasional visitor'. Mansfield (1967b) notes that because of its localized distribution the Inuit often know where to find it, and that in Ungava Bay, southern Baffin Island and southern Southampton Island it has been eliminated from some localities. Any isolated populations that are permanent residents of freshwater would be especially susceptible.

This species is normally considered quite sedentary, but the extent to which local populations are isolated from one another is unknown. The localized movements that are often reported appear to be related to migrations of prey fish. The ice-inhabiting form largha of the Bering (and perhaps Beaufort) Sea appears to be more mobile than the other groups (Johnson et al. 1966; Fedoseev 1971; Naito and Nishiwaki 1975).

POPULATION STRUCTURE

There have been no studies of the reproductive biology, age and sex structure, or population dynamics of harbour seals in the Canadian Arctic. Specimens have been collected opportunistically during the course of other work by personnel of the Arctic Biological Station (Mansfield et al. 1975b). An ageing method based on analysis of layers in the cementum of the canine teeth exists for this species (Mansfield and Fisher 1960), and some aspects of reproductive status can be evaluated by histological analyses (e.g., Bigg 1969). Thus the population biology is amenable to study if it is possible to overcome biases resulting from age and sex differences in collectability. Because of the minor economic importance of the harbour seal in the Canadian Arctic (Friesen 1975), the biology of this species in other areas has not been summarized here (see Bigg 1969, Bigg and Fisher 1974, Boulva 1975 and Pitcher and Calkins 1977 for reviews and references).

CURRENT HARVEST AND UTILIZATION

Based on incomplete R.C.M.P. game reports from 1962 to 1971, Smith and Taylor (1977) reported that the mean annual harvest of harbour seals in the Northwest Territories (apparently excluding Port Burwell) was 42, with 17 of these being at Frobisher Bay, 13 at Coral Harbour, four at Eskimo Point and zero to two at other settlements. However, Kemp (1975) states that hunters in the North Bay area near Lake Harbour normally take five to ten annually. At Frobisher Bay 13 to 17 were traded annually at the Hudson's Bay Co. store in the mld-1960's (Meldrum 1975). The 'best estimate' of the annual take in the Port Burwell area in 1973 to 1975 was 44 (JBNQNHRC 1976) - the highest figure for any settlement in the N.W.T. Elsewhere along the coasts of northern Quebec the 'best estimate' was 65 per year, with 58 of these being from Ungava Bay.

The figures quoted above are probably imprecise and are not current. Both Smith and Taylor (1977) and Bissett (1967b) caution that harbour and ringed seals are not always recorded separately. in addition, seals used domestically may not be reported.

Figures listed above do not include harbour seals wounded or killed but not retrieved. No estimates of hunting losses are available for the Arctic. Bigg (1969:30) estimates that during the periods when a bounty was offered for harbour seals killed along the British Columbia coast, only 50% of those killed were recorded in the bounty files.

HARP SEAL

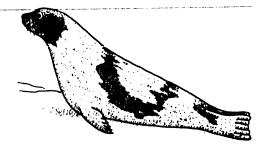
DISTRIBUTION

The three largely distinct stocks of harp seals whelp and moult near Newfoundland, near Jan Mayer Island (north of Iceland) and in the White Sea during late winter and early spring. They then migrate northward to spend the summer. The Newfoundland stock moves north to the Canadian Arctic and west Greenland (Figure 15); other stocks do not enter this area, and are not discussed here. This species has been studied intensively since 1949 in the Newfoundland area, where it is the main object of the controversial seal hunt.

The 'Newfoundland stock' whelps and moults in two sub-areas — in the Gulf of St. Lawrence and on the ice 'front' east of the Strait of Belle Isle. There is some exchange between these areas (Mansfield 1970; Sergeant 1971). Adults migrate north in April and May; the young-of-the-year or 'beaters' follow separately (Sergeant 1965a). Harp seals are deflected eastward across Davis Strait by the ice. The vanguard of adults reaches south and southwest Greenland in May, and the peak catch in this area is in June (Kapel 1975b). The young apparently do not begin to arrive until June (Sergeant 1965a). Very few harp seals of the 'Newfoundland stock' move east beyond Cape Farewell, the southern tip of Greenland (Sergeant 1965a, 1973d).

Some harp seals remain in Davis Strait and off southwest Greenland in summer, but many continue to the west or north. Some move west into Hudson Strait, Frobisher Bay and Cumberland Sound. Some, including Juveniles, continue west along Hudson Strait and south to James Bay (Mansfield 1968; Sergeant 1976a). Harp seals are rare in northern Foxe Basin (Anders 1965). Considerable numbers of harp seals continue up the west coast of Greenland and reach northwest Greenland (Umanak, Upernavik) and Thule District in June and July. Only small numbers reach Smith Sound and inglefield Land (Degerbøl and Freuchen 1935; Vibe 1950). However, many cross Baffin Bay to the Bylot Island area, Lancaster and Jones Sounds, and adjacent channels (Figure 15). Migration into the Canadian high Arctic occurs mainly in July and August (Tuck 1957; Finley 1976; Greendale and Brousseau-Greendale 1976; Johnson et al. 1976; Riewe 1977). Those entering Cumberland, Lancaster and Jones Sounds have been reported to be mainly adults (Anders et al. 1967; Greendale and Brousseau-Greendale 1976; Riewe 1977).

Harp seals begin to leave the Canadian high Arctic in September, although a few remain in Lancaster Sound in October (Miller 1955; Sergeant 1965a; Bissett 1967a; Finley and Johnston 1977). Some remain in Cumberland Sound to mid-January and a few may winter in the area (Anders et al. 1967. A considerable number remain along the west coast of Greenland until February (Kapel 1975b). Most adults apparently migrate south close to the Labrador coast in October to December (Anderson 1934; Sergeant 1965a; Evans 1968), and it is



only a fraction of the immatures and especially the young-of-the-year that tend to lag behind and, in some cases, to overwinter in the Davis Strait area (Fisher 1955; Sergeant 1965a; Imperial et al. 1978).

There have been a few isolated records of harp seals in the western Arctic (western Alaska, Wrangel Island, Aklavik, Cambridge Bay — Anderson 1934; Dunbar 1949; Smith and Taylor 1977). However, eastern Viscount Melville Sound and Peel Sound are the western margin of the normal range in the high Arctic (Finley and Johnston 1977; Smith and Taylor 1977).

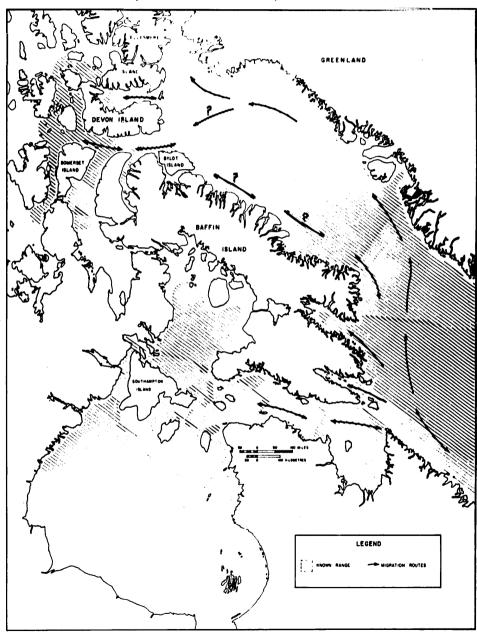
STATUS AND SIZE OF POPULATIONS

The western Atlantic harp seal population is believed to have included several million animals before the period of heavy exploitation in the 19th and 20th centuries. Numbers had declined by the early 1900's, but increased during a period of limited exploitation between and during World Wars I and II. The first surveys by aerial photography, conducted in 1950-51, indicated that about 645,000 pups were produced annually by a total population (excluding pups) of about 3,300,000 seals (Fisher 1952, 1955). More recent studies of potential biases indicate that the 1950-51 estimates may have been low by about 20% (Sergeant 1965b).

The western Atlantic population has declined since 1950-51 (Sergeant 1975). At present it includes about 1,250,000 seals (excluding pups), and produces about 300,000 pups each year. The precise values and current trends of these parameters have been and are the object of much study and controversy (for reviews, see Allen 1975; Sergeant 1975, 1976a, c; Lett and Benjaminsen 1977; Winters 1978). Prevailing opinion is that the hunting quotas and regulations have now been adjusted such that the decline has been stopped and a slow increase in stock initiated. This is the intent of the management strategy adopted by the Canadian Government and the International Commission for the Northwest Atlantic Fisheries.

The number of harp seals that enter the Arctic each summer is determined primarily by the historical trends in harvest of the stock in more southern areas.

FIGURE 15 Distribution and Migration Routes of Harp Seals in the Canadian Eastern Arctic. (Based on sources cited in text.)



The reported harvest in Greenland, which is small relative to the harvest farther south, declined rather steadily from 1948 to 1971 (Kapel 1975b). Records from the Canadian Arctic, where the harvest is even smaller than in Greenland, are too incomplete to permit a similar assessment. Assuming that the decline in the breeding population has been arrested, the availability of the harp seal in the Canadian Arctic should also stabilize and then increase. Since those entering the Canadian high Arctic are apparently mainly adults (see above), population trends there may lag behind those in more southerly regions.

On a long-term basis, tho summer distribution of harp seals in the Arctic seems to be correlated with climatic conditions. In western Greenland, harp seals tended to move farther north before 1810 and after 1910 than in the intervening colder years (Vibe 1967). If this correlation represents a direct climatic effect, future climatic changes may affect the local status of harp seals in the Arctic.

Numbers of harp seals occurring in various parts of the Canadian Arctic in summer are poorly known. Tuck (1957:38) counted about 150,000 migrating west along the north coast of Bylot Island into Lancaster Sound from late June to early August of 1957. Greendale and Brousseau-Greendale (1976) saw only about 16,000 migrating west in the same area in July 1976. The aerial surveys of Johnson et al. (1976) provide good evidence that there was little westward migration through the area in June or August 1976, and that most of the 1976 migration into Lancaster Sound was along the south shore past the observation site. The reason for the apparent 89% decline between 1957 and 1976 is unclear, since the overall decline of age 1 + harp seals in the western Atlantic population during the period was only about 32% (Lett and Benjaminsen 1977). Maximum numbers seen or estimated to be present in Barrow Strait and Peel Sound In various periods during 1974 to 1976 have not exceeded about 2,500 (Finley 1976: Finley and Johnston 1977). Duvall and Handley (1946) saw 'thousands' in Broe [Brae?] Bay, North Devon Island, on 2 September 1946, and Sergeant (1965a) lists an estimate of 10,000 east of Coburg island on 28 September 1963. The maximum reported annual kills of 2,071 at Pangnirtung, 677 at Frobisher Bay and 1,939 at Lake Harbour (see below) place lower limits on the numbers that sometimes occur in these general areas.

POPULATION STRUCTURE AND DYNAMICS

The ages of harp seals can be determined by counting annual layers in the dentine of the canine teeth, although ages beyond 15 or 20 years are often difficult to determine precisely (Fisher 1952; Rasmussen 1957).

REPRODUCTIVE BIOLOGY

Harp seals of the western Atlantic whelp on ice-pans 30 to 60 cm thick northeast and west of Newfoundland (Sergeant 1963), mainly in early March. Whelping tends to be a few days later on the 'Front' than in the Gulf of St. Lawrence (Sergeant 1965a). The single pup (twins are very rare) is nursed for about two weeks, during which time its weight increases from about nine to 35 kg (Sergeant 1973b). The males, which have been in the area, approach the females at the end of lactation, and females reportedly mate with one or more males, usually in the water (Sergeant 1965a, 1976a). Implantation is delayed, so development of the foetus takes less than the apparent gestation period of about 11.5 months. In April and May, before migrating north, the adult and immature (ages 1 + years) harp seals haul out on the ice to moult. The adult females tend to do so later than other groups (Sergeant 1985a).

The age at which female harp seals become physiologically mature (i.e. ovulate for the first time) has been found to vary from three to nine years, with the mean value being positively correlated with population size (Fisher 1955; Sergeant 1973c, 1976c; Lett and Benjaminsen 1977). The mean age of first ovulation for the western Atlantic population was 5.5 years in 1951-54, about 4.5 years in 1961-65, about 4.8 years in 1968-71, and 3.8 years (Front only) in 1976. Fewer data concerning age of physiological maturity are available for males, and the values are even more variable. Testes appeared to become mature at an average age of 7.5 years in 1952-57 and 5.5 years in 1971 in the western Atlantic population, and at 4.0 years in 1958-64 in the White Sea population (Sergeant 1973c).

In 1976 at least 95% of the mature females from the Front ovulated (Sergeant 1976c). Data from the White Sea suggest that a much lower percentage of the mature females ovulated, but these data may be biased by failure to recognize some follicles that did ovulate (Nazarenko 1975). Nazarenko's data do show that a higher proportion of the old (22 to 29 years) than of the younger mature females fail to ovulate.

Fisher (1952) found in 1951-52 that 80% of 70 mature females were pregnant in January, shortly before whelping. More recent estimates of pregnancy rates are higher — generally over 90%. However, Winters (1978) suggested that Fisher's sample was anomalous, and that there is no clear evidence of an increase in fertility rate as the population size declined.

¹ Recent reviews of harp seal status include Lavigne (Queen's Quarterly 85: 377-388, 1978), Lavigne et al. (Polar Rec. 19: 381-385, 1979), Mohn (J. Fish. Res. Board Can. 36: 404-410, 1979) and Mohn and Winters (J. Fish. Res. Board Can. 36: 1527-1532, 1979).

AGE AND SEX STRUCTURE

Many samples of harp seals have been studied to de termine age and sex structure. However, because of age and sex-related differences in seasonal distribution and catchability, it has been very difficult to estimate the structure of the population. Furthermore, this structure has changed from year to year because of variable hunting intensity and the variable age and sex structure of the kill. Sergeant (1971, 1976c) and Lett and Benjaminsen (1977) have summarized the available data and have estimated the probable age and sex structure at various places and times. The natural sex ratio is believed to be 1:1 and a few harp seals reach the age of 30 or even 35 years (Sergeant 1965b, 1973b). Because of the historical development of the annual hunt, the proportion of females in the breeding population is believed to have become as high as 54.9% in 1971, and to have declined to 52.9% in 1976 (Lett and Benjaminsen 1977).

Samples of harp seals killed near Baffin Island in 1967 and 1969 contained fewer zero to two year olds than one would expect on the basis of the estimated population composition (Sergeant 1971; cf. Lett and Benjaminsen 1977). In contrast, many samples from western Greenland contain many zero to two year olds (Kapel 1975c). These results are consistent with previously cited evidence that harp seals entering the Canadian high Arctic are mainly adults.

MORTALITY FACTORS

The main source of mortality to the western Atlantic harp seal population is man. Both young-of-the-year and older animals are taken during the annual harvest off Newfoundland, in the mid-1970's about 40 to 45% of the pups and two to three per cent of the older animals (1 + years) were harvested annually (Sergeant 1976a; Lett and Benjaminsen 1977).

Known natural sources of mortality include killer whales (Degerbel and Freuchen 1935), ice movements (Popov 1975; Sergeant 1976a) and presumably disease, ice rafting in storm conditions can kill large numbers of young, and occasionally adults are also crushed (Sergeant 1976a). However, natural mortality rates in the 'first week or so' after birth are reportedly very low (0.01 or less — Sergeant 1971). Natural mortality rates for age zero to one and one to two harp seals are not accurately known; the rate for adults was estimated as 0.08 to 0.10 by Sergeant (1976a) and 0.10 by Winters (1978). Lett and Benjaminsen (1977) estimated the natural adult mortality rate of age 2 + harp seals to be 0.114.

POPULATION DYNAMICS

Various parameters of harp seal populations are believed or suspected to be density dependent, and thus to be part of a population regulation mechanism. The positive correlation between age of sexual maturity and population size is the best documented. Earlier attainment of sexual maturity when the population size is reduced has also been reported in several other species of marine mammals (Guiland 1971; Sergeant 1973c). Eberhardt and Siniff (1977) have evaluated the effects of such an adjustment on the birth rate. Second, the natural mortality rate of pups may be density dependent, but the evidence is inconclusive (Lett and Benjaminsen 1977:1166). Third, it has been suggested that the proportion of mature females producing a calf each year is higher when the population size is low than when it is high, but this is not proven (cf. Winters 1978).

The dynamics of western Atlantic harp seals have been intensively studied and are comprehensively discussed by Sergeant (1975, 1976a, b). Allen (1975) developed a linear model of the population, and Lett and Benjaminsen (1977) developed a more comprehensive model incorporating more recent data, certain density-dependent functions and a stochastic element. The latter model, which takes harvest in Greenland and arctic Canada into account, predicts that the maximum sustainable yield would be about 200,000 pups and 40,000 older seals (age 1 + years) annually, and would be achieved if the population size of age 1 + seals were about 1,600,000, including about 375,000 breeding females. Winters (1978) gives slightly higher values.

It is beyond the scope of this report to review the details of the models. However, the significance of the Canadian Arctic catch to the population is considered here. Lett and Benjaminsen (1977:1181) assume a mean catch of 1,294 age 1 + years seals and no juveniles in the Canadian Arctic. In fact, a few percent of the harp seals taken in the Canadian Arctic are juveniles (Sergeant 1971, 1976a). Also, the current annual kill of age 1 + years harp seals in the Canadian Arctic, allowing for sinking losses, is several thousand (see below). Furthermore, adults are apparently over-represented in the age 1 + kill in the Canadian Arctic (Sergeant 1971).

Adult harp seals, especially young adults, are more valuable than pups in terms of future reproductive potential (Allen 1975). Lett and Benjaminsen (1977: 1185) found that an increase of 10,000 in the assumed annual take of 1+ years seals would have a dramatic effect on the future size of the harp seal population. Thus the apparent underestimation of the current arctic kill of adults should be assessed and taken into account in the models, and the potential effects of any increase in the arctic kill should be carefully evaluated. Assuming that the population is now increasing, the effects of any increased arctic harvest would depend on the year in which the increase occurred, and could be partially compensated for by a downward adjustment of the southern kill, it is important to note, however, that the reduction in harvest of pups would have to exceed the increase in the arctic harvest of adults in order to prevent a population decline.

CURRENT HARVEST AND UTILIZATION

ANNUAL HARVEST

The western Atlantic harp seals have been harvested on the whelping and moulting areas near Newfoundland since about 1750 (for reviews, see Fisher 1952, 1955; Sergeant 1963, 1965b, 1978a). The peak kills were in 1820-60, with a one-year maximum of 687,000 seals (including a small proportion of hooded seals) in 1831, when 300 ships and 10,000 men took part in the harvest. The Newfoundland area harvest of harp seals increased in the late 1940's after the wartime lull, with a peak of about 450,000 in 1951 (Sergeant 1978a). Thereafter, the harvest declined gradually and averaged 143,000 (82% pups) in 1972-75. The total permitted kill was 170,000 in 1977 and 180,000 in 1978, including allowance for a take of about 10,000 harp seals in western Greenland and the Canadian Arctic.

The annual harvest of harp seals in western Greenland was estimated as about 24,000 in 1948, 20,000 in 1953, 8,550 in 1962 and 6,000 from 1969-71 (Kapel 1975b). These figures are derived from the community catch of gams' lists, which are believed to be reasonably accurate, at least for the central west and northwest Greenland districts where most of the harp seals are taken.

The most recent available figures for reported harvest in the Canadian Arctic are given in Table 10. Values for northern Quebec are 'best estimates' of take and are believed to be reasonably accurate. However, as many as 1,500 harp seals were reportedly taken in nets at Port Burwell annually during the 1960's (JBNQNHRC 1976). Values for the Northwest Territories are from the Fur Export Tax Returns, which underestimate accurate numbers taken (for discussion, see ringed seal account). According to these figures, by far the largest harvest in the Canadian Arctic comes from Cumberland Sound (as represented in the Pangnirtung records).

Peak annual harvests in some other communities during the 1962-71 period (Smith and Taylor 1977) were considerably higher than those in 1975-76. The Port Burwell net fishery has already been mentioned. At Frobisher Bay, 337, 677 and 673 harp seal skins were traded at the Hudson's Bay Co. store in 1963-64, 1964-65 and 1965-66 (Meldrum 1975). A total of 1,939 harp seals were reported in one year at Lake Harbour, but the average figure was much lower (Smith and Taylor 1977). At Grise Flord, a maximum of 677 harp seals were taken in one year, according to R.C.M.P. game records summarized by Smith and Taylor, However. Riewe (1977) does not mention this figure, and instead reports a maximum of 70 in each of 1962-63 and 1964-65 at Grise Fiord. Smith and Taylor (1977) also list peak reported harvests of 30 at Resolute, 32 at Clyde River, and 125 at Cape Dorset. The changing total population size of the harp seal further complicates in-

TABLE 10
Reported Harvest of Harp Seals in the Canadian Arctic.

Community	19751,2	19761
Resolute Bay	-	1
Grise Flord	142	109
Arctic Bay	19	4
Pond Inlet	6	48
Clyde River	_	8
Broughton Island	36	35
Pangnirtung	2071	1516
Frobisher Bay	218	112
Lake Harbour	8	68
Cape Dorset		3
Hail Beach	_	2
gloolik	4	-
Coral Harbour	6	,
Eskimo Point	3	-
Pelly Bay		10
Great Whale River	3	No Data
nukjuag	16	
Akudlivik	8	**
Sugluq	134	**
Nakeham Bay	153	**
Koartak	12	**
Payne Bay	7	**
ort Chimo	40	**
Beorge River	16	••
Port Burwell	363	**
Totals	3265	(1916)

'Upper part of table from data aupplied by Fisheries and Marine Service based on data from Fur Export Tax Returns gathered by N.W.T. government.

*Lower part of table from JBNQNHRC (1976).

terpretation of the 1962-71 figures compiled by Smith and Taylor.

The current total annual harvest in the Canadian Arctic is not accurately known. The estimate of 3,000 to 4,000 mentioned by Friesen (1975) and Mansfield et al. (1975b) does not appear to include much allowance for hunting losses or domestic use.

HUNTING LOSS

The buoyancy of harp seals is very low when they first arrive in the Arctic and increases gradually through the summer. This is evident both indirectly from Sergeant's (1973b) seasonal measurements of blubber thickness and condition factor (girth × 100/length), and directly from hunting losses (e.g., Degerbøl and Freuchen 1935; Anders et al. 1967; Bissett 1967a). When the lean seals first arrive, most sink within a few seconds after being shot; during the break-up hunt in Cumberland Sound about 65% of a sample of 46 killed were lost (Anders et al. 1967). During the open water hunt, 50% of 34 were lost during late July, and 37% of 38 were lost in August. Sinking losses continued to

decline in September and October (Anders et al. 1967). Riewe and Amsden (in press) found the loss rate to be 61% in a sample of 61 harp seals shot during the open water season in Jones Sound. The overall loss rate is unclear, since the above samples are small and the seasonal distribution of the kill is only approximately known. If the average annual harvest in the Canadian Arctic is 3,000 and the loss rate is 40% to 60%, the annual kill could be 5,000 to 7,500. This does not include wounded animals that die later.

Hunting losses in Greenland are unknown. However, most of the harp seals are killed among the drift ice or in open water (Kapel 1975b), and significant losses seem inevitable.

Losses in the harvest near Newfoundland are rarely mentioned. The harvest figures for the take of 1 + year old seals on the moulting areas represent only those recovered, and in the past the percentage loss was 'quite high' (Fisher 1955). According to Sergeant (1963), this percentage has been lowered by better marksmanship and one observer in 1962 estimated it at about seven per cent.

SEASONAL AVAILABILITY

Availability of harp seals in the Canadian Arctic is determined by the timing of migration into and from the various areas (see 'Distribution' section, above). In most areas harp seals appear soon after break-up of ice and remain until freeze-up begins. Some harp seals remain in the southeastern Baffin Island area until January or later, but even there most of the harvest is in July to October (Anders et al. 1967). At Port Burweil, most harp seals taken are obtained during the southward migration in October to December (Sergeant 1965s: Evans 1968).

HUNTING TECHNIQUES

Anders et al. (1967) have described the hunting methods used for harp seals in Cumberland Sound, the area of the Canadian Arctic where the largest numbers of harp seals are taken. During break-up, harp seals surfacing in small areas of open water are shot by Inuit on the ice and retrieved by boat. When possible, the seal is wounded, approached and finally dispatched from close range; this reduces sinking losses. In the open water period harp seals are shot from a boat. Early in the season, when harp seals sink rapidly after death, only those that surface near the boat (<90 m away) are shot, in Greenland kayaks and harpoons are occasionally still used (Kapel 1975b).

In the Port Burwell area harp seals are captured in nets during the southward migration in late autumn (Sergeant 1965a; Evans 1968). Nets were also used in Greenland in earlier years (Kapel 1975b).

UTILIZATION

Mature harp seals weigh an average of 135 kg, with maies being only slightly heavier than remales. One year olds weigh 40 to 65 kg (Sergeant 1973b). In the Canadian Arctic, the skins are both traded and used domestically; the proportion traded varies with price (Riewe 1977). In 1978, there was no market for harp seal skins at Grise Flord and many seals were left unskinned (LGL Ltd. unpubl. data). The meat is used for dog food, but the importance of this has no doubt declined.

HOODED SEAL

The flooded seal is not of significant importance to inuit in the Northwest Territories (Friesen 1975; Smith and Taylor 1977). However, offshore waters of Davis Strait are an important breeding and migration area for this species.

DISTRIBUTION

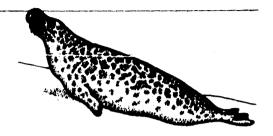
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Hooded seals are closely associated with the edge of the pack ice from Newfoundland through Davis Strait, southwest, south and southeast Greenland, Denmark Strait and Jan Mayen Island to Spitsbergen. Hooded seals assemble during March in heavy pan ice at three main whelping areas — near Jan Mayen Island north of iceland, in Davis Strait, and near Newfoundland. The Davis Strait whelping area was known in the 19th century and rediscovered in 1974; in various years its latitude has varied from that of northern Labrador to that of Cumberland Sound (Sergeant 1974, 1976b; Imperial et al. 1978). Most of the Newfoundland population whelps on the 'Front' east of northern Newfoundland and southern Labrador, but a few whelp in the Gulf of St. Lawrence.

In April, after whelping and breeding. Newfoundland hooded seals start to migrate north to Davis Strait and southwest Greenland. Migrating hooded seals begin to reach coastal waters off southwest and central west Greenland in early April (Rasmussen 1960; Kapel 1975b), but these early arrivals are probably from the Davis Strait group, not from Newfoundland, Young-ofthe-year begin to arrive about 10 days after the older animals (Rasmussen 1960), From southwest Greenland, most apparently migrate southeast to south Greenland, where the main catch is in May and early June (Kapel 1975b). However, the catch per hunter is much higher in south than southwest Greenland. which suggests that hooded seals approach south Greenland from the southwest or west as well as the northwest.

From south Greenland, many hooded seals apparently migrate northeast to their main moulting area in Denmark Strait between Greenland and Iceland (Rasmussen 1980; Kapel 1975b). There is only one published record of a hooded seal marked near Newfoundland being caught off eastern Greenland (Sergeant 1974), but distributional evidence and observations of migrating animals provide substantial evidence that many Davis Strait and/or Newfoundland seals do move to Denmark Strait (Rasmussen 1960). Seals from the Jan Mayen whelping group also migrate to the Denmark Strait area and moult there in late June and early July.

Some hooded seals of the Davis Strait and/or Newfoundland stocks remain off southern or western Greenland during the moulting period, especially in heavy ice years, and those that moulted in Denmark Strait begin to return to Davis Strait by late July (Ras-



mussen 1960; Kapel 1975b). Their distribution in late summer and fall is poorly known. The few seen and hunted off northwest Greenland and the Thule District are recorded in June through September (Vibe 1950; Kapel 1975b).

There are also occasional summer records from the Canadian aide of Baffin Bay, particularly from the Bylot Island area (Low 1906; Anderson 1934; Degerbel and Freuchen 1935; Miller 1955; Tuck 1957; Blaeett 1967b; Johnson et al. 1976). One individual has been found as far west as Radstock Bay, southwest Devon Island (Stirling and Archibaid 1977), There have been a few records in Jones Sound (Riewe 1977) and off eastern Ellesmere Island and in Kane Basin (Vibe 1950). There have also been occasional records in Cumberland Sound (Kumilen 1879; Anders et al. 1967) and in eastern Hudson Strait (Dunbar 1949). Mansfield (1968) and Bruemmer (1972) mention single sightings in southwest and east Hudson Bay.

Southward migration parallel to the Labrador coast has been recorded in late September (Rasmussen 1960), but some hooded seals, probably mainly of the group that whelps in Davis Strait, remain there through the winter (Kapel 1975b; Imperial *et al.* 1978).

There have been several extralimital records of the hooded seal in the western Canadian Arctic — near Herschel Island and Tuktoyaktuk (Porsild cited by Dunbar 1949), near Sachs Harbour (Usher 1966) and at Read Island off southwest Victoria Island (Smith and Taylor 1977). In general, however, this species does not move appreciably west from Davis Strait or Baffin Bay.

STATUS AND SIZE OF POPULATIONS

Hooded seals have been hunted commercially at the Newfoundland and Jan Mayen whelping areas for over 150 years, and were also taken at the Denmark Strait moulting area up to 1981. The Denmark Strait harvest presumably took seals from all three whelping areas. There has also been a smaller harvest along the Greenland coast for a similarly prolonged period. The imprecise information about population sizes and trends that is available is almost all derived from hunt statistics.

The catch of hooded seals off Newfoundland, south and southwest Greenland and eastern Baffin Island declined sharply in the 1920's (Rasmussen 1960: Anders et al. 1967; Vibe 1967; Sergeant 1974). The number whelping near Jan Mayen Island apparently increased around the same time, perhaps because of a reallocation of seals among whelping areas in response to the climatic amelioration then in progress (Rasmussen 1960). Sergeant (1974) has argued that such a reallocation is feasible because all three groups whelp simultaneously in March, because all apparently mix in Denmark Strait in early summer, and because at least a few of the juveniles wander widely. Since 1965 the catches in Greenland and Newfoundland have increased again (Kapel 1975b; Sergeant 1976b), perhaps due to the heavier ice present in recent years, the cessation of the Denmark Strait hunt in 1961, or both (Sergeant 1976a, b). Off Newfoundland, the catch per ship as well as the total catch averaged higher in the 1966 to 1973 period than in 1929 to 1965 (Sergeant 1974).

Rasmussen (1980) suggested that the total population in the late 1950's was about 500,000 to 750,000, with about 10% of these breeding near Newfoundland. This crude estimate was based on the facts that about 75,000 hooded seals were then being harvested annually, exclusive of the small Greenlandic and Soviet catches, and that the total population was apparently declining slowly. A moulting group of 230,000 was recorded in Denmark Strait in 1959, but this was believed not to represent all seals in the area.

The recently rediscovered Davis Strait whelping population included roughly 50,000 adults in 1974 and possibly a similar number in 1977 (Sergeant 1974; Imperial et al. 1978) but fewer were found in 1976 (Sergeant 1976b) and 1978 (about 34,000 — MacLaren Marex Inc. 1979). None of these estimates was based on comprehensive coverage.

The number of hooded seals whelping near Newfoundland has not been estimated directly. This group is estimated to have produced about 27,000 young annually in 1971 to 1976 (Sergeant 1976b). This estimate is derived from an indirect method involving several assumptions, a regression analysis based on only five points, and extrapolation of the regression line beyond the range of the data. If the estimate is correct, the

number of adults near Newfoundland would be about 54,000, assuming a 1:1 sex ratio and 100% fertility. Additional immature animals would also be present.

in summary, the status of the 'populations' of hooded seals is unclear because estimates of population sizes are imprecise and because the degree and causes of exchange among populations are uncertain. If exchange is extensive, year-to-year trends in catch in one area cannot be interpreted without knowledge of trends in other areas. The fact that the Davis Strait group was not accounted for until 1974 makes interpretation of trends especially difficult. In the absence of a reliable estimate of the size of the Newfoundland stock, it is impossible to evaluate the conclusion by Sergeant (1974) that this heavily exploited stock is maintained by immigration of seals from the little-exploited Davis Strait stock.

POPULATION STRUCTURE AND DYNAMICS

Hooded seals have not been studied in the Northwest Territories. Samples of the animals from the Newfoundland and Jan Mayen whelping populations, the Denmark Strait moulting aggregation and the Greenland coastal catch have been examined at various times, in general, the population biology of the hooded seal is less well known than that of the harp seal or the ringed seal. Hooded seals can be aged by counting layers in the dentine or cementum of the canine teeth, Ageing can be very reliable for ages zero to 10 years, but there is an uncertainty of ±1 year for ages 11 to 15 (Kapel 1975b) and presumably also for older animals.

The hooded seal has been said to be monogamous, but may be to some degree polygynous (Miller and Boness 1979). The male remains on the ice with the female during the whelping period in March (Rasmussen 1957; Mansfield 1967a). The single pup is nursed for lease than two weeks (variously reported as eight to 12 days — Rasmussen 1957; Mansfield 1967a; Sergeant 1976a) and then is abandoned. Copulation occurs at the end of lactation, so the total gestation period is about 11.5 months. However, implantation is delayed.

Age of first breeding by females is usually three years off Newfoundland (Oritsland and Benjaminsen 1975) but was usually four years off Jan Mayen in the 1950's (Rasmussen 1960); the first pup is produced one year later. Thereafter breeding is usually annual. Males apparently become mature considerably later (10 years — Sergeant 1976b).

Age and sex structure has been studied using animals from the commercial and native seal hunts. Such samples are usually biased. For example, females associate more closely with the pups than do males, so sex ratios in kills at whelping patches are biased. The sex ratios in samples of hooded seals (excluding young-of-the-year) from Greenland and Denmark Strait, where

bias is less likely, are close to 1:1 (Rasmussen 1980; Kapel 1975b). Similarly, the ratio is near 1:1 for pups off Newfoundiand (Oritisand and Benjaminsen 1975). Age atrusture is difficult to assess because immatures are infrequent in the whelping areas and because young-of-the-year apparently do not migrate to the Denmark Strait moulting area (Rasmussen 1980; Sergeant 1976b). However, few hooded seals are proportionately rarer than old harp seals. The mean age of the moulting animals in Denmark Strait seemed to be decreasing in the late 1950's just before the hunt there was abolished (Rasmussen 1960). All these results come from heavily exploited populations; the age and sex structure of pre-exploitation populations and of the lightly exploited (see below) Davis Strait population are unknown.

The main source of mortality to adult and young hooded seals is doubtleas hunting. The average annual take of pups off Newfoundland in 1988-75 was 7,369, or 27% of the eatimated 27,000 pups produced annually in 1971-76. Natural pup and immature mortality are unknown; few immatures (one to three years) are harvested. Natural mortality rates for adults are unknown, since hunting is a major factor in all populations that have been studied. Widely varying and often inconsistent estimates (nine to 23%) of total annual adult mortality have been quoted for various locations, years and sex classes (Sergeant cited in Kapel 1975b; Oritsland and Benjaminsen 1975; Sergeant 1976a). Neither natural nor total mortality of any age or sex category of the Davis Strait population is known; total mortality is presumably less than for the Newfoundland and Jan Mayen populations (see below).

Dynamics of the populations whelping near Jan Mayen island and Newfoundland have not been examined in detail, and the Davis Strait group is unstudied. Detailed analysis will remain difficult until the extent of exchange among populations is known. The significance of current harvests is uncertain since total population sizes are poorly known.

CURRENT HARVEST AND UTILIZATION

Extremely few hooded seals are harvested by inuit in the Canadian Arctic (Friesen 1975; Smith and Taylor 1977), and there is no evidence that the harvest was appreciably greater in the past. Pond inlet accounts for most of the catch; in 1978, about 10 hooded seals were taken — all were males (LGL Ltd., unpublished data).

Hooded seals that whelp in Davis Strait are presumably exploited in Greenland during spring and summer, but it is not known what proportion of the total Greenland catch is from this population. The south and west Greenland catch, presumably from both the Davis Strait and Newfoundland populations, was relatively high before 1919 (6,500 to 7,500 annually in Julianehaab district atone in 1916-18), low thereafter, and higher again since 1985 (about 2,000 annually) (Rasmussen 1960; Kapel 1975b). The number of seals killed but not retrieved or reported is unknown but potentially significant because of the difficult drift-loe conditions (Kapel 1975b). In addition, up to 1961 the thenunrecognized Davis Strait population was presumably exploited while moulting in Denmark Strait.

Harvests of the Jan Mayen and Newfoundland populations were summarized by Raamussen (1960) and Sergeant (1965b, 1974, 1976a, b). The Denmark Strait hunt ended in 1961, and increasing restrictions have been placed on the Jan Mayen and Newfoundland hunts (annual quotas of 30,000 and 15,000, respectively, by 1972-74). From 1966-75, the average annual hervest off Newfoundland waa 7,369 pupp and 5,370 older hooded seals — the latter being predominantly breeding females (Sergeant 1976b).

RINGED SEAL

This small seal is widespread in the Canadian Arctic where it forms the basis of the resource-harvesting economics of most of the coastal Inuit communities. The ringed seal is the best studied of the arctic marine mammals. Because of its economic importance and the quantity and quality of information available, the following discussion is necessarily somewhat more detailed than are the accounts of the other species of marine mammals.

DISTRIBUTION

The ringed seal is the most widespread species of marine mammal in the Canadian Arctic. It occurs in all marine waters south to James Bay and northern Newfoundland and north to the Arctic Ocean, north of Ellesmere Island (Dunbar 1949; Mansfield 1967a). The ringed seal has a similar wide range throughout circumpolar arctic regions.

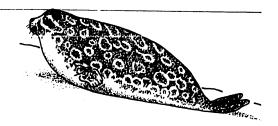
The ringed seal is usually a permanent resident in most of its range; it overwinters under the sea ice through which it maintains breathing holes (Degerbøl and Freuchen 1935; Vibe 1950; McLaren 1958a; Mansfield 1967a; Smith 1973a). Throughout most of its Canadian range it is thought to be sedentary, undertaking only local movements in response to changing ice conditions. However, in the western Arctic there is some evidence that regular, annual movements occur along the northern coast of Alaska (Burns 1970; Burns and Harbo 1972) and in the Canadian sector of the Beaufort Sea (Smith 1976a; Smith and Stirling 1978).

The distribution of ringed seals is highly dependent on the presence of stable fast ice where adults maintain breathing holes throughout the winter. Thus, the species tends to be coastal in distribution with smaller numbers occurring offshore in zones of moving pack ice.

STATUS AND SIZE OF POPULATIONS

There is no systematic, quantitative information on historic levels of harvest of ringed seals. There has been no commercial (non-native) exploitation for at least 50 years and current population levels are believed to be similar to historic levels.

There has been a great deal of recent research on methods of estimating the sizes of ringed seal populations (McLaren 1958b, 1961, 1966b; Burns and Harbo 1972; Smith 1973a, b, 1975a; Finley et al. 1974; Stirling et al. 1975, 1977; Finley 1976, 1978; Braham et al. 1977b). Since population estimates derived from some of these studies have been used to determine the potential sustainable harvest levels of ringed seals in various geographic regions, it is important to evaluate the accuracy and consistency of the procedures that have been used. It will be noted that although the



methods are apparently similar, there are important differences that greatly affect the comparability of the studies. The following evaluation considers the census techniques that are used, the basic assumptions implicit in the techniques, the estimation procedures used and the population estimates that have been derived.

CENSUS TECHNIQUES

Two basic survey techniques have been used to census ringed seals:

- 1. boat surveys during the open water season, and
- 2. aerial surveys during spring.

Surveys from boats were conducted and evaluated by McLaren (1961) and have been used in Russia by Potelov (1975a). However, because of the short open water season, the large areas to be surveyed and the costs and logistic problems associated with operating in ice-infested waters, boat surveys of ringed seals have not been widely used and are not discussed here.

Aerial surveys have been widely used and offer the advantages of high speed and long range; thus, large areas can be surveyed and replicate surveys can be conducted to determine confidence limits. Ringed seals haul out onto the surface of fast ice in late May, June and early July to moult their pelage. At this time they are conspicuous on the light-coloured ice and they can be easily counted.

The proportion of the seals on ice that are counted during aerial surveys depends on a variety of factors. These factors include type of survey alrcraft, its speed and altitude, the positions of the observers in the aircraft, the width of the transect that is being surveyed, and the experience, concentration and visual acuity of the observers. The biases of the aerial survey technique have not received enough attention and surveys by different investigators have not been standardized. A few examples will illustrate these points.

Survey altitudes have varied from 30 m (McLaren 1966b) to 152 m (Stirling et al. 1977). Survey speeds have varied from 170 km/h (Finley et al. 1974) to 240 km/h (Stirling et al. 1977) or are not stated (Smith 1975a). Transect widths have varied from 0.4 km (Finley et al. 1974; Johnson et al. 1976) to 1.6 km (Stirling et al.

1975) or to the limit of visibility (McLaren 1966b). Surveys have been conducted by the pilot and an observer in the two front seats (Burns and Harbo 1972). one observer in the front and one in the rear (Smith 1975a; Finley 1976), and two observers in rear seats (Stirling et al. 1977). in a series of studies by LGL Ltd., it was found that observer differences in detection of seals can amount to 40% in extreme cases and that observers in front seats see 11 to 15% more seals than observers in rear seats at speeds of 210 km/h and altitudes of 90 m (Finley 1976). When an above-average observer is in the front seat and survey speeds are slow (170 km/h), the combined effects of observer bias and seat position can be substantial (about 60% in one study - Johnson et al. 1976). These biases do not occur with all observers and seating arrangements but they can be substantial and should be examined in each study.

ESTIMATION PROCEDURES

The question of what proportion of ringed seals hauled out on the ice are actually counted was discussed above. Of more concern is what proportion of the seals present in an area are actually hauled out on the ice at the time of the survey. Ringed seals exhibit diurnal and seasonal patterns of haul out with peaks during midday (10:00 to 16:00 h) and mid to late June (McLaren 1966b; Burns and Harbo 1972; Smith 1973a, b; Finley 1976). However, Finley (1978) has shown that timing of haul-out behaviour is a complex function of location, diurnal and seasonal patterns, and weather, Finley (1978) also suggests that much of the supposed increase in frequency of haul-out in late June is, in fact, caused by the influx of additional (presumably subadult) seals from adjacent areas rather than by increased haul-out behaviour of resident seals.

Smith (1973a) estimated that during peak haul-out periods, only 50% of the seals present were actually hauled out on the ice. Finley (1978) estimated that over 70% of the seals are hauled out during peak periods in the central high Arctic. Fedoseev (1971) cites Shustov to the effect that 83 to 84% are hauled out at one time. Thus, correction factors to account for seals under the ice range from 1.2 to 2.0. Obviously, more work is required to refine these estimates.

McLaren (1958b, 1966b) noted that numbers and distribution of ringed seals in June were in general determined by the type and amount of fast ice present in an area. Fast ice along complex coasts supported higher densities of seals than did ice along simple coasts and ice close to shore supported more seals than did ice further from shore. Thus, he extrapolated densities from a small number of aerial surveys of various ice types along southeastern Baffin Island to ice distribution patterns in other areas to determine population sizes. These estimates were intended as first approximations but have since been used to assess potential yields (see various Area Economic Surveys produced by D.I.A.N.D. and also JBNQNHRC 1976).

Smith (1973a, b) has pointed out several problems with McLaren's (1958b, 1966b) preliminary extrapolations. In addition, recent work (Stirling et al. 1975, 1977; Finley 1976, 1978; Smith and Stirling 1978) has shown that seals are not distributed only according to simple ice type nor is distribution necessarily similar from year to year, at least in the western Arctic.

The estimates by McLaren (1958b) are not sufficiently precise for use in determination of potential harvestable yield of ringed seals. However, the method of relating seal density to ice type probably can be modified to provide more reliable estimates.

POPULATION ESTIMATES

McLaren (1958b) estimated a population of nearly one million seals in the eastern Arctic south of Lancaster Sound but including Hudson Bay. As noted above, this estimate is suspect.

Smith (1973a) estimated the populations of ringed seals in Home Bay, Hoare Bay and Cumberland Sound on the east coast of Baffin Island to be about 71,000, 36,000 and 59,000, respectively. These estimates are based on a correction factor of 2 X to account for animals under the ice during the surveys and a correction factor of + 0.1149 to account for sub-adult animals that were believed to be present in offshore areas. The uncorrected estimates for the three areas are about 33,000, 17,000 and 27,000.

Smith (1975a) estimated that Hudson Bay supported 455,000 ringed seals and James Bay supported 61,000. These estimates include a correction factor of 2 X for animals under the ice. Smith used unweighted average densities for his extrapolations of numbers. If the extrapolations are weighted for length of transect, the population estimates are 407,000 and 56,000. The uncorrected estimates from weighted data are 203,000 and 28,000.

Stirling et al. (1975, 1977) have made the most systematic estimates of ringed seal numbers. Based on a large number of aerial surveys and a partially stratified design, they estimated the population of ringed seals in the Canadian Beaufort Sea to be 41,983 (95% confidence interval of $\pm 8,152$) in 1974 and 21,661 (95% confidence interval of $\pm 4,919$) in 1975. These estimates were not corrected for seals under the ice. The large sample size and careful design of these surveys make these estimates much more reliable than those cited above, which were based on few aerial surveys. It should be noted that even this survey of the Beaufort Sea produced a 95% confidence interval of about $\pm 20\%$.

STOCKS

There is no evidence to suggest that isolated stocks of ringed seals exist in the Canadian Arctic. Large-scale movements of seals have been documented in the Beaufort Sea (Stirling et al. 1977). Local movements along the east coast of Baffin Island have been in-

ferred for the Cumberland Sound area. Smith (1973a) believes that the heavily exploited Cumberland Sound 'population' is maintained by immigration of seals from surrounding areas.

POPULATION STRUCTURE AND DYNAMICS

The age of ringed seals can be stermined by examination of canine teeth from the lower jaw. McLaren (1958a) and Smith (1973a) counted dentinal annuli to determine the age of the animal. McLaren (1958a) reported that this method was unreliable for some animals over 10 years of age and for most animals over 20 because the dentinal annuli were highly compacted. Stirling et al. (1975) aged ringed seals by staining and counting cementum layers in the teeth. They found this technique to be very accurate.

REPRODUCTIVE BIOLOGY

Nothing is known about the social system of ringed seals but they are assumed to be promiscuous (Stirling 1975). Adult ringed seals maintain breathing holes in stable fast ice and the single pup is born on the ice in the last half of March or the first half of April (Vibe 1950; McLaren 1958a; Fedoseev 1965a; Johnson et al. 1966; Smith 1973a; Smith and Stirling 1975) in all areas studied. The pups are born in birth lairs hollowed out of snowdrifts in the lee of pressure ridges and hummocks in the fast ice (Degerbøl and Freuchen 1935; McLaren 1958a; Smith and Stirling 1975). Lactation lasts for 1.5 to two months after which the female abandons the pup (McLaren 1958a; Smith 1973a). The duration of lactation is partly a function of ice stability. Fedoseev (1975) found that ringed seals inhabiting drift ice in the Sea of Okhotsk nursed for only three

The breeding season extends from mid-March to mid-May; copulation occurs in water under the ice (McLaren 1958a; Smith 1973a; Stirling 1975). Many females with pups ovulate during lactation. Implantation is delayed for about three months and occurs in August (McLaren 1958a).

Sexual maturity is attained by males at ages six to eight years with most becoming mature in their seventh year (McLaren 1958a; Fedoseev 1965a, 1968, 1975; Johnson et al. 1966; Smith 1973a). Females are considered to be sexually mature when they first ovulate. If breeding occurred, the first pup would be produced in the following year. McLaren (1958a) found that 12% of the four year-olds (= in fifth year), 22% of five year-olds, 78% of six year-olds and 100% of seven year-olds had ovulated (N = 65) along southwest Baffin Island. The corresponding figures for the Chukchi Sea coast of Alaska are 8%, 60%, 55% and 93% (N = 45) (Johnson et al. 1966) and for the east coast of Baffin Island (Home Bay) they are 41%, 59%, 85% and 86%

(N = 225) (Smith 1973a). Figures for Russian portions of the Chukchi Sea, Bering Sea and Sea of Okhotsk are similar (Fedoseev 1965b, 1975).

Ringed seals are annual breeders. However, not all adult females ovulate or are pregnant every year. Thus the effective birth rate per adult female is less than 1.0 and can be quite variable. There is confusion in the literature about the ovulation rate of ringed seals. Smith (1973a, 1975b) calculated that the mean ovulation rate was 0.80 for a sample of 665 females from Home Bay, Baffin Island, Stirling et al. (1977) adjusted this figure to 0.92 by excluding the incompletely mature four and five year-old age classes. In actual fact the mean ovulation rate of this large sample (four and over) is 0.87 when the age distribution of the actual sample is considered. This rate rises to 0.91 if four and five year-olds are excluded. McLaren (1958a) found that the ovulation rate in six year-olds from southwest Baffin Island was 0.78; however, the rate for 42 older females from various areas in the eastern Arctic was 0.93 (McLaren 1958b). The ovulation rate for a sample of 280 seals older than six years from the Chukchi Sea off Alaska was 0.94 (Johnson et al. 1966 as recalculated by Stirling 1971). A small sample (27) from the Beaufort Sea in 1972 yielded an ovulation rate of 0.74 (Stirling et al. 1977).

Two types of variation in the ovulation rate have been found: age-specific and year-specific. Most workers have found that young females (five, six and seven year-olds) have a lower ovulation rate than older females (e.g., McLaren 1958b; Smith 1973a). McLaren (1958b) thought that old females (over 30 years) had a reduced ovulation rate but Smith (1973a) found no evidence of this. Studies in the Beaufort Sea (Stirling et al. 1975, 1977) have documented major year-to-year differences in the ovulation rate of mature females: 0.74 (N = 27, 1972), 0.49 (N = 80, 1975) and 0.39 (N = 23, 1974). This annual variability will be discussed later but it is noted here that long term studies in other areas have not found similar variations (Fedoseev 1968 — Sea of Okhotsk; Smith 1973a — eastern Baffin Island).

Smith (1973a) assumed that virtually all females that ovulated did become pregnant and hence he and other workers have used the ovulation rate as a good approximation of pregnancy rate and birth rate. Studies that have examined pregnancy rates have found them to be somewhat lower than the average ovulation rates cited above. Pregnancy rates after implantation were 0.86 (Johnson et al. 1966) and 0.73 (Fedoseev 1975) in the Chukchi Sea, 0.73 in the Bering Sea (Fedoseev 1968). The last of these studies was based on a sample of 481 females taken over three years and the annual rate varied from 0.83 to 0.87.

AGE AND SEX STRUCTURE

The age structure of ringed seal populations is fairly well known based on the work of McLaren (1958b), Fedoseev (1968), and the detailed studies by Smith (1973a, 1975b). These studies show that approximately half of the female population consists of mature females and half of immature animals. It is extremely difficult to collect unbiased samples of ringed seals since there are major differences in the distribution of breeding and non-breeding age classes, some differences in distribution of sexes, and differences in the ease of collecting the various age classes. McLaren (1958b) and Smith (1973a) give good discussions of these potential biases.

The maximum longevity of ringed seals in the wild has been difficult to evaluate because of the difficulties of 'reading' the dentinal layers in teeth from old animals. McLaren (1962) records one male that was at least 43 years old but very few ringed seals live past 30 years of age (McLaren 1958b; Smith 1973a).

The sex ratio of ringed seals is 1:1 in all age classes (McLaren 1958a; Fedoseev 1965a, b; Johnson et al. 1966; Smith 1973a).

MORTALITY FACTORS

The ringed seal is the basis for substantial native hunting economies throughout most of its circumpolar arctic range. Aspects of mortality through hunting are discussed in later sections.

Predation by polar bears and arctic foxes apparently is the principal source of natural mortality to ringed seals. Other potential sources identified by McLaren (1962) include parasites and diseases (unimportant), tooth wear in old animals that may cause death before physiological maximum longevity is reached (possibly important in unhunted populations — I. A. McLaren, pers. comm.), and for immatures on unstable pack ice accidental death by being crushed or trapped without access to air (no quantitative data).

Arctic foxes have long been known to move onto the sea ice in winter and scavenge at the remains of seals killed by polar bears. However, recent studies in the western Arctic (Amundsen Gulf, south of Banks Island) have shown that arctic foxes are significant predators of ringed seal pups (Smith 1976b). In a three year study, Smith (1976b) estimated that an average of 26% of the ringed seal pups were taken by arctic foxes, which dug through the snow covering the seal birth lairs: the annual rates were 9%, 40% and 34%. The reasons for The variability in fox predation rates are unclear. A potential bias of this study is that the dog used to find the birth lairs of seals may have been attracted to those lairs that had already been found and marked (with urine and scats) by the foxes (Stirling and Smith 1977). Nonetheless, predation by arctic foxes is clearly an important source of mortality to ringed seal pups in the western Arctic. There are no data on the extent of this predation in other parts of the Canadian Arctic.

but arctic foxes occur throughout the area and there is no reason to assume that substantial predation does not occur.

The polar bear is probably the principal source of natural mortality of ringed seals. Stirling and Archibald (1977) examined ringed seals killed by bears and found that bears primarily took immature, non-breeding ringed seals. Over 80% of the ringed seals killed in the spring were two years old or less in normal population years (Stirling and Smith 1977). However, in the western Arctic in 1974 and 1975 when seal numbers and reproduction rates were very low, more adults were taken

Smith (1975a) hints at the potential importance of bear predation on seals. He estimated that there were 516,000 ringed seals in Hudson and James Bay (should be 463,000 - see preceding section) and that the estimated 600 bears occupying the denning area in southern Hudson Bay consumed between 5,000 and 21,000 ringed seals per year, based on the assumption that the bears occupy sea ice for half the year. The higher estimate was based on the finding by Stirling (1974) that one seal was killed per five bear days in Radstock Bay, southwest Devon Island, in the early summer. Smith (1975a), citing C. Jonkel, suggests that the population of bears in Hudson and James Bays could be as high as 2,000 to 3,000 animals. If there are 3,000 bears in the area and if each does take one seal per five days in the sea ice, then the kill of seals by bears would be about 110,000. Since most predation (about 85%) in normal years is on sub-adult (less than six years old) sea. (Stirling and Archibald 1977) and since about 50% of the population are sub-adults (McLaren 1958b; Smith 1973a), then about 40% of the sub-adults are taken annually by polar bears. Obviously, this could not happen on a long-term basis, and one or more of the above values is probably seriously in error.

The above exercise illustrates several important points. The polar bear is an important predator of ringed seals. Management of ringed seals requires a knowledge of the numbers of bears preying on the seal population and the number of seals per year required by bears of different age and sex classes. (The annual rate of eight to 35 seals per bear used by Smith [1975a] needs to be refined.) Management of ringed seals requires that the combined effects of predation by polar bears, arctic foxes and Inuit be considered. Clearly, the three predators are in a state of potential conflict for the available surplus of ringed seals. The conflict is further complicated by the fact that Inuit are also predators of polar bears and arctic foxes. Future management will have to balance the relative Inuit demand for ringed seals, polar bears and arctic foxes with the demand for ringed seals by polar bears and arctic foxes.

POPULATION DYNAMICS

Evaluations of the population dynamics of ringed seals have been confounded by the difficulty of obtaining unbiased age samples from the populations. Various

investigators (McLaren 1958b; Smith 1973a) have tried to correct for these biases but it is not known how accurate the corrections have been. The most important biases have been in the estimation of numbers and survival of pups and sub-adult classes.

The annual increment of pups into the population has been estimated at 18.2% (southwest Baffin Island — corrected for a 1:1 sex ratio — McLaren 1958b) and 19.51% (Home Bay, eastern Baffin Island — Smith 1973a). These estimates assume that pregnancy (McLaren) or ovulation (Smith) rates equal birth rates. The increment of pups into the Sea of Okhotsk ringed seal population averaged 21% per year over a six year period based on observed pregnancy rates (range 19% to 23% — Fedoseev 1968).

Estimates of first year mortality (including hunting) are 0.31 (McLaren 1958b) and 0.41 (Smith 1975a). However, because of biased sampling of pups, these estimates are based on comparisons of the number of pups inferred from ovulation rates with the number of seals in the 1+ year class. Fedoseev (1968) found an average mortality rate of 0.35 for seals in their first year based on comparisons of the numbers of seals in the 0+ and 1+ age classes. He felt that his data were free of age-specific sampling biases. McLaren (1958b) estimated that the natural mortality (exclusive of hunting) of pups was 25%.

Mortality rates in relation to age are typically U-shaped with high mortality to pups but low mortality to older age classes. Mortality rates are assumed to gradually increase for seals over 15 years of age (McLaren 1958b; Smith 1973a). Fedoseev (1968) found an average annual natural mortality rate of 0.11 for animals aged one to 12 years. McLaren's (1958b) estimate of natural mortality for these classes was 0.06. Smith (1975b) constructed a model of a hypothetical unhunted population and found that the crude death rate (= natural mortality for the population was 0.08. The overall mean mortality rate for the population at Home Bay, Baffin Island, was 0.17 (includes hunter kill).

Several authors have estimated the potential sustainable yields of ringed seal populations. McLaren (1958b, 1962) calculated that the total hunting kill of his population was 7,000 per year. He then constructed a hypothetical life table using data from specimens from the area and several assumptions. The life table assumes a balanced population of stable size and age distribution and that kill was at the maximum sustainable level. The sustainable yield was 7-10% of the population (pups included) and 8% was thought the best approximation. It is important to note that there is no evidence to confirm or deny that the 7,000 animals were being taken from a stable population. If the population was declining then 8% is an overestimate of sustainable yield.

Smith (1973a), who had larger samples, constructed a hypothetical life table for an unexploited population and found that the maximum sustainable yield was about 11% of the population. Smith felt that this esti-

mate was too high and was in part caused by the arbitrariness of the age-specific survival rates assigned to the model. Smith (1973a) calculated the annual sustainable yield of the population hunted at Home Bay, Baffin Island, to be 7.2%. This again assumed that the population was balanced and that the observed kill was equal to the maximum sustainable kill. The estimated yield of 7.2% was determined by dividing the total annual kill by the population size. This estimate is now used for management purposes so it is important to evaluate potential sources of error in the estimate.

The kill figures used by Smith (1973a) were derived by adjusting the number of pelts traded to account for sinking loss and pelts not traded to arrive at an estimate of total kill. A correction factor of 5% was applied to the number of pelts traded to account for sinking loss during the winter and pelts not traded. Sinking loss in winter has, in fact, been found to be between 7 and 10% (McLaren 1958b; Anders et al. 1967; Higgins 1968) and the number of pelts not traded was as high as 33% in one year at Holman (Smith and Taylor 1977). Clearly, there could be substantial errors in the estimates of total kill.

The estimate of population size used to calculate sustainable yield may also be inaccurate. 'The estimates of numbers (70,684) arrived at in this investigation only indicate the approximate size of the real populations' (Smith 1973a:31). In the most comprehensive aerial surveys of ringed seals conducted to date, Stirling et al. (1977) had a 95% confidence interval of $\pm 20\%$ around their population estimates. The less systematic and comprehensive surveys by Smith (1973a) should have at least as broad a confidence interval. Thus, there is a 95% chance (at most) that the actual population was between 56,500 and 84,800. In addition, Smith (1973a) used a correction factor of 2X to account for animals under the ice during the surveys. This factor is also an estimate and has unknown confidence limits associated with it.

The combined 95% confidence limits that apply to the estimate of 70,684 seals cannot be determined at this time, but are probably at least ±30%. Since this estimate and the imprecise estimate of annual kill are used to determine the sustainable yield, the confidence limits for the sustainable yield estimate would also be at least ±30%. Thus, the potential annual sustainable yield could be as little as 5% or as much as 10% of the population, based on the above arguments. While the above differences amount to only a few percentage points, they are quite significant when translated into allowable catches. For example, the difference between 5 and 10% amounts to 50,000 seals in a population of one million.

Smith's (1973a) estimates have been discussed in detail because they are clearly the best information available. However, the estimates will need to be refined if the harvest of ringed seals increases significantly.

Fedoseev (1968, 1975, 1976) estimated that the sustain-

able yield of ringed seal populations was about 4%. However, this estimate appears to be based on oversimplifications concerning the estimates and interpretations of the proportion of one year old seals in the population (15%) and the average annual mortality rate (0.11) of the population (excluding young-of-the-year).

Finally, the assumption that a single rate of sustainable yield can be applied equally to all populations in all years needs to be re-examined. Stirling et al. (1975, 1977) have documented major, naturally-occurring fluctuations in the numbers, distribution and reproductive rates of ringed seals and bearded seals in the Beaufort Sea. They note that 'quotas that were safe for a healthy population could be devastating to a reduced population with lowered productivity'.

LIMITING FACTORS

McLaren (1958a, 1962) thought that because ringed seals feed on many parts of the food web and on at least two different trophic levels, their numbers and distribution were not limited by food availability. Ringed seal populations may be limited by the amount of stable fast ice available to breeding adults. The older breeding adults occupy the most stable fast ice found in bays, flords and along complex coasts. In the less stable ice along simple coasts and offshore from complex coasts the densities of seals are lower and most of the animals are immature or young adults; seals at the floe-edge are Immatures (McLaren 1958a, 1962; Vibe 1967; Smith 1973a, b; Smith and Stirling 1975). McLaren (1958a) found that ringed seals born in less stable ice were smaller and often starved. Degerbøl and Freuchen (1935) found that seals along outer, exposed coasts tended to be smaller than those in flords in Greenland, and Fedoseev (1975) found that ringed seals in populations occupying drift ice were smaller than those on fast ice.

The factors that determine the numbers of ringed seals that occur on stable fast ice are not known (McLaren 1962). Finley (1978) found that breathing holes were randomly dispersed in bays. Stirling and McEwan (1975) noted that male ringed seals are aggressive under the ice and this may reduce under-ice movement or exclude sub-adult seals from stable fast ice areas. It is not known if the males maintain territories under the ice (Stirling 1975). Burns and Harbo (1972) and Finley (1978) suggest that available food under the fast ice may determine the numbers of seals that can occupy these areas. The number of breeding seals that can establish birth lairs is in part determined by the presence of snowdrifts in the lee of pressure ridges and hummocks in the fast ice (Smith and Stirling 1975).

Thus, although the amount and stability of fast ice determines the theoretical upper size limit of seal populations, a variety of other factors are also involved. There is a need for studies of the natural population regulation mechanisms of ringed seals and

the manner in which these mechanisms act in various ice types and geographical areas.

CURRENT HARVEST AND UTILIZATION

ANNUAL HARVEST

Ringed seals are harvested at virtually all coastal communities in the Arctic. Mansfield (1967a) estimated that the annual harvest in the mid-1960's was about 70,000 ringed seals. Current harvest information is summarized in Table 11. The figures for 1975 and 1976 are based on 'Fur Export Tax Returns' and indicate that the annual number of raw pelts exported from the Northwest Territories was about 35,000 in 1975 and 46,000 in 1976. An additional 15,500 seals were harvested by native communities in Quebec (Table 11).

The Fur Export Tax Returns were not designed explicitly to measure the harvest of seals. The returns underestimate the actual harvest of ringed seals for the following reasons:

- 1. retention of pelts for domestic use.
- incomplete reporting from settlements (see Table 11 — e.g., Cape Dorset and Repulse Bay),
- 3. use of pelts for handicrafts, and
- 4. pelts damaged and not traded.

These biases have been recognized and discussed by many authors (Stephansson 1975; Usher 1975; Berger 1977; Smith and Taylor 1977) and will not be pursued here. No means of adjusting or correcting the Fur Export Tax Returns to indicate actual harvest have been developed. Thus, the figure of 46,000 pelts exported in 1976 represents an unknown fraction of the total harvest. It is of some interest that if the maximum annual reported harvests from each community in the N.W.T. for the period 1940 to 1972 are summed then about 100,000 ringed seals would have been taken. Smith (1975a) used this approach to indicate potential harvest of ringed seals in Hudson Bay.

The figures presented for the Quebec communities (Table 11) are based on interviews with hunters in each community and are thought to be reliable estimates of annual harvest levels.

HUNTING LOSS

The proportion of ringed seals that are killed but not retrieved is probably lower than for some of the other seals. However, the numbers lost can be substantial. McLaren (1958b) examined seasonal variations in the amount of blubber on ringed seals and found that blubber thickness (and buoyancy) declined in May and June during the moult and then slowly increased during July and August. During break-up in June and July, melting ice and freshwater inflows lower water salinity and reduce water density. The lower density of seawater and reduced buoyancy of the seals in June and July lead to high sinking losses (McLaren 1958b) and

TABLE 11 Harvest of Ringed Seals in the Canadian Arctic.

	Fur Expor	Peak Annual	
Community	1975	1976	Harvest 1940-1972²
Arctic Bay	1773	1101	
Broughton Island	4673	1161	2917
Cape Dorset	218	8050	7425
Clyde River	2165	2034	5716
Frobisher Bay	2295	3392	2700
Grise Flord	688	2612	3137
Hall Beach	392	598	1000
igloolik	2133	127	444
Lake Harbour		3079	3914
Pangnirtung	1886	2020	4053
Pond Inlet	7168	9688	13091
Resolute Bay	1627	1674	4000
Sanikiluag	109	243	670
Bathurst Inlet	1728	212	2351
Cambridge Bay	3	105	900
Chesterfield Inlet	105	126	1759
Coppermine	101	175	950
Coral Harbour	1869	2279	8068
Eskimo Point	1008	574	2340
	406	206	
Gjoa Haven	375	140	3000
Holman	2384	4971	550
Pelly Bay	835	683	5500
Rankin Inlet	87	106	289
Repulse Bay	<u></u>		1441
Spence Bay	496	1072	1896
Whale Cove	195	117 96	2401
Paulatuk			1200
Sachs Harbour	61	72	_
Tuktoyaktuk	_	29 8	2186
Sub-totals	4	18	850
	34,781	45,928	
ebec Communities and Port Burwell ⁴			
	1973-75		
Akudlivik	1207		
Fort Chimo	752		_
Fort George	0		388
George River	635		235
Great Whale River	1210		_
nukjuag			3446
Koartak	2322		3977
eaf Bay	895		
Payne Bay	213		_
Port Burwell	1123		1092
Povungnituk	789		-
Buglua	_		1395
Vakeham Bay	1583		3862
	4809		2366
Sub-total	15,538		2000

Based on data gathered by N.W.T. government and provided by Fisheries and Marine Service, Yellowknife. In a few instances seals classed as 'other seals' have been included here as ringed seals.

¹From Smith and Taylor (1977). Highest annual harvest based on records from Hudson's Bay Company for 1940 to 1972 and R.C.M.P.

^{3&#}x27;-' indicates no report for community.

^{*}Data from JBNQNHRC (1976).

Best estimate of annual harvest during the two year period 1973-74 and 1974-75.

TABLE 12
Loss of Ringed Seals Through Sinking.

		Number	Per cent	
Date	Type of Hunt	Killed	lost	Source
February	breathing hole	12	8.3	Higgins 1968
March-April	fast-ice?	40	7.5	McLaren 1958b
May-June	fast-ice	31	9.7	Anders et al. 1967
July	fast-ice	26	23.1	Riewe and Amsden (in press)
Feb., March, June	floe-edge	19	47.4	Higgins 1968
June-July	break-up	206	16.0	Anders et al. 1967
July-Sept.	open water	59	50.8	Riewe and Amsden (in press)
July	open water	42	52.4	McLaren 1958b
July	open water	10	40.0	Higgins 1968
June-July	open water	344	27.9	Anders et al. 1967
August	open water	113	15.9	Anders et al. 1967
August	open water	58	15.5	McLaren 1958b
September	open water	112	3.6	McLaren 1958b
July-August	shoreline*	69	4.3	Riewe and Amsden (in press)
June	open water	ns**	38.	Smith and Taylor 1977
July	open water	ns	52.	Smith and Taylor 1977
August-Sept.	open water	ns	◄10 .	Smith and Taylor 1977

^{*} Seals are shot in shallow water from shore .

hunting is reduced in some communities at this time. The few studies of rates of sinking loss are reviewed in Table 12. There is quite good agreement among the estimates although larger sample sizes would be desirable.

Clearly, sinking loss is an important component of the total kill of ringed seals. Since the loss rate varies with season, any adustments of harvest figures to account for sinking loss need to be based on harvest figures that include data on the seasonality of the harvest. McLaren (1958b) presented a model for predicting the rate of sinking loss for various areas and seasons. This model should be updated with the information in Table 12 and with new information.

There are no data on loss of animals that are wounded and die at a later date.

HUNTING TECHNIQUES

Several techniques are currently used to hunt ringed seals. They have been described in great detail by many authors (Degerbøl and Freuchen 1935; Vibe 1950; McLaren 1958b; Anders 1965; Anders et al. 1967; Bissett 1967a, b; Higgins 1968; Beaubier et al. 1970; Kapel 1975b; Treude 1977). Briefly, the technique used depends on season. Ringed seals are shot at their breathing holes (agluit) or cracks in the fast ice. Nets are occasionally used in cracks, 'Set-guns' which are tripped by the seal when it surfaces to breathe in the breathing hole are used by a few Inuit. Ringed seals are hunted on the fast ice during the haul-out period in May and June. Most hunters use a screen to hide their approach from the seals but approaches are often made without a screen. A substantial hunt in many areas is conducted along the edge of the fast ice (floe-edge). The seals are shot in the water from the ice and are retrieved by means of a small boat. During the open water season, seals are shot from canoes, larger decked boats and shore. Nets are occasionally used.

UTILIZATION

Ringed seals weigh about 4.5 kg at birth. Adult males average 65 to 70 kg and adult females slightly smaller (Mansfield 1967a). Harvests often concentrate on younger animals and Riewe (1977) found that the average ringed seal killed at Grise Fiord weighed 48 kg.

The importance of the ringed seal to the Inuit extends beyond economic considerations into social and cultural matters (Rasmussen 1931 cited by Wenzel 1978). In economic terms, it is the basis for the subsistence economies of most communities. The ringed seal is a principal source of food and the skin is used for a variety of clothing and handicraft items. Ringed seals are also an important source of dog food in some communities.

Ringed seal pelts have recently become an important source of cash income. Most communities began significant trading of seal pelts in the 1950's and the increase in fur prices in the 1960's increased the trade (Smith and Taylor 1977). Wenzel (1978) reviews the average prices paid to hunters for mature ringed seal pelts:

1955	\$1.50	1974	\$14.00
1963	\$12.25	1977 (June)	\$14.00
1967	\$2.50	1977 (Aug.)	\$10.00
1971	\$13.00	1977 (Nov.)	\$1.00

The price for top quality pelts was \$10.00 in the winter of 1978-79 at Pond Inlet. However, most pelts bring lower returns or are unsaleable. The price of furs has fluctuated significantly. Fur prices affect the numbers of seals killed and the proportion of those killed that are traded. Riewe (1977) found that the proportion of the harvest that was traded as skins varied from 13% to 61% and averaged 37% at Grise Fiord between 1965 and 1972. It is not known whether these figures are typical of other communities or whether they still apply in Grise Fiord.

^{**}ns = sample size not stated

BEARDED SEAL

DISTRIBUTION

The bearded seal or squareflipper is a large, solitary seal found throughout the Canadian and Eurasian Arctic (Mansfield 1967a; Benjaminsen 1973). In Canada it occurs south into James Bay and along the Labrador coast, and north as far as the limit of the permanent ice (Mansfield 1967a).

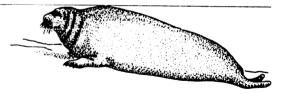
The bearded seal is primarily a bottom feeder and its distribution is somewhat determined by the presence of relatively shallow water. However, the depth to which bearded seals can dive is a subject of some debate. Vibe (1950) gives the maximum depth as 80 m whereas Braham et al. (1977b) list 200 m as the maximum depth. Stirling et al. (1977) found that bearded seals in the Beaufort Sea preferred waters 25 to 75 m deep. The bearded seal is strongly associated with moving pack ice and pan ice where it is widely dispersed (Burns 1970; Burns and Eley 1977). Although bearded seals can maintain breathing holes in fast ice, they rarely do so (Vibe 1950; Burns 1967).

In many areas, bearded seals are quite sedentary and make only local movements in response to ice-conditions (Vibe 1950; McLaren 1962; Fedoseev 1973). In some areas, regular long-distance migrations are undertaken but again these are in response to movements of ice fields (Burns 1967; Benjaminsen 1973; Stirling et al. 1977). There is some evidence for differential distribution and movements of various age groups (Benjaminsen 1973; Potelov 1975a).

STATUS AND SIZE OF POPULATIONS

There is very little information about the numbers of bearded seals in the Canadian Arctic. The species occurs in small numbers in virtually all coastal areas and it is extremely difficult to census. There are many references to bearded seals being more common in one area than in another area but these differences have not been quantified. For example, bearded seals have been reported to be especially common in Jones Sound (Degerbøl and Freuchen 1935), in Ungava Bay (Dunbar 1949), along the west coast of Hudson Bay (Mansfield et al. 1975b), in northern Foxe Basin (Mansfield et al. 1975b).

McLaren (1958b) roughly estimated the numbers of bearded seals in the eastern Arctic by determining the ratio of bearded seals to ringed seals observed during shipboard surveys and applying that ratio to the numbers of ringed seals estimated to occur on the spring fast ice. These estimates of ringed seals were themselves extrapolations (see ringed seal account). The results obtained from southern Baffin Island were then extrapolated to the rest of the eastern Arctic south of Lancaster Sound but including Hudson and Ungava



Bays. The derived population estimate was 186,000 animals. This estimate is extremely crude (McLaren 1958b), but there are no other population estimates for the eastern Canadian Arctic.

Recent aerial surveys in the Canadian Beaufort Sea produced estimates of 2,757 (95% confidence interval: ± 728) bearded seals in 1974 and 1,197 (± 239) bearded seals in 1975 (Stirling et al. 1977). These estimates apply to an area of about 143,000 km² and are not corrected for unseen animals since no such correction factors exist.

The Bering Sea population of bearded seals is thought to be 300,000 to 450,000 (Braham et al. 1977b) and the Sea of Okhotsk population was estimated at 180,000 to 200,000 animals (Fedoseev 1973).

POPULATION STRUCTURE AND DYNAMICS

It has only recently been confirmed that bearded seals can be aged by counting the annual cementum layers on the roots of the upper canine teeth (Benjaminsen 1973). Previous workers used growth ridges on the claws for ageing; this technique gave reliable results only up to nine to 16 years depending on the specimen (McLaren 1958c; Burns 1967).

The only studies of bearded seals in Canada (McLaren 1958c; Stirling et al. 1977) were conducted as sidelines to studies of ringed seals and polar bears; there have been no Canadian studies specifically of bearded seals (Mansfield et al. 1975b).

REPRODUCTIVE BIOLOGY

The mating system of bearded seals is not well known but the males are probably polygamous (Burns 1967). The single young is born on the ice in late April or early May although a few are born in early April and late May (Chapskii 1938; Dunbar 1949; McLaren 1958c; Burns 1970; Potelov 1975b). The lactation period is brief, lasting only 12 to 18 days during which time the young increases in weight from about 34 kg to 85 kg (Burns 1967, 1970). The pup is abandoned by the female at the end of the lactation period (Chapskii 1938). The peak of mating occurs from mid-April to mid-May although

some occurs before and after this period in some areas (Chapskii 1938; McLaren 1958c; Burns 1967), Implantation is delayed for about 2.5 months (McLaren 1958c).

Most females in the eastern Arctic reach sexual maturity (ovulate) at age six years (McLaren 1958c) although a few were mature at five. Burns (1967) found that 60% ovulated at age five years in the Bering Sea and Potelov (1975b) found that 80% of the five year-olds were mature in the Barents, Kara and White Seas. Males reach maturity at six or seven years (McLaren 1958c; Burns 1967; Potelov 1975b).

McLaren (1958c), based on a small sample, thought that mature females gave birth in alternate years in the eastern Arctic. Chapskii (1938) suggested a two-year cycle but did not have enough data to be conclusive. Recent studies suggest that bearded seals are annual breeders. Burns (1967) found an ovulation rate of 0.84 (N = 133) and a pregnancy rate of 0.85 (N = 26) in mature females from the Bering Sea. The pregnancy rate in bearded seals (over nine years old) in the Sea of Okhotsk was 0.84 (N = 19) (Fedoseev 1973). Stirling et al. (1977) suggest that there can be important annual differences in ovulation rates in the Beaufort Sea (1974 — ovulation rate 1.00 — N = 9; 1975 — ovulation rate 0.46 — N = 24).

It is presumed that bearded seals are annual breeders in Canadian waters but McLaren's (1958c) findings remain unexplained. There have been no other studies in the eastern Canadian Arctic. Manning (1974) has shown that bearded seals in the eastern and western Canadian Arctic are distinct subspecies.

AGE AND SEX STRUCTURE

The sex ratio of bearded seals is 1:1 at birth (Burns 1967) and remains the same through adulthood (Chapskii 1938; Burns 1967; Fedoseev 1973).

The age structure of populations has not been determined. This is in part due to the lack of an ageing technique for older animals at the times when the large samples of the earlier studies were collected. Benjaminsen (1973) gives the age distribution for a biased sample of 175 animals from Svalbard (Spitsbergen). The oldest male that he found was 25 years of age and the oldest female was 31. Burns (1967), in a sample of 390, found that 46% were six years old or over; however, he thought that the adult classes were underrepresented in his sample and that adults (six years or more) actually comprised 55 to 60% of the population.

MORTALITY FACTORS

Little is known about mortality of bearded seals apart from hunting, which is discussed later. Chapskii (1938) thought that natural pup mortality was probably high and that polar bears were the primary source of mortality. Some bearded seals were lost to killer whales and parasites. Stirling and Archibald (1977) examined the carcasses of 15 bearded seals killed by bears in the

Beaufort Sea and found that most of these seals were sub-adults. However, more adults were taken in years when the seal population was low.

There has been no quantitative assessment of the rates of predation by polar bears. There is also no information about mortality to bearded seals while they inhabit the shifting pack ice where there may be a significant risk of being crushed or trapped and drowned.

POPULATION DYNAMICS

Knowledge of the dynamics of bearded seal populations is very sketchy. Burns (1967) thought that mature females comprised 27 to 30% of the pre-whelping population. Since the pregnancy rate was 0.80 to 0.85, the annual increment of pups into the population was between 22 and 25% of the Bering Sea population. Fedoseev (1973) estimated that only 19% of the pre-whelping population (Sea of Okhotsk) consisted of pregnant females.

Burns (1967) believed that the pup mortality rate was high but could not quantify it. Fedoseev (1973, 1976) determined mortality in the first year of life to be 0.22 to 0.25.

Fedoseev (1973, 1976) calculated the average annual mortality rate for animals over one year of age to be 0.14. Benjaminsen (1973) found that the average annual mortality of bearded seals over eight years old was also 0.14.

Fedoseev (1973) stated that the annual sustainable kill of bearded seals in the Sea of Okhotsk is less than 5%. McLaren (1958c) suggested that a safe first approximation of maximum sustainable yield in the eastern Canadian Arctic was also 5%. However, this estimate was based primarily on a comparison with his estimate of 8% for ringed seals with intuitive corrections for alternate year breeding and lower mortality rates for bearded seals (McLaren 1962). However, the latter two points have not been proven. Since the estimates of population size in the Canadian Arctic and of percentage sustainable yield are both very imprecise, the actual sustainable yield cannot be estimated.

LIMITING FACTORS

There is too little information about bearded seals to determine the factors that limit the size of unexploited populations. The numbers are thought to be related to the presence of reasonably shallow, productive banks that are free of fast ice in winter (McLaren 1962). However, bearded seals do occupy pack ice over deep waters in some areas during winter.

Male bearded seals are aggressive and often fight (Chapskii 1938; Burns 1967). However, the 'strong evidence of territoriality' (Mansfield et al. 1975b:7) has not been published. The latter authors (p. 7) suggest that 'predation by polar bears appears to be an important factor in controlling the population size in some areas'. There are, as yet, no published quantitative data on this question.

CURRENT HARVEST AND UTILIZATION

ANNUAL HARVEST

Few data are available on the harvest of bearded seals in the Canadian Arctic. The Fur Export Tax Returns do not distinguish between bearded and other seals. In addition, a high proportion of the skins are retained for domestic use and thus are not traded (JBNQNHRC 1976).

Smith and Taylor (1977) summarized the harvest records from R.C.M.P. Game Reports for the period 1962 to 1971. Bearded seals are taken in small numbers in most coastal communities. Settlements that have taken over 100 bearded seals in a single year during the period include Pangnirtung, Frobisher Bay, Lake Harbour, Cape Dorset, Eskimo Point, Igloolik and Sachs Harbour (Smith and Taylor 1977).

Inuit communities along the Quebec coast were estimated to harvest about 1800 bearded seals per year in the mid-1970's (JBNQNHRC 1976). Settlements along Hudson Strait took about 600 of these and communities in Ungava Bay took 675. It is of interest that the current Hudson Strait harvest is about double the sustainable yield estimated by McLaren (1958b).

Information on the harvest levels of bearded seals in the N.W.T. is not being collected at the present time.

HUNTING LOSS

Bearded seals are generally less buoyant than ringed seals and losses through sinking can be high at all seasons (McLaren 1958b; Smith and Taylor 1977). There are few quantitative data. Burns (1967) noted that retrieval of killed bearded seals in Alaska may be as low as 40% in open water hunts. Higgins (1968) in a small sample (four killed) from southern Baffin Island found a loss rate of 25%. Riewe and Amsden (in press) found a loss rate of 70% in a small sample (10) from Jones Sound. Clearly, many more quantitative data are required to evaluate the extent of the hunting loss.

HUNTING TECHNIQUES

Bearded seals are shot when they haul out on the ice, either from boats or from the ice itself. Loss of these animals can be high as they often reach the water before dying. A few inuit in Thule District of Greenland take bearded seals with harpoons at breathing holes (Vibe 1950).

During the open water season there is much hunting from boats. Rifles are used and the loss rate through sinking is high. Since bearded seals usually sink shortly after death, the hunters attempt to wound them so that they can be approached close enough to be harpooned and then dispatched.

The hunting of bearded seals requires considerable skill as demonstrated by the fact that 92% of the harvest in Quebec communities was obtained by older hunters (JBNQNHRC 1976).

UTILIZATION

Adult bearded seals can reach 340 kg weight (Mansfield 1967a) but most of those taken are smaller (e.g., 236 kg for 25 taken in summer in Alaska — Burns 1967).

Most skins are retained for domestic use. Hides are used for making boot soles, dog team traces, whip lashes, straps, harpoon lines, kayaks and umlaks. The carcass provides food for humans and dogs and formerly oil for lamps (Dunbar 1949; Vibe 1950; McLaren 1958c, 1962; Smith and Taylor 1977).

Note added in proof: New data concerning bearded seals off Alaska are contained in Burns, J. J. and K. J. Frost. 1979. The natural history and ecology of the bearded seal, Erignathus barbatus. Final Rept., OCSEAP Contract 02-5-022-53, Alaska Dept. Fish and Game, Fairbanks. 77 p.

CONCEPTS OF SUSTAINABLE YIELD

MAXIMUM SUSTAINABLE YIELD

The basis for the concept of sustainable yield is that, at population sizes below the carrying capacity of the environment, average birth rate normally exceeds average death rate. The 'surplus' of annual births over deaths represents the number of animals that, in theory, can be cropped without reducing the population size. Maximum sustainable yield is attainable at the one particular population size where the surplus is largest.

The sustainable yield from a particular population size can, in theory, be calculated if population size and the birth and natural death rates at that population size are known. As previously shown, these parameters are rarely well defined for populations of arctic marine mammals. Furthermore, when harvesting takes disproportionate numbers of certain age or sex classes, the simple calculation method becomes inapplicable.

The sustainable yield from a given population can also, in theory, be achieved by trial and error - if population size decreases, reduce the harvest; if it increases, increase the harvest. This approach requires a reliable index of population size. Average 'catch per unit effort' over several years would be an appropriate statistic to use, but at present neither catch nor unit effort is accurately recorded for most species. A further complication with the 'trial and error' method is that the harvest is often taken primarily from the older age classes. An adjustment in harvest level will rapidly affect rate of production of young, but there will be a time lag of several years before the adjustment is reflected in rate of recruitment of animals into the older, harvestable population. If only the latter is monitored, the 'iteration time' in the trial and error process must be several years in duration. This severely limits responsiveness to changes in population size, environmental conditions, harvest patterns, utilization, etc. 'Trial and error' management may be adequate when hunting pressure is light and relatively constant, but it is not sufficiently responsive to ensure maintenance of populations when hunting pressure is stronger or more variable, or when environmental or socio-economic conditions are rapidly changing.

Maximum sustainable yield (MSY) is much more difficult to achieve or calculate than is sustainable yield. Trial and error methods are an impractical way to achieve MSY; many decades would be required to evaluate the sustainable yield from various population sizes. Before MSY could be estimated, it would likely change because of changes in environmental or other conditions.

The central problem in calculating MSY is that MSY depends on the functional relationships between the population size (N) and the birth and death rates. Density-dependent rates have proven to be very difficult to determine.

Furthermore, the relationship between MSY, N and the carrying capacity is uncertain. Most models suggest that MSY would be achieved when N is around or slightly above 50% of the carrying capacity (Ricker 1975; Gulland 1977). However, a recent analysis suggests that MSY would occur when N is only slightly less than carrying capacity and well above the 50% level (Eberhardt and Siniff 1977; see also Royce 1975). Even this generalization is difficult to use as a basis for defining MSY, since the size of the unexploited population (which presumably approximates the carrying capacity) is not known accurately for any marine mammal breeding in the Canadian Arctic.

OPTIMUM SUSTAINABLE YIELD

This concept was introduced in the 'Information Required for Management' section. The basic idea is that the concept of MSY is oversimplified because it considers one species in isolation, and because it fails to take into account indirect effects on other species and the investment of resources necessary for the harvest. An optimum sustained population, and the associated optimal sustainable yield, would represent the levels 'at which the species contributes most to the well being of the ecosystem' (Eberhardt and Siniff 1977).

Interactions among species are a major reason why the MSY concept is an undesirable oversimplification in the case of arctic marine mammals. As discussed in the ringed seal account, the effects of a change in population size and harvest can only be anticipated if the responses of competitors and predators (which may also be significant to man) are taken into account.

A further limitation of the MSY concept that should be considered in defining an optimum sustainable yield is that no specific allowance is made for a safety factor. As Holt and Talbot (1978) point out, knowledge is limited and management processes — even if based on reliable data — are imperfect. Thus, a conservative policy should be adopted to ensure that options are maintained and the risk of irreversible change or long-term adverse effects is minimized.

The year-to-year variability of arctic conditions and of population responses thereto is an important factor in management. Existing data for some of the betterstudied species show that birth and mortality rates can vary, probably dramatically, from year to year (see Stirling et al. 1977). Thus, recruitment rates must be variable, and the size and age structure of the population must be uneven and variable over time, even in the absence of a harvest. As a result, sustainable harvest will vary, perhaps dramatically, from year to year. In the absence of anything more than the present vague knowledge of this variability, a conservative management strategy would clearly be prudent. The optimal sustainable yield of each species would, in these terms, be achieved at a population size somewhere between the MSY level and the carrying capacity.

SUMMARY OF GAPS IN MANAGEMENT INFORMATION

In order to actively manage a species or population to permit sustainable harvests, it is necessary to know the size of the population and the sustainable yield (either present, maximum or optimum) of that population. The numbers of individuals available for harvest can then be determined. The foregoing is a simplification. In practical terms several types of information are required. These include

- Distribution It is necessary to know the summer and winter range of the species and the routes used during seasonal movements. A migratory species may be hunted in different areas and may be subject to different natural and man-induced stresses in different parts of its range. In migratory species the sustainable yield must be apportioned among the various harvesting areas.
- 2. Status and Size of Populations Many species contain more or less semi-isolated populations or stocks. It is important to know whether a stock is isolated and receives little or no recruitment from neighbouring stocks (e.g., belugas in Cumberland Sound) or whether the sub-population is not isolated and is replenished with surplus individuals from adjacent areas (e.g., ringed seals in Cumberland Sound). The numbers and boundaries of stocks are determined by a complex of environmental factors and vary from species to species. Management should be based on the concept of stocks and the number of animals in each stock should be accurately determined.
- Population Structure and Dynamics Several biological properties of a species combine to determine the productivity and mortality rates and hence the potential yield for that species. This complex of properties combined with the size of stock and immigration and emigration rates for the stock determine the allowable harvest levels. Many of the inherent biological properties of the population can change in response to harvesting and as part of density-dependent population regulation mechanisms. These changes can, in turn, cause changes in the levels of allowable harvest. Ideally, the population dynamics of the populations should be well understood; in practice, such understanding is extremely difficult to obtain.
- 4. Kill Statistics Rational management requires that accurate data on the numbers of animals killed during the hunt be known. The kill includes the number harvested, the number killed and not retrieved, and the number that are wounded and die after the hunt. Kill statistics should include information on the age and sex of the animals killed since concentration on certain ages or sexes can change the dynamics and potential yields of the species. In addition, if the kill statistics include information on the catch per

unit effort then information on changes in the status or distribution of the population can be derived.

The amount and quality of the information required for management were reviewed in some detail in the preceding species accounts. In the remainder of the present section, we summarize the major gaps in the management information for each of the important species of marine mammals. Not all of the gaps are of equal importance for practical management of the various species of arctic marine mammals. Furthermore, certain data gaps can be filled in either of two ways, and the second type of information is not essential (although useful for corroboration) if the first type has been obtained. However, if future management is to become predictive, then most of the following gaps should be filled.

BELUGA (WHITE WHALE)

DISTRIBUTION

Knowledge of the summer distribution of belugas is quite good although more information is required for eastern Hudson Bay, Hudson Strait, Ungava Bay and Foxe Basin. The migration routes and main wintering areas for the Lancaster Sound population are unknown. It is not known if more than a small proportion of the Hudson Bay population actually winters in the bay. Similarly, the wintering areas of Cumberland Sound and Ungava Bay populations are only generally known.

STATUS AND SIZE OF POPULATIONS

Estimates of the beluga populations in the Beaufort Sea, Lancaster Sound and Cumberland Sound are believed to be quite accurate although the numbers of animals in Jones and Smith Sounds and their relationship to the Lancaster Sound animals are poorly understood.

Sergeant and Brodle (1975) estimated that there were 10,000 belugas in Hudson Bay and 1,000 in Ungava Bay and Hudson Strait. The relationships between these two groups, and among these groups and those in Foxe Basin and eastern Hudson Bay, are unknown. The current estimates cannot be correct since the Quebec communities along Hudson Strait and Ungava Bay currently take about 450 belugas, or 45% of the estimated population, annually. Clearly, either the Hudson Strait population is larger than estimated, or many of the belugas from Hudson Bay migrate through Hudson Strait, or both. Knowledge of stock discreteness, numbers and movements of belugas in Hudson Bay, Foxe Basin and Hudson Strait is incomplete.

POPULATION STRUCTURE AND DYNAMICS

The age of belugas is determined by counting dentinal layers of the teeth and by assuming that two layers correspond to one year of age. This assumption has not been proven and is currently the subject of debate. Until an ageing technique has been verified, information on population dynamics must be treated with great caution. All age-related properties of the population (e.g., age at first breeding, age-specific mortality, reproductive longevity) are suspect.

If the ageing technique is verified then the available data are very useful. However, larger sample sizes are needed to refine some estimates such as birth rate and reproductive longevity. There are no adequate estimates of sex-specific and age-specific mortality rates, particularly calf mortality.

The assumption that males are polygamous needs to be verified since some hunts concentrate on large males and may bias the sex ratio towards females. This bias will not necessarily decrease productivity if males are polygamous and breed more than one female. However, it has been suggested that disruption of dominance patterns involving supremacy of one or a few males could cause reductions in reproductive rates and survival (Holt and Talbot 1978).

The rate of recruitment of calves into the total population has been estimated at 0.09 to 0.12. However, in the absence of unbiased information about age-specific natural mortality rates these estimates cannot be translated into estimates of sustainable yield of adults and large immatures. The density-dependence of the population parameters has not been studied.

KILL STATISTICS

Harvest statistics have been inadequate and may have underestimated the total harvest in the Canadian Arctic (including Quebec and Manitoba) by half. In addition, the harvest data exclude animals lost by sinking. The loss rate in some areas can exceed 50% of the belugas killed but is much lower in other areas. Estimates of loss rate need to be determined for various areas and hunting techniques. Recent harvest statistics are thought to be improved but their reliability should be verified.

An estimated 500 to 1,000 belugas are harvested annually in west Greenland but it is not known what proportion of these animals are from populations that also frequent Canadian waters.

NARWHAL

DISTRIBUTION AND NUMBERS

There is no information on the numbers and movements of narwhals that frequent northern Hudson Bay and Foxe Basin. The current estimate of the number of narwhals in the eastern high Arctic is 20,000 to 30,000 animals. This estimate is unacceptably vague and needs to be verified. The summer distribution of this population is only partly known and the migration routes and wintering areas have only been surmised on the basis of a few records.

POPULATION STRUCTURE AND DYNAMICS

No satisfactory technique for ageing narwhals has been found. The basic biology and population dynamics of narwhals have been assumed to be similar to belugas. In view of the incompleteness of the information about belugas and the lack of evidence about potentially important interspecific differences, it is prudent to consider that the potential sustainable yield of narwhal populations is unknown.

There is no information about the carrying capacity of arctic marine waters for narwhals or natural limiting factors that would place upper limits on narwhal population size.

KILL STATISTICS

Recent harvest statistics are thought to be fairly reliable and the recent imposition of a quota system may further improve the reliability. However, periodic evaluations of the data collection systems should be performed. Assessments of harvest levels for Canadian narwhal populations must include the proportion of the Greenland kill that comes from Canadian populations. Such information is not available.

The loss rates (due to sinking) of narwhals killed during some hunts can be exceedingly high. Loss rates for various types of hunts need to be quantified so that the harvest statistics can be adjusted to reflect the actual kill. Information on the proportion of the harvest taken by each type of hunt is not gathered but would be useful for refinement of kill estimates.

Current harvests are concentrated in a few restricted areas. It is not known whether the age and sex structure of animals killed in these areas are typical of the whole population or if certain age or sex classes are being inadvertently overharvested. It is thought that the hunters select adult males because of their tusks but it is not known how effective this selection is.

BOWHEAD WHALE

DISTRIBUTION AND NUMBERS

The historic range and movements of bowheads are known in a very general sense but there is no information on the current population level in any part of the Canadian Arctic. The populations have been assumed to be recovering froin the severe overexploitation by the commercial whalers but this assumption has not been proved. The international Whaling Commission considers this species to be endangered. In view of the likelihood of increased pressure on the Minister of Fisheries to issue permits for the kill of bowheads by natives, the lack of any systematic data on current bowhead numbers is very unfortunate because it makes rational decisions about issuance of permits impossible.

POPULATION DYNAMICS

There is no information about the population dynamics of bowheads and no estimates of sustainable yield can be made. The possibility that the bowhead population is distributed too sparsely to permit the excess of births over deaths normally expected in a depleted population should be considered.

WALRUS

DISTRIBUTION AND NUMBERS

The general range of the walrus is well known but there are major gaps in knowledge of the limits of local populations and interchange among these stocks. There are quantitative estimates from only two restricted areas in the eastern Arctic and one of these estimates (from northwest Hudson Bay) is undoubtedly low. The current status of the Baffin Bay population (formerly very large) is unknown and there are no estimates of the size of the Foxe Basin population, which is believed to be large. The size and movements of the Hudson Strait group are poorly known and the relationships of this group to populations in Foxe Basin and Hudson Bay are not understood.

POPULATION STRUCTURE AND DYNAMICS

Knowledge of the reproductive biology of the wairus in the eastern Arctic is based on small samples. Larger samples of the Pacific wairus show some differences from the eastern Arctic samples. The birth rate was 0.43 in Alaska versus 0.35 in the Canadian Arctic. It is not known whether this difference of 23% is real or is a function of the small sample size (N = 17) from the eastern Arctic. Natural mortality rates are unknown and no age-specific mortality rates have been calculated for eastern Arctic wairuses. Estimates of the annual increment of calves into the wairus population are

11% for the eastern Arctic versus 14% for Alaska; again this difference may be a sampling artifact. The lack of age-specific and sex-specific mortality estimates, particularly for calves and sub-adults, makes it impossible to calculate accurate estimates of sustainable yield. The density-dependence of the population parameters is not known.

The numbers and distribution of walruses are probably ultimately limited by the availability of productive feeding areas in shallow water (less than 80 m). However, there are very few quantitative data on the standing crops of the bottom-dwelling food organisms and there are no data on the productivity of these organisms in the Canadian Arctic. Thus, carrying capacity of these areas cannot be determined.

KILL STATISTICS

Harvest statistics are not considered reliable although recent estimates may be more accurate. The loss rate for killed walruses is variable but can be high. There are few quantitative data on losses. Typical loss rates for various kinds of hunts need to be determined so that reported harvest statistics can be adjusted to reflect the actual kill. Management of the Baffin Bay 'stock' should reflect the kill of these animals in Greenland.

HARBOUR SEAL

The harbour seal has a localized distribution in the eastern Arctic. It was formerly moderately common in certain areas but there are no quantitative estimates of its current or former status. Small numbers are harvested but it is not known whether populations are currently over or under harvested. The species has apparently been eliminated from some localities. There have been no studies of the biology of this species in the Canadian Arctic.

HARP SEAL

DISTRIBUTION AND NUMBERS

The numbers of harp seals that enter Canadian Arctic waters each summer are not known and observed annual variations (e.g., 150,000 vs 16,000 observed entering Lancaster Sound) are unexplained. The distribution of harp seals in the Canadian Arctic is known in only a general sense and the numbers present in most areas are unknown

POPULATION STRUCTURE AND DYNAMICS

The population dynamics of harp seals have been the subject of intensive studies due to the commercial seal fishery off eastern Canada. The critical management decisions are currently made in conjunction with this fishery. The kill of harp seals in the Arctic is comparatively small but is not well documented. Accurate information on arctic harvest levels is needed for the management models being used.

Significant increases in the kill of harp seals in the Arctic will have implications for the hunt off eastern Canada and would require re-allocation of harvest quotas. The age structure of the harp seal kill in the Arctic is not adequately known, but differs from that off eastern Canada. This information is needed to determine the effects of increasing the arctic kill.

Of the marine mammal species considered here, the harp seal is the only one for which some information about the density dependence of certain population parameters is available.

KILL STATISTICS

The magnitude and age structure of the current harvest of harp seals in the Arctic arc not well documented. The Fur Export Tax Returns underestimate the harvest but it is not known by how much.

More information on non-retrieval of harp seals is required. Since sinking loss rates decrease progressively during the summer and autumn hunt period, information on the seasonal distribution of the kill is required.

HOODED SEAL

Although large numbers of hooded seals use Canadian arctic waters, most remain offshore in the pack ice where they are inaccessible to coastal harvesting. Few are taken by Inuit and few are likely to be taken in future without large sealing vessels.

RINGED SEAL

The ringed seal is the most abundant marine mammal in the Canadian Arctic and in some respects it is the easiest species to study. The available data about ringed seals are superior in quantity and hence quality to the data available for any other marine mammal in the Arctic. However, there are difficulties in determining sustainable yield levels. In addition, the long-term studies of ringed seals and their chief predators (polar bears and arctic foxes) are raising important questions that are central to the management of arctic marine mammals but have previously been unrecognized. These questions involve the high annual variability in arctic marine ecosystems and the close ecological interrelationships among at least some species of mammals and, by implication, the Inuit as predators.

DISTRIBUTION

The distribution of ringed seals is well known although long distance and local migrations have not been well documented. The degree to which areas of offshore pack ice are used by breeding seals is poorly understood but given the large areas involved, the numbers could be significant.

STATUS AND SIZE OF POPULATIONS

There is thought to be reasonably free interchange among ringed seal populations in adjacent areas although sedentary adult sub-populations may exist. There is evidence that local populations can be overharvested and Bradley (1970) has suggested that intense hunting can cause ringed seals to alter their behaviour and distribution in some areas. This has not been conclusively demonstrated but has implications for the derivation of harvest strategies.

Ringed seals can be relatively easily counted during spring when they haul out on fast ice. Almost all population estimates are based on the results of aerial surveys. Most such estimates are based on inadequate design, inadequate analyses of survey biases and questionable correction factors for unseen animals. There is a pressing need for development and standardization of survey techniques and for biological research to determine appropriate correction factors.

POPULATION STRUCTURE AND DYNAMICS

The basic reproductive biology and dynamics of ringed seal populations are quite well known. However, the difficulty of obtaining unbiased age samples has prevented determination of mortality rates of pups and young immatures. Estimates of maximum sustainable yield are still imprecise and are based on inadequate census techniques and little information about density-dependent processes. One current estimate has 95% confidence limits of more than ±30%.

In theory, knowledge of the characteristics of fast-ice cover and of the factors that control seal numbers on fast ice can be combined to predict maximum populations that can exist in an area. More information is required to develop a reliable prediction system.

The large scale year-to-year variability in numbers, distribution and productivity of ringed seals in the Beaufort Sea makes it essential that variability be examined by long-term studies in other parts of the Arctic.

KILL STATISTICS

Current harvest statistics underestimate, by an unknown amount, the number of ringed seals harvested. This underestimation can be quite severe in certain situations and should be quantified. More data on seasonal variations in sinking loss are also required in order to refine the correction factors to be applied to reported harvest.

BEARDED SEAL

Although this large seal is quite common and widespread, and is utilized by Inuit, it has not been specifically studied in Canada.

DISTRIBUTION AND NUMBERS

The general range of the bearded seal is well known but reliable estimates of abundance are lacking for virtually all areas. Movements of bearded seals are poorly understood in most areas.

POPULATION STRUCTURE AND DYNAMICS

Most information on bearded seals comes from Alaskan and Soviet populations and it is not known whether eastern Arctic populations are similar. For example, the bearded seal is an annual breeder in Alaska but the results from a small sample in the eastern Arctic suggest a two-year breeding cycle. This question needs to be examined in more detail. The general lack of data from Canadian populations makes it impossible to determine current, maximum or optimum sustainable yield levels.

KILL STATISTICS

There is no information on the current harvest levels of bearded seals. Estimates of the percentage nonretrieval of killed animals are inadequate.

CONCLUSIONS AND RECOMMENDATIONS

The basic conclusion of this report is that with current levels of information it is not possible to determine the maximum or optimum sustainable yield of any species of marine mammal in the Canadian Arctic. The 'ad hoc' management policies used to date have been reasonably useful in the recent past, which has been a period of generally declining harvests. However, demographic trends Indicate that the current growth (about a 20-year doubling time) in inuit populations will continue.

The Inuit have clearly stated their desire to retain close ties with the land and to maintain a viable marine mammal harvesting component in their way of life. It seems clear that some populations of marine mammals can support increased harvests resulting from increases in the numbers of hunters. However, it is also clear that sustainable harvest levels may be less than the future demand by inuit. It is not currently possible to calculate the potential sustainable yields of marine mammals in the Canadian Arctic. Nevertheless, these data are necessary for management of the marine mammal resources and to permit rational judgements about the future of the resource harvesting component in Inuit society.

CURRENT MANAGEMENT

Little management-oriented research is now being conducted on marine mammals (other than polar bears) in the Canadian Arctic. The near-term future of management research appears bleak due to major reorganization and budget reductions within the federal Department of Fisheries and Environment, Internal government committees have recommended that the Arctic Biological Station, which has responsibility for management research on arctic marine mammals, be closed. It is not clear whether the research function will be transferred to Fisheries and Marine Service in Winnipeg where administrative responsibility for management currently resides. Regardless of organizational changes and upheavals, it is clear that a major change in governmental priorities will be necessary to allow for adequately funded, longer-term research necessary to manage arctic marine mammals.

ROLE OF INUIT

Effective management of marine mammals requires that the users (Inuit) of the resource be fully informed and agree with the goals of management programs. Management is further complicated by Inuit land claims negotiations and Inuit desires to assume certain responsibilities in the management of marine mammals. In our experience, many Inuit are skeptical of government scientists and there is strong opposition to the recently enacted quotas on the harvest of narwhals and walruses. The recently established Northwest Territories Game Advisory Council is designed, in part, to allow interchange between the game managers and the Inuit. It is perhaps too early to determine whether the council will achieve its objectives.

Management must be a cooperative effort and the Inuit should have an effective voice in the decision-making process. Concurrently, some inuit should receive training in wildlife biology. Small-scale programs currently exist, but these provide training only at the technical level. University level training is also needed although the full slate of courses taught at southern universities is probably unnecessary.

MANAGEMENT PRIORITIES

The following sections discuss general priorities for marine mammal research. Details of studies of particular species or problems are not outlined as they are beyond the scope of this report.

RELIABLE HARVEST DATA

Management of hunted animal populations requires that accurate kill statistics be available. Many workers have commented on the inadequacies in the kill statistics that have been gathered. The collection system has apparently improved but its accuracy has not been tested. The system needs to be refined and additional data collected from at least some communities. Information on the geographic and seasonal distribution of the kill and on the sex and age structure of the kill can provide important insights into the distribution and health of the hunted population. Seasonal data are needed to assess hunting losses and, in some cases, the part of the population that is hunted.

A joint program by Fisheries and Marine Service, Canadian Wildlife Service and the Northwest Territories Government is planned to gather some but not all of the required information. The future of this program (in the planning stages since autumn 1977) is uncertain. The Baffin Region Inuit Association has plans for resource harvesting studies in each of the Baffin Island communities but again not all of the information required would be gathered. An industry-funded re-

source harvest study currently being conducted in Pond Inlet and planned to be expanded to Grise Fiord and Clyde River will provide a fuller complement of useful management data. The key to success of any of these projects is the involvement and support of the Inuit hunters. This type of program can provide invaluable data for ongoing management research programs (discussed later).

HUNTING LOSS

A critical component of any management strategy is knowledge of the numbers of animals that are killed but not retrieved. These losses can be significant (see preceding sections of this report). Studies to accurately determine loss rates and the factors affecting these rates are required. Experiments to test methods to reduce the loss rate should be conducted. Better hunting techniques could significantly increase harvests without increasing the kill or the stress on the population.

IMMEDIATE MANAGEMENT PROBLEMS

It is with great trepidation that we discuss problems of immediate concern. The available knowledge of arctic marine mammals is insufficient to identify all of the species or populations that are being overharvested. Overharvesting is almost certainly occurring in several situations that are presently unrecognized. Thus, the following discussion of immediate management problems includes only those that are recognized. There are undoubtedly others! Absence from this discussion should not be construed to imply that a particular population is not being overharvested.

The apparently isolated beluga population in Cumberland Sound shows signs of severe overharvesting. Surveys in 1978 indicate a decline in numbers of over 30% in the past two years to a total of about 500 animals (B. Kemper personal communication). The decline was presumably related to the extremely high kill in 1977.

The status of the belugas inhabiting Hudson Strait. Ungava Bay and northeastern Hudson Bay is a matter of concern. Sergeant and Brodie (1975) estimated this population at 1,000 animals. However, the annual kill of these animals is 600 (JBNQNHRC 1976). The harvest data are thought to be reliable; thus, the population estimate must be wrong. It seems likely that belugas from western Hudson Bay are using Hudson Strait during migration. Even so, the total annual kill (including a guess at hunting loss) for all of Hudson Bay, Hudson Strait and Ungava Bay is greater than the published estimates of sustainable yield (maximum 10%) for this population. In addition, the estimates of sustainable yield are thought to be unrealistically high. A further concern is that the major hydroelectric projects in Manitoba and Quebec will probably affect coastal habitat used by belugas. No studies of this potential impact are being conducted.

The status of the Lancaster Sound narwhal population is unclear. Recent estimates of 20,000 to 30,000 ani-

mals are based on extrapolations and need to be verified. The retrieval rate of narwhals killed at Pond Inlet and Arctic Bay is not fully known but recent studies at the Pond Inlet ice edge indicate that only about 30% of the narwhals killed are actually retrieved (LGL Ltd. unpublished data). Thus, the existing quotas of 100 for each settlement could lead to the killing of over 600 narwhals. If the animals killed at other high Arctic settlements and in Greenland are taken from this population, then overharvesting may be occurring. Also, the harvests are concentrated in a few areas; if subpopulations occur, some of these could be under severe pressure. Clearly, better knowledge of the Lancaster Sound narwhal population is urgently required.

Concern has been expressed about the status of walrus populations in western Foxe Basin. However, so little is known about this population that it is impossible to assess its present condition.

FUTURE MANAGEMENT PRIORITIES

Basic management research programs should be instituted immediately. Harvest levels will increase as Inuit populations increase. This will lead to very heavy hunting pressure around communities and will undoubtedly lead to local depletion of mammal populations. Inuit hunters would then have to travel farther at greater cost. This could be a serious hardship for those Inuit trying to fashion a way of life that combines partial wage employment with resource harvesting. The current government program to support the establishment of outpost camps will tend to disperse the hunting pressure away from the major communities. However, it is not known how popular the outposts will be.

Sound marine mammal management including knowledge of sustainable yields is clearly necessary to allow rational decisions about the size and distribution of harvest that can be sustained at each settlement or outpost camp. The degree of isolation of heavily exploited populations from less exploited populations is of special importance. Such predictive management information is not currently available.

The principal gaps in required information for each species were discussed in detail in preceding sections of this report. We discuss here those species that will most likely be subject to increased harvest levels in the near future. These are the species on which management research is required immediately.

The ringed seal is the most important species harvested by Inuit. Hunters in many communities (e.g., Pond Inlet and Igloolik) have already noted that they must travel farther from the communities to hunt ringed seals. This is an indication of local overharvesting. Pressure on ringed seal populations will increase.

Bearded seals are taken whenever they are encountered and are important to the inuit. Very little is known about the biology of this species. Population sizes and sustainable yields are unknown. It is probable, however, that demand for the species will increase.

Demand for wairuses has declined recently with the demise of dog teams. However, there are signs that the kill is now increasing because of high prices paid for wairus ivory. Many animals are now being taken solely for their ivory with no or little use made of the rest of the carcass. The demand is likely to further increase and will place pressure on wairus populations, at least in local areas.

Similarly, the value of narwhal tusks has caused an increased demand for these animals. The current quota system is extremely unpopular with the Inuit and pressure for increased harvests will be intense. Problems associated with narwhal management were discussed previously.

Some populations of belugas are already being overharvested and pressure on others will increase as inuit populations increase. Current knowledge is not sufficient for safe management of beluga stocks.

The five species of marine mammals discussed above should receive top priority in any program of management research. This research is by necessity a long-term proposition, especially in the Arctic where major year-to-year fluctuations in reproduction and, to a lesser degree, population levels can be caused by natural environmental conditions. These studies should begin soon. Without this information, major problems and declines seem almost inevitable in the not too distant future. These problems will be most pronounced in certain local areas, but population-wide problems can be anticipated.

Two other species deserve comment here. The endangered bowhead whale is extremely poorly known in the Canadian Arctic. There is virtually no useful information on the status of this species in the eastern Arctic. The prudent course is to allow no exploitation of the bowhead. However, there will probably be requests by Inuit to take bowheads. If these requests are to be seriously entertained then more work on bowhead populations should be undertaken.

The kill of harp seals in the Canadian Arctic appears to be underestimated in models used to establish quotas for commercial exploitation off eastern Canada. If the kill by Inuit increases substantially, corresponding changes in the commercial quotas off eastern Canada will be necessary.

IMPACT ASSESSMENT vs MANAGEMENT OF POPULATIONS

In recent years, a number of major industrial activities have been planned for the Canadian Arctic. Many of these have direct implications for marine mammal populations. These projects have generated many impact-related studies funded by government and industry. Some of these studies have provided information useful for management. However, it seems to us that government responses to industrial proposals have been largely at the expense of management research. Manpower and funds have been diverted to impact of the control of

pact assessment, and management research is often only possible if it is disguised as an impact-related study. This has led to some studies that are not adequate for either management or impact-related purposes.

Basic biological knowledge is necessary for both management and impact assessment purposes. However, such knowledge cannot be gained if investigators must relocate their study areas in response to each new industrial project. Several years are required for a thorough study of any population. Appropriate information cannot be gained by studying a different population every year or two. Impact assessment research is very important but reliable impact predictions and mitigation measures are only possible if good biological information is available. In many cases government impact studies have duplicated industry-funded studies and provided very little new or additional information.

In the long term, the major identifiable threat to marine mammal populations in the Canadian Arctic will probably be the increased hunting pressure by Inuit. In many ways, this will also be the most difficult problem to deal with. A sound knowledge of the population dynamics of each major species of marine mammal is a prerequisite for rational decision-making and problem avoidance. This knowledge can only be attained through sustained, long-term management-oriented research. We believe that it is imperative that this type of management research be conducted. Impact assessment studies of industrial projects should be conducted in addition to basic management research, not instead of it.

The following general comment by Krebs (1972:361) is particularly appropriate to the management of marine mammals in the Canadian Arctic:

"Management of forest, fishery, and wildlife resources is presently based more on rules of thumb and empirical results than on scientific knowledge and forecasting, and one of the great challenges of modern ecology is to place resource management on a scientific basis. We can all be very good at managing yesterday's populations. When will we be equally adept at managing tomorrow's?"

LITERATURE CITED

- Abrahamson, G. 1968. Tuktoyaktuk Cape Parry: an area economic survey. A.E.S.R. 62/2. Dept. Indian Affairs and Northern Development, Industrial Division, Ottawa. 83 p.
- Alexander, V., R. Horner and R. C. Clasby. 1974. Metabolism of arctic sea ice organisms. Institute of Marine Science, University of Alaska, Fairbanks. IMS Report R74-4. 120 p.
- Allen, K. R. and D. G. Chapman. 1977. Whales. *In:* J. A. Gulland (ed.). Fish Population Dynamics. John Wiley & Sons, London, p 335-358.
- Allen, M. B. 1971. High-latitude phytoplankton. Ann. Rev. Ecology and Systematics 2: 261-276.
- Allen, R. L. 1975. A life table for harp seals in the northwest Atlantic. Rapp. P.-V. Reun, Cons. Int. Explor. Mer 169: 303-311.
- Anders, G. 1965. Northern Foxe Basin: An area economic survey. Dept. Indian Affairs and Northern Development, Ottawa, 139 p.
- Anders, G., A. Haller, D. Foote and P. Cove. 1967. The east coast of Baffin Island: an area economic survey. A.E.S.R. 66/4. Dept. Indian Affairs and Northern Development, Ottawa, 196 p.
- Anderson, R. M. 1934. Mammals of the Eastern Arctic and Hudson Bay. In: W. C. Bethune (ed.). Canada's Eastern Arctic. Its history, resources, population and administration. Dept. of Interior, Ottawa. pp. 67-108.
- Andrews, J. T. 1972. Recent and fossil growth rates of marine bivalves, Canadian Arctic, and Late-Quaternary Arctic marine environments. *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology* 11: 157-176.
- Andriyashev, A. P. 1954. Fishes of the northern seas of the U.S.S.R. Smithsonian Institution and the National Science Foundation, Washington, D.C. 617 p. (Translated from Russian by the Israel Program for Scientific Translations.)
- Anraku, M. and M. Omori. 1963. Preliminary survey of the relationships between the feeding habit and the structure of the mouth parts of marine copepods. Limnol. Oceanogr. 8: 116-126.
- Apollonio, S. 1961. The chlorophyll content of arctic sea-ice. Arctic 14: 197-200.
- Apollonio, S. 1965. Chlorophyll in arctic sea ice. Arctic 18: 118-122.
- Apollonio, S. 1973. Glaciers and nutrients in Arctic seas. Science 180: 491-493.
- Apollonio, S. 1976a. Primary production in coastal waters of the Arctic Ocean. Bigelow Laboratory, Contrib. No. 76008 (Unpubl. MS). 48 p.
- Apollonio, S. 1976b. Primary production in the Canadian arctic archipelago, 1961-1963. Bigelow Laboratory, Contrib. No. 76016 (Unpubl. MS), 88 p.

- Bain, H. and A. D. Sekerak. 1978. Aspects of the biology of Arctic cod, *Boreogadus saida*, in the central Canadian Arctic. Unpubl. Rept. by LGL Ltd. for Polar Gas Project. 104 p.
- Bain, H., D. Thomson, M. Foy and W. Griffiths. 1977.
 Marine ecology of fast-ice-edges in Wellington
 Channel and Resolute Passage, N.W.T. Unpubl.
 Rept. by LGL Ltd. for Polar Gas Project. 262 p.
- Banfield, A. W. F. 1974. The Mammals of Canada. University of Toronto Press, Toronto. 438 p.
- Barnard, J. L. 1959. Epipelagic and under-ice amphipods of the central Arctic Basin. In: Scientific Studies at Fletcher's Ice Island, T-3, 1952-1955. Vol. 1: 115-152.
- Beaubier, P. H., M. J. Bradley and J. G. Vestey. 1970. Human Ecological Studies — Igloolik, N.W.T. Final Rept. submitted to I.B.P. Human Adaptability Project. McGill Dept. of Geography, Montreal. 180 p.
- Beck, B., T. G. Smith and A. W. Mansfield. 1970. Occurrence of the Harbour Seal, *Phoca vitulina*, Linnaeus in the Thlewiaza River, N.W.T. Can. Field-Nat. 84: 297-300.
- Benjaminsen, T. 1973. Age determination and the growth and age distribution from cementum growth layers of bearded seals at Svalbard. FiskDir. Skr. Ser. HavUnders. 16: 159-170.
- Berger, T. R. 1977. Northern Frontier, Northern Homeland. The report of the Mackenzie Valley pipeline inquiry. Vol. 2. Terms and Conditions. Ministry of Supply and Services Canada, Ottawa. 268 p.
- Best, R. C. and H. D. Fisher. 1974. Seasonal breeding of the narwhal (Monodon monoceros L.). Can. J. Zool. 52: 429-431.
- Bigg, M. A. 1969. The harbour seal in British Columbia. Bull. Fish. Res. Board Can. 172, 33 p.
- Bigg, M. A. and H. D. Fisher. 1974. The reproductive cycle of the female harbour seal off southeastern Vancouver Island. *In:* R. J. Harrison (ed.), Functional anatomy of marine mammals. Vol. 2. Academic Press, pp. 329-347.
- Bissett, D. 1967a. Resolute. An area economic survey. A.E.S.R. 67/1. Dept. Indian Affairs and Northern Development, Ottawa. 175 p.
- Bissett, D. 1967b. Northern Baffin Island: An area economic survey. Vol. 2. A.E.S.R. 67/1. Dept. Indian Affairs and Northern Development, Ottawa. 131 p.
- Blacker, R. W. (ed.). 1968. Symposium on the ecology of pelagic fish species in arctic waters and adjacent seas. Rapp. P.-V. Réun. Cons. Perm. Int. Explor. Mer 158.
- Bohn, A. and R. O. McElroy. 1976. Trace metals (As, Cd, Cu, Fe, and Zn) in Arctic cod, *Boreogadus salda*, and selected zooplankton from Strathcona Sound,

- northern Baffin Island. J. Fish, Res. Board Can. 33: 2836-2840.
- Boulva, J. 1975. Temporal variations in birth period and characteristics of newborn harbour seals. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 169: 405-408.
- Bradley, M. 1970. Ringed seal avoidance behaviour in response to Eskimo hunting in northern Foxe Basin. Unpubl. Master's Thesis, Dept. Geography, McGill Univ., Montreal. 113 p.
- Bradstreet, M. S. W. 1976. Summer feeding ecology of seabirds in eastern Lancaster Sound, 1976. Unpubl. Rept. by LGL Ltd. for Norlands Petroleums Ltd. 187 p.
- Bradstreet, M. S. W. 1977. Feeding ecology of seabirds along fast-ice edges in Wellington Channel and Resolute Passage, N.W.T. Unpubl. Rept. by LGL Ltd. for Polar Gas Project. 149 p.
- Bradstreet, M. S. W. and K. J. Finley. 1977. Distribution of birds and marine mammals along fast-ice edges in Barrow Strait, N.W.T. Unpubl. Rept. by LGL Ltd. for Polar Gas Project. 315 p.
- Braham, H., B. Krogman and C. Fiscus. 1977a. Bowhead (Balaena mysticetus) and beluga (Delphinapterus leucas) whales in the Bering, Chukchi and Beaufort Seas. Environmental Assessment of the Alaskan Continental Shelf, Vol. I: 134-160. N.O.A.A., U.S. Dept. Commerce, Boulder, Colorado.
- Braham, H.W., C. H. Fiscus and D. J. Rugh. 1977b. Marine mammals of the Bering and southern Chukchi seas. Environmental Assessment of the Alaskan Continental Shelf, Vol. I: 1-99. N.O.A.A., U.S. Dept. Commerce, Boulder, Colorado.
- Brakel, W. D. 1977. Socio-economic importance of marine wildlife utilization. Beaufort Sea Project, Tech. Rept. 32: Environment Canada, Victoria.
- Brodie, P. F. 1969. Mandibular layering in *Delphinapterus leucas* and age determination. Nature 221: 956-958.
- Brodie, P. F. 1971. A reconsideration of aspects of growth, reproduction, and behavior of the White Whale (*Delphinapterus leucas*), with reference to the Cumberland Sound, Baffin Island, population. J. Fish. Res. Board Can. 28: 1309-1318.
- Brooks, J. W. 1954. A contribution to the life history and ecology of the Pacific Walrus. Spec. Report No. 1, Alaska Coop. Wildl. Res. Unit. 103 p.
- Brown, R. 1868. Notes on the history and geographical relations of the Cetacea frequenting Davis Strait and Baffin's Bay. Proc. Zool. Soc. London 1868: 533-556.
- Buchanan, R. A., W. E. Cross and D. H. Thomson. 1977. Survey of the marine environment of Bridport Inlet, Melville Island. Unpubl. Rept. by LGL Ltd. for Petro-Canada. 265 p.

- Buckley, J. L. 1958. The Pacific Walrus a review of current knowledge and suggested management needs. U.S. Fish and Wildl. Serv., Spec. Sci. Rept. — Wildl. No. 41. 29 p.
- Buckley, J. R., T. Gammelsrød, J. A. Johannessen, O. M. Johannessen and L. P. Røed. 1979. Upwelling: oceanic structure at the edge of the arctic ice pack in winter. Science 203(4976): 165-167.
- Burns, J. J. 1965. The walrus in Alaska its ecology and management. Fed. Aid in Wildl. Restoration Project W-6-R-5. Alaska Dept. Fish and Game, Juneau. 48 p.
- Burns, J. J. 1967. The Pacific bearded seal. Fed. Aid in Wildl. Restoration Projects W-6-R and W-14-R. Alaska Dept. Fish and Game, Juneau. 66 p.
- Burns, J. J. 1970. Remarks on the distribution and natural history of pagophilic pinnipeds in the Bering and Chukchi Seas. J. Mamm. 51: 445-454.
- Burns, J. J. and T. J. Eley. 1977. The natural history and ecology of the bearded seal (*Erignathus barbatus*) and the ringed seal (*Phoca hispida*). Environmental Assessment of the Alaskan Continental Shelf, Vol. I: 226-302. N.O.A.A., U.S. Dept. Commerce, Boulder, Colorado.
- Burns, J. J. and S. J. Harbo, Jr. 1972. An aerial census of ringed seals, northern coast of Alaska. Arctic 25 279-290.
- Bursa, A. 1961a. Phytoplankton of the Calanus Expeditions in Hudson Bay, 1953 and 1954. J. Fish. Res. Board Can. 18: 51-83.
- Bursa, A. S. 1961b. The annual oceanographic cycle at Igloolik in the Canadian Arctic. II. The phytoplankton. J. Fish. Res. Board Can. 18: 563-615.
- Bursa, A. S. 1968. Marine life of Hudson Bay. Part 1. Marine plants. In: C. S. Beals (ed.). Science, history and Hudson Bay. Vol. 1. Dept. Energy, Mines and Resources, Ottawa. pp. 343-351.
- Bursa, A. S. 1971. Biological oceanographic observations in Frobisher Bay. III. Phytoplankton tables 1967. Fish. Res. Board Can. Tech. Rept. No. 267. 21 p.
- Carey, A. G., Jr. and R. E. Ruff. 1977. Ecological studies of the benthos in the western Beaufort Sea with special reference to bivalve molluscs. *In:* M. J. Dunbar (ed.), Polar Oceans, Arctic Institute of North America. pp. 505-530.
- Carey, A. G., Jr., R. E. Ruff, J. G. Castillo and J. J. Dickinson. 1974. Benthic ecology of the western Beaufort Sea continental margin: preliminary results. In: J. C. Reed and J. E. Sater (eds.), The Coast and Shelf of the Beaufort Sea, Arctic Institute of North America. pp. 665-680.
- Chapskii, K. K. 1938. The bearded seal (Erignathus barbatus Fabr.) of the Kara and Barents Seas. Trudy arkticheskogo instituta 123: 7-70. Canada Fish. and Mar. Serv., Transl. Series No. 3162. 145 p.

- Clarke, A. J. 1978. On wind-driven quasi-geostrohpic water movements near fast-ice edges. Deep-Sea Res. 25: 41-51.
- Conover, R. J. 1962. Metabolism and growth in Calanus hyperboreus in relation to its life cycle. Rapp. Proc. Verb. Réun. Cons. Perm. Int. Expl. Mer 153: 190-197.
- Corlett, J. 1968. Capelin in the northwestern Barents Sea. Rapp. P.-V. Réun. Cons. Perm. Int. Explor. Mer 158: 11-18.
- Craig, P. C. and W. Griffiths. 1978. Beaufort Sea barrier island-lagoon ecological process studies: Ecology of fishes in Simpson Lagoon, 1977. Envir. Assess. Alaskan Cont. Shelf, Annu. Rept. Prin. Invest., March 1978. Vol. VII, pp. 587-664. Nat. Oceanic and Atmos. Admin., Boulder, Col.
- Crisp, D. J. 1975. Secondary productivity in the sea. In: Productivity of World Ecosystems. National Academy of Sciences, Washington, D.C. pp. 71-89.
- Currie, R.D. 1968. Western Ungava. An area economic survey. Dept. Indian Affairs and Northern Development, Ottawa.
- Curtis, M. A. 1977. Life cycles and population dynamics of marine benthic polychaetes from the Disko Bay area of West Greenland. Ophelia 16: 9-58.
- Davis, R. A., W. J. Richardson, S. R. Johnson and W. E. Renaud. 1978a. Status of the Lancaster Sound narwhal population in 1976. Rept. Int. Whal. Commn. 28: 209-215.
- Davis, R. A., W. R. Koski and K. J. Finley. 1978b. Numbers and distribution of Walruses in the central Canadian high arctic. Unpubl. Rept. by LGL Ltd. for Polar Gas Project, Toronto. 50 p.
- Degerbøl, M. and P. Freuchen. 1935. Mammals. Report Fifth Thule Expedition, 1921-24. Vol. 2, No. 4-5.
- Divoky, G. J. 1976. The pelagic feeding habits of Ivory and Ross' gulls. Condor 78: 85-90.
- Doan, K. H. and C. W. Douglas. 1953. Beluga of the Churchill region of Hudson Bay. Bull. Fish. Res. Board Can. No. 98: 1-27.
- Dunbar, M. J. 1941. On the food of seals in the Canadian Eastern Arctic. Can. J. Res. D 19: 150-155.
- Dunbar, M. J. 1946. On *Themisto libellula* in Baffin Island coastal waters. J. Fish. Res. Board Can. 6: 419-434.
- Dunbar, M. J. 1949. The Pinnipedia of the arctic and subarctic. Fish. Res. Board Can., Bull. 85: 1-22.
- Dunbar, M. J. 1951. Resources of arctic and subarctic seas. Trans. Roy. Soc. Canada XLV III. Sec. 5: 61-67.
- Dunbar, M. J. 1954a. The amphipod crustacea of Ungava Bay, Canadian Eastern Arctic. J. Fish. Res. Board Can. 11: 709-798.

- Dunbar, M. J. 1954b. The status of the Atlantic walrus, Odobenus rosmarus (L.), in Canada. The Arctic Circular 8: 11-14.
- Dunbar, M. J. 1957. The determinants of production in northern seas: a study of the biology of *Themisto libellula* Mandt. Can. J. Zool. 35: 797-819.
- Dunbar, M. J. 1959. Arctic marine zoogeography. In: G. R. Lowther (ed.), Problems of the Pleistocene and Arctic Area. McGill University Museums Publ. No. 1: 55-63.
- Dunbar, M. J. 1968. Ecological development in polar regions. Prentice-Hall, Englewood Cliffs, New Jersey. 119 p.
- Dunbar, M. J. 1973. Glaciers and nutrients in Arctic fjords. Science 182: 398.
- Duvall, A. J. and C. O. Handley, Jr. 1946. Report of a wildlife reconnaissance of the eastern Canadian Arctic. U.S. Dept. Int., Fish Wildl. Serv. 142 p.
- Eberhardt, L. L. 1969. Population analysis. In: R. H. Giles (ed.). Wildlife management techniques. Wildl. Society, Washington, pp. 457-495.
- Eberhardt, L. L. 1977. "Optimal" management policies for marine mammals, Wildl. Soc. Bull. 5: 162-169.
- Eberhardt, L. L. and D. B. Siniff. 1977. Population dynamics and marine mammal management policies. J. Fish. Res. Board Can. 34: 183-190.
- Eley, T. J., Jr. 1978. A possible case of adoption in the Pacific walrus. Murrelet 59: 77-78.
- Eilis, D. V. 1955. Some observations on the shore fauna of Baffin Island. Arctic 8: 224-236.
- Ellis, D. V. 1960. Marine infaunal benthos in arctic North America. Arctic institute of North America Tech. Paper No. 5. 53 p.
- Emlen, J. M. 1973. Ecology: an evolutionary approach. Addison-Wesley, Reading, Mass. 493 p.
- English, T. S. 1959. Primary production in the central North Polar Sea drifting station Alpha 1957-58. Paper presented at First International Oceanographic Conf., New York, 1959.
- Evans, J. 1968. Ungava Bay: an area economic survey. A.E.S.R. 58/1. Dept. Indian Affairs and Northern Development, 72 p.
- Fay, F. H. 1957. History and present status of the Pacific walrus population. Trans. North Am. Wildl. Conf. 22: 431-445.
- Fay, F. H. 1960. Carnivorous walrus and some arctic zoonoses. Arctic 13: 111-122.
- Fay, F. H. 1974. The role of ice in the ecology of marine mammals of the Bering Sea. In: D. W. Hood and E. J. Kelley (eds.), Oceanography of the Bering Sea with emphasis on renewable resources. Inst. Mar. Sci., Univ. Alaska. pp. 383-399.

- Fay, F. H., H. M. Feder and S. W. Stoker. 1977. An estimation of the impact of the Pacific Walrus population on its food resources in the Bering Sea. U.S. Marine Mammal Comm. Rep. No. MMC-75/06 and MMC-74/03. U.S. Nat. Tech. Inform. Serv. Cat. No. PB-273 505. 38 p.
- Fedoseev, G. A. 1965a. Comparative characteristics of ringed seal populations in the Chukotskii Peninsula coastal waters. Izvestlya TINRO 59: 194-212. (Transl. Bureau, Canada Dept. of Secret. of State, 1975).
- Fedoseev, G. A. 1965b. Age and sex composition of the kill of the ringed seal (Phoca hispida ochotensis Pall.) as an index of the age structure of the population. Morskie Miekopitayushchie, Akademiya Nauk SSSR, pp. 105-112. (Fish. Res. Board Can., Transl. Series No. 799).
- Fedoseev, G. A. 1968. Determining numbers and basis for establishing the catch quota of Ringed Seals in the Sea of Okhotsk. *In:* V. A. Arsen'ev and K. I. Panin (eds.), Pinnipeds of the North Pacific, VNIRO, Moscow, pp. 175-183.
- Fedoseev, G. A. 1971. The distribution and numbers of seals on whelping and moulting patches in the Sea of Okhotsk. *In:* K. K. Chapskii and E. S. Mil'chenko (eds.), Research on Marine Mammals. Canada Fish. Mar. Serv. Transl. Ser. No. 3185: 135-158.
- Fedoseev, G. A. 1973. Biological description of and basis for the kill limit on bearded seals in the Sea of Okhotsk, Izvestiya TINRO 86: 148-157. Canada Fish. Mar. Serv., Transl. Ser. No. 3282.
- Fedoseev, G. A. 1975. Ecotypes of the ringed seal (Pusa hispida Schreber, 1777) and their reproductive capabilities. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 169: 156-160.
- Fedoseev, G. A. 1976. Principal populational indicators of dynamics of numbers of seals of the family Phocidae. Ekologiya 5: 62-70.
- Finley, K. J. 1976. Studies of the status of marine mammals in the central District of Franklin, N.W.T. June-August, 1975. Unpubl. Rept. by LGL Ltd. for Polar Gas Project, 183 p.
- Finley, K. J. 1978. Behaviour and densities of ringed seals (*Phoca hispida*) during haul out in the high Arctic, June 1977. Unpubl. Rept. by LGL Ltd. for Polar Gas Project. 107 p.
- Finley, K. J., R. A. Davis and W. J. Richardson. 1974. Preliminary studies of the numbers and distribution of marine mammals in the central Canadian Arctic 1974. Unpubl. Rept. by LGL Ltd. for Polar Gas Project. 68 p.
- Finley, K. J. and W. G. Johnston. 1977. An investigation of the distribution of marine mammals in the vicinity of Somerset Island with emphasis on Bellot Strait, August-September 1976. Unpubl. Rept. by LGL Ltd. for Polar Gas Project. 91 p.
- Fiscus, C. H. and W. M. Marquette. 1975. National

- Marine Fisheries Service field studies relating to the bowhead whale harvest in Alaska, 1974. Northwest Fisheries Center Processed Rept., National Marine Fisheries Serv.. Seattle. 23 p.
- Fisher, H. D. 1952. Harp seals of the Northwest Atlantic. Fish. Res. Board Can. General Series No. 20. St. Andrews. N.B. Sept. 1952. 4 p.
- Fisher, H. D. 1955. Utilization of Atlantic harp seal populations. Trans. Twentieth N. Amer. Wild. Conf. 1955; 507-518.
- Fraker, M. A. 1977a. The 1977 whale monitoring program Mackenzie Estuary, N.W.T. Unpubl. Rept. by F. F. Slaney and Co. Ltd. to Imperial Oil Ltd. 53 p.
- Fraker, M. A. 1977b. The 1976 white whale monitoring program, Mackenzie Estuary, N.W.T. Unpubl. Rept. by F. F. Slaney and Company Ltd. to Imperial Oil Limited, Calgary, 76 p. + Appendices.
- Fraker, M. A. 1979. Spring migration of bowhead (Balaena mysticetus) and white whales (Delphinapterus leucas) in the Beaufort Sea. Can. Fish. Marine Serv., Tech. Rept. 859. 36 p.
- Fraker, M. A., D. E. Sergeant and W. Hoek. 1978. Bowhead and white whales In the Southern Beaufort Sea. Beaufort Sea Project, Tech. Rept. No. 4. Dept. of Fisheries and the Environment. Victoria, B.C.
- Fraser, J. H. 1962. The role of ctenophores and salps in zooplankton production and standing crop. Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer 153: 121-123.
- Freeman, M. M. R. 1968. Winter observations on beluga (*Delphinapterus leucas*) in Jones Sound, N.W.T. Can. Field-Nat. 82: 276-286.
- Freeman, M. M. R. 1969/70. Studies in maritime hunting I. Ecologic and technologic restraints on walrus hunting, Southampton Island N.W.T. Folk 11-12: 155-171.
- Freeman, M. M. R. 1974/75. Studies in maritime hunting II. An analysis of walrus hunting and utilization: Southampton Island, N.W.T. 1970. Folk 16-17: 147-158.
- Freeman, M. (ed.). 1976. Inuit land use and occupancy project. Vol. 1: land use and occupancy, and Vol. 2: supporting studies. Dept. of Indian and Northern Affairs, Ottawa.
- Freuchen, P. 1921. Om hvalrossens forekomst og vandringer ved Grønlands vestkyst. Dan. Naturhist. Foren., Vidensk. Medd. 72: 237-249. Fish. Res. Board Can., Transl. Ser. No. 2383, 1973.
 - Freuchen, P. and F. Salomonsen. 1958. The Arctic Year. G. P. Putnam's Sons, New York, N.Y. 438 p.
 - Friesen, B. F. 1975. Potential Inuit benefits from commercial and sports use of arctic renewable resources. Vol. 10. Inuit Tapirisat of Canada, Renewable Resources Project. 176 p.

- Frost, K. J., L. F. Lowry and J. J. Burns. 1978. Offshore demersal fishes and epibenthic invertebrates of the northeastern Chukchi and western Beaufort Seas. Outer Cont. Shelf Envir. Assess. Prog., Annu. Rept. Prin. Invest., March 1978. Vol. I, pp. 231-353. Nat. Oceanic and Atmos. Admin., Boulder, Col.
- Grainger, E. H. 1971. Biological Oceanographic Observations in Frobisher Bay. I. Physical, Nutrient and Primary Production Data, 1967-1971. Fish. Res. Board Can. Tech. Rept. No. 265. 75 p.
- Grainger, E. H. 1974. Nutrients in the southern Beaufort Sea. *In:* J. C. Reed and J. E. Sater (eds.). The coast and shelf of the Beaufort Sea. Arctic Institute of North America. pp. 589-605.
- Grainger, E. H. 1975. Biological productivity of the Southern Beaufort Sea: the physical-chemical environment and the plankton. Beaufort Sea Tech. Rept. No. 12a. 82 p.
- Green, J. M. and D. H. Steele. 1975. Observations on marine life beneath sea ice, Resolute Bay, N.W.T. In: Proc. Circumpolar Conference on Northern Ecology, Nat. Res. Counc. Can., Ottawa, pp. II — 77-86.
- Greendale, R. G. and C. Brousseau-Greendale. 1976. Observations of marine mammal migrations at Cape Hay, Bylot Island during the summer of 1976. Fisheries and Marine Service Tech. Rept. No. 680, 25 p.
- Greisman, P. and G. Ingram. 1977. Nutrient distribution in the St. Lawrence estuary. J. Fish. Res. Board Can. 34: 2117-2123.
- Griffiths, W. and P. C. Craig. 1978. Beaufort Sea barrier island-lagoon ecological process studies: Invertebrates in Simpson Lagoon 1977. Envir. Assess. Alaska Cont. Shelf, Annu. Rept. Prin. Invest., March 1978. Vol. VII, pp. 665-757. Nat. Oceanic and Atmos. Admin., Boulder, Col.
- Gulland, J. A. 1971. The effect of exploitation on the numbers of marine animals. pp. 450-467 In: P. J. den Boer and G. R. Gradwell (eds.). Dynamics of Populations, Cent. Agric. Publ. Doc., Wageningen, The Netherlands.
- Gulland, J. A. (ed.). 1977. Fish population dynamics. J. Wiley & Sons, London. 372 p.
- Harington, C. R. 1966. Extralimital occurrences of walruses in the Canadian Arctic. J. Mamm. 47: 506-513.
- Hay, K. 1976. Preliminary report on narwhal studies in northern Baffin Island, summer 1976. Fish. Res. Board Can. MS Rept. 9 p.
- Hay, K. and D. E. Sergeant. 1976. Interim Technical Report, Arctic Whale Project, Environmental-Social Program, Northern Pipelines (Arctic Islands Pipeline). Fish. Res. Board Can. 41 p.
- Heyland, J. D. and K. Hay. 1976. An attack by a Polar Bear on a juvenile Beluga. Arctic 29: 56-57.
- Higgins, G. 1968. The south coast of Baffin Island: an

- area economic survey. A.E.S.R. 67/2. Dept. Indian Affairs and Northern Development, Ottawa. 235 p.
- Hognestad, P. T. 1968. Observations on Polar cod in the Barents Sea. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 158; 126-130.
- Holt, S. J. and L. M. Talbot. 1978. New principles for the conservation of wild living resources. Wildl. Monograph 59: 1-33.
- Horner, R. A. 1977. History and recent advances in the study of ice biota. *In:* Polar Oceans, M. J. Dunbar (ed.). Arctic Institute of North America. pp. 269-283.
- Hsiao, S. I. C., M. G. Foy and D. W. Kittle. 1977. Standing stock, community structure, species composition, distribution, and primary production of natural populations of phytoplankton in the southern Beaufort Sea. Can. J. Botany 55: 685-694.
- Imperial Oil Ltd., Aquitaine Co. of Can. Ltd., and Canada Cities Services Ltd. 1978. Environmental impact statement for exploratory drilling in Davis Strait region. Imperial Oil Ltd., Calgary, Alberta.
- JBNQNHRC (James Bay Northern Quebec Native Harvesting Research Committee.) 1976. Research to establish present levels of harvesting by native peoples of Northern Quebec. Phase I. Part II. A Report on the harvests by the Inuit of Northern Quebec. 230 p. + Appendices.
- Johnson, M. L., C. H. Fiscus, B. T. Ostenson and M. L. Barbour. 1966. Marine mammals. In: N. J. Willimovsky and J. N. Wolfe (eds.). Environment of the Cape Thompson region, Alaska. U.S. Atomic Energy Commission, Oak Ridge, Tenn. pp. 877-924.
- Johnson, S. R., W. E. Renaud, R. A. Davis and W. J. Richardson. 1976. Marine mammals recorded during aerial surveys of birds in eastern Lancaster Sound, 1976. Unpubl. Rept. by LGL Ltd. for Norlands Petroleums Ltd. 180 p.
- Jonkel, C. J. 1969. White whales wintering in James Bay. J. Fish. Res. Board Can. 26: 2205-2207.
- Jonsgård, Å. and P. B. Lyshoel. 1970. A contribution to the knowledge of the biology of the killer whale Orcinus orca (L.). Nytt Mag. Zool. 18; 41-48.
- Kanwisher, J. W. 1966. Photosynthesis and respiration in some seaweeds. *In:* H. Barnes (ed.). Some contemporary studies in marine science. Allen and Unwin, London, pp. 407-420.
- Kapel, F. O. 1975a. Preliminary notes on the occurrence and exploitation of smaller Cetacea in Greenland. J. Fish. Res. Board Can. 32: 1079-1082.
- Kapel, F. O. 1975b. Recent research on seals and seal hunting in Greenland. Rapp. P.-V. Réun. Int. Explor. Mer 169: 462-478.
- Kapel, F. O. 1975c. Age analyses and catch of the harp seal in northwest Greenland, 1953-72. ICNAF Res. Bull. 11: 93-106.

- Kapel, F. O. 1977. Catch of belugas, narwhals and harbour porpoises in Greenland, 1954-75, by year, month and region. Rep. Int. Whal. Commn. 27: 507-520.
- Kemp, W. B. 1975. The harvest potential of Inuit camps. Unpubl. Rept. to D.I.N.A., Ottawa. 72 p.
- Kenyon, K. W. 1965. Food of harbor seals at Amchitka Island, Alaska. J. Mamm. 46: 103-104.
- Kiliaan, H. P. L. and I. Stirling. 1978. Observations on overwintering walruses in the eastern Canadian High Arctic. J. Maπιm. 59: 197-200.
- Kleinenberg, S. E., A.V. Yablokov, B. M. Bel'kovich and M. N. Tarasevich. 1964. Beluga (Delphinapterus leucas) investigation of the species. Akad. Nauk SSSR, Institut Morfologii Zhivotnykh Im. A. N. Severtsova, Moscow. 450 p. (Translated into English, 1969, Israel Program for Scientific Trans., Jerusalem. 376 p.)
- Kosygin, G. M. 1971. Feeding of the bearded seal Erignathus barbatus nauticus (Pallas) in the Bering Sea during the spring-summer period. Izv. TINRO 75: 144-151, Can. Fish. Mar. Serv. Transi. Ser. 3747. 14 p.
- Kosygin, G. M. and ∀. ⋈. Gol'tsev. 1971. Data on the morphology and ecology of the Harbour Seal of the Tatar Strait. In: K. K. Chapskii and E. S. Mil'chenko (eds.), Research on marine mammals. Canada Fish. Mar. Serv. Transi. Ser. No. 3185: 384-410.
- Krebs, C. J. 1972. Ecology the experimental analysis of distribution and abundance. Harper and Row, New York. 694 p.
- Krylov, V. I. 1965. Determination of age, rate of growth and analysis of the age structure of the Pacific walrus catch. *In:* Morskie mlekopitayushchie. Akademiya Nauk SSSR. Izdatel'stova "Nauka", Moskva. p 201-210. Fish. Res. Board Can. Transi. Ser. No. 1004, 1968.
- Krylov, V. I. 1971. The feeding of the Pacific Walrus (Odobaenus [sic] rosmarus divergens III.). In: K. K. Chapskii and E. S. Mil'chenko (eds.), Research on marine mammals. Canada Fisheries and Marine Serv, Transi. Ser. No. 3185. pp. 177-189.
- Kumlien, L. 1879. Contributions to the natural history of Arctic America, made in connection with the Howgate Polar Expedition, 1877-78. U.S. Nat. Mus. Bull. No. 15. 179 p.
- Lalli, C. M., R. Buchanan, D. Thomson and F. Wells. 1973. Polar Gas Preliminary Environmental Study: Marine Ecology Report. Unpubl. McGill Univ. Rept. for Polar Gas Project. 98 p.
- Larkin, P. A. 1977. An epitaph for the concept of maximum sustained yield. Trans. Am. Fish. Soc. 106(1): 1-11.
- Lee, R. F. 1974. Lipid composition of the copepod Calanus hyperboreas from the Arctic Ocean. Changes with depth and season. Mar. Biol. 26: 313-318.

- Lee, R. K. S. 1973. General ecology of the Canadian arctic benthic marine algae. Arctic 26: 32-43.
- Lett, P. F. and T. Benjaminsen. 1977. A stochastic model for the management of the northwestern Atlantic harp seal (Pagophilus groenlandicus) population. J. Fish. Res. Board Can. 34: 1155-1187.
- Lindsay, D. G. 1975. Sea ice atlas of arctic Canada 1961-1968. Dept. Energy, Mines and Resources, Ottawa, 213 p.
- Lorenzen, C. J. 1976. Primary production in the sea. In: D. H. Cushing and J. J. Walsh (eds.). The Ecology of the Seas. W. B. Saunders Company, Philadelphia. pp. 173-185.
- Loughrey, A. G. 1959. Preliminary Investigation of the Atlantic walrus *Odobenus rosmarus rosmarus* (Linnaeus). Can. Wildl. Serv., Wildl. Manage. Bull (Series 1) No. 14. 123 p.
- Low, A. D. 1906. The cruise of the Neptune, 1903-4. Report on the Dominion Government Expedition to Hudson Bay and the arctic islands on board the D.G.S. Neptune, 1903-1904. Government Printing Bureau, Ottawa.
- Lowry, L. F., K. J. Frost and J. J. Burns. 1977. Trophic relationships among ice inhabiting phocid seals. Final report of Beaufort Sea activities. *In:* Env. Assessment of the Alaskan Continental Shelf. Vol. I. N.O.A.A., Boulder, Colorado. pp. 391-432.
- Lowry, L. F., K. J. Frost and J. J. Burns. 1978. Food of ringed seals and bowhead whales near Point Barrow, Alaska. Can. Field-Naturalist 92: 67-70.
- Lubbock, B. 1937. The arctic whalers. Brown, Son and Ferguson Ltd., Glasgow. 483 p.
- Lubinsky, I. 1972. Marine bivalve molluscs of the Canadian Arctic. Ph.D. Thesis, McGill Univ. 735 p.
- MacGinitie, G. E. 1955. Distribution and ecology of the marine invertebrates of Point Barrow, Alaska. Smithsonian Misc. Coll. 128(9), 201 p.
- MacLaren Marex Inc. 1979. Report on aerial surveys of marine mammals and birds in southern Davis Strait and eastern Hudson Strait in March, 1978. Unpubl. Rept. for Esso Resources Canada Ltd., Aquitaine Co. of Canada Ltd. and Canada Cities Services Ltd. Arctic Petroleum Operators Association.
- Mann, K. H. 1972. Ecological energetics of the seaweed zone in a marine bay on the Atlantic coast of Canada. II. Productivity of the seaweeds. Marine Biology 14: 199-209.
- Manning, T. H. 1974. Variations in the skull of the bearded seal, *Erignathus barbatus* (Erxleben). Biol. Pap. Univ. Alaska No. 16. 21 p.
- Manning, T. H. 1976. Birds and mammals of the Belcher, Sleeper, Ottawa and King George Islands, and Northwest Territories. Can. Wildl. Serv., Occas. Paper 28, 40 p.

- Mansfield, A. W. 1958. The biology of the Atlantic walrus Odobenus rosmarus rosmarus (Linnaeus) in the eastern Canadian Arctic. Fish. Res. Board Can., MS Rept. Ser. (Biol.) No. 653. 146 p.
- Mansfield, A. W. 1966. The walrus in Canada's Arctic. Can. Geogr. Journal 73: 88-95.
- Mansfield, A. W. 1967a. Seals of arctic and eastern Canada. Fish. Res. Board Can. Bulletin No. 137. 35 p.
- Mansfield, A. W. 1967b. Distribution of the harbor seal, *Phoca vitulina* Linnaeus, in Canadian arctic waters, J. Mamm. 48: 249-257.
- Mansfield, A. W. 1968. Seals and walrus. In: C. S. Beals (ed.). Science, history and Hudson Bay, Vol. I. Dept. Energy, Mines and Resources, Ottawa. pp. 378-387.
- Mansfield, A. W. 1970. Population dynamics and exploitation of some arctic seals. *In:* M. W. Holdgate (ed.). Antarctic ecology. Vol. 1. Academic Press. pp. 429-446.
- Mansfield, A. W. 1971. Occurrence of the Bowhead or Greenland Right Whale (Balaena mysticetus) in Canadian Arctic Waters. J. Fish. Res. Board Can. 28: 1873-1875.
- Mansfield, A. W. 1973. The Atlantic walrus *Odobenus* rosmarus in Canada and Greenland. IUCN Publ. New Series, Suppl. Paper 39: 69-79.
- Mansfield, A. W. and H. D. Fisher. 1960. Age determination in the harbour seal, *Phoca vitulina* L. Nature (London) 186: 92-93.
- Mansfield, A. W., T. G. Smith and B. Beck. 1975a. The narwhal, Monodon monoceros, in eastern Canadian waters. J. Fish. Res. Board Can. 32: 1041-1046.
- Mansfield, A. W., D. E. Sergeant and T. G. Smith. 1975b. Marine mammal research in the Canadian Arctic. Environment Canada, Fisheries and Marine Service Tech. Rept. 507: 1-23.
- Marquette, W. M. 1977. The 1976 catch of bowhead whales (Balaena mysticetus) by Alaskan Eskimos, with a review of the fishery, 1973-1976, and a biological summary of the species. Northwest and Alaska Fisheries Center Processed Rept., Nat. Marine Fisheries Serv., Seattle. 96 p.
- Marshall, N. 1970. Food transfer through the lower trophic levels of the benthic environment. *In:* J. H. Steele (ed.), Marine food chains. Oliver and Boyd, Edinburgh. pp. 52-66.
- Matheke, G. E. M. and R. Horner. 1974. Primary productivity of the benthic microalgae in the Chukchi Sea near Barrow, Alaska. J. Fish. Res. Board Can. 31: 1779-1786.
- M'Clintock, F. L. 1859. The voyage of the 'Fox' in the Arctic seas. A narrative of the discovery of the fate of Sir John Franklin and his companions. John Murray, London.

- McLaren, I. A. 1958a. The biology of the ringed seal (Phoca hispida Schreber) In the eastern Canadian Arctic. Fish. Res. Board Can. Bull. 118: 1-97.
- McLaren, I. A. 1958b. The economics of seals in the eastern Canadian arctic. Fish. Res. Board Can., Arctic Cir. 1: 1-94.
- McLaren, I. A. 1958c. Some aspects of growth and reproduction of the bearded seal, *Erignathus barbatus* (Erxleben). J. Fish. Res. Board Can. 15: 219-227.
- McLaren, I. A. 1961. Methods of determining the numbers and availability of ringed seals in the eastern Canadian Arctic. Arctic 14: 162-175.
- McLaren, I. A. 1962. Population dynamics and exploitation of seals in the eastern Canadian Arctic. *In:* E. D. LeCren and M. W. Holdgate (eds.). The exploitation of natural animal populations. Blackwell Scientific Publ., Oxford. pp. 168-183.
- McLaren, I. A. 1966a. Taxonomy of harbor seals of the western North Pacific and evolution of certain other hair seals. J. Mamm. 47: 466-473.
- McLaren, I. A. 1966b. Analysis of an aerial census of ringed seals. J. Fish. Res. Board Can. 23: 769-773.
- McLaren, I. A. 1969. Population and production ecology of zooplankton in Ogac Lake, a landlocked flord on Baffin Island. J. Fish. Res. Board Can. 28: 1485-1559.
- McLaren, I. A. and A. W. Mansfield. 1960. The netting of sea mammals. A report on the Belcher Islands experiment, 1960. Fish. Res. Board Can., Arctic Unit Circ. 6. 13 p.
- McLaren, P. L., M. A. McLaren and L. A. Patterson. 1977. Numbers and distribution of birds during migration in the District of Keewatin, northern Manitoba and northwestern Ontario, 1976. Appendix B. Harbor seals in southern Keewatin and northern Manitoba. (p. 284). Unpubl. Rept. by LGL Ltd. for Polar Gas Project. 284 p.
- McRoy, C. P. and J. J. Goering. 1974. The influence of ice on the primary productivity of the Bering Sea. In: D. W. Hood and E. J. Kelley (eds.), Oceanography of the Bering Sea. Institute of Mar. Sci., Univ. of Alaska, Fairbanks. pp. 403-421.
- McVay, S. 1973. Stalking the Arctic whale. American Scientist 61: 24-37.
- Medvedev, L. P. 1971. Information on the feeding of the Beluga in the Dikson region. In: K. K. Chapskii and E. S. Mil'chenko (eds.), Research on marine mammals. Canada Fisheries and Marine Service Transi. Ser. No. 3185. pp. 92-104.
- Meldrum, S. M. 1975. Frobisher Bay: An area economic survey. A.E.S.R. 66/3. Dept. Indian Affairs and Northern Development. Ottawa. 170 p.
- Miller, E. H. and D. J. Boness. 1979. Remarks on display functions of the snout of the grey seal, Hall-

- choerus grypus (Fab.), with comparative notes. Can. J. Zool. 57: 140-148.
- Miller, R. S. 1955. A survey of the mammals of Bylot Island, Northwest Territories. Arctic 8: 167-176.
- Milne, A. R. and B. D. Smiley. 1978. Offshore drilling in Lancaster Sound: possible environmental hazards. Institute of Ocean Sciences, Dept. Fisheries and Environment, Sidney, B.C. 95 p.
- Mitchell, E. D. 1973. The status of the world's whales. Nature Canada 2(4): 9-25.
- Mitchell, E. 1975a. Review of biology and fisheries for smaller cetaceans. J. Fish. Res. Board Can. 32: 889-983.
- Mitchell, E. 1975b. Porpoise, dolphin and small whale fisheries of the world status and problems. I.U.C.N. Mono. No. 3, 129 p.
- Mitchell, E. 1975c. Trophic relationships and competition for food in northwest Atlantic whales. Can. Soc. Zool. Proc. Ann. Meeting. pp. 123-133.
- Mullin, M. M. 1969. Production of zooplankton in the ocean; the present status and problems. Oceanogr. Mar. Biol. Ann. Rev. 7: 293-314.
- Naito, Y. and M. Nishiwaki. 1975. Ecology and morphology of *Phoca vitulina largha* and *Phoca kurilensis* in the southern Sea of Okhotsk and northeast of Hokkaldo. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 169: 379-386.
- Nazarenko, Y. I. 1975. Sexual maturation, reproductive rate, and missed pregnancy, in female harp seals. In: K. Ronald and A. W. Mansfield (eds.). Biology of the seal. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 169: 413-415.
- Nemoto, T. 1970. Feeding patterns of baleen whales in the ocean. *In:* J. H. Steele (ed.). Marine Food Chains. Oliver & Boyd. pp. 241-252.
- Ockelmann, W. K. 1958. The zoology of East Greenland; Marine Lamellibranchiata. Medd. om Grønland 122(4): 1-256.
- Odum, H. T. and E. P. Odum. 1955. Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll. Ecological Monographs 25: 291-320.
- Oritsland, T. and T. Benjaminsen. 1975. Sex ratio, age composition and mortality of Hooded Seals at Newfoundland. ICNAF Res. Bull. 11: 135-143.
- Parsons, J. L. 1977. Metabolic studies on ringed seals (*Phoca hispida*). M.Sc. Thesis, University of Guelph. 82 p.
- Pitcher, K. and D. Calkins. 1977. Biology of the harbor seal, *Phoca vitulina richardi*, in the Gulf of Alaska. Environmental Assessment of the Alaskan Continental Shelf, Vol. I. N.O.A.A., U.S. Dept. Commerce, Boulder, Colorado. pp. 189-225.
- Platt, T. and D. V. Subba Rao. 1975. Primary production

- of marine microphytes. In: J. P. Cooper (ed.). Pt-otosynthesis and productivity in different environments. Cambridge University Press, Cambridge. pp. 249-280.
- Ponomarenko, V. P. 1967. Feeding of larvae and try of the Arctic cod, Boreogadus saida Lepechin, in the Barents and Kara Seas. Polyarn. Nauchno-it sled. Praektnyi Inst. Morsk. Rybn. Khoz. Okeanogr., Materialy Rybokhoz. Issled. Severnago Bas: eina. 10: 20-27. (Transl. from Russian by U.S. Bur. 3port Fish. Wildl., 1968).
- Popov, L. A. 1975. The Influence of hydrometeorological conditions in the White Sea on the behaviour of harp seals in the breeding season. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 169: 371-373.
- Porsild, M. P. 1918. On "Savssats": a crowding of arctic animals at holes in the sea ice. Geog. Fleview 6(3): 215-228.
- Potelov, V. A. 1975a. Biological background for determining the abundance of bearded seals (*Erig nathus barbatus*) and ringed seals (*Pusa hispida*). Rapp. P.-V. Réun. Cons. Int. Explor. Mer 169: 553.
- Potelov, V. A. 1975b. Reproduction of the bearded seal (Erignathus barbatus) in the Barents Sea. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 169: 554.
- Poulet, S. A. 1976. Feeding of *Pseudocalanus minutus* on living and non-living particles. Marine Biol. 34: 117-125.
- Prokhorov, V. S. 1968. Materials on the ecology of Capelin in the Barents Sea. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 158: 23-31.
- Rasmussen, B. 1957. Exploitation and protection of the east Greenland seal herds. The Norwegian Whaling Gazette 2: 45-59.
- Rasmussen, B. 1960. On the stock of hood seels in the northern Atlantic. Fisken og Havet. Populeere rapporter og meldinger fra Fiskeridirektoratets Havforskningsinstitutt, Bergen. No. 1, 23 p. (Fish Res. Board Can. Transl. Ser. No. 387. 29 p.)
- Reeves, R. H. 1978. Atlantic wairus (Odobenus rosmarus rosmarus): A literature survey and status report. U.S. Fish and Wildl. Serv., Wildl. Research Rept. 10. Washington, D.C. 41 p.
- Rice, D. W. 1974. Whales and whale research in the eastern North Pacific. *In:* W. E. Schevill (ed.), The Whale Problem: A Status Report, Harvard University Press, pp. 170-195.
- Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Fish. Res. Board Can. Bull. 191. 382 p.
- Riewe, R. R. 1977. The utilization of wildlife in the Jones Sound region by the Grise Fiord Inuit. In: L. C. Bliss (ed.), Truelove Lowland, Devon Island, Carada: A High Arctic Ecosystem. Univ. Alberta Press. Edmonton. pp. 623-644.

- Riewe, R. R. and C. W. Amsden. (in press). Harvesting and utilization of Pinnipeds by Inuit hunters in Canada's Eastern High Arctic. Mercury Series, Archaeological Survey of Canada, National Museum of Man, Ottawa.
- Rodin, L. E., N. I. Bazilevich and N. N. Rozov. 1975. Productivity of the world's main ecosystems. *In:* Productivity of World Ecosystems. National Academy of Sciences, Washington, D.C. pp. 13-26.
- Roedel, P. M. (ed.). 1975. Optimum sustainable yield as a concept in fisheries management. Spec. Publ. No. 9, Am. Fish Soc., Washington, D.C. 89 p.
- Roman, M. R. 1977. Feeding of the copepod Acartia tonsa on the diatom Nitzschia closterium and brown algae (Fucus vesiculosus) detritus. Marine Biol. 42: 149-155.
- Ross, W. G. 1974. Distribution, migration, and depletion of Bowhead whales in Hudson Bay, 1860 to 1915. Arctic and Alpine Res. 6: 85-98.
- Ross, W. G. 1975. Whaling and Eskimos: Hudson Bay 1860-1915. Nat. Mus. Canada, Publ. in Ethnology No. 10: 1-164.
- Royce, W. F. 1975. Use of yield models in fishery management. pp 9-12. *In:* Roedel (1975).
- RRCS (Renewable Resources Consulting Services Ltd.). 1977. Aerial surveys of marine mammals of Lancaster Sound, 1975-1976. Unpubl. Rept. to Norlands Petroleums Ltd. 100 p.
- Ryther, J. H. 1969. Photosynthesis and fish production in the sea. Science 166: 72-76.
- Ryther, J. H. and W. M. Dunstan. 1971. Nitrogen, phosphorus and eutrophication in the coastal marine environment. Science 171: 1008-1013.
- Salter, R. E. 1978. Normal behaviour and disturbance responses of Walruses (Odobenus rosmarus L.) during terrestrial haul-out, eastern Bathurst Island, N.W.T., July-August 1977. Unpubl. Rept. by LGL Ltd. for Polar Gas Project. 68 p.
- Scammon, C. M. 1874. The marine mammals of the north-western coast of North America together with an account of the American Whale-Fishery. J. H. Carmany and Co., San Francisco. 324 p.
- Scoresby, W. 1820. An account of the Arctic regions with a history and description of the northern whale-fishery. Edinburgh, Constable. 2 vols.
- Sekerak, A. D., D. Thomson, H. Bain and J. Acreman. 1976a. Summer surveys of the marine ecology of Creswell Bay, Somerset Island and Assistance Bay, Cornwallis Island, N.W.T. 1975. Unpubl. Rept. by LGL Ltd. for Polar Gas Project. 215 p.
- Sekerak, A. D., R. A. Buchanan, W. B. Griffiths and M. G. Foy. 1976b. Biological oceanographic studies in Lancaster Sound, 1976. Unpubl. Rept. by LGL Ltd. to Norlands Petroleums Ltd. 239 p.

- Sergeant, D. E. 1963. Report on aerial photographic survey of harp seals, 1963. Fish. Res. Board Can. MS. 5 p.
- Sergeant, D. E. 1965a. Migrations of harp seals Pagophilus groenlandicus (Erxleben) in the northwest Atlantic. J. Fish. Res. Board Can. 22: 433-464.
- Sergeant, D. E. 1965b. Exploitation and conservation of harp and hood seals. Polar Record 12: 541-551.
- Sergeant, D. E. 1968. Whales. In: C. S. Beals (ed.). Science, history and Hudson Bay, Vol. I. Dept. Energy, Mines and Resources, Ottawa. pp. 388-396.
- Sergeant, D. E. 1969. Feeding rates of Cetacea. Fisk-Dir. Skr. Ser. HavUnders. 15: 246-258.
- Sergeant, D. E. 1971. Calculation of production of harp seals in the western North Atlantic. ICNAF Redbook 1971. Part III. pp. 157-184.
- Sergeant, D. E. 1973a. Biology of White Whales (Delphinapterus leucas) in western Hudson Bay. J. Fish. Res. Board Can. 30: 1065-1090.
- Sergeant, D. E. 1973b. Feeding, growth, and productivity of northwest Atlantic harp seals (*Pagophilus groenlandicus*). J. Fish. Res. Board Can. 30: 17-29.
- Sergeant, D. E. 1973c. Environment and reproduction in seals. J. Reprod. Fert., Suppl. 19: 555-561.
- Sergeant, D. E. 1973d. Transatlantic migration of a harp seal, *Pagophilus groenlandicus*. J. Fish. Res. Board Can. 30: 124-125.
- Sergeant, D. E. 1974. A rediscovered whelping population of hooded seals Cystophora cristata Erxleben and its possible relationship to other populations. Polarforschung 44: 1-7.
- Sergeant, D. E. 1975. Estimating numbers of harp seals. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 169: 274-280.
- Sergeant, D. E. 1976a. History and present status of populations of harp and hooded seals. Biol. Conserv. 10: 95-118.
- Sergeant, D. E. 1976b. Research on Hooded Seals Cystophora cristata Erxleben in 1976. ICNAF Res. Doc. 76/X/126 (Revised). 8 p.
- Sergeant, D. E. 1976c. Studies on harp seals of the western North Atlantic population in 1976. ICNAF Res. Doc. 76/X/124 (Revised). Serial No. 4010. 32 p.
- Sergeant, D. E. and P. F. Brodie. 1969. Body size in white whales, *Delphinapterus leucas*. J. Fish. Res. Boarc €an. 26: 2561-2580.
- Sergeant, D. E. and P. F. Brodie. 1975. Identity, abundance, and present status of populations of white whales, *Delphinapterus Ieucas*, in North America. J. Fish. Res. Board Can. 32: 1047-1054.
- Sergeant, D. E. and W. Hoek. 1974. Seasonal distribution of bowhead and white whales in the eastern Beaufort Sea. *In:* J. C. Reed and J. E. Sater (eds.),

- The coast and shelf of the Beaufort Sea. The Arctic Institute of North America. pp. 705-719.
- Shaughnessy, P. D. 1975. Biochemical comparison of the harbour seals *Phoca vitulina richardi* and *P.v. largha*. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 169: 70-73.
- Shaughnessy, P. D. and F. H. Fay. 1977. A review of the taxonomy and nomenclature of North Pacific harbour seals. J. Zool. (Lond.) 182: 385-419.
- Shustov, A. P. 1970. Daily dynamics of seal rookerles in the Sea of Okhotsk. Izv. TINRO 71: 283-288. Canada Fish. Mar. Serv. Transl. Ser. No. 2402: 1-14.
- Smith, T. G. 1973a. Population dynamics of the Ringed Seal in the Canadian eastern Arctic. Fish. Res. Board Can. Bull. 181: 1-55.
- Smith, T. G. 1973b. Censusing and estimating the size of ringed seal populations. Fish. Res. Board Can., Tech. Rept. No. 427: 1-26.
- Smith, T. G. 1973c. Management research on the Eskimo's Ringed Seal. Can. Geog. J. 86: 118-125.
- Smith, T. G. 1975a. Ringed seals in James Bay and Hudson Bay: Population estimates and catch statistics. Arctic 28: 170-182.
- Smith, T. G. 1975b. Parameters and dynamics of ringed seal populations in the Canadian eastern Arctic. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 169: 281-295.
- Smith, T. G. 1976a. The icy birthplace of the ringed seal. Can. Geog. J. 93: 58-63.
- Smith, T. G. 1976b. Predation of ringed seal pups (Phoca hispida) by the arctic fox (Alopex lagopus). Can. J. Zool. 54: 1610-1616.
- Smith, T. G. and I. Stirling. 1975. The breeding habitat of the ringed seal (*Phoca hispida*). The birth lair and associated structures. Can. J. Zool. 53: 1297-1305.
- Smith, T. G. and I. Stirling. 1978. Variation in the density of ringed seal (*Phoca hispida*) birth lairs in the Amundsen Gulf, Northwest Territories. Can. J. Zool. 56: 1066-1070.
- Smith, T. G. and D. Taylor. 1977. Notes on marine mammal, fox and polar bear harvests in the Northwest Territories 1940 to 1972. Fish. Mar. Serv., Tech. Rept. No. 694. Environment Canada, Ottawa. 37 p.
- Soper, J. D. 1928. A faunal investigation of southern Baffin Island. Natl. Mus. Can. Bull. 53.
- Spalding, D. J. 1964. Comparative feeding habits of the fur seal, sea lion, and harbour seal on the British Columbia coast. Fish. Res. Board Can. Bull. No. 146. 52 p.
- Squires, H. J. 1967. Decapod Crustacea from *Calanus* collections in Hudson Bay in 1953, 1954 and 1958-61. J. Fish.Res. Board Can. 24: 1873-1903.
- Squires, H. J. 1968. Decapod Crustacea from the

- Queen Elizabeth and nearby Islands in 1962. J. Fish. Res. Board Can. 25: 347-362.
- Steele, D. H. 1961. Studies in the marine amphipoda of eastern and northeastern Canada. Ph.D. Thesis, McGill University, Montreal. 350 p. + Appendices.
- Stephansson, S.E. (ed.). 1975. What is the need? Report No. 1 of Federal-Territorial Study Group on the Status of Marine Mammal Resources in the Northwest Territories. Resource Management Branch, Fisheries and Marine Service, Winnipeg. 33 p.
- Steven, D. M. 1974. Primary and secondary production in the Gulf of St. Lawrence. Marine Sciences Centre, McGill Univ., Manuscript Rept. No. 26. 116 p.
- Stirling, I. 1971. Population dynamics of the Weddell Seal (Leptonychotes weddelli) in McMurdo Sound, Antarctica, 1966-1968. Antarctic Research Series 18: 141-161. Amer. Geophysical Union, Wash., D.C.
- Stirling, I. 1974. Midsummer observations on the behavior of wild polar bears (Ursus maritimus). Can. J. Zool. 52: 1191-1198.
- Stirling, I. 1975. Factors affecting the evolution of social behaviour in the Pinnipedia. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 169: 205-212.
- Stirling, I. and W. R. Archibald. 1977. Aspects of predation of seals by polar bears. J. Fish. Res. Board Can. 34: 1126-1129.
- Stirling, I., R. Archibald and D. DeMaster. 1975. Distribution and abundance of seals in the eastern Beaufort Sea. Beaufort Sea Project, Tech. Rept. No. 1, 58 p. Dept. of Environment, Victoria.
- Stirling, I., W. R. Archibald and D. DeMaster. 1977. Distribution and abundance of seals in the eastern Beaufort Sea. J. Fish. Res. Board Can. 34: 976-988.
- Stirling, I. and E. H. McEwan. 1975. The caloric value of whole ringed seals (*Phoca hispida*) in relation to polar bear (*Ursus maritimus*) ecology and hunting behavior. Can. J. Zool. 53: 1021-1027.
- Stirling, I. and T. G. Smith. 1977. Interrelationships of Arctic Ocean mammals in the sea ice habitat. *In:* Circumpolar Conference on Northern Ecology. National Research Council of Canada, Ottawa. pp. II 129-136.
- Templeman, W. 1968. Review of some aspects of Capelin biology in the Canadian area of the north-west Atlantic. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 158: 41-53.
- Thomson, D., S. Woods and J. Acreman. 1975. Marine ecology survey in the central portion of the Canadian Arctic Islands, 1974. Unpubl. Rept. by McGill Univ. for Polar Gas Project. 77 p.
- Thomson, D., W. E. Cross, H. Bain and L. Patterson. 1978. Aspects of the spring and summer marine environment of Brentford Bay, Boothia Peninsula, N.W.T. Unpubl. Rept. by LGL Ltd. for Polar Gas Project. 203 p.

- Tomilin, A. V. 1957. Mammals of the USSR and adjacent countries. (Cetacea). Akad. Nauk SSR, Moscow, 9: 1-756 (translated into English, 1967, Israel Program for Scientific Translations, Jerusalem, 717 p).
- Treude, E. 1977. Pond Inlet, northern Baffin Island; the structure of an Eskimo resource area. Polar Geography 1(2): 95-122.
- Tuck, L. M. 1957. Wildlife investigations in the Cape Hay region, Lancaster Sound, 1957. Unpubl. Canadian Wildlife Service Rept. No. 760. 36 p. + plates.
- Tuck, L. M. 1960. The murres. Canadian Wildl. Serv. Mono. Ser. 1. 260 p.
- Usher, P. J. 1966. Banks Island: an area economic survey 1965. Industrial Division, Dept. Indian and Northern Affairs, Ottawa, 91 p.
- Usher, P. J. 1975. Historical statistics approximating fur, fish and game harvests within inuit lands of the N.W.T. and Yukon 1915-1974, with text. Vol. 3. Inuit Tapirisat of Canada, Renewable Resources Project. 101 p.
- Vibe, C. 1950. The marine mammals and the marine fauna in the Thule District (northwest Greenland) with observations on ice conditions in 1939-41. Meddelelser om Grønland 150(6): 1-117.
- Vibe, C. 1967. Arctic animals in relation to climatic fluctuations. Meddelelser om Grønland 170(5): 1-227.
- Welch, H. E. and J. Kalff. 1975. Marine metabolism at Resolute Bay, Northwest Territories. *In:* Proc. Circumpolar Conference on Northern Ecology, Nat. Res. Counc. Can., Ottawa. pp. II — 67-75.
- Wenzel, G. 1978. The harp-seal controversy and the Inuit economy. Arctic 31: 2-6.
- Wildish, D. J. 1977. Factors controlling marine and estuarine sublittoral macrofauna. Helgoländer wiss. Meeresunters 30: 445-454.
- Williams, T. 1977. The raw material of population dynamics. pp. 27-45. In: J. A. Gulland (ed.), Fish population dynamics. J. Wiley & Sons, London. 372 p.
- Wing, B. L. 1976. Ecology of Parathemisto libellula and P. pacifica (Amphipoda: Hyperiidea) in Alaskan coastal waters. Northwest Fish. Center, Auke Bay Fish. Lab. Processed Rept. 266 p.
- Winters, G. H. 1978. Production, mortality, and sustainable yield of northwest Atlantic harp seals (*Pagophilus groenlandicus*). J. Fish. Res. Board Can. 35: 1249-1261.
- Youngman, P. M. 1965. Walrus on Prince Patrick Island, Northwest Territories, Canada. J. Mamm. 46(1): 104.

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