Canadian Bulletin of Fisheries and Aquatic Sciences 216



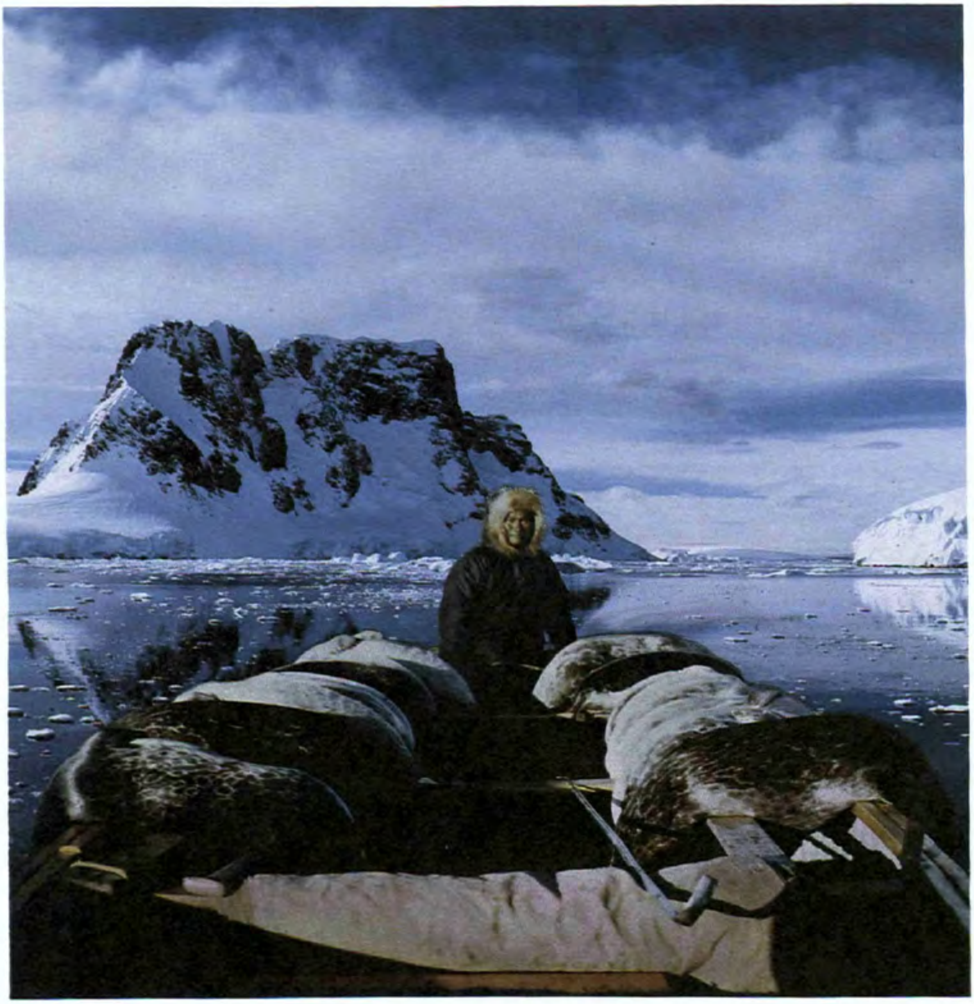
# The Ringed Seal, *Phoca hispida*, of the Canadian Western Arctic

Thomas G. Smith



Fisheries and Oceans    Pêches et Océans

# The Ringed Seal, *Phoca hispida*, of the Canadian Western Arctic



*Jimmy Memorana of Holman, Northwest Territories, with a day's catch of ringed seals.*

Canadian Bulletin of Fisheries and Aquatic Sciences 216

# The Ringed Seal, *Phoca hispida*, of the Canadian Western Arctic

**Thomas G. Smith**

*Department of Fisheries and Oceans*
*Arctic Biological Station*
*555 St-Pierre Blvd.*
*Sainte-Anne-de-Bellevue, Quebec H9X 3R4*

DEPARTMENT OF FISHERIES AND OCEANS
*Ottawa 1987*

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

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

---


**Information and Publications Branch**

| | |
|---|---|
| Dixi Lambert | Director General |
| Johanna M. Reinhart, M.Sc. | Director and Editor |
| Gerald J. Neville | Editorial and Publishing Services |

**Editorial Office:** Department of Fisheries and Oceans
Communications Directorate
Information and Publications Branch
200 Kent Street
Ottawa, Ontario, Canada K1A 0E6

---

Typesetter: K.G. Campbell Corporation Ltd., Ottawa, Ontario
Printer: Kromar Printing Ltd., Winnipeg, Manitoba
Cover Design: André, Gordon and Laundreth Inc., Ottawa, Ontario


---




Available from authorized bookstore agents, other bookstores
or you may send your prepaid order to the
Canadian Government Publishing Centre
Supply and Services Canada, Ottawa, Ont. K1A 0S9.

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

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

| | |
|---|---|
| Canada: $8.00 | Cat. No. Fs94-216E |
| Other countries: $9.60 | ISBN 0-660-12463-7 |

*Price subject to change without notice*




Correct citation for this publication:

SMITH, T.G. 1987. The ringed seal, *Phoca hispida*, of the Canadian Western Arctic. Can. Bull. Fish. Aquat. Sci. 216: 81 p.

## Contents

## *Dedication*

To Jimmy Memorana, who will not be able to read this, because there were no schools when he was a youth. He learned his lessons in the way of the Inuit, by observation and experience. I'm proud to have him as a friend and teacher. *Koanapargonaktok Inumarialuk.*

# Abstract

SMITH, T.G. 1987. The ringed seal, *Phoca hispida*, of the Canadian western arctic. Can. Bull. Fish. Aquat. Sci. 216: 81 p.

I studied ringed seals, *Phoca hispida*, during the years 1971 to 1983 from Holman in Amundsen Gulf, N.W.T., and several other localities in the southeastern Beaufort Sea. The highest densities of ringed seals (2.84/$km^2$) were found in Prince Albert Sound, Amundsen Gulf. Each year this becomes an area of good stable landfast ice which is consistently used as a breeding habitat. Age structure of the catches indicates segregation of older animals occupying fast-ice areas in the winter and spring, with all age classes being present in the summer open-water period. In the autumn, young-of-the-year and adolescents move west along the coast of Amundsen Gulf and southeastern Beaufort Sea. Seals tagged in this study were recovered as far west as Point Barrow, Alaska and Injun, Siberia. Prime breeding ice in Amundsen Gulf is characterized by being stable with ice hummocks or pressure ridges which provide areas for accumulation of snow in which subnivean lairs are constructed. Lairs serve the dual function of providing protection from predators and as a thermal shelter. Both polar bears, *Ursus maritimus*, and arctic foxes, *Alopex lagopus*, kill seals in their lairs. Arctic foxes are the most important predators of ringed seal pups in the western Canadian arctic. Strong territoriality exists in the breeding habitat. A limited form of polygyny exists in the ringed seal breeding population; one male maintains a territory which includes several females with their sub-territories of birth-lair complexes. A significant decrease in the number of birth lairs found during dog searches was documented in 1974 and 1975. In 1975 it was also found that the number of lairs occupied by rutting males was severely reduced. Predation by arctic foxes was at a peak in the spring of 1973, one year prior to the highest fox trapping harvest yet recorded for the area. High fox predation continued in the springs of 1974 and 1975 even though the number of ringed seal pups born had been severely reduced. Ringed seal pups are born in mid April. Ovulation occurs on average, 21 May, with implantation of the blastocyst on 18 August. There is an active gestation of 241 days with a delay of implantation of 89 days. Females are sexually mature at 5.61 years with the mean age of first reproduction being attained at 7.67 years. The pup sex ratio at birth is 1:1. Mean reproductive rates in normal years are calculated as 0.56. In 1974 and 1975 ovulation rates were reduced to the low values of 0.41 and 0.38, respectively, compared to the mean rate of 0.89 in other years. The index of body condition of adult seals was also significantly reduced in both 1974 and 1975. The length at birth of seals in this study area is calculated to be 632 mm (STL) with a foetal growth rate of 2.2 mm/day; post-natal growth to weaning is 6.1 mm/day; and post-weaning growth is reduced to a low of 0.099 mm/day for the remainder of the year. There is an indication of severe stunting in 4% and moderate stunting in 11% of the seals measured in this study. It appears to be related to date of birth and poor feeding conditions during the first year of life. Ringed seals feed on a variety of crustaceans during the open water season including *Parathemisto libellula, Thysanoessa raschii* and *Mysis oculata*. Arctic cod, *Boreogadus saida*, is the most important food of all ages of ringed seals during the ice covered period. There is evidence of feeding competition between adolescents and adults as shown by different prey items and diurnal feeding times. All age classes lose body condition from spring through to early September. Autumn feeding on arctic cod by groups of adult ringed seals occurs regularly, and this is an important time for the seals to regain body condition. It is also probably the proximate cause, through territorial exclusion, of the migration of young and adolescents westward along the mainland coast towards the Beaufort and Bering Seas. Survivorship values estimated from catch curves do not present either a clear or accurate picture of the annual changes in a ringed seal population. They reflect the drastic reduction in recruitment documented from reproductive data and breeding habitat evaluation in 1974 and 1975, but would not be sensitive enough to point to the nature of the change on their own. The inadequacy of a $kl_x$ type life table is underlined by the changes in recruitment documented in this study, which violates the basic assumptions of population stability needed for such an analysis. The marked decrease in recruitment of 1974 and 1975 seems to be about equally influenced by reduced ovulations and increased pup mortality from fox predation. Many changes have occurred in the Canadian arctic in the past 20 years. The subsistence culture of the Inuit is being replaced by a cash–revenue economy. Modern Inuit depend on the sale of furs and seal pelts to finance their hunts which provide the main source of food for their growing population. Recent European anti-sealing campaigns have severely affected the ability of the Inuit to generate enough cash from hunting to pay their operating costs. Recent concerns of the Inuit and environmentalists involve the impacts of industrial development especially from the petroleum industry on seals. Oil spills, which have not yet occurred on a large

scale are not thought to pose as serious a threat to seals as was once envisaged. Adult ringed seals are able to withstand and recover from immersion in oil, but the effects on newborn seals would be more severe. Other oil-related impacts such as disturbance from ice-breaking tankers and underwater noise are more difficult to assess empirically. The effect of contaminants such as heavy metals and chlorinated hydrocarbons is not thought to be a major problem in the Canadian north. Integrated ecosystem research is needed to identify the mechanisms involved in regulation of marine mammal populations. This study has documented a significant reduction in ovulation in 1974 and 1975 which resulted in reduced recruitment. This was correlated to a significant reduction in body condition in the same years, but we have no quantitative information about fish or their availability, or on other levels of production in the ecosystem. New techniques including radio telemetry and satellite remote sensing are available and should be used to study ringed seals. The projected doubling of the Inuit population by the year 2000 will place more pressure on ringed seal populations, which will be increasingly used as human food.

## Résumé

SMITH, T.G. 1987. The ringed seal, *Phoca hispida*, of the Canadian western arctic. Can. Bull. Fish. Aquat. Sci. 216: 81 p.

Au cours des années 1971 à 1983, j'ai étudié les phoques annelés, *Phoca hispida*, de la région de Holman, dans le golfe d'Amundsen, Territoires du Nord Ouest, et de plusieurs autres localités au sud est de la mer de Beaufort. Les plus fortes densités de phoques annelés (2,84/km$^2$) furent retrouvées au détroit du Prince Albert, au golfe d'Amundsen. Cette région se transforme à chaque année en une zone de bonne glace côtière stable laquelle est utilisée de façon régulière comme habitat de reproduction. La structure d'âge des prises indique qu'une ségrégation des animaux plus âgés se produit en hiver et au printemps aux zones de glace côtière stable alors que toutes les classes d'âge sont présentes au cours de la période estivale. En automne les jeunes de l'année et les adolescents occupent les zones côtières du golfe d'Amundsen lesquelles servent de zone de reproduction après le gel. Les phoques marqués au cours de cette étude furent retrouvés aussi à l'ouest de Pointe Barrow en Alaska et Inchoun en Sibérie. Dans le golfe d'Amundsen, la glace de meilleure qualité pour la reproduction est caractérisée par sa stabilité, par la présence de glace hummoquée ou crètes de pression lesquelles créent des zones d'accumulation de neige où seront creusés les repères de naissance sous-nivéens. Ces repères possèdent la double fonction de protéger des prédateurs et de servir d'abris thermiques. Toutefois, les ours blancs, *Ursus maritimus*, et les renards arctiques, *Alopex lagopus*, tuent les phoques dans leurs repères. Les renards arctiques sont les prédateurs les plus importants des blanchons des phoques annelés dans l'ouest de l'Arctique Canadien. Une forte territorialité existe dans la zone de reproduction. Il y a une forme de polygynie limitée dans la population de phoques annelés; le mâle défend un territoire qui regroupe plusieurs femelles avec leur complexe de sous-territoires et de repères de naissances. Une diminution significative du nombre de repères de naissance, trouvés par les chiens, fut documentée en 1974 et 1975. En 1975, j'ai aussi découvert que le nombre de repères occupés par les mâles en rut était fortement réduit. La prédation par les renards arctiques a atteint un sommet en 1973–74, soit un an avant le plus haut record de récolte de renards par le piégeage. Une prédation élevée par les renards fut aussi documentée en 1974–75 en dépit du fait qu'il y eut une réduction sérieuse du nombre de naissance de phoques annelés. Les jeunes phoques annelés naissent au milieu d'avril. En moyenne, l'ovulation se produit le 21 mai et le blastocyste s'implante le 18 août. La période active de gestation dure 241 jours et le délai de l'implantation est de 89 jours. Les femelles atteignent la maturité sexuelle à 5,61 ans et l'âge moyen de la première reproduction est de 7,67 ans. La proportion des sexes à la naissance est de 1:1. On calcule qu'aux années de reproduction normale, les taux moyens sont de 0,56. En 1974 et 1975 les taux d'ovulation ont été réduits respectivement aux valeurs de 0,41 et 0,38 lesquelles sont basses comparativement au taux moyen de 0,89 des autres années. L'indice de condition physionomique des phoques adultes était aussi significativement réduit en 1974 et en 1975. On calcule que la longueur des jeunes à la naissance est de 632 mm (STL) dans la région d'étude et que le taux de croissance fétale est de 2,2 mm/jour; la croissance post-natale jusqu'au sevrage est de 6,1 mm/jour alors que la croissance de la première année suivant le sevrage est réduite à une base valeur de 0,099 mm/jour. Cette recherche indique que 4% des phoques mesurés possédaient une taille beaucoup inférieure à la moyenne de leur classe d'âge respective et 11% une

taille modérément inférieure à la moyenne. La date de naissance et les conditions d'alimentation médiocres pendant la première année d'existance en serait la cause. Les phoques annelés se nourrissent d'une variété de crustacés au cours de la saison sans glace, comprenant *Parathemisto libellula, Thysanoessa rashii* et *Mysis oculata*. Pendant la période de couverture de glace, la morue arctique, *Boreogadus saida*, constitue l'aliment le plus important de toutes les classes d'âges de phoques annelés. Les sortes de proies différentes et les périodes d'alimentation diverses démontrent qu'il existe une compétition pour l'alimentation entre les adolescents et les adultes. Du printemps jusqu'au début de septembre, les indices de condition de toutes les classes d'âge décroissent. L'utilisation de la morue arctique comme nourriture par les groupes de phoques annelés adultes se produit chaque automne et cette saison est une période importante au cours de laquelle les phoques améliorent leur condition physionomique. Puisqu'ils sont alors exclus du territoire, ceci constitue vraisemblablement la cause immédiate de la migration des jeunes et des adolescents vers l'ouest, le long du continent, vers la mer de Beaufort et la mer de Bering. L'analyse des taux de survie estimés à partir des courbes de capture ne mêne pas à une image claire ni précise des changements annuels à l'intérieur d'une population de phoques annelés. Même si ces données réflètent la baisse drastique de recrutement qui fut documentée, en 1974 et 1975, par le biais des données de reproduction et de l'évaluation de l'habitat de reproduction, la sensibilité des courbes de capture n'aurait pas été suffisante pour permettre de démontrer les causes précises de ces changements. L'imperfection d'une table de survie de type $kl_x$ est mise en évidence par les variations de recrutement documentées dans cette étude, lesquelles défient les hypothèses de base reliées à la stabilité de population qui sont requises pour ce genre d'analyse. Depuis 20 ans, plusieurs changements se sont produits dans l'Arctique canadien. La culture des Inuit fondée sur la subsistance se transforme en une économie de revenus. Les Inuit modernes dépendent de la vente des fourrures et des peaux de phoques pour le financement de leur chasse laquelle fournit la principale source de nourriture pour leur population croissante. Les campagnes européennes récentes contre la chasse aux phoques ont durement affecté la capacité des Inuit de générer suffisamment de revenus de leur chasse pour défrayer leurs coûts d'opérations. Les Inuit et les environnementalistes se soucient actuellement des effets possibles, sur les phoques, du développement industriel, particulièrement de l'industrie pétrolière. Les déversements d'huile accidentels, qui ne se sont pas encore produits à grande échelle, ne sont plus considérés comme une menace sérieuse pour les phoques, contrairement à ce qu'on avait initialement envisagé. Les phoques annelés adultes peuvent résister à une immersion dans l'huile et s'en remettre; toutefois, les conséquences sur les blanchons seraient plus graves. D'autres effets reliés à l'huile tel que les dérangements causés par les bateaux-citernes, brises-glace et les bruits sous-marins sont plus difficiles à évaluer de façon empirique. L'effet des contaminants tel que les métaux lourds et les hydrocarbones chlorés ne semble pas constituer un problème majeur au Nord canadien. Il est néeessaire de conduire une recherche intégrée sur l'écosystème afin d'identifier les mécanismes régissant les populations de mammifères marins. La présente étude a révélé qu'une diminution significative du taux d'ovulation s'était produite en 1974 et 1975 et avait causé une réduction du recrutement. Ceci fut corrélé à une diminution significative de l'indice de condition des phoques aux mêmes années,mais nous n'avons pas d'information quantitative sur les poissons et leur disponibilité ou sur les autres niveaux de production de l'écosystème. Des nouvelles techniques, incluant la radiotélémétrie et la télédétection par satellite sont disponibles pour l'étude des écosystèmes arctiques. Le doublement de la population Inuit, prévu pour les années 2000, engendrera une plus grande pression sur les populations de phoques annelés qui constitueront une source de nourriture de plus en plus utilisée.

# Introduction

The aboriginal people of the western North American arctic have been dependent on sea mammals since their first occupation of the coastal regions of Alaska, western Canada, and Greenland over 6 000 years ago (Jenness 1925; Collins and Henry 1958; Giddings 1967; Bandi 1969; McGhee 1974; McGhee and Tuck 1976). Because the ringed seal, *Phoca hispida*, is the most abundant of the arctic marine mammals, adapted to life in land-fast sea ice and thus available throughout the year, it formed the basis of the very stable coastal Inuit economy (Maxwell 1979). In recent times ringed seals and to a much lesser extent bearded seals, *Erignathus barbatus*, are an important source of protein and until recently a primary part of the cash income of most Canadian arctic coastal villages.

In the mid-1960's (Foote 1967) and again starting in 1977 (Wenzel 1979) the anti-seal hunting protests adversely affected the demand for arctic seal pelts. Ringed seals are also the main prey species of the polar bear, *Ursus maritimus*, (Stirling 1974; Stirling and McEwan 1975; Stirling and Archibald 1977; Smith 1980a) and an important food item in the diet of the arctic fox, *Alopex lagopus* (Smith 1976a). Both these species also play a prominent role in the cash income of modern Inuit hunters (Smith 1980b). Inuit from four villages, Tuktoyaktuk, Paulatuk, Sachs Harbour, and Holman (*Ulukhartok*) currently harvest seals from Amundsen Gulf and the Beaufort Sea.

In the last decade exploration for oil and gas has led to the discovery of considerable reserves in the offshore areas of the southeastern Beaufort Sea. Initial concerns about the impact of industrial activities on the environment were directed at the possible effects of accidents such as oil spills resulting from blowouts of offshore wells (Milne and Herlinveaux 1977; Blood 1977). A number of studies were conducted to evaluate the quantity and dispersion of oil which would result from offshore oil well blowouts in the Beaufort Sea (Milne 1977); and also attempted to assess the short-term effects of contact and ingestion of oil on ringed seals (Geraci and Smith 1976a, 1976b, 1977; Englehardt et al. 1977; Geraci and St. Aubin 1979). Some direct and measurable adverse effects were demonstrated, but it was generally concluded that many of these were reversible over time and would be of considerably less consequence than had been previously assumed. While some animals such as sea birds (Brown et al. 1973; Nettleship 1977) and polar bears (Øritsland et al. 1981) would suffer considerable mortality should they contact oil directly, seals and whales (Brown et al. 1983; Geraci et al. 1983; Smith et al. 1983) would probably sustain relatively minor damage.

Recent thought ascribes more importance to other less direct, but possibly more harmful effects of industrial activity in the arctic. Year-round ice-breaking tanker traffic, which will be used to transport oil and gas, has a potential of directly destroying the fast-ice breeding habitat of ringed seals in the path of the ice-breaking ships or, on a large scale, by destabilization of ice edges such as those bordering the Bathurst polynya in Amundsen Gulf.

The ability to assess the effect of man-made impacts on ringed seals will depend on being able to quantify the amount of annual variability in their distribution, numbers and population parameters over large geographical areas in the arctic. Past studies of ringed seal populations were usually based on one or a few years of data from a small area, with the unstated assumption that the population had a stable age structure and that annual recruitment was constant (McLaren 1958a; Smith 1973a). These assumptions made in the absence of any supporting data were necessary for calculating population parameters from a life table based on shot specimens obtained from the Inuit harvest. Recent studies in the Canadian Beaufort Sea and Amundsen Gulf have provided direct evidence of significant annual changes in the numbers (Stirling et al. 1977; Stirling et al. 1982) and recruitment (Smith and Stirling 1978) of ringed seals.

This study spans the years 1971 to 1983. It documents the distribution, movements, feeding and vital parameters of the ringed seals occupying Amundsen Gulf and the southeastern Beaufort Sea. I examine the variability in numbers, body condition, food, annual recruitment, mortality, and attempt to elucidate the underlying causes and the mechanisms of population change.

## The Study Area

### Sampling Sites, Bathymetry, and Oceanography

Studies were conducted at Herschel Island (69°30′N, 139°00′W), Brown's Harbour (70°05′N, 124°22′W), Sachs Harbour (71°59′N, 125°13′W) and Holman (70°43′N, 117°43′W), bordering on the southeastern Beaufort Sea and Amundsen Gulf (Fig. 1). The eastern Beaufort Sea is heavily influenced by the large plume of sediment-rich fresh water from the Mackenzie River extending 30–65 km offshore and affecting a large area out from the river mouth (Grainger 1975). This part of the Beaufort Sea has a shallow shelf, averaging less that 50 m in depth, which extends 80–110 km outwards from the coastline (Henry 1975). Off the shelf there are deep-water areas, reaching a maximum depth of more than 3 500 m north of Herschel Island (Burns 1973). In Amundsen Gulf, depths in excess of 500 m have been measured. Maximum depths of 350 m and 268 m have been recorded in the large bays of Prince Albert Sound and Minto Inlet on western Victoria Island.

Surface currents in the Beaufort Sea are anticyclonic. The gyre is centred at approximately 80°N and 140°W coinciding with the atmospheric-pressured anticyclonic winds (Herlinveaux and De Lange Boom 1975). Little is known of the surface currents or water masses in the Amundsen Gulf. Local knowledge and personal observations indicate that the surface currents are possibly anticyclonic as shown by a northerly current on the west and a southerly current on the east side of Prince of Wales Strait.

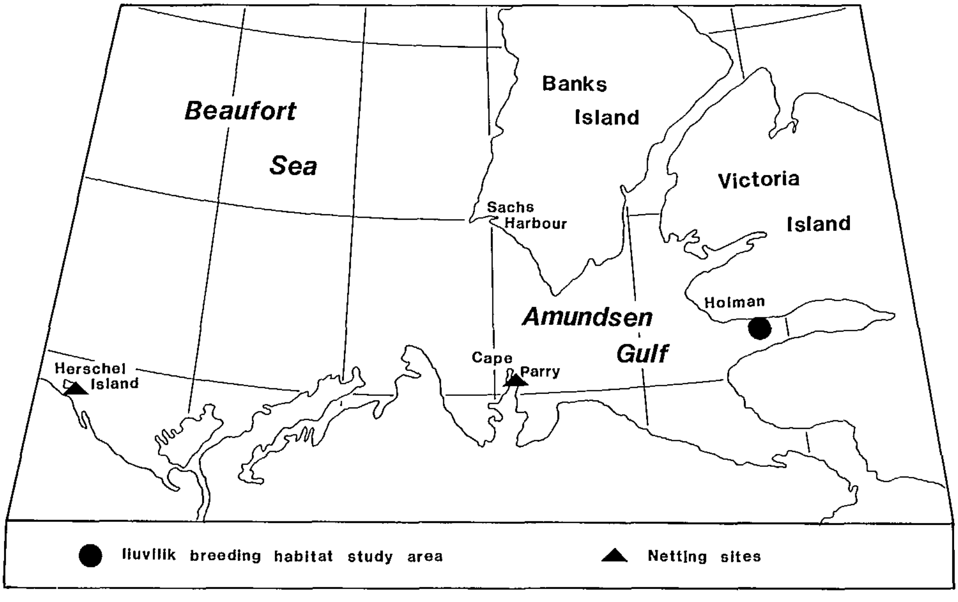



FIG. 1. Location of seal netting sites, collecting and study areas, in Amundsen Gulf and southeastern Beaufort Sea area.

Tides in the eastern Beaufort Sea and Amundsen Gulf have a maximum amplitude of less than 1 m (Canadian Hydrographic Service 1984). Wind and sea states often mask these tides completely.

## Climate and Sea Ice Conditions

The Beaufort Sea–Amundsen Gulf Region has mean air temperatures of 12°C in July and of – 35°C in January (Unpublished report of Fenco Consultants and F.F. Slaney Co. 1978). In the Beaufort Sea the land-fast sea ice begins to form in late September and extends some 16 to 50 km offshore (Usher 1970; Burns 1973). A shear zone, often seen as a large open-water lead, extends in a northeasterly direction. In some years it reaches almost to the west coast of Banks Island in the area between Sachs Harbour and Norway Island (Milne 1977). This marks the boundary between the annual fast-ice and the mixed-age polar pack-ice of the northern Beaufort Sea.

In Amundsen Gulf, sea ice is almost exclusively of the first-year type. Freeze-up begins in the northern part of the gulf in the third week of September. Often an area of open water exists off the southern tip of Banks Island extending west to Cape Bathurst. The location and extent of the Bathurst polynya, as it is sometimes called, varies considerably from year to year (Lindsay 1975, 1978). In some years it does not occur; in others it may extend from Cape Bathurst, to as far east and north as the west coast of Victoria Island near the village of Holman.

Marko and Fraker (Unpublished report by Arctic Sciences Ltd. and L.G.L. Ltd. 1981) examined ice cover data back to 1973. They indicate that the fast ice boundary usually forms along lines linking Cape Bathurst on the mainland to Cape Kellett or Cape Lambton on the west coast of Banks Island. Hammill (1986), in examining an even larger data set dating back to 1964, showed the variability in the formation and extent of the Bathurst polynya in more detail (Table 1). He concluded that the formation and maintenance of the Bathurst polynya depended primarily on the offshore winds prevailing in the area during April and May, as was also shown in Markham (1975) for the southeastern Beaufort Sea. Hammill (1986) showed that the locations of the high and low pressure weather systems are directly related to ice retreat patterns. In the Amundsen Gulf wind direction appears to be the single most important factor in influencing ice retreat. In years of early ice break-up southeast winds predominate in the spring, which clear ice out of the gulf quickly and prevent Beaufort Sea ice from blocking the western exit. There was also a strong negative correlation between the time of ice break-up and the timing of the following freeze-up in Amundsen Gulf. It appears that years of early break-up followed by late ice advance may be related to the persistence of spring barometric pressure patterns resulting in a southeasterly wind component throughout the summer and into the autumn. Timing of break-up in the Beaufort Sea (Markham 1975) corresponded to that of Amundsen Gulf in 7 of 11 years examined.

## Marine Biological Studies in the Area

The Canadian sector of the southeastern Beaufort Sea is relatively low in primary and secondary productivity (Grainger 1975). While some studies of the phytoplankton (Hsiao 1975; Hsiao et al. 1977), zooplankton (Grainger 1965, 1971; Mohammed and Grainger 1974; Grainger and Grohe 1975), nutrients (Grainger 1974) and marine fish (Hunter 1979) exist for the Mackenzie Delta and Canadian Beaufort Sea, little is known of the productivity or distribution of the marine fauna of Amundsen Gulf (Shih and Laubitz 1978).

Virtually no data exist on the food of ringed seals in the western Canadian arctic. In the Alaskan Beaufort Sea, Lowry et al. (1980) indicate that pelagic euphausiids (*Thysanoessa* spp.), hyperiid amphipods (*Parathemisto libellula*) and Arctic cod (*Boreogadus saida*) are

TABLE 1. Location and extent of the Bathurst polynya, the date of formation and breakup of ice cover in Amundsen Gulf, Northwest Territories for the years 1964–83 (from Hammill 1986).

| Year | Location of polynya | Date of Breakup | Date of Freeze-up | Open water | Ice cover in June | | |
|---|---|---|---|---|---|---|---|
| | | | | | $^{5}/_{10}$ pack | $^{6-9}/_{10}$ pack | Fast ice |
| 1964 | No polynya | Late | Early | | | | |
| 1965 | Cape Lambton to Cape Parry east to Darnley Bay | Medium | Medium | | | | |
| 1966 | Extended east to Holman | Late | Medium | | | | |
| 1967 | No polynya | Late | Early | | | | |
| 1968 | No polynya | Early | Late | | | | |
| 1969 | In normal location | Medium | Late | | | | |
| 1970 | In normal location | Early | Medium | | | | |
| 1971 | Extended east to Holman | Early | Late | | | | |
| 1972 | Small polynya off Sachs Hbr. | Medium | Medium | | | | 100% |
| 1973 | No polynya | | | 8% | | | 92% |
| 1974 | Narrow, Sachs Hbr. to C. Bathurst | | | | | | 100% |
| 1975 | | | | | | | 100% |
| 1976 | | | | | | | 100% |
| 1977 | | | | 26% | 1% | 30% | 43% |
| 1978 | Very broken up well into Amundsen Gulf | | | 23% | 12% | 30% | 35% |
| 1979 | | | | | | | 100% |
| 1980 | | | | | | | 100% |
| 1981 | | | | 56% | | 15% | 29% |
| 1982 | | | | | | 1% | 99% |
| 1983 | | | | | | 9% | 91% |

important to the ringed seal. This is particularly so because these species occur in concentrations which can be efficiently exploited by the seals. Arctic cod, which are the main prey in autumn and winter, show considerable variability in their distribution from year to year in some areas (Quast 1974; Lear 1979; Craig et al. 1982; Sekerak 1982). Their summer distribution in the western Beaufort Sea appears to be closely linked to the receding ice edge. Significant variability in the size of different age classes (Frost and Lowry 1981) and absence of certain cohorts of the cod (Hunter 1979), could indicate large annual changes in primary productivity and food availability.

## Previous Seal Studies in the Area

Early descriptions of the distribution of marine mammals of the southeastern Beaufort Sea were given by Stefansson (1913a, 1913b, 1914, 1921). Resource utilization studies with notes on the distribution of marine mammals of the Canadian Beaufort Sea are provided by Abrahamson (1963) and Abrahamson et al. (1964). Usher (1965a, 1965b, 1970) describes the economics of seal hunting at Holman and Sachs Harbour. Data on the size composition of a ringed seal harvest at Sachs Harbour are analysed in Usher and Church (1969a, b). Stirling (1973) studied the underwater vocalizations of ringed seals from western Victoria Island. Burns and Harbo (1972) conducted aerial surveys of ringed seals in the western Beaufort Sea, while Smith (1973b), Stirling et al. (1977) and Stirling et al. (1982) made aerial censuses of ringed and bearded seals in the eastern Beaufort Sea and Amundsen Gulf. Smith et al. (1973), Smith and Geraci (1975) and Smith (1976b) describe the capture–recapture techniques, catch, condition and movements of ringed seals taken in nets at Herschel Island and Brown's Harbour. Smith and Stirling (1975, 1978) describe the breeding habitat of the ringed seal and variation in annual recruitment from 1973 to 1976 in the Amundsen Gulf area. Smith (1976a, 1980a) and Stirling and Archibald (1977) comment on the role of arctic foxes and polar bears as predators of ringed seals. Smith and Geraci (1975), Geraci and Smith (1976a, 1976b, 1977) and Englehardt et al. (1977) describe experiments to determine the effects of contact and ingestion of oil on ringed seals of the Beaufort Sea. Addison and Smith (1974), Addison et al. (1986) and Smith and Armstrong (1975, 1978) report on the organochloride residue levels and heavy metal content in ringed seal tissues from Amundsen Gulf.

## Materials and Methods

### Collection and Treatment of Materials

During the 1970's with the high price for seal pelts the Inuit of the western arctic were taking large numbers of ringed seals. This enabled me to organize collections of specimens from several communities. The canine teeth from lower jaws and reproductive tracts of ringed seals were purchased from Inuit hunters who had been provided with labels, maps on which to plot their catches and containers with preservatives. Table 2 lists the number of specimens obtained during the period 1971 to 1983. Additional information was obtained including: body measurements, body weight, tissues, stomach contents and adrenal glands. These were taken from seals which we collected by shooting on the ice, from boats, at the breathing hole, or from animals which had drowned in our nets. We emphasized collections of specimens from the Inuit hunters during the summer open-water season because these

TABLE 2. Number of ringed seal specimens collected and examined by year and locality during this study.

| Year | Location | Number of specimens |
|---|---|---|
| 1966 | Sachs Harbour | 49 |
| 1971 | Holman, Herschel Island | 2 540, 124 |
| 1972 | Holman, Sachs Harbour<br>Brown's Harbour, | 410, 313<br>208, |
| 1973 | Holman | 194 |
| 1974 | Holman, Brown's Harbour | 272, 83 |
| 1975 | Holman, Brown's Harbour,<br>Paulatuk | 422, 30,<br>32 |
| 1976 | Holman, Brown's Harbour | 604, 48 |
| 1977 | Holman, Brown's Harbour | 731, 43 |
| 1978 | Holman | 762 |
| 1979 | Holman | 167 |
| 1980 | Holman | 637 |
| 1981 | Holman | 814 |
| Total | | 8 483 |

seem to provide the least biased age frequency samples (Smith 1973a). I collected seals during the winter and autumn to obtain more detailed information on food, reproductive rates, and body condition.

*Tooth Sections* – Teeth were cut in cross section or longitudinally using the methods described in Smith (1973a). Most age determinations were made by reading the dentinal annuli of cross sections under transmitted light. Usually I made duplicate readings of the tooth, the second reading following shortly after the first. When difficult old teeth were examined duplicate or triplicate readings were made. In these cases cementum readings were also done if the pulp cavity was almost or completely closed. No measurements of precision were calculated for these determinations.

*Tissues and Stomach Contents* – Stomach contents, muscle, blubber and organ tissues were preserved in 10% formalin. Female reproductive tracts were treated as in Smith (1973a). Stomach contents were examined for fish otoliths, a dry random subsample of which was removed prior to preservation of the other specimens in buffered formalin. In the laboratory, contents were measured volumetrically and by weight and classified as a percentage into zooplankton, benthos and fish. Identification was made to species whenever possible.

*Body Measurements* – These were standard length, axillary girth and blubber thickness over the sternum as described in American Society of Mammalogists (1967). Foetuses were measured in a straight line from crown to rump. Whole body weights uncorrected for blood loss of shot animals were measured using a spring scale accurate to ±2 lb.

## Breeding Habitat Surveys

The sea-ice breeding habitat was searched for breathing holes and subnivean lairs using trained Labrador Retriever dogs (Smith and Stirling 1975, 1978). The same bitch (Bug) was used for the searches from 1973 to 1981. In 1983 her male offspring (Beau) who had been trained and run with her in 1980 and 1981 was used as the principal survey dog. The dogs were trained to search out areas and indicate the presence of breathing holes or subnivean lairs by digging. Their olfactory sense is remarkably efficient, enabling them to detect breathing holes or lairs in drifted snow as deep as 200 cm, while working in winds of up to 20–25 knots. Lairs are sometimes detected from distances of 1500 m or greater.

Activity of ringed seals in three subnivean lairs was monitored by inserting microphones through the roof of the structures near the breathing hole via a ½-inch diameter P.V.C. pipe. These lairs were located by the dogs and their extent delimited by probing with a steel rod. The three microphones were linked to a Uher 4000 Report stereophonic tape recorder located in a heated shelter approximately 200 m from the subnivean lairs. Temperature inside the lairs was monitored by inserting a thermistor through the same pipe and linking them to two Rustrak two-channel chart recorders, also located in the heated shelter. One thermometer, which was sheltered from the sun by snow blocks, was placed outside the lairs at approximately 10 cm above the surface of the snow. Wind speeds were monitored using a continuous-run anemometer, placed on the surface of the snow, clear of all obstructions in a radius of 100 m around it.

## Aerial Surveys

Two aerial surveys of the reconnaissance-type were flown on 21 June to 23 July, 1972 and 29 June to 6 July, 1973. Counts of the ringed and bearded seals on the ice followed the procedures described in Smith (1973a, 1973b).

### Capture and Marking of Ringed Seals

Seals were captured in nets at Herschel Island as described in Smith et al. (1973) and at Brown's Harbour in 1972, 1974, 1975, 1976, and 1977. At Brown's Harbour, in 1972, seals were individually marked on the back with hot iron brands using up to three numbers. They were also tagged in the web of one hind flipper using plastic Rototags. The age of each seal was estimated from visual examination of the bands in the claws of the foreflippers; the axillary girth was measured and sex recorded before each was released. Seals caught in subsequent years at Brown's Harbour were not released, but used in physiological experiments (Geraci and Smith 1976a; Englehardt et al. 1977; St. Aubin and Geraci 1977; St. Aubin et al. 1978). They were marked with Rototags only and kept in chain link enclosures in a seawater lagoon near the camp.

All seals that drowned during the netting programs were measured and sampled as described above.

### Data Analysis

Data analysis was carried out using STATPAC (I.B.M. Corporation) and S.A.S. (S.A.S. Institute Inc., North Carolina, 27511, USA) subroutines on a mainframe computer. Many of the routines used were adapted from Fortran programs described in Smith (1970).

## Abundance and Distribution

### Density and Distribution from Aerial Surveys

Reconnaissance aerial surveys were flown in June 1972 and 1973. Amundsen Gulf was completely covered by first-year land-fast ice in both years. Weather conditions for surveying and ice surface conditions were similar in each survey.

Flight paths from both surveys are shown in Fig. 2. For the purpose of analysis the position of each two-minute survey quadrat was located on the track and its distance from the nearest land was measured. In this way the survey was divided into three categories of ice: that within 15 miles of coastline; ice further than 15 miles from shore; and the stable ice in large inlets, sounds and straits.

The densities of seals from the two surveys in the three different ice categories are given in Table 3. Seal numbers per two-minute quadrat were transformed using $\text{Log}_{10}$. Differences in the mean number of seals per quadrat for different categories of ice were examined using Student's $t$ test. Prince Albert Sound in both years and Minto Inlet in 1973 only, had higher densities than all other categories of ice censused ($t = 3.37$, $P < 0.001$ in all cases). No significant difference in density existed between ice within or greater than 15 miles distance from the coast.

In 1972 densities of seals were higher than in 1973 for both the extensive inshore and offshore ice areas of Amundsen Gulf ($t = 5.6$, $P < 0.001$). There were, however, no between-year differences in the densities of the Prince Albert Sound area ($t = 0.65$, $P > 0.5$). In Minto Inlet the density of ringed seals increased drastically from 0.62 per $km^2$ in 1972 to 3.66 $km^2$ in 1973.

### Seasonal and Spatial Segregation of Age Classes

The large collection of ringed seal specimens from the western Victoria Island coast and Prince Albert Sound provides a good picture of the seasonal dispersion and spatial segregation of age classes. The distribution of young-of-the-year (0+), adolescents (1+ to

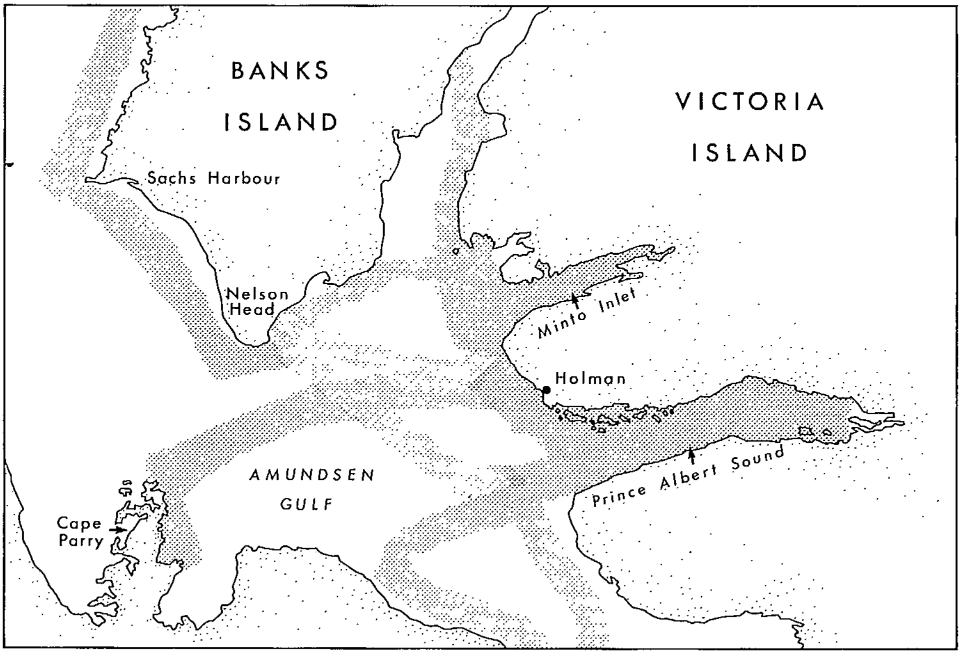



FIG. 2. Flight paths flown during the 1972 and 1973 aerial surveys in Amundsen Gulf and the southeastern Beaufort Sea.

TABLE 3. Densities of ringed seals hauled out on the ice of Amundsen Gulf and southeastern Beaufort Sea from aerial counts in 1972 and 1973. Number of 2-minute quadrats on which mean densities are based are given in parentheses.

| Ice type | Location | 1972 Survey density/km$^2$ | | 1973 Survey density/km$^2$ | |
|---|---|---|---|---|---|
| Within 15 km of coast | Amundsen Gulf and W. Banks Island | 1.43/km$^2$ | (202) | 0.89/km$^2$ | (231) |
| 25 km of coast | Amundsen Gulf | 1.47 | (65) | 0.74 | (74) |
| In large bays, inlets and sounds | Prince Albert Sound | 2.84 | (99) | 2.45 | (152) |
| | Minto Inlet | 0.62 | (35) | 3.66 | (62) |
| | Large Bays on N. Victoria Island | | | 0.31 | (58) |

6+ years) and adults ($\geq$ 7 years) during the summer, autumn and winter– spring periods is shown in Fig. 3. In the summer all age classes appear to be represented in the population, as is the case in other areas where ringed seals have been studied (McLaren 1958a; Smith 1973a).

In the autumn, usually 3 weeks to a month prior to freeze-up, there appears to be an influx of ringed seals into the Prince Albert Sound area. Weather conditions at this time of year are usually not good for hunting from boats, but in 1971 and 1973 I was able to collect samples of these seals during September and early October. Seals during this period are usually found in groups, sometimes numbering upwards of 30 individuals, and are very old

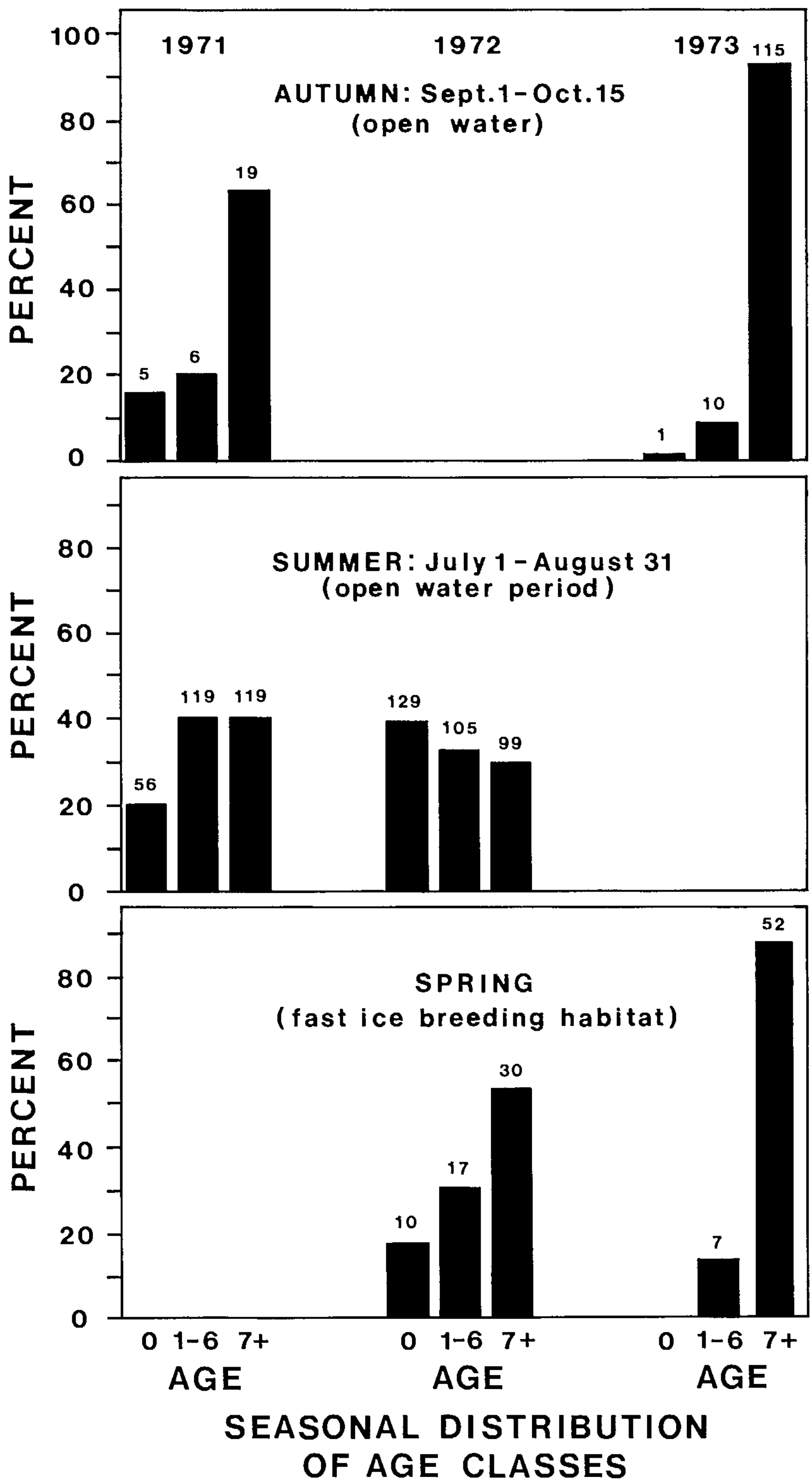



FIG. 3. Seasonal distribution of age classes of seals collected in the Holman, Amundsen Gulf area during the years 1971–73. Sample size is shown above the histogram.

consisting mostly of adults with few adolescents and rarely any young-of-the-year. This is the only time of year when ringed seals are seen together in the water. They are feeding intensely on dense schools of arctic cod which are found in the area at this time in most years. This apparently is of common occurrence in Amundsen Gulf and the southeastern Beaufort Sea. It has been observed at other localities such as Sachs Harbour, Letty Harbour, and Read Island (Bill Joss, Holman, personal communication). Inuit of the area maintain that these are "travelling seals" which have come into the area from a considerable distance away. It is not apparent what forms the basis of this opinion.

In the autumn along the mainland coast most seals caught in our nets are young-of-the-year. Recent observations of groups of seals in the southeastern Beaufort Sea during Bowhead whale surveys (Renaud and Davis 1981. Unpublished report by L.G.L. Ltd. for Dome Petroleum Ltd.), could either be of these young seals moving west towards the Alaskan slope or of feeding groups of older seals preparing to occupy winter habitats.

Seals taken in the spring months, from the fast-ice breeding habitat of Prince Albert Sound, are collected by shooting them when they are hauled out on the ice, or by killing them in their breathing holes. The age composition of this catch is much like the autumn sample, showing a preponderance of sexually mature seals, with only a low number of adolescent and young-of-the-year. Young, that are included in the catches from prime breeding ice, are neonates. Most adolescents in these areas have been collected from early forming leads, or near the end of the fast-ice period, just prior to the ice break-up. In the months of March through June most adolescents collected in areas of good breeding habitat show heavy scarring and fresh bite marks indicating strong aggressive behaviour on the part of the adults holding breeding territories (Smith and Hammill 1981).

In 1971 a large expanse of open water persisted throughout the winter in Amundsen Gulf. The floe-edge of the Bathurst polynya extended as far as the area just offshore of Holman and local hunters were able to kill large numbers of seals, mostly adolescents, in the open water during the period March through May (Fig. 4.). Since the floe-edge hunting area was contiguous with land-fast ice occupied by adult breeding animals, it was inevitable that a number of sexually mature specimens were also killed. These adults may have been involved in actively preventing adolescents from entering the fast-ice breeding areas since there was a very high incidence of bite marks on the bodies of adolescent seals taken along the floe-edge in 1971. It is possible, however, that these marks may also have resulted from competition among the adolescents for food.

A more detailed examination of the age structure of the floe-edge catch reveals an under-representation of neonates (0+) and yearling seals (Fig. 4.) and an expected representation of the remaining adolescent year-classes. It was possible to examine individual catches, taken within a few hours from the same place along the floe-edge, between 13 March and 7 June 1971. Of these catches 32% (13) departed significantly in favour of adolescents from the proportion of adult to adolescent seen in the summer open water catches for Holman in 1971–72 ($\chi^2 > 3.84$ in all cases; $P < 0.05$). Also 43% (16) of the catch showed a significantly greater proportion of male ringed seals ($\chi^2 > 3.84$ in all cases; $P < 0.05$).

## Movements of Marked Seals and Age Structures of Net Catches

Seals were captured in nets at Herschel Island in 1971 and at Brown's Harbour in 1972 and 1974 to 1977.

At Herschel Island 177 ringed seals were captured in nets of which 121 were branded, tagged and released. In 1972, 327 were caught at Brown's Harbour of which 108 were marked and set free. Table 4 lists the details of the four marked seals, which were recaptured. The low recovery of 1.7% (4/229) in 5 years was not unexpected, in view of the small sample size, the large area involved and the small number of Inuit hunters in the few coastal villages of the region. We recovered only one of the four lower jaws of these

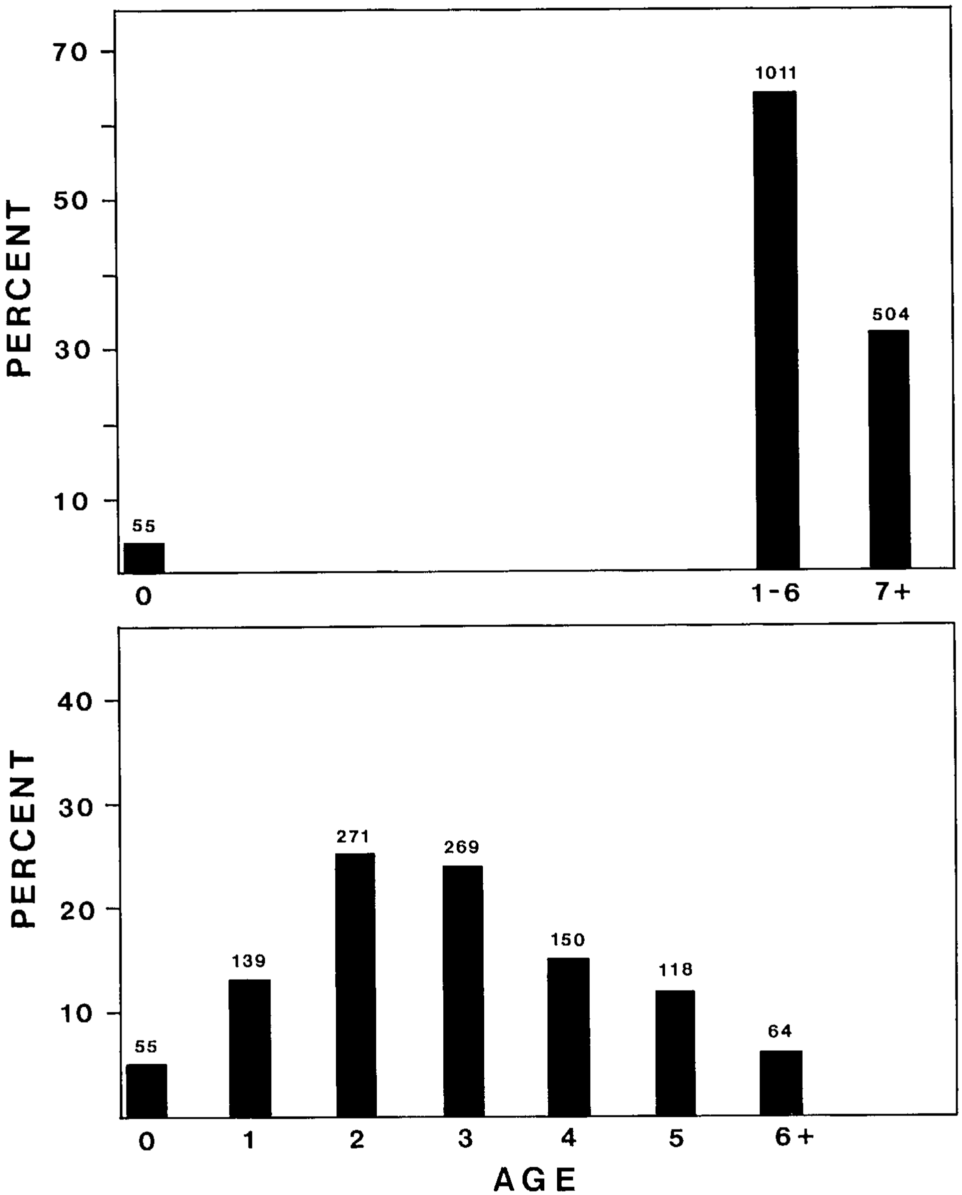



FIG. 4. Age structure of ringed seal catches at the floe-edge during March to the end of May 1971. Sample size is shown above the histogram.

seals. This was determined to be 4 years old which agreed with the date of original capture and the estimate of age we had made at that time.

The netting effort spanned the period mid-July to early October (Table 5). While there was a marked year-to-year variation in the number of seals caught, peak catches regularly occurred in the first 2 weeks of September. Since we pulled out our nets just at freeze-up, we know nothing of the extent of seal movements after early October.

TABLE 4. Information on ringed seals tagged or branded and later shot by Inuit hunters.

| Date and area of capture and release | Age from claw ridges at capture | Sex | Area and date of recapture | Age from tooth at recapture | Distance from original capture site (naut. miles) |
|---|---|---|---|---|---|
| 69°35′N × 139°00′W Herschel Is. Sept. 1971 | Adolescent (2–6 years) | ? | 70°45′N × 117°50′W Holman area June 1973 | 6 years | 435 |
| Herschel Is. Sept. 1971 | 1 year | ? | 71°57′N × 125°15′W Sachs Hbr. 14/7/74 | 4+ years | 305 |
| Herschel Is. Sept. 1971 | 1 year | F | 66°18′N × 170°15′W Injun, East Cape Chuthotsk Penn. Siberia, 20/6/73 | ? | 720 |
| 78°07′N × 124°22′W Brown's Hbr. 10/9/72 | 3 years | M | 71°20′N × 156°40′W Point Barrow, Alaska, April 1974 | ? | 620 |

TABLE 5. Date of capture and number of ringed seals caught in nets at Herschel Island in 1971 and Brown's Harbour in 1972, 1974–77.

| Location and year | Total net days | July | | | | August | | | | September | | | | October |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Herschel Is. 1971 | 34 | | | | | | | 14 | 16 | 81 | 45 | 23 | | |
| Brown's Hbr. 1972 | 41 | | | | | | 41 | 40 | 44 | 32 | 79 | 61 | | |
| Brown's Hbr. 1974 | 52 | | | | | | | | 17 | 22 | 45 | | | |
| Brown's Hbr. 1975 | 54 | | | | 1 | 1 | 7 | 2 | 3 | 10 | 0 | 6 | | |
| Brown's Hbr. 1976 | 45 | | | | | | | 18 | 4 | 14 | 3 | 3 | 24 | 2 |
| Brown's Hbr. 1977 | 67 | 6 | 0 | 2 | 0 | 3 | 0 | 5 | 2 | 5 | 3 | | | |

TABLE 6. Frequency and percent age composition of ringed seals caught in nets at Herschel Island in 1971 and Brown's Harbour in 1972, 1974–77.

| Age (years) | Herschel Is. 1971 | | Brown's Hbr. 1972 | | Brown's Hbr. 1974 | | Brown's Hbr. 1975 | | Brown's Hbr. 1976 | | Brown's Hbr. 1977 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | f | (%) | f | (%) | f | (%) | f | (%) | f | (%) | f | (%) |
| 0+ | 46 | (37) | 215 | (77) | 22 | (26) | 7 | (22) | 40 | (91) | 31 | (100) |
| 1+ to 6+ | 39 | (32) | 53 | (19) | 28 | (34) | 8 | (25) | 3 | (7) | | |
| 7 | 38 | (31) | 10 | (4) | 33 | (40) | 17 | (53) | 1 | (2) | | |

The largest proportion of seals caught in nets are young-of-the-year (Table 6). While there was considerable variation in the age composition from year to year an overall 61% (361/591) of the net catches were of 0+ year-old seals. Adolescents (1+ to 6+ years) made up 22% and adults (≥7 years) 17% of the total net catch.

## Discussion

Aerial surveys of ringed seals hauled out on the ice in early summer is the main method used to estimate population size. There are various problems associated with this technique including the reassortment of the age classes at this time of year (Smith 1973a), movement of individuals in from other areas to haul out on the remaining ice (Smith and Hammill 1981), and other unidentified oceanographic factors increasing the availability of food or creating local conditions promoting an uneven distribution of seals. The probability of estimates derived from the early summer aerial survey being representative of the resident winter population of the area, especially in view of the inherent imprecision of aerial counts (Kingsley 1985), is thus likely to be very low. Aerial survey estimates should probably be considered indices of abundance and reflections of ice and other environmental conditions prevailing during the time the surveys were conducted.

Our brief survey in Amundsen Gulf during 1972 and 1973 showed that the highest densities of seals are found in Prince Albert Sound. This area has long been recognized by the Inuit as the prime breeding habitat of the region. Stefansson (1913a) in 1911, found the largest concentration of Inuit in the region living on ringed seals, which they hunted from their snowhouse village, on the ice of Prince Albert Sound. These people, the *Kaneriuargmiut* (*Kaneriuak* = Prince Albert Sound, *miut* = people of) hunted ringed seals at the breathing holes with harpoons. When the seals were depleted around their village they simply moved to a new site where seals were abundant. Stefansson found three abandoned villages as he travelled eastward into Prince Albert Sound in search of the "Copper Eskimo".

Ringed seal densities in 1972 and 1973 were similar in Prince Albert Sound. Overall densities in the remainder of Amundsen Gulf decreased from 1972 to 1973, but not significantly. There was however a significant increase seen in the densities observed in Minto Inlet in 1973, the only other large bay on the west coast of Victoria Island (Fig. 5).

Densities of seals calculated from aerial surveys vary considerably from year to year in Amundsen Gulf and do not appear to relate simply or directly to prevailing ice conditions. This might be caused by the present rather crude and imprecise methods available in the

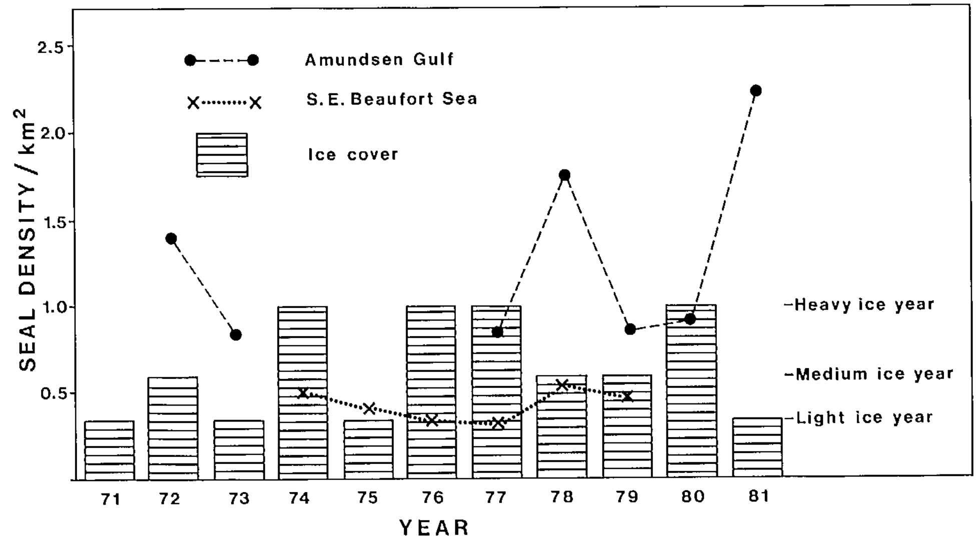



FIG. 5. Ringed seal densities and ice conditions in Amundsen Gulf and the southeastern Beaufort Sea during the years 1971–81.

quantification and description of ice available from large-scale coverage techniques such as ice observer flights and satellites. Significantly increased densities of seals (Kingsley 1984, 1985) were found in 1981 over 1980 and 44% decrease was detected between the 1982–83 and his 1984 estimates. In 1981 break-up was much earlier and there was much more open water in Amundsen Gulf. The high densities of northern Amundsen Gulf that year were attributed to an influx of seals from the open-water area. At the same time they did not observe a density decrease away from the ice-edge. My 1973 surveys also showed what might have been an influx of seals by the marked increase in densities of Minto Inlet, even though the overall densities in Amundsen Gulf were much lower than in 1972.

Stirling et al. (1982) documented a large decrease in density of ringed seals in the southeastern Beaufort Sea during the period 1974 through 1977. They attribute this to the heavy ice of 1974. Their population densities continued to decline through 1977, then increased significantly in 1978–79. A corresponding increase in seal densities of Amundsen Gulf appears to have taken place in 1978 (Fig. 5). From the few data available, it appears that fluctuations of densities of ringed seals in the southeastern Beaufort Sea and Amundsen Gulf correspond in timing. These changes in abundance also seem to be related to changes in reproductive rates and body conditions (see sections on Growth and Reproduction). It is, however, difficult to explain why some of Amundsen Gulf appears to show different densities in some years while Prince Albert Sound appears to remain fairly constant. The differences may relate to yet undetectable differences in ice or snow conditions or to oceanographic features influencing the distribution of seals in the early summer. There is also a difficulty in identifying the exact conditions during which the maximum number of seals will haul out on the ice. Smith and Hammill (1981) showed that between 23 and 80% of the maximum estimated number of seals would be lying on the ice during the months of May and June.

Movements of seals manifest themselves both as seasonal reassortment of age classes in the nearshore areas of Amundsen Gulf and as a migration westward along the mainland coast towards the Beaufort and Chukchi Seas.

The seasonal age structure of the Inuit catch shows adult ringed seals to occupy the coastal areas in the autumn months and use the fast-ice breeding habitat to the exclusion of adolescents, in the winter and spring. The catches from the open water period in the summer appear to contain all the age classes in the population. This is a very similar situation to that shown by McLaren (1958a) and Smith (1973a) along the east coast of Baffin Island. Seals taken from the open water and broken pack-ice, which existed in Amundsen Gulf in 1971, were predominantly adolescent seals. The yearling age classes were under-represented, suggesting perhaps that they had moved further away from the area during the previous autumn migration. Individual catches from Inuit hunting at the floe-edge also showed that there was sexual segregation in their catches with a preponderance of males in the harvest. This might be related to the fact that adolescent males were most likely to occupy the areas on the fringe of the fast-ice breeding habitat, to attempt to copulate with sexually receptive females.

Catches from our netting sites and returns from our tagged seals indicate a migration to the west along the coast of Amundsen Gulf and the southeastern Beaufort Sea in the autumn. This reached its peak in the first half of September. The majority of ringed seals involved in this movement are young-of-the-year. This probably is prompted by intraspecific competition for food and territorial exclusion by sexually mature seals which are seen to be moving into areas such as Prince Albert Sound and feeding heavily on *Boreogadus saida* (see section on Feeding). Areas in the western Beaufort, Chukchi and Bering seas remain clear of ice during the winter and some of the more southern areas have a much higher marine productivity and a greater variety of feeding niches. Young seals which have undeveloped hunting abilities would probably have an easier time surviving there where competition for food and territorial aggression from adult seals is reduced.

## The Breeding Habitat

### Description of the Sea Ice Habitat

The ringed seal is an occupant of the land-anchored (land-fast) ice where it maintains breathing holes sometimes through 2 m or more ice by abrading it with its foreflippers. The Inuit culture was able to establish itself in the arctic primarily because of the year-round availability of ringed seals. By building their snow houses on the sea ice and hunting the nearby seals they were assured of a supply of blubber for heating and light, food for maintenance of people and dogs and skins for clothing.

The sea ice is a heterogeneous habitat subject to the influence of wind and tidal deformation. Surface features such as pressure ridges and ice hummocks created by ice deformation are important to the ringed seals since they accumulate snow, thus providing sufficient depth in which the seals can dig out their subnivean lairs. The degree of stability of the ice cover as reflected by the spacing of ridges and hummocks appears to be a key factor in determining whether a specific area of sea ice will become good breeding habitat in a particular year.

Both the overall extent of land-fast ice and surface features in the same region varies considerably from year to year and as a result prime breeding habitat is not always located in exactly the same place. Snow cover is also variable, not depending on total precipitation as much as the duration and extent of wind. Unfortunately, current remote sensing technology does not give fine enough resolution to permit large-scale evaluation of ice as breeding habitat.

In Amundsen Gulf freeze-up begins around mid-October. The landward ends of Minto Inlet and Prince Albert Sound (Fig. 1) begin freezing at this time and are usually completely frozen by mid-December depending on wind. It is during this period of the year that wind shapes the surface features of the ice. Ice pushed up into hummocks and ridges is usually around 20–40 cm thick indicating deformation has occurred within the first two months of freeze up. Prince Albert Sound, around the area called Iluvilik has long been a known productive breeding habitat for ringed seals. It is there that I conducted my birth habitat surveys over the period 1972 to 1983.

From observations in the late autumn just before or during freeze up large groups of adult ringed seals are seen to move into these areas which will later become breeding habitat. The age structure of these groups of adult males and females collected during October 1971 and 1973 is very similar to the age of seals taken in the breeding habitat of the same area the following spring (Fig. 6). Without direct evidence it thus appears that breeding seals occupy the Prince Albert Sound breeding ice near the beginning of freeze up, but the exact timing of construction of the subnivean lairs varies. Smith and Stirling (1975) described the different types of lairs and their spatial distribution, commenting on snow depth required for their construction. Simple haul-out lairs have been found as early as the first week of January. In most years the maximum snow accumulation occurs in March and April. Winds and snowstorms result in the very rapid, sometimes overnight, creation of deep drifts around obstructions such as ice hummocks and pressure ridges. These areas contain seal holes since they were once open cracks. As they are covered with snow they quickly become haul-out sites and birth lairs (Fig. 7). In the *Iluvilik* study area, both pressure ridges and ice hummocks exist in close proximity almost every year. It appears that extensive fields of ice hummocks, each separated by a few hundred metres of flat stable ice, provide the most important type of breeding habitat. Pressure ridges are the second most important site of lair construction. The Inuit of Ulukhartok (Holman) recognize two types: the "*ayorak*", medium-relief ridges of considerable length, which often form in the same place year after year; and the "*koglornerk*" which is really only a crack with a small amount of pressured ice along the edges. The *ayorak* is a stable ridge of sufficient relief to cause snow accumulation to a depth of 60–200 cm, ideal for lair construction. By contrast, the

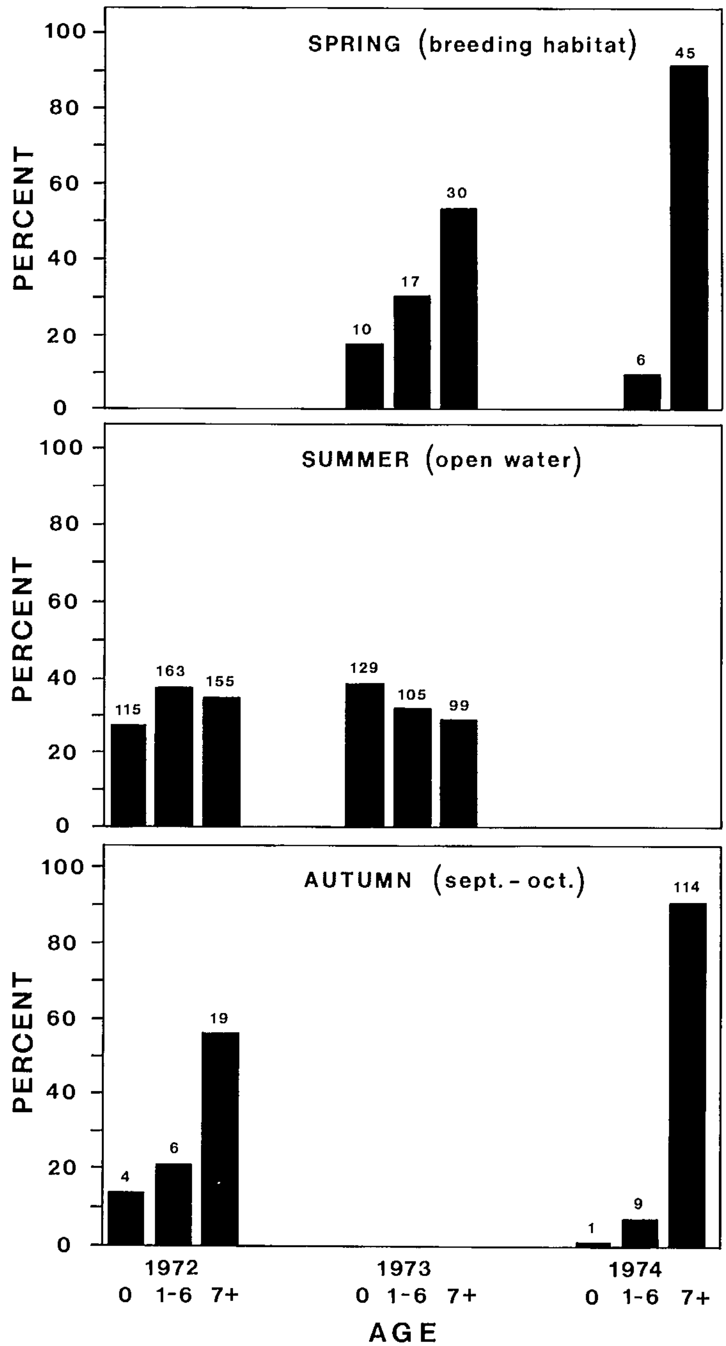



FIG. 6. Age structure of ringed seals occupying the breeding habitat in autumn, spring, and summer.

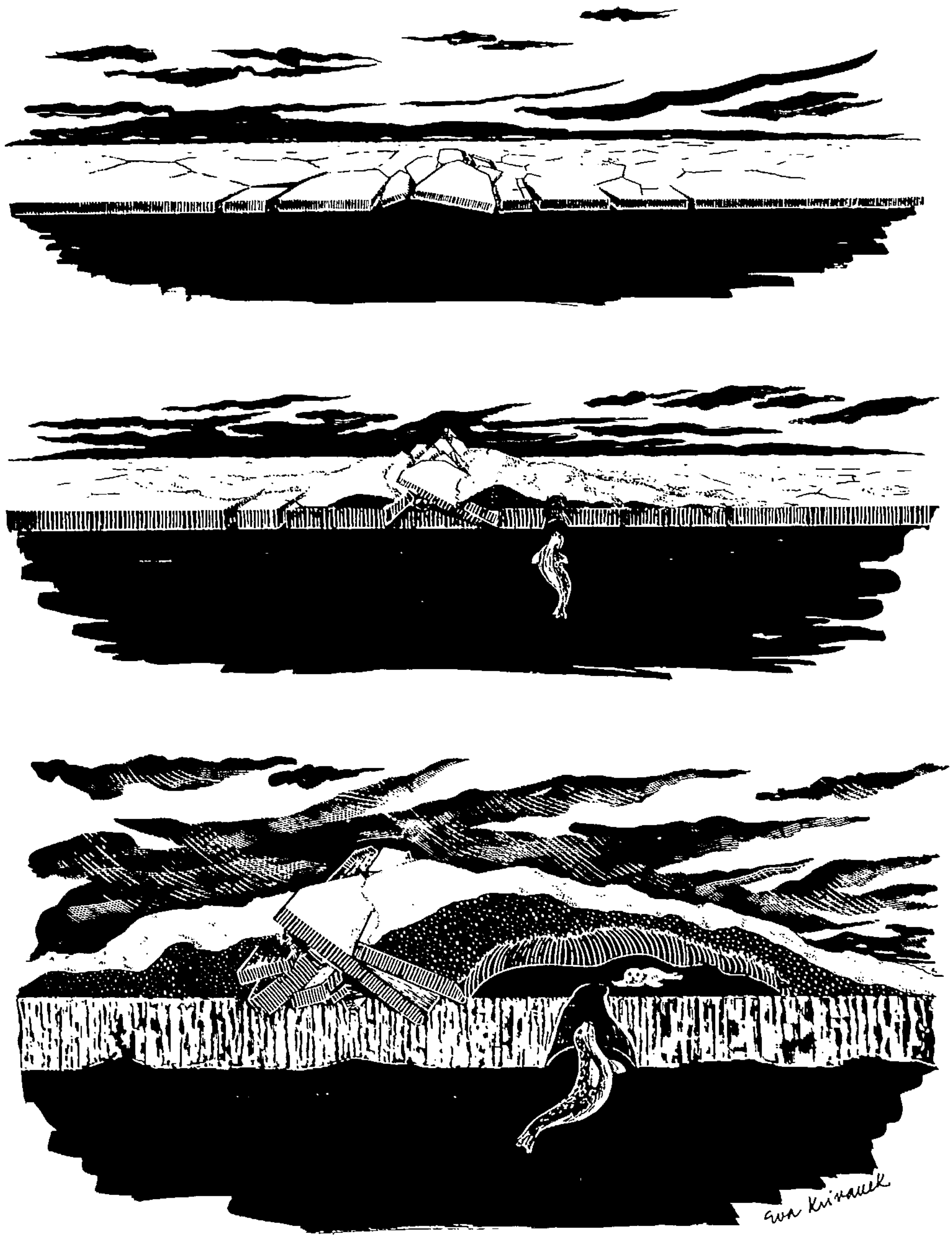


FIG. 7. Development of the subnivean birth lair of the ringed seal (from Smith and Stirling 1975).

*koglornerk* usually does not have much snow along its border and is an unstable crack, opening and closing throughout the winter. It is much less favoured by adult seals for building lairs because of the instability and is often only used by sub-adults as the site for breathing holes.

Occasionally in flat-ice areas with little snow accumulation, a refrozen lead can be seen. These apparently occur in early winter when wind stresses create an opening which refreezes without any pressure deformation along its axis. Often these features have many seal holes along them. They are usually in flat ice, but should snow drifts form over them, they can quickly become sites of subnivean lair construction.

Lairs are distributed around ice hummocks and along pressure ridges (Fig.8). This map was made using the plane table survey technique, and can be considered to be fairly typical showing the location of the subnivean structures as they relate to surface features and to each other.

We recognize two basic lair types. The haul-out or resting lair (*nunariak* or *nunarjak*) is usually single-chambered, measuring approximately 1.5 × 2.0 m with a ceiling of 30 cm and is found in snow of approximately 60 cm in total depth (Smith and Stirling 1975). Some lairs (*tiggaksitit*) can be further recognized as being used by adult sexually active males, called "*tiggak*" by the Inuit because of their very distinct pungent and lingering odour. Birth lairs, *netsiarsitit*, are much larger structures, with the main chamber dimensions of approximately 2.5 × 3.5 m. They are positively identified as birth lairs by tunnels dug off the main chamber by the pup. White hairs, the natal lanugo are frequently found frozen into the snow. Occasionally remains of the placenta are found on the floor of the birth lair. Birth lairs are found in slightly deeper snow than haul-out lairs (65 cm) and are usually close to one or two other birth lairs, which we believe to form part of a birth lair complex used by one female and her pup (Smith and Stirling 1975, 1978; Smith and Hammill 1981).

The Inuit recognize a suckling lair, *miluktitivik*, as part of the birth lair complex, but we fail to differentiate these from birth lairs on a structural basis. Local Inuit also recognize a small haul-out lair near the birth lair complex as a structure to which a neonate will swim unaccompanied by the mother which they call an *ayoarhavik*, which means a "learning lair". We were unable to corroborate this with our data, neither do we have any direct

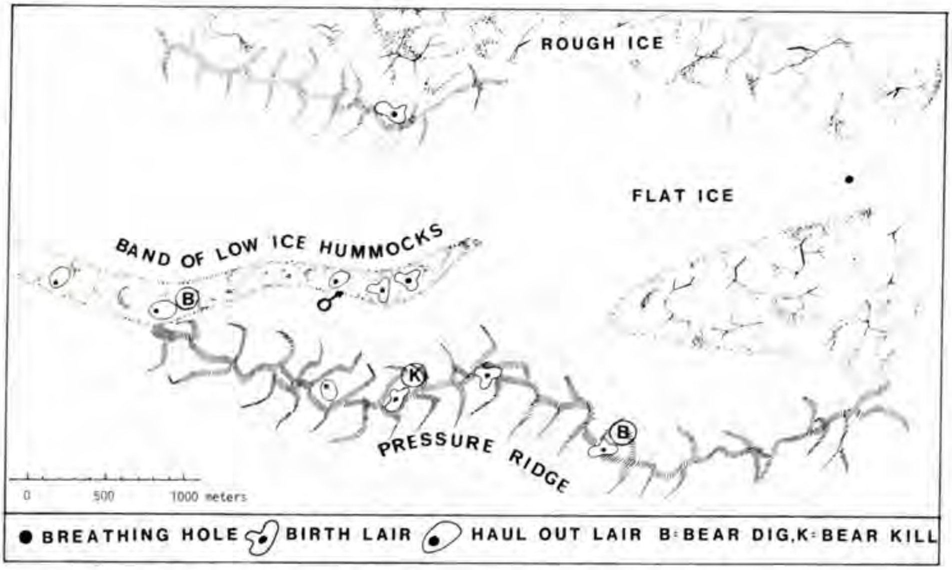



FIG. 8. A plane table map of ringed seal subnivean lairs showing their relationship to surface features of the sea ice.

behavioural observations which would either confirm or deny it. Rarely, one other type of structure called a *kalgik*, is found. I have only detected a few of these along pressure ridges, which have depressions formed by their freezing up while the crack was open. These depressions fill with snow and are dug out as large chambers, which in some cases are used by several seals together. The impression has been that these are sub-adult seals not involved in maintaining territories.

## Age Structure and Behaviour

To date almost nothing is known about the behaviour of ringed seals when they are hidden from view in their subnivean lairs and restricted in movement to a small number of self-maintained breathing holes. Yet this period in their life cycle probably constitutes the single most important one, since they spend considerable time in the same area where food limitations and social interactions will directly influence the future production of the population.

The age structure of ringed seals collected during March through May in the *Iluvilik* area is quite old (Table 7). Sub-adults are missing from the catch until mid-May and the first neonates are seen in late April.

Bite wounds resulting from intraspecific fighting were recorded for all seals collected. Bites were observed in the axilla, on the hind flippers, on the ventral surfaces and sometimes around the genitalia of both males and females. Some extreme wounds were seen on occasion, usually on sub-adult seals, found either dead in haul-out lairs or hauled out onto the surface of the ice. Of the years 1972 to 1978, the maximum number of intraspecific wounds were seen in 1972 and 1974. Bites occurred both on sub-adult males (16%, $n = 32$) and next on adult males (13%, $n = 54$) taken at *Iluvilik*, the difference was not significant. Incidence of fresh bite wounds reached a peak (8%) (6/72) during the period 15–31 May and declined almost to nothing after 15 June.

Of the adolescent males with bite marks, three of the five specimens were almost mature at 5 and 6 years of age. Pups were never found to have been bitten and only (6/74 = 8%) adult females showed bite wounds in the hind flippers, which were relatively light and might have been inflicted during courtship chases.

Starvelings are occasionally found in the breeding habitat. The majority of these show evidence of intraspecific bite wounds. The majority of such seals are yearlings (1+ year old) or neonates. Most of the starveling neonates are found wandering on the surface of the ice, after having failed to relocate their breathing holes (Smith and Memogana 1977). Quite frequently yearlings are found dead hauled out in subnivean lairs. More rarely sub-adult seals are found, either in subnivean lairs, or partially frozen while hauled out on the sea ice.

The increased number of adult males and females caught in subnivean lairs in the period mid-May to mid-June (Table 7) shows a redistribution of adult seals in the breeding territory

TABLE 7. Number of different age and sex classes of ringed seals collected from the study area at Iluvilik, western Victoria Island, N.W.T. and percentage of those taken from subnivean lairs.

| | Adult females | | Adult males | | 1–6 years females | | 1–6 years males | | Pups (0+ years) | |
|---|---|---|---|---|---|---|---|---|---|---|
| Date | *n* | (%) | *n* | (%) | *n* | (%) | *n* | (%) | *n* | (%) |
| March | 3 | (33) | 0 | | 0 | | 0 | | 0 | |
| Apr. 1–15 | 6 | (33) | 5 | (60) | 4 | (75) | 2 | (100) | 0 | |
| Apr. 16–30 | 13 | (54) | 11 | (36) | 4 | (0) | 6 | (17) | 2 | (50) |
| May 1–15 | 23 | (35) | 11 | (18) | 13 | (38) | 18 | (44) | 9 | (56) |
| May 16–31 | 22 | (45) | 16 | (44) | 2 | (0) | 3 | (33) | 1 | (0) |
| June 1–15 | 7 | (43) | 11 | (45) | 4 | (50) | 3 | (0) | 8 | (13) |

and likely indicates a peak in mating activity at that time (see section on Reproduction). Prior to weaning of the pup, adult females appear to stay away from the territorial males and defend their birth lair complexes from them (Smith and Hammill 1981).

Adult male ringed seals emit a strong pungent odour from as early as late January until late May. They are known throughout the arctic as *tiggak* by the Inuit. The function of this odour is not adequately explained. There is very limited and inconclusive evidence that polar bears, arctic fox and survey dogs tend to avoid or bypass male lairs indicating a possible anti-predator function. The odour is associated with the male rut and appears more likely to serve as a means of marking territory prior to mating. While no scent glands have been found in the Phocidae, ringed seals have well developed apocrine sweat glands in the facial area around the lips, under the vibrissae and up to the level of the eyes. The odour appears to emanate from the oily secretion in the facial mask. The dark face of rutting males appears to be caused by this secretion. The occurrence of odoriferous males decreases from 58% (7/12) in April to 11% (2/18) in late May ($\chi^2 = 3.95$, $P < 0.05$) when mating has occurred and the sea-ice breeding territories are breaking down.

The sex ratio of adult animals collected in the breeding habitat does not depart significantly from unity except in the period 1 to 15 May (Table 7; 23 females: 11 males $\chi^2 = 4.24$,

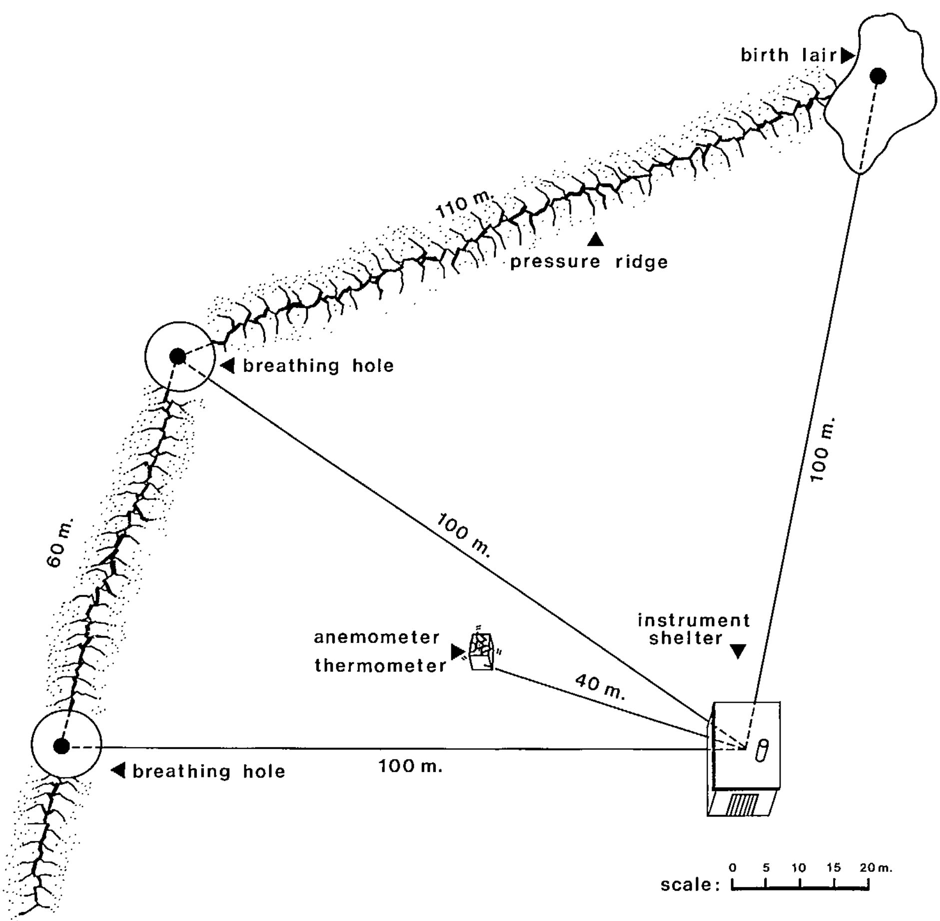



FIG. 9. Map of three subnivean lairs and the equipment shelter used to house the temperature and acoustic recorders.

$P < 0.05$). this might indicate an increase in sexual activity and strong territorial behaviour by the males, perhaps making them more vulnerable to being shot at this time of year.

Activity was monitored in three lairs near Iluvilik during the period 1 to 5 May 1983. Presence or absence of seals and their breathing rate was recorded using microphones which had been installed in the ceiling of the lairs. After opening the lair at the end of the experiment it was found that two of them were no longer being used as areas for seals to haul out and that the third was a possible birth lair with small tunnels visible, but there was no lanugo present (Fig. 9). During this study it was not possible to recognize the individual animals involved in the activity. The first two lairs were only used as breathing holes which were occupied 14% of the time monitored (18.33 hours) over a 5-day period. The third lair where a seal actually hauled out, was occupied continuously for 3 of the 5 days of the study. On 5 May the seal remained in this lair for the complete observation period lasting 9.17 hours. With the small sample size in two of the lairs I was not able to discern any patterns of change in diel activity. Seals using these lairs as breathing sites would remain in the hole for less than 2 min. and take from 30 to 39 breaths per minute. The seal remaining in the presumed birth lair respired much more slowly, at a rate of 19–30 breaths per minute.

Ringed seals begin to haul out on the sea ice in early May. In the Iluvilik area the annual peak in numbers occurs around mid-June (Fig. 10) with the diurnal peak between 09:00 and

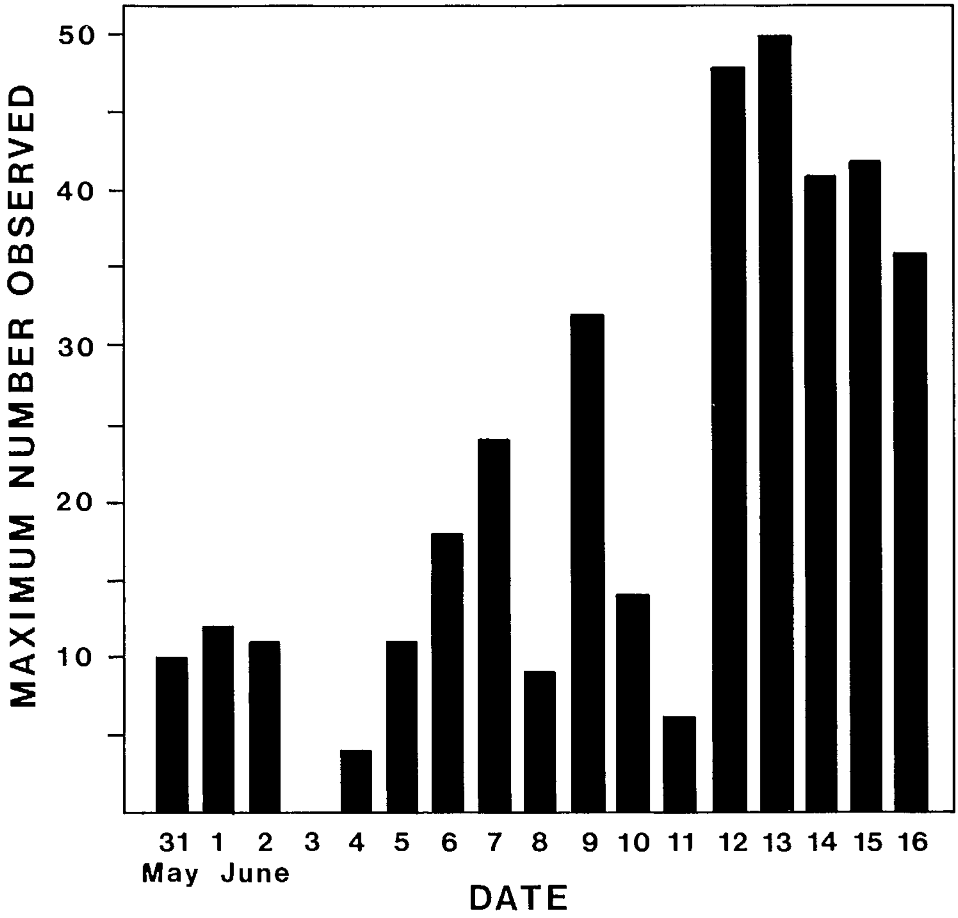



FIG. 10. Seasonal accummulation of ringed seals hauled-out on the land-fast sea ice.

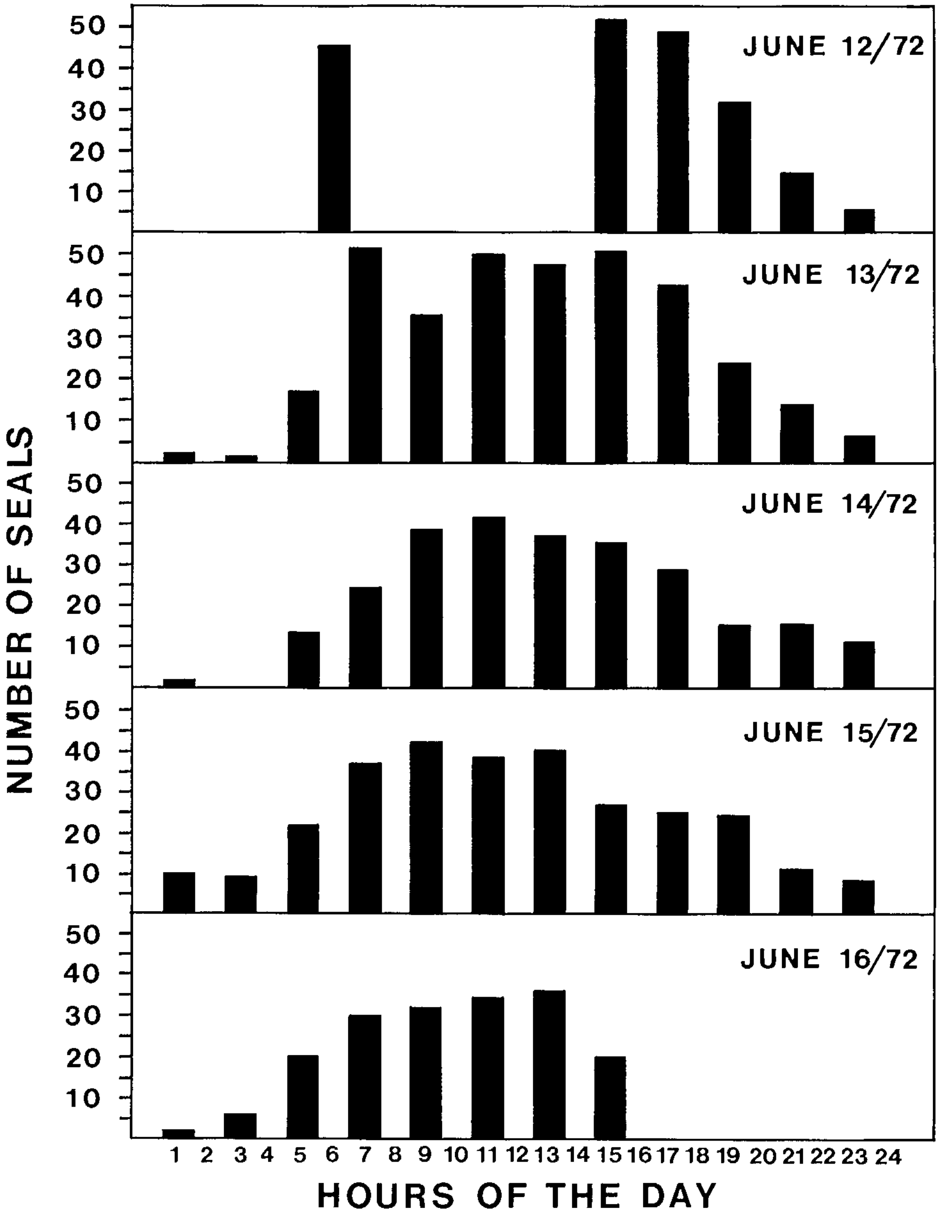



FIG. 11. Diurnal haul-out regime of ringed seals counted on the land-fast ice at Iluvilik during June 1972.

15:00. (Fig. 11). Surface melt conditions vary from year to year. In years with high temperatures and little wind, considerable surface melt water accumulates for a period of 1–2 weeks in late June. This can affect the number and distribution of ringed seals hauled out on the ice. This condition does not occur each year and is almost impossible to predict.

## Annual Variation in Density of Subnivean Lairs

With the exception of the 1980 dog searches, which were done only in early February, the breeding habitat surveys covered the period April through early June, thus spanning the period of parturition (Table 8).

The highest proportion of birth lairs (60%) was found in 1972 and lowest number of minutes searched per birth lair (10.9 min) was during the 1973 season. The proportion of birth lairs decreased in 1974 leading to a low in 1975 with a subsequent increase beginning in 1976 (Fig. 12). The same trend occurred for all types of lairs found per unit search time (Table 8), though not so pronounced as for birth lairs, indicating that 1974 and 1975 had the lowest density of subnivean structures. In 1975 and 1976 the majority of subnivean structures were haul-out lairs. In 1975, which had the lowest density of birth lairs (89 min per birth lair found), no lairs of reproductively active males were found (Table 8). Search results for the years 1977, 1978, 1981 and 1983 indicate a return close to the high densities of total lairs and birth lairs seen in 1972 and 1973.

## Predation on Newborn Seals

Smith (1976a) described the methods used by arctic foxes to enter ringed seal birth lairs and kill the pups within. The predation rates on newborn pups in the birth lairs found during the dog searches of the sea ice near *Iluvilik* for 9 spring seasons from 1973 to 1983 were documented (Table 9). The 1980 season is excluded because the searches were done before the birth period. Peak predation mortalities occurred during the spring months of 1973 and 1974. Trapping records from 1972 to 1982 indicate that there was a large increase in the size of the fox population in 1974. That year the harvest of arctic fox in the western Canadian arctic was one of the highest recorded. On neighbouring Banks Island one trapper reported a take of 1 650 foxes, the highest single harvest ever reported.

While predation rates are not directly correlated with the annual fox harvest figures they do show a positive correlation with the number of lairs marked by foxes with urine or scats ($r = 0.93$). The 2 years with the highest predation rates were initiated by a fairly low fox catch in 1972–73 and followed by an extremely high fox catch in the second year 1973–74. Birth lair densities in the year following the second highest predation rates (1974–75) were the lowest recorded in 8 years of searches.

TABLE 8. Number, percentage, type of subnivean ringed seal lairs and amount of search time from dog surveys in all types of ice features, in the inshore fast-ice study area of Iluvilik, Prince Albert Sound, N.W.T.

| Season | Birth lairs | | Haul-out lairs | | Male haul-out lairs | | Breathing holes | | Lairs marked by foxes | | Total lairs | Lairs found in timed search | Search time (min) | Min/ Lair | Min/ Birth Lair |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *n* | (%) | *n* | (%) | *n* | (%) | *n* | (%) | *n* | (%) | | | | | |
| 1972 | 52 | (60) | 25 | (29) | 3 | (4) | 6 | (7) | 30 | (35) | 86 | —— | NO DATA | | —— |
| 1973 | 28 | (48) | 19 | (33) | 9 | (16) | 2 | (4) | 47 | (81) | 58 | 45 | 185.0 | 4.1 | 10.9 |
| 1974 | 25 | (22) | 57 | (50) | 14 | (12) | 18 | (16) | 61 | (54) | 114 | 12 | 133.0 | 11.1 | 33.3 |
| 1975 | 2 | (9) | 11 | (50) | 0 | (0) | 9 | (41) | 2 | (9) | 22 | 8 | 89.0 | 11.1 | 89.0 |
| 1976 | 3 | (14) | 9 | (43) | 8 | (38) | 1 | (5) | 7 | (33) | 21 | 21 | 95.7 | 4.6 | 31.9 |
| 1977 | 10 | (15) | 26 | (41) | 17 | (27) | 11 | (17) | 8 | (13) | 64 | 64 | 197.0 | 3.1 | 19.7 |
| 1978 | 19 | (39) | 12 | (24) | 5 | (10) | 13 | (27) | 16 | (33) | 49 | —— | NO DATA | | —— |
| 1980[a] | 0 | (0) | 21 | (39) | 17 | (31) | 16 | (30) | 1 | (2) | 54 | 54 | 139.9 | 2.6 | 0 |
| 1981 | 15 | (20) | 23 | (31) | 11 | (15) | 25 | (34) | 25 | (34) | 74 | 71 | 239.8 | 3.4 | 16.0 |
| 1983 | 18 | (22) | 41 | (51) | 2 | (2) | 20 | (25) | 8 | (10) | 81 | 81 | 279.6 | 3.5 | 15.3 |

[a]Searched only during period 4–11 February.

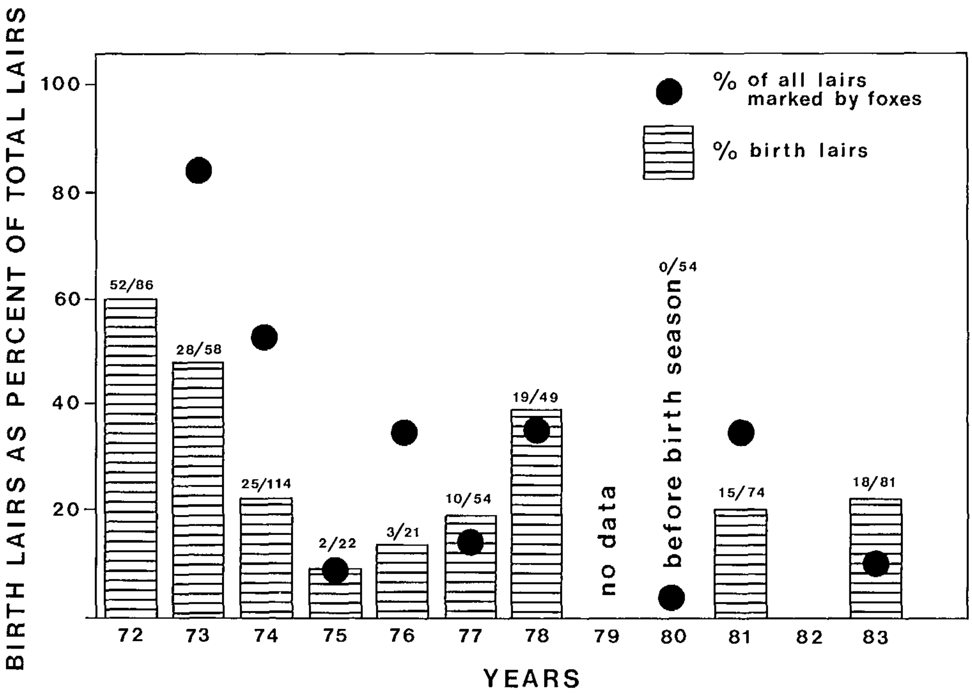



FIG. 12. Annual variation in the proportion of ringed seal birth lairs found by survey dogs in the Iluvilik, Prince Albert Sound, N.W.T. area.

TABLE 9. Frequency and percent of neonate ringed seals killed in their subnivean lairs by arctic foxes, *Alopex lagopus* and the total fox harvest from the Holman area, western Victoria Island, N.W.T.

| Trapping season | Birth-lairs in which pups were killed *n* | *f* | (%) | All types of lairs marked by foxes *n* | *f* | (%) | Reported annual fox harvest from Holman[a] | Average price per fox pelt[a] |
|---|---|---|---|---|---|---|---|---|
| 1971–72 | 45 | 4 | (9%) | 86 | 30 | (35%) | 2 215 | $11.31 |
| 1972–73 | 38 | 15 | (40%) | 58 | 47 | (81%) | 703 | $18.31 |
| 1973–74 | 32 | 11 | (34%) | 114 | 61 | (54%) | 3 892 | $30.20 |
| 1974–75 | 0 | | | 22 | 2 | (9%) | 1 923 | $17.58 |
| 1975–76 | 3 | 1 | (33%) | 21 | 7 | (33%) | 356 | $25.67 |
| 1976–77 | 10 | 1 | (10%) | 64 | 8 | (13%) | 1 432 | $35.30 |
| 1977–78 | 19 | 2 | (11%) | 49 | 16 | (33%) | 2 740 | |
| 1978–79 | | | | | | | 596 | $39.26 |
| 1979–80 | | | | | | | 1 887 | $42.38 |
| 1980–81 | 15 | 2 | (13%) | 74 | 25 | (34%) | 3 503 | $29.81 |
| 1981–82 | 18 | 1 | (6%) | | | | 3 174 | $31.71 |

[a]From the records of the Northwest Territories Department of Fish and Game.

## Discussion

Adult ringed seals appear to occupy in the early autumn months the areas of land-fast coastal ice, which will later in the spring become breeding habitat (Lukin and Potelov 1978). In the Prince Albert Sound area seals collected at that time are almost all adults and are often seen to be actively feeding in groups, on schools of Arctic cod. Young of the year and adolescent seals appear to leave the areas at this time and begin a westward migration along the mainland coast towards the west. The initial stimulus for occupation of favoured areas by adult seals which will later become breeding habitat, and the movement away by young animals may be directly related to competition for Arctic cod (see section on Feeding Ecology).

In the nearshore *Iluvilik* breeding habitat, ice hummocks and pressure ridges are the most important surface features of the sea ice around which subnivean lairs are constructed. Ice stability and snow of 60–65 cm are necessary qualities of good breeding ice. In other Canadian arctic areas, snow depth differs quite markedly, resulting in a somewhat different distribution of subnivean lairs. Along the fjord - indented southeastern Baffin Island coast (latitudes 60° to 72°N) prime breeding habitat is found in deep bays where the ice is extremely flat and free of hummocks or pressure ridges (Smith et al. 1979; Smith and Hammill 1980a, 1981). Precipitation is much higher in these areas, allowing ringed seals enough snow to build their lairs along refrozen leads, which form across the mouths of fjords and bays. These leads or cracks are apparently created by tidal influences, which in some areas are quite substantial. Lairs are also sometimes found in the tidal pressure zones along the coast (McLaren 1958a), but because of their instability these cracks do not appear to be prime sites for birth lairs (Smith and Hammill 1980b, 1981).

In the high arctic, an area of very low annual precipitation, lairs are rarely found in the stable flat ice of large bays (Smith et al. 1979). In Parry Channel, an area containing multi-year and annual fast-ice, densities of subnivean lairs are highest offshore in first-year ice along pressure ridges and around ice hummocks which accumulate sufficient snow. In general, ringed seals avoid multi-year ice, a fact clearly reflected in the diminished density of subnivean structures in the western areas of Parry Channel (Smith and Hammill 1980b). In Svalbard, and probably also in western Greenland ringed seals form lairs in the snow accumulated around bergy bits at the foot of active glaciers (Lydersen and Gjertz 1984, 1986). Again depth of snow seems to be the primary factor involved in site selection.

Lairs appear to have the dual function of thermal shelter and protection from predators (Stirling 1974b; Stirling and Archibald 1977; Smith and Stirling 1978; Lukin 1980). Ringed seals are the smallest of the phocids, with pups of approximately 4–6 kg at birth. It is possible that this indicates that the anti-predator function of the lairs has been the most important selective response since other antarctic and northern pack-ice phocids have developed large bodies as an adaptation to the cold. Temperature differences of as much as 30°C have been measured between the inside and exterior of an occupied lair. Taugbol (1984) showed a critical temperature of −25°C for dry newborn ringed seal pups and about 0°C for pups with wet lanugo. With prevailing ambient temperatures of −24°C to −31°C in April when pups are born, it is apparent that a thermal shelter is needed for the survival of the neonate, especially when it must on occasion, enter the water to escape predation from arctic foxes (Smith 1976a), or polar bears (Stirling 1974a, b; Stirling and Archibald 1977; Smith 1980a).

The birth lair and existence of several alternate lairs to which a female can take her pup should she be disturbed by foxes or bears, appears to be essential in light of the high mortalities imposed on ringed seal populations by natural predators (Smith 1976a, 1980a; Stirling and Archibald 1977; Smith and Hammill 1981). I have observed female ringed seals grasping their pups by the neck with their teeth and attempting to move them to an adjacent lair. Inuit and polar bears hunt adult female ringed seals by catching the pup and waiting for the mother to return (Kumlein 1879; Stirling and McEwan 1975). They take advantage of the strong mother-pup bond, which often results in the death of the adult female. Predation pressure by foxes, bears and indigenous man appears to be the strongest selective force shaping the maternal behaviour of the ringed seal.

Most seals found in the fast-ice breeding habitat are adult animals, especially those occupying the birth and haul-out lairs along the pressure ridges and in the hummocked ice. Some adolescents are found, usually along the low snow covered unstable cracks *(koglornerk)*. Their numbers appear to begin to increase in early May, but they are evidently actively excluded from breeding sites, which are located around birth lairs, until mid-June. Adolescent males, which are approaching sexual maturity, show the highest proportion of bite wounds, evidence of agonistic encounters, probably with territorial adults.

Starveling yearlings found in the breeding habitat are usually badly bitten and sometimes dead. These are pups born the previous year, which because they get a poor start in life for whatever reason, stayed throughout the winter in the coastal breeding ice. It is possible that they seek thermal shelter in subnivean lairs of other seals, are badly treated and eventually die, either in the lairs or hauled out on the surface of the ice. Lost neonates, sometimes wandering long distances over the ice, are also frequently found (Smith and Memogana 1977). These sometimes show a large weight loss and are often partially frozen.

The increase in adult males caught in birth lairs and of adult females caught in lairs used by rutting males in mid-May to mid-June indicates that mating occurs at this time (see section on Reproduction). This period is also correlated to the highest incidence of bite wounds in both adolescent and adult males.

Smith and Hammill (1981) indicated that males appear to hold territories in which a few adult females maintain birth lair complexes. We speculated that the male and female subterritories, as well as being part of the reproductive strategy, might serve to provide space for feeding and escape from predators during the long period of occupation of the breeding habitat. The strong male odour, apparently stronger than in other phocids probably serves in scent marking. The fact that males emit this odour as early as 2 February and have been found to be in reproductive condition by late January (Nazarenko 1965), supports the hypothesis that winter territories could be held as feeding areas as well as breeding sites.

The adult sex ratio from seals collected during the probable mating period from mid-May to mid-June was 2.09 females:1 male. This is very similar to the sex ratio found in the east Baffin breeding habitat studied by Smith and Hammill (1981), adding support to the hypothesis that ringed seals display a limited form of polygyny.

Monitoring of activity in the subnivean lairs indicates that seals vary in their behaviour in different types of structures. The long period of time (9.17 hours) spent in one lair by a seal of unknown age indicates that they are quite important as resting areas. Burns and Kelly (unpublished Annual Report, NOAA Project No: RU232, 1982), studying an area of low seal density in the Beaufort Sea, found that three radio tagged seals each apparently only used a single lair. One was a mature seal possibly with a pup and the other two were adolescent females. They spent from 17 to 24% of their time in the lairs over the period 17 April to 24 May, showing a lack of synchrony in the early period. Later in the year their haul-out behaviour became more synchronous and peaked between 08:00 and 18:30, which is similar to the observed peak of haul-out for ringed seals on the surface of the ice in other studies (Smith 1973a; Finley 1979).

Varying conditions including surface wetness and the depth of snow pits in which the seals are lying appear to have a considerable affect on the diurnal and seasonal timing of the peak of haul-out. More detailed microclimate studies are needed in order to identify the variables affecting seal numbers on the sea ice, especially if they are to be applied as correction factors to total population estimates from aerial surveys (Smith and Hammill 1981; Kingsley 1985). There is also a potential for using remote sensing satellites to count seal population over large areas by the characteristic drainage patterns which sometimes exist around seal holes (Digby 1984). More detailed ground truthing is required to properly assess this technique.

The decrease in density of subnivean structures to a low in 1974 and 1975, with the extreme low of birth lairs in 1975, indicates a real change in the numbers and recruitment of the ringed seal population in the area. Such changes have already been indicated for the southeastern Beaufort sea by Stirling et al. (1977) and Smith and Stirling (1978). The extremely high proportion (60%) of birth lairs among subnivean structures found in 1972 might reflect a major difference in the surface features of the sea ice or better conditions for breeding females such as increased food in the *Iluvilik* area that year. In 1972 there were extensive fields of ice hummocks well surrounded with deep snow drifts. Virtually all birth lairs were parts of complexes with two or sometimes three associated lairs. This ideal type of surface condition has not been observed again to the same extent. Thus the increased proportion of birth lairs over 1973 might not actually reflect a real increase in number of breeding females but simply that each female maintained more lairs in her "complex". Unfortunately there are no search time data for 1972.

In 1975, the poorest year for birth lairs, there were also almost no lairs of breeding males in the *Iluvilik* area. This might be a direct indication that because of reduced ovulation in 1974, or poor feeding conditions in 1975 (see section on Reproduction), many breeding males failed to return to the breeding habitat, thus lengthening the period of reduced recruitment in the population. Searches for lairs for the years 1978 to 1983 indicate a gradual return to the densities of birth lairs seen in the 1972 and 1973 periods.

Predation on neonate ringed seals in their birth lairs resulted in extremely high mortalities in the years 1973 and 1974 (Smith 1976a). Predation of pups by foxes in the eastern Baffin and the high-arctic areas appears to be much lower (Smith et al. 1979; Smith and Hammill 1980a, b), probably because the fox populations never reach the high densities seen around Banks and Victoria Islands. Burns and Kelly (1982) and Lydersen and Gjertz (1986) record similar high predation rates of 30 and 31%, respectively, in the western Beaufort Sea and Spitzbergen.

The highest rate of predation by foxes recorded in the *Iluvilik* area occurred in 1973 when birth lairs were plentiful and again in 1974 when birth lairs were much less dense. From fox harvests it appears that the high predation rate, started in 1973 by a rather weak fox population, might have helped to stimulate a large increase in the number of foxes in 1974 (Hammill 1983). It was in fact one of the best trapping years ever documented. The large fox population of 1974 continued its high predation on what appears to have been a ringed seal population already showing a strong decline in recruitment (see section on Reproduction).

## Reproduction

### Season of Birth and the Ovarian Cycle

The earliest recorded birth of a ringed seal in the study area was of a pup found dead on the ice on 7 April 1974; another was recorded killed by a fox on 10 April and a recently born pup with a fresh 6 cm long umbilicus was caught on 19 April. A lactating female was taken on 19 April and the earliest moulted neonate was found on 7 May. The birth season can extend quite late as shown by a lactating female which was shot on 2 July. This was exceptionally late, most females evidently cease lactating by early June. The latest pup with it's white lanugo partially moulted, was collected on 11 June.

Seasonal changes in the ovaries of ringed seals have been described in detail by McLaren (1958a) and Smith (1973a). Essentially the same pattern was observed in this study except that birth and ovulation were slightly later. Newly formed large corpora lutea were seen from 10 May to 17 June. These were only partially luteinized with the sites of recent eruption of the follicle still evident on the ovary. Of the 21 ovaries in 1971, which were collected just before or after ovulation, there is a suggestion that the youngest nulliparous females ovulate some one to three weeks earlier than the older post partum multiparous females. The latter had borne pups that year and were still lactating. The high frequency of

TABLE 10. Calculation of mean date of ovulation of ringed seals in Amundsen Gulf after the method of Caughley (1977).

| Period | Period code $x$ | Number of recent ovulations $f$ | $fx$ | $fx^2$ |
|---|---|---|---|---|
| 1–10 May | 0 | 4 | 0 | 0 |
| 11–20 May | 1 | 6 | 6 | 6 |
| 21–30 May | 2 | 7 | 14 | 28 |
| 31 May–9 June | 3 | 2 | 6 | 18 |
| 10–19 June | 4 | 2 | 8 | 32 |
| | | $\Sigma f = 21$ | $\Sigma fx = 34$ | $\Sigma fx^2 = 84$ |

females with ovaries about to, or just having ovulated, between 1 May and 19 June (Table 10) indicates that the mean date of ovulation was May 21 (SD = 9.6) (Caughley 1977).

## Implantation and Gestation

The earliest and latest dates of implantation of a blastocyst, shown by a swelling of the uterine cornus, were on 2 August and 29 September, a spread of 58 days. Smith (1973a) used 1 April as the nominal birth date of ringed seals on eastern Baffin Island. The peak of births in the present area appears to take place at least 2 weeks later. Using 21 May as the mean conception date, a linear regression of foetal crown-rump length against time for 105 foetuses, collected from 2 August to 17 April, yielded the equation; crown-rump length (cm) = $-249.4 + 2.77$ (days), with $r^2 = 0.91$. From this it is calculated that the mean date of implantation is 18 August. With 21 May as the mean date of ovulation this gives a delayed implantation of 89 days with an active gestation of 241 days.

Twins were observed once in this study. A female 26–30 years old, collected on 21 February 1981, contained two foetuses, a male and a female, measuring 480 and 460 mm, respectively.

## Sexual Maturity and Age at First Reproduction

No females younger than 4+ years showed any follicular activity. Using the presence of either large follicles or corpora lutea as indications of ovulation, the mean age of sexual maturity for this region is estimated to be 5.61 years (DeMaster 1978).

Reproductive tracts were examined and classified as nulliparous, primiparous or multiparous (Table 11). The average age of first pregnancy based on the number of females which showed at least one previous birth (primi- or multiparous tract) was 7.67 years (York 1983). Only female reproduction was examined in the present study. Several studies are in agreement that male ringed seals attain sexual maturity on average at age 7 years (McLaren 1958a; Nazarenko 1965; Smith 1973a).

## Sex Ratio of Pups

The sex ratio of pups killed in the *Iluvilik* breeding habitat did not depart from unity (57 females: 63 males). In 1972 when pups were taken in nets during the autumn at Brown's

TABLE 11. Evidence of sexual maturity and age (last birthday) at first reproduction based on presence of large follicles (≥ 5 mm) or corpora lutea in the ovaries and on the state of the uterine cornua, for a sample of ringed seals taken near Holman, N.W.T.

| Age | Sample size | With follices ≥ 5 mm in diam. or a corpus luteum | Stage of the uterine cornua | | |
|---|---|---|---|---|---|
| | | | Nulliparous | Primiparous | Multiparous |
| 0 | 4 | 0 | 4 | | |
| 1 | 29 | 0 | 29 | | |
| 2 | 48 | 0 | 48 | | |
| 3 | 39 | 0 | 39 | | |
| 4 | 28 | 7 | 28 | | |
| 5 | 38 | 20 | 33 | 5 | |
| 6 | 23 | 14 | 16 | 2 | 5 |
| 7 | 25 | 25 | 10 | 3 | 12 |
| 8 | 25 | 25 | 0 | 7 | 18 |
| 9 | 27 | 27 | 1 | 5 | 21 |
| 10 | 12 | 12 | 0 | 0 | 12 |
| 11 | 228 | 228 | 1 | 9 | 218 |

Harbour a significantly greater proportion of males were caught (87 males:57 females), $\chi^2 = 6.25$, $P < 0.001$. In the other 4 years of catches at Brown's Harbour (1974–77) the sex ratio of pups was near unity.

## Annual Changes in Reproduction

The percentage of seals ovulating as indicated by the presence of an active corpus luteum during the years 1971 to 1980 showed a clear reduction in ovulation in the Iluvilik breeding habitat in 1974 to a low in 1975, and a similar pattern in the summer and autumn in the hunting area, with a return to normal levels of ovulation in 1976–77 (Fig. 13).

Sexually inactive females comprised 2, 13, 29, 49, 3, and 1% of the samples in 1972, 1973, 1974, 1975, 1976, and 1977 respectively and were not seen in other years (Table 12). Failure to ovulate did not appear to be age related.

There appears to have been a significant change in the age structure of reproducing females over the years. It is known that females taken in the autumn and in the breeding habitat are significantly older than those taken in the summer open water season (see section on Breeding Habitat). This is reflected in Table 12 for the catches of 1973 and 1974, which were all from the breeding habitat. However, the 1977 catch from the *Iluvilik* breeding habitat, with a mean age of 10.04 years is significantly younger when it is compared to the 1972 to 1974 mean ages ($t$ = minimum 4.24, $P < 0.01$).

In 1974 and 1975 when ovulation was severely reduced there were significant reductions in the indices of condition of those females which had not successfully ovulated. The mean measured indices of condition (see section on Growth and Condition) for female ringed seals of 6+ years or greater which had either ovulated or failed to do so are given in Table 13.

Macroscopic examination of the ovaries and reproductive tracts revealed some abnormalities such as haemorrhagic and attretic follicles, regressing copora lutea and non-functional ovaries (Smith 1973a). Small tumors on the ovaries and on the uterine cornua were also occasionally discovered. When compared to the combined incidence from other years (Table 14), the years 1974 and 1975 had a significantly higher proportion of abnormalities ($\chi^2 > 17.8$, $P < 0.001$). Only one abortion was ascertained. The most common abnormalities were haemorrhagic follicles. Of those showing such follicles (29), there was an almost equal number of females which ovulated (14) and which were inactive.

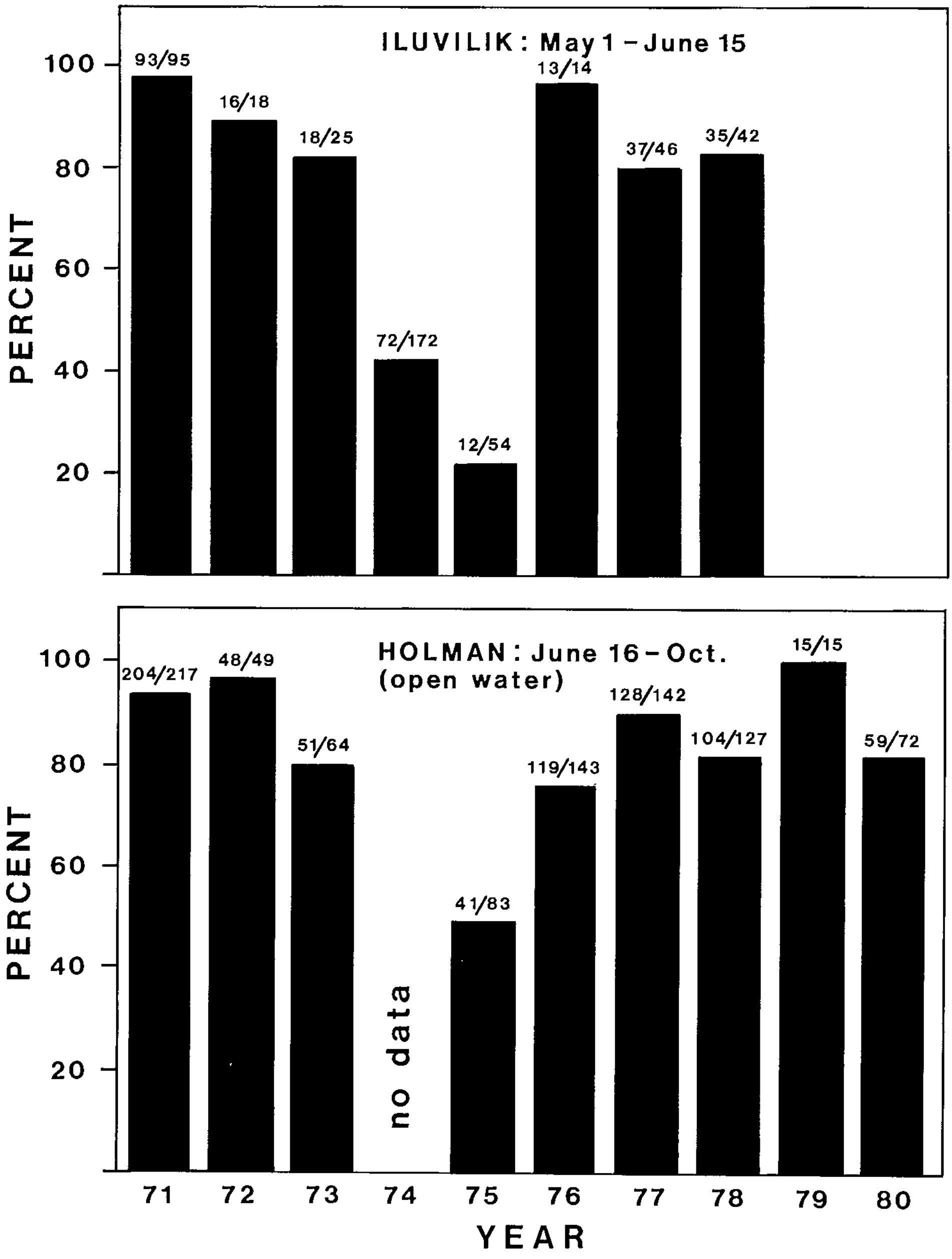



FIG. 13. Annual changes in the percentage of adult (≥7) female ringed seals with active corpora lutea during the spring and open-water seasons.

TABLE 12. Age frequencies of mature female ringed seals with frequencies (in parentheses) of sexually inactive (non-ovulating) individuals. Mean ages are calculated from the age-grouped data.

| Age | 1971 | 1971 (Sept. only) | 1972 | 1973 | 1974 | 1975 | 1976 | 1977 | 1977 (Iluvilik only) | 1978 | 1969 | 1980 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 4 | 9 | | | | | | | | | 1 | | |
| 5 | 32 | 1 | | 1 | | 2 | 3 | 1 | 1 | 4 | | 1 |
| 6 | 17 | 1 | 1 | 1 | 1 | 2 | 13 | 9 | 7 | 15 | | |
| 7 | 32 | | | 1 | 2 | 8 (4) | 8 | 19(1) | 10 | 13 | | 1 |
| 8 | 34 | | 1 | 4 | 3(2) | 14(10) | 11(1) | 28(1) | 17 | 24 | 1 | 6 |
| 9 | 31 | 2 | | 1 | 4(1) | 20(12) | 18 | 23 | 12 | 19 | 2 | 6 |
| 10 | 26 | 1 | 3 | 4(2) | 10(2) | 22 (9) | 21(1) | 27 | 14 | 14 | 2 | 10 |
| 11 | 31 | 2 | 2 | 5 | 4(1) | 25 (9) | 28 | 20 | 7 | 9 | | 5 |
| 12 | 30 | 1 | 3 | 7(1) | 10(4) | 17 (8) | 23(1) | 26 | 10 | 10 | | 5 |
| 13 | 19 | 1 | 3 | 1 | 18(9) | 6 (3) | 18 | 25 | 6 | 9 | 3 | 5 |
| 14 | 19 | | 4 | 12(3) | 13(3) | 5 (1) | 14(1) | 16 | 4 | 4 | 1 | 8 |
| 15 | 28 | 4 | 5 | 3 | 4(1) | 4 (2) | 10(1) | 9 | | 5 | 1 | 3 |
| 16 | 17 | 1 | 8(1) | 3 | 9(5) | 7 (2) | 6 | 8 | 3 | 3 | 2 | 2 |
| 17 | 16 | 4 | 4 | 4 | 13(6) | 3 (3) | 5 | 5 | 3 | 4 | | 3 |
| 18 | 9 | 3 | 3 | 5(1) | 7(3) | | 1 | 3 | | 3 | 1 | 1 |
| 19 | 5 | 1 | 3 | 4 | 7(4) | | | 2 | | 2 | 1 | |
| 20 | 3 | 1 | 1 | 2 | 5 | | 1 | 2 | | 3 | | 2 |
| 21 – | 26 | 4 | 9 | 16(1) | 22(9) | 3 (3) | 2 | 5 | 1 | 1 | | 2 |
| 26 – | 15 | 3 | 6 | 8(2) | 10(5) | | 1 | | | | | 1 |
| 31 – | | | 1 | 3(2) | 2(1) | | | 1 | | | | |
| 36 ≥ | | | 1 | | 1 | | | | | | | |
| TOTAL | 399 | 30 | 58 | 85 | 145 | 138 | 183 | 229 | 95 | 143 | 14 | 61 |
| % inactive | 0 | 0 | 2 | 14 | 39 | 46 | 3 | 1 | 0 | 0 | 0 | 0 |
| $\bar{x}$ age | 12.15 | 16.63 | 17.39 | 17.38 | 16.64 | 10.93 | 11.29 | 11.32 | 10.04 | 11.11 | 13.07 | 12.56 |
| SD | 5.79 | 6.17 | 5.57 | 6.76 | 5.78 | 3.14 | 3.45 | 3.73 | 3.09 | 4.20 | 3.50 | 4.26 |

TABLE 13. Measured mean index of body condition (actual weight · ST length$^{-1}$) for ovulating and sexually inactive ringed seals from 1971 to 1978.

| | Proportion ovulating | | Mean $x$ condition of those ovulating | | | Mean $x$ condition of those inactive | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Sampling period | $n$ | % | $x$ | SD | $n$ | $x$ | SD | $n$ | Student $t$ | $P$ |
| 1 May – 26 June 1971 | 25 | 92% | 76 | 13 | 20 | | | | | |
| 10 Sept. – 4 Oct. 1971 | 58 | 100% | 131 | 18 | 13 | | | | | |
| 31 May – 16 June 1972 | 16 | 100% | 87 | 12 | 11 | | | | | |
| 1 Aug. – 29 Aug. 1972 | 25 | 100% | — | — | — | | | | | |
| 30 Apr. – 1 June 1973 | 26 | 69% | 100 | 15 | 12 | 87 | 13 | 4 | 1.57 | $P<0.1$ |
| 10 Sept. – 4 Oct. 1973 | 63 | 84% | — | — | — | — | | | | |
| 23 Mar. – 1 June 1974 | 171 | 57% | 88 | 11 | 44 | 64 | 12 | 56 | 10.1 | $P<0.001$ |
| 4 Mar. – 19 Apr. 1975 | 27 | 0% | — | — | — | — | — | — | | |
| 7 July – 8 Sept. 1975 | 34 | 65% | 91 | 14 | 15 | 75 | 13 | 7 | 2.55 | $P<0.02$ |
| 10 Apr. – 28 July 1977 | 74 | 100% | 96 | 15 | 52 | | | | | |
| 19 Apr. – 27 June 1978 | 36 | 100% | — | — | — | | | | | |

TABLE 14. Incidence and type of reproductive abnormalities from adult female ringed seals collected in Amundsen Gulf during the years 1971–80.

| Season | Total abnormalities | Haemorrhagic follicles | Attretic follicles | Regressing corpus luteum | Uterine or ovarian tumor | Abortion | One active ovary only |
|---|---|---|---|---|---|---|---|
| 1971 | 9/352 | 3 | 1 | 1 | 2 | 1 | 1 |
| 1972 | 4/67 | | | 1 | 1 | | 2 |
| 1973 | 6/83 | 3 | | 1 | 2 | | |
| 1974 | 19/160 | 17 | 1 | 1 | | | |
| 1975 | 17/146 | 12 | 4 | 1 | | | |
| 1976 | 8/192 | 7 | | 1 | | | |
| 1977 | 14/237 | 10 | 1 | | 3 | | |
| 1978 | 3/153 | 3 | | | | | |
| 1979 | 0/15 | | | | | | |
| 1980 | 0/69 | | | | | | |

Three of the five females with one ovary non-functional were over 26 years old suggesting that senility was perhaps involved.

It is instructive to look at the percentage occurrence of "recent" corpora albicantia as evidence of ovulation the year previous to their formation (Fig. 14). Here the pattern is much less clear, in fact not showing the reduction in ovulation until 1975 and indicating a low through 1977.

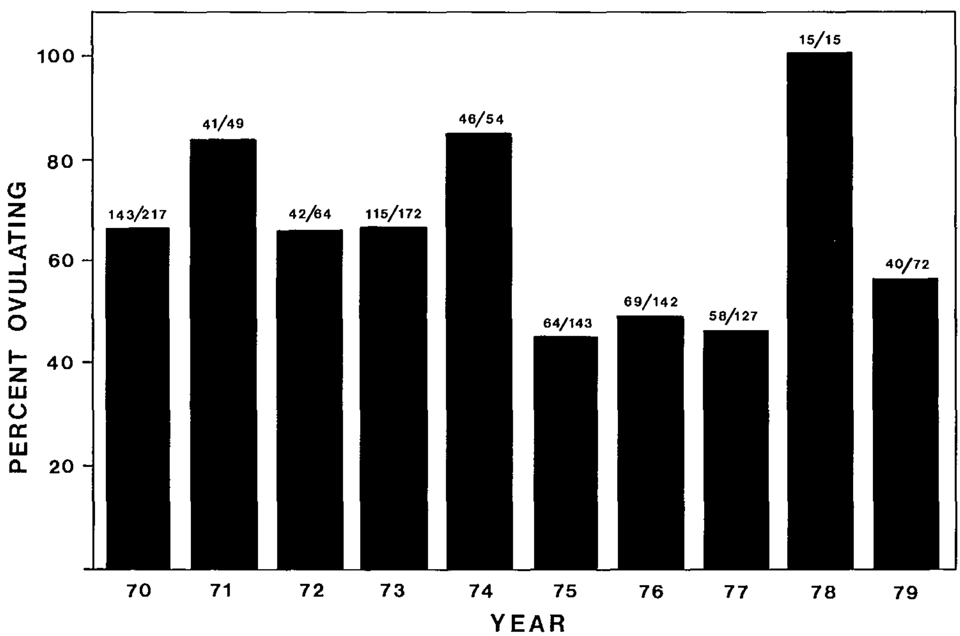



FIG. 14. Percent of ≥7 year old female ringed seals with corpora albicantia of year $x + 1$ as indicators of ovulation in year $x$.

## Reproduction Rates

The presence of a foetus or swelling in a uterine cornus was used as the basis for calculating age specific reproductive rates. Since the years 1973, 1974 and 1975 showed a real decline in ovulation and number of pups produced (see also Breeding Habitat and section on Age Structures), these were excluded from the analyses in Table 15.

TABLE 15a, b. Age-specific reproductive rates based on the presence of a blastocyst chamber or a foetus in the uterine cornua (excludes data from years 1973–75).

| | Age (years) | Number with foetus | Proportion pregnant | Smoothed proportion pregnant |
|---|---|---|---|---|
| (a) | 4+ | 1/3 | 0.333 | 0.196 |
| | 5+ | 1/2 | 0.500 | 0.288 |
| | 6+ | 1/7 | 0.142 | 0.390 |
| | 7+ | 1/6 | 0.166 | 0.494 |
| | 8+ | 5/9 | 0.555 | 0.604 |
| | 9+ | 12/13 | 0.923 | 0.706 |
| | 10+ | 7/8 | 0.875 | 0.802 |
| | ≥11 | 50/57 | 0.833 | 0.877 |
| (b) | 4+ | | 0.131[a] | 0.082 |
| | 5+ | | 0.304[a] | 0.174 |
| | 6+ | 1/7 | 0.142 | 0.291 |
| | 7+ | 1/6 | 0.166 | 0.425 |
| | 8+ | 5/9 | 0.555 | 0.564 |
| | 9+ | 12/13 | 0.923 | 0.698 |
| | 10+ | 7/8 | 0.875 | 0.817 |
| | ≥11 | 50/57 | 0.833 | 0.911 |

[a]Based on percent with primi- or multiparous reproductive tracts (Table 11).

The age-specific percentage of females with blastocyst chambers or foestuses collected after the mean date of implantation of 18 August was transformed to arc sine (Sokal and Rohlf 1969) and regressed against age giving a smoothed distribution of the reproductive rates (arc sine $y = 1.73 + 6.16$ (age), with $r^2 = 0.56$) and a mean reproductive rate of 0.54. Alternatively because of the low sample size in the youngest age classes we may use the proportions of females in age classes 4+ and 5+ showing a primiparous or multiparous reproductive tract (Table 15b). The regression smoothing technique in this case yields expected age-specific reproductive rates from the equation, arc sine $y = -15.21 + 8.0$ (age), with $r^2 = 0.78$.

## Discussion

The peak of pupping in the Holman area at 72°N appears to occur around mid-April which is approximately two to three weeks later than on southeastern Baffin Island at 60°N (McLaren 1958a; Smith 1973a; Smith and Hammill 1980a) suggesting a latitudinal gradient in the time of pupping.

Pups appear to remain with the females for approximately 1.5–2 months Ovulation occurs near the end of May, probably just prior to the end of lactation and not, as previously had been thought, shortly after parturition (Smith 1973a). This is confirmed by direct ovarian evidence of females which were accompanied by unweaned pups (Smith and Hammill 1980a). It is supported by examination of newly erupted follicles, indicating a mean ovulation date of 21 May. Boyd (1983) showed that plasma progesterone titers increased late in the lactation period of grey seals, *Halicoerus grypus*, indicating that ovulation occurred prior to weaning of the pup. Evidence of timing of reproductive activity from behaviour studies (Smith and Hammill 1981) and from the present work (see Breeding and Habitat section) confirms that ovulation and mating occur at this time.

Female ringed seals taken in this study first ovulated at an average age of 5.61 years. This is similar to calculated values from the data of Smith (1973a) giving 5.25 years on east Baffin, but younger than that derived from data by Fedoseev (1965) of 7.18 years for the Okhotsk Sea and the calculated estimate of 6.18 years from the data of Johnson et al. (1966) in Alaska. These estimates were recalculated by the methods of DeMaster (1978) and are based on females showing either large follicles or active corpora lutea as a sign of ovulation. Corpora albicantia were not used since the period of retention appears to be highly variable in the ringed seal, thus making them unreliable indicators of past reproductive states as in several other species of Phocidae such as harbour seals, *Phoca vitulina*, and grey seals (Boulva and McLaren 1979; McLaren and Smith 1985; Boyd 1984).

Mean age at first reproduction, as calculated by the method of York (1983), was 7.67 years in this study. This is comparable to 7.73 years for southeastern Baffin calculated from data in McLaren (1958a) and 7.18 for the east Baffin coast (Smith 1973a).

The sex ratio of neonates killed in the breeding habitat did not depart from unity, which was similar to the findings in other ringed seal studies. A sample of 144 ringed seal pups caught in nets at Brown's Harbour showed a significant preponderance of males, but smaller net catches taken in 4 other years at the same locality did not show this. The preponderance of males is perhaps explained by some sexual segregation or difference in timing of migration for the two sexes. Direct evidence of sexual segregation among adolescents taken along the spring floe-edge near Holman in 1971 has already been presented in this study (see section on Movements).

A major decline in the reproductive rate was first seen in 1974 and it reached a low in 1975, evidently caused mainly by failure to ovulate. Ovarian abnormalities such as haemorrhagic follicles were also higher in those years, but were not significantly correlated to the failure of ovulation. Stirling and Archibald (1977) documented similar low ovulation rates (0.39 and 0.49) for the 1974 and 1975 years from their ringed seal samples collected in the southeastern Beaufort Sea. Intrauterine mortality did not appear to play a significant part in the reproductive changes. The physical condition of females failing to ovulate was significantly lower in 1974 and 1975.

In 1975 no adult male lairs were detected in the breeding habitat (see Breeding Habitat section), but this could have been a result of the reduced ovulation in 1974 and other unfavourable conditions in the area rather than the primary cause of the reproductive low in 1975.

The annual incidence of corpora albicantia fails to give a clear picture of the past ovulation rates. The large variability in retention time of these scars, along with the difficulties in identifying and measuring them makes them unreliable as indicators of recent ovulations. The lack of evidence of a decrease in reproduction in 1974 and 1975 indicated by the frequency of corpora albicantia formation for those years suggests that ovaries which remain inactive might retain their corpora albicantia for several years (Fig. 14).

The unweighted mean reproductive rates from the smoothed data for the present study (Amundsen Gulf) is 0.54 while on east Baffin (Smith 1973a) it was 0.62 (Table 16). I think the low sample sizes in age classes 4+ to 7+ cause an underestimation of this parameter. The low sample sizes of these young reproductive females are possibly due to their active exclusion from the breeding habitat by the older more dominant sexually active females. It is evident that it is difficult to calculate a meaningful reproductive rate for the whole population. Apart from year-to-year variation in rates (see also Helle 1977) there is a need

TABLE 16. Comparison of age-specific reproductive rates of ringed seals from Amundsen Gulf and eastern Baffin Island (Home Bay). Smoothing was by linear regression of angular transformations.

| Age | Amundsen Gulf | | Home Bay (Smith 1973a) | |
|---|---|---|---|---|
| 4+ | 0.196 | (3) | 0.329 | (0) |
| 5+ | 0.288 | (2) | 0.420 | (3) |
| 6+ | 0.390 | (7) | 0.500 | (4) |
| 7+ | 0.494 | (6) | 0.586 | (4) |
| 8+ | 0.604 | (9) | 0.667 | (8) |
| 9+ | 0.706 | (13) | 0.743 | (6) |
| 10+ | 0.802 | (8) | 0.814 | (1) |
| 11+ $\hat{I}$ | 0.877 | (50) | 0.875 | (38) |
| Unweighted $\bar{x}$ | 0.54 | | 0.62 | |

for standardization in the way such rates are calculated. Clearly, rates should be based on the age-specific frequencies of females showing blastocyst chambers or foetuses after the latest date of implantation. Ovarian evidence from early in the season is also needed to ascertain that there is a normal proportion of sexually functional (ovulating) females in the sample. The wide range of reproductive rates presented by various authors ranging from 0.261 (Helle 1977) to 0.857 (Johnson et al. 1966) attests to the difficulty of estimating this parameter. The effect of changed age structure of reproducing females and the possibility of sexual senescence should also be examined whenever ringed seal populations are being monitored. While sexual senescence was only slightly indicated in my material, other authors (Fedoseev 1965: Helle 1977, 1980a) have indicated a significant decline of reproduction with increased age. Lowered reproduction has also been shown to be associated with a pathological condition known as uterine stenosis (Helle 1980b) which might in turn be related to the high PCB levels found in the Bay of Bothnia (Helle et al. 1976a, b).

Perhaps the best comparison for reproductive rates between different populations should be based on age specific data for the age classes from 10+ to 20+ in order to avoid the sampling problem at both ends of the sexually mature age distribution.

## Growth and Condition

### Foetal Growth

A problem in describing foetal growth through to birth is that usually the smaller foetuses are measured from crown to rump and the later near-term foetuses are described using standard length. The three linear measurements (Fig. 15) usually taken on foetuses are related to weight for 45 specimens (Table 17). because of the curvature of foetuses the best single measurement is the nose to tail length taken over the curvature of the body. Nose−tail length (NTL) is related to crown−rump (CRL), standard length (STL), and weight (WT) by the following linear regression equations:

(1) $\text{Log}_{10}\,\text{NTLcm} = 0.449 + \text{Log}_{10}\,0.855\,(\text{CRLcm}),\ R^2 = 0.96;$

(2) $\text{NTLcm} = 1.15\,(\text{STLcm}),\ R^2 = 0.99;$

(3) $\text{Log}_{10}\,\text{NTLcm} = 5.408 + \text{Log}_{10}3.244\,(\text{WT}_g),\ R^2 = 0.98;$

Most of the original foetal measurements were crown-rump and were converted to NTL length by equation (1). The late term foetuses originally recorded as standard length were converted to NTL length by equation (2).

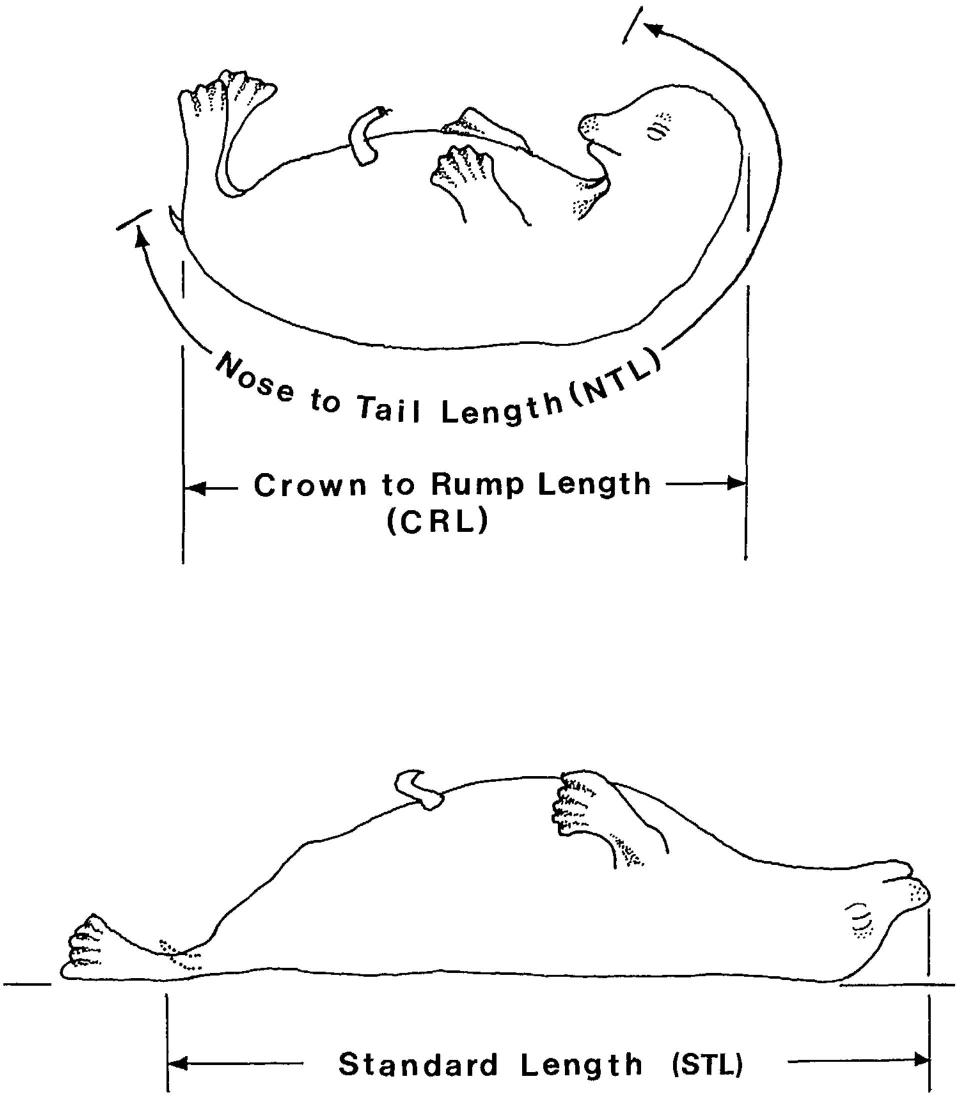



FIG. 15. Linear measurements usually taken from foetuses. Crown–rump (CRL) and nose–tail (NTL) are taken along the curvatures, but standard length (STL) is taken in a straight line over the body.

Foetal growth to term is described by the linear regression equation, NTLcm = $-2.31 + 2.77$ (days), $R^2 = 0.91$, indicating a NTL length at birth of 66.5 cm (57.8 cm standard length). With an active gestation of 241 days this indicates that the foetal growth rate is 2.8 $mm \cdot d^{-1}$.

## Growth to Weaning

A sample of 15 pups, which had milk in their stomachs, were collected up to 38 days after the nominal mean birth date of 15 April. The youngest pups, judged to be approximately 3 days old by the appearance of their umbilical cords (Thomas and DeMaster 1979),

TABLE 17. Crown–rump, nose–tail, standard length and weight of 45 ringed seal foetuses.

| Crown–rump length (mm) | Nose–tail length (mm) | Standard length (mm) | Weight (g) |
|---|---|---|---|
| 38 | 61 | · | 2.80 |
| 13 | 28 | · | 0.30 |
| 49 | 69 | · | 4.20 |
| 49 | 68 | · | 2.50 |
| 22 | 44 | · | 0.60 |
| 65 | 86 | 71 | 7.90 |
| 17 | 31 | · | 0.15 |
| 46 | 64 | 50 | 2.50 |
| 26 | 50 | · | 1.00 |
| 89 | 130 | 96 | 29.50 |
| 11 | 23 | · | · |
| 72 | 112 | 89 | 15.50 |
| 33 | 58 | · | 1.50 |
| 26 | 47 | · | 0.80 |
| 32 | 56 | · | 0.70 |
| 49 | 67 | · | 4.70 |
| 12 | 24 | · | · |
| 22 | 39 | · | 0.70 |
| 11 | 33 | · | 0.20 |
| 48 | 71 | · | 3.80 |
| 42 | 64 | · | 2.50 |
| 15 | 28 | · | 0.20 |
| 35 | 59 | · | 2.00 |
| 50 | 75 | 57 | 4.60 |
| 24 | 42 | · | 0.60 |
| 49 | 66 | · | 4.10 |
| 13 | 28 | · | 0.30 |
| 24 | 46 | · | 0.80 |
| 74 | 107 | 82 | 19.90 |
| 65 | 93 | 67 | 10.10 |
| 65 | 92 | 69 | 11.70 |
| 137 | 197 | 163 | 191.60 |
| 47 | 71 | · | 3.60 |
| 67 | 90 | · | 10.00 |
| 72 | 104 | 81 | 21.60 |
| 66 | 92 | 71 | 14.50 |
| 103 | 139 | 114 | 78.90 |
| 88 | 129 | 99 | 47.80 |
| 200 | 455 | 305 | 1 050.00 |
| · | 725 | 620 | 5 300.00 |
| · | 670 | 595 | 4 100.00 |
| · | 660 | 575 | 4 400.00 |
| · | 735 | 640 | 6 500.00 |
| · | 600 | 590 | 5 800.00 |
| 410 | 625 | 535 | 4 300.00 |

measured $\bar{x}$ = 70.9 cm ($n$ = 5) and weighed $\bar{x}$ = 6.13 kg ($n$ = 4). Regression of standard length and weight of these pups against age yielded the equations: STL (cm) = 69.08 + 0.61 (days), ($R^2$ = 0.73) and weight (kg) = 3.41 + 0.76 (days), ($R^2$ = 0.94) indicating preweaning growth rates of 6.1 $mm \cdot d^{-1}$ and 0.76 $kg \cdot d^{-1}$.

## Growth and Condition in the First Year of Life

Regression of standard lengths on time (0–365 days) were compared for male and female pups using an analysis of variance with General Linear Models Procedures (S.A.S.). The slopes were found not to differ significantly ($F = 0.20$, $P = 0.81$), and the sexes of pups were grouped for further analyses. A non-linear regression fit by least squares using the von Bertalanffy (1934) model $STL = Bo\,(1 - e^{-B1x - B2})$ was done using the non-linear regression procedure (S.A.S. Institute Inc.). The Gauss–Newton iterative method of regressing residuals onto the partial derivatives of the model was used until iterations converged (Hartley 1961). Specimens were limited to the period 21 March to 2 October. Growth is described by $STL(cm) = 93.93\,(1 - e^{-0.060x - 0.891})$ indicating an average growth of 0.099 $mm \cdot d^{-1}$ for the first year of life, but the equation indicates that pups reach their asymptotic growth after 74 days. Based on the nominal birth date of 15 April and the mean date of ovulation (which is assumed to be the mean date of weaning) of 21 May, pups have achieved the length of 86.7 cm or 93% of their first year's growth during the suckling period. Active growth in length appears to cease for most pups around the end of June which is about the time of breakup of the land-fast sea ice.

The condition of pups (actual weight ÷ standard length), increases noticeably from birth through the suckling period then decreases somewhat during July and August (Fig. 16). It appears to begin to increase again in late August and into September. There appears to be a significant relation between the body condition and standard length achieved by pups in

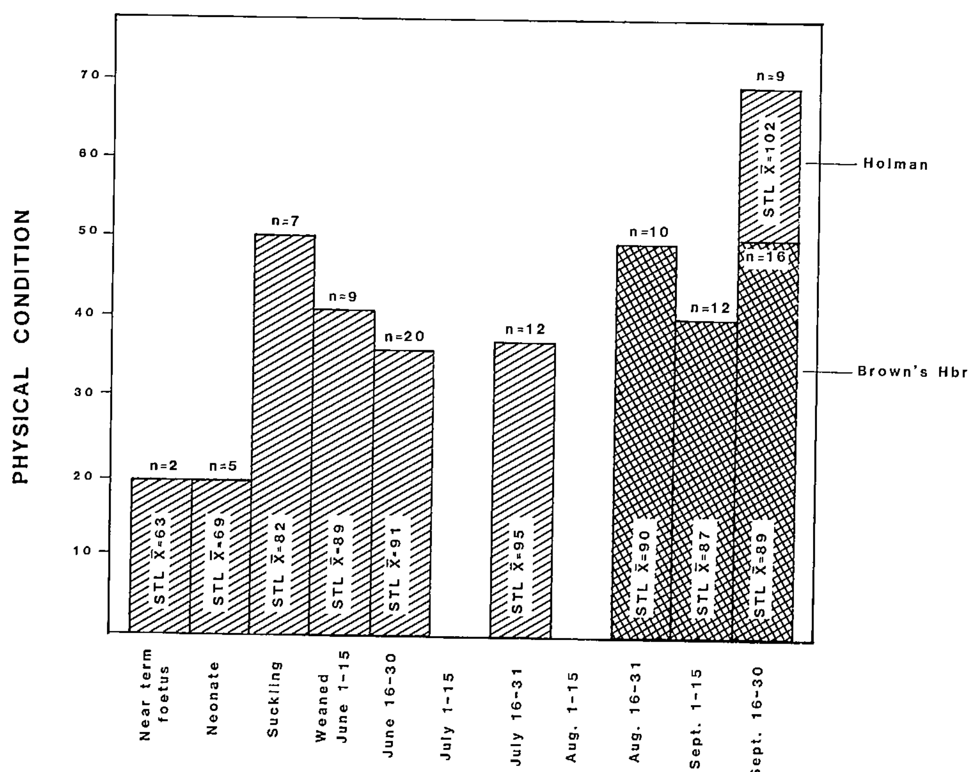



FIG. 16. Physical condition of pups from near-term foetuses through weaning to approximatcly 6 months of age from the Holman and Brown's Harbour catches.

their first year of growth in specimens taken from both the Holman and Brown's Harbour areas; Holman pups Condition = $-17.351 + 0.450$ (STL); $R^2 = 0.22$; $F = 35.07$, $P < 0.001$; Brown's Harbour pups Condition = $-2.803 + 0.280$ (STL); $R^2 = 0.20$; $F = 23.15$, $P < 0.001$. Unfortunately there are no data to show what happens during the winter months.

## Growth and Weight to Maturity

Male and female growth from age one year was calculated by fitting the von Bertalanffy model as described previously (Table 18). Asymptotic length for males is 131.21 cm (± 3.53; $P < 0.05$) and females 126.85 cm (± 4.12). Females attain 86.3% of their asymptotic length at first reproduction (7.67 years); males attain 89.6% of their length, if their age at sexual maturity is taken to be 7 years of age.

Growth in weight, was estimated from the equation: weight (kg) = $0.0023\ \text{length}^{1.204} \times \text{girth}^{1.857}$ (Usher and Church 1969b). Asymptotic weights from the von Bertalanffy model for males and females were 63.4 kg (± 9.63, $P < 0.05$) and 61.1 kg (± 11.97), respectively.

## Seasonal and Annual Changes in Condition

An index of body condition was constructed by using the equation girth ÷ standard length × 100. All age classes show a decline in physical condition through the summer months, with an increase beginning in mid-September. None showed any sex-specific differences in their seasonal condition. Adolescents and adults show declines in body condition (Fig. 17 and 18), reaching a low in early August though not as drastic as in the

TABLE 18. Standard length at age for male and female ringed seals of Amundsen Gulf, N.W.T., using the von Bertalanffy model fitted by the S.A.S. Institute (1985) non-linear regression procedure. 0+ age class is not included in the calculation.

| | Male | | | Female | | |
|---|---|---|---|---|---|---|
| Age | Mean length | SD | *N* | Mean length | SD | *N* |
| 0 | | | | | | |
| 1 | 95.36 | 8.63 | 49 | 92.61 | 10.70 | 26 |
| 2 | 101.10 | 8.45 | 30 | 99.44 | 8.05 | 27 |
| 3 | 104.34 | 9.60 | 23 | 102.64 | 12.81 | 17 |
| 4 | 107.88 | 7.26 | 18 | 104.22 | 9.01 | 9 |
| 5 | 114.89 | 11.52 | 19 | 104.57 | 10.44 | 21 |
| 6 | 117.60 | 7.16 | 25 | 111.95 | 12.93 | 24 |
| 7 | 119.35 | 10.46 | 34 | 113.03 | 7.07 | 31 |
| 8 | 124.32 | 6.81 | 25 | 120.26 | 13.16 | 46 |
| 9 | 124.89 | 8.76 | 47 | 119.48 | 8.43 | 33 |
| 10 | 128.65 | 9.03 | 32 | 121.58 | 9.28 | 50 |
| 11 | 126.23 | 9.15 | 38 | 122.61 | 7.19 | 42 |
| 12 | 126.06 | 7.42 | 30 | 122.73 | 7.98 | 41 |
| 13 | 124.95 | 8.26 | 24 | 123.14 | 9.07 | 42 |
| 14 | 128.81 | 7.50 | 22 | 123.64 | 5.43 | 25 |
| 15 | 124.33 | 6.73 | 18 | 122.23 | 8.39 | 21 |
| 16 | 128.30 | 12.27 | 13 | 127.68 | 10.83 | 32 |
| 17 | 128.75 | 6.07 | 4 | 122.20 | 9.24 | 20 |
| 18 | 127.60 | 9.52 | 5 | 127.41 | 8.30 | 12 |
| 19 | 136.33 | 7.09 | 3 | 120.21 | 8.23 | 14 |
| 20 | 136.33 | 7.09 | 3 | 122.14 | 7.10 | 7 |

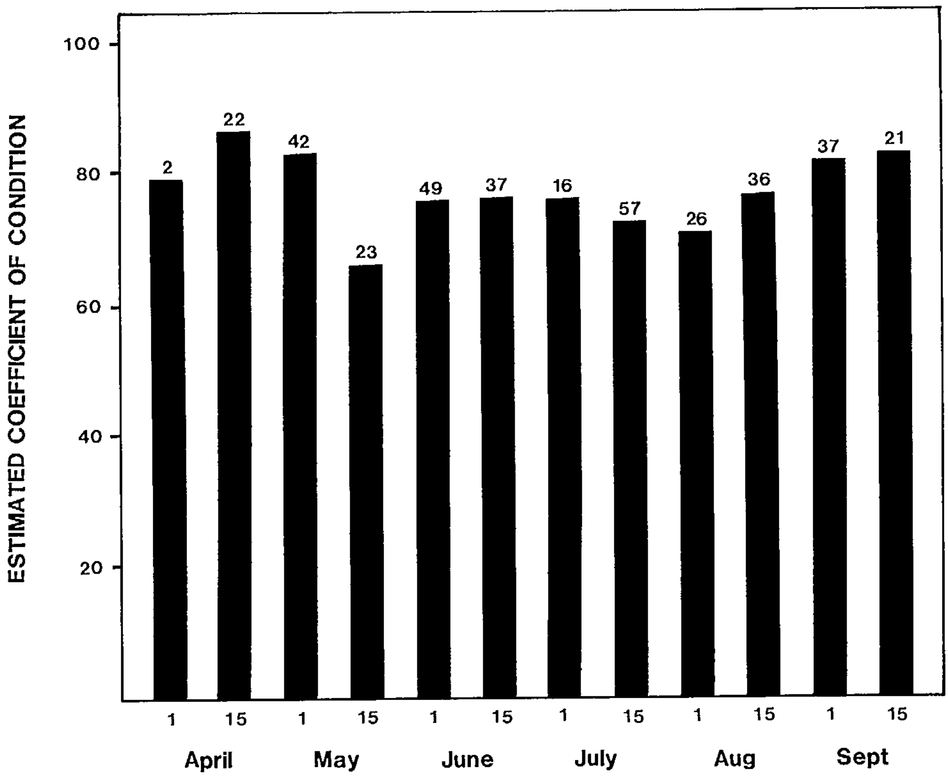



FIG. 17. Seasonal variation in the mean body condition of adolescent ringed seals (1+ to 6+ years old).

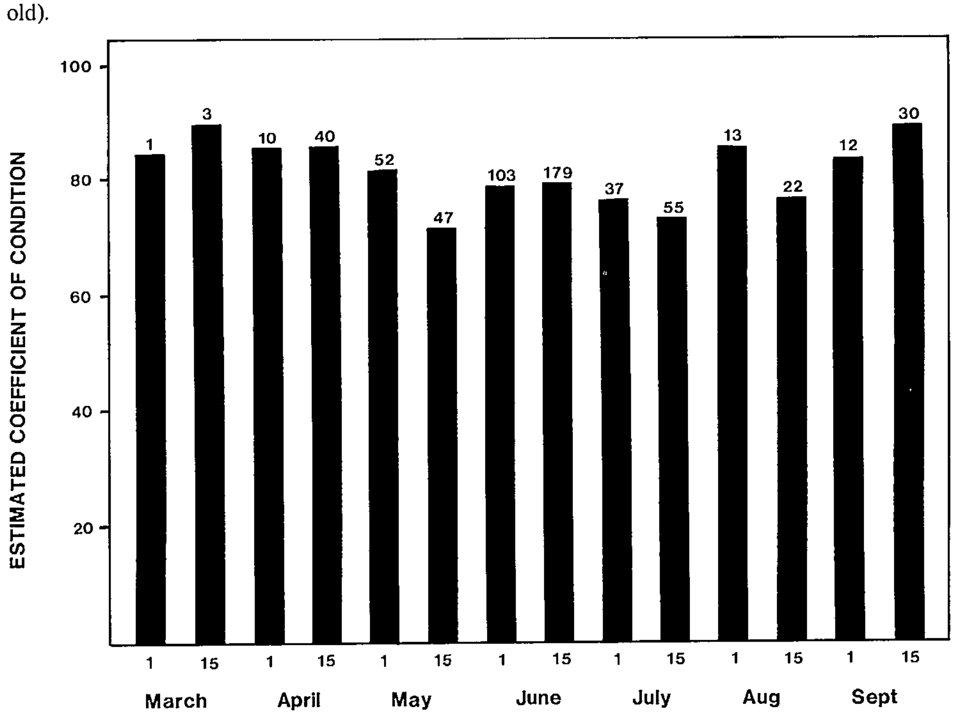



FIG. 18. Seasonal variation in the mean body condition of adult ringed seals (≥7 years old).

pups. The seasonal change in condition is further documented by the percentage of seals lost through sinking during the open-water hunt. This reaches a peak in late July when 48% of seals shot are not retrieved (Fig. 19).

Mean condition for seals taken in the same months for the years 1971–72, 1976–78 were lumped and compared to the mean condition for male and female pups (0+), adolescents (1+–6+) and adults (≥ 7) for the years 1973, 1974, 1975 using a Student's *t* test. Significantly lower conditions are found for adults and adolescents in 1974 and 1975 (Table 19). Adolescents were also in poorer conditions in 1973, 1974, 1975, but the differences were not significant, probably because of low sample sizes.

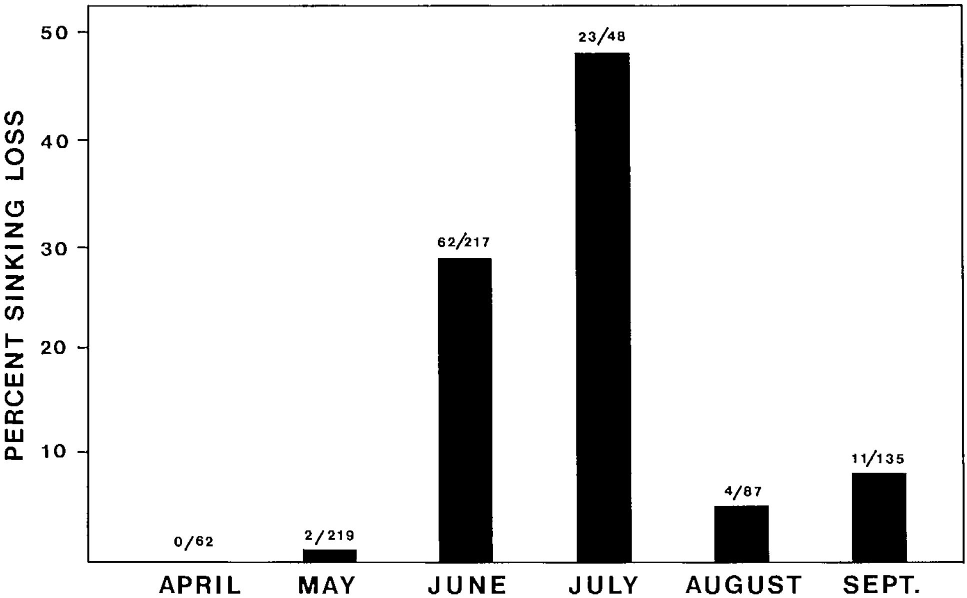



FIG. 19. Percentage of ringed seals lost through sinking during the open-water hunt.

TABLE 19. Differences in mean condition indices, (Girth ÷ NTL) × 100, for both sexes of pups (0+), adolescents (1–6+) and adults from Amundsen Gulf. Comparisons were for the lumped data from 1971–72, 1976–78 and the idividual years of 1973, 1974, 1975.

| Age class | Year | Difference in mean index of condition | *t* | *P* | *n* |
|---|---|---|---|---|---|
| Pups (0+) | 1973 | −0.4 | 0.11 | 0.91 | 13:582 |
| | 1974 | +0.4 | 0.52 | 0.60 | 20:582 |
| | 1975 | +0.2 | 0.79 | 0.45 | 2:582 |
| Adolescent (1–6+) | 1973 | −3.5 | 0.50 | 0.61 | 11:362 |
| | 1974 | −2.8 | 1.10 | 0.27 | 33:362 |
| | 1975 | −0.8 | 1.37 | 0.19 | 11:362 |
| Adults (≥ 7) | 1973 | −2.2 | 1.62 | 0.10 | 55:616 |
| | 1974 | −3.8 | 5.65 | 0.001* | 260:616 |
| | 1975 | −1.9 | 2.41 | 0.01* | 162:616 |

*Significantly different.

When Actual Weight ÷ NTL × 100 is used as the condition index adolescents for 1974 as well as adults for 1974 and 1975 are shown to be in significantly poorer condition.

## The Occurrence of Short Seals

Of 1469 seals, 34 were two standard deviations less than the mean length for their respective age class. Pups in this severely stunted group all had indices of condition of $< 20.0$, indicating a very poor state of nutrition. Seals older than pups varied in condition from low to normal. All age classes including pups had normal distributions of their standard lengths which were slightly negatively skewed.

Normal reproduction was reduced in the most stunted seals. Of the seals which were 2 SD shorter than average length only 13% (1/8) had ovulated compared to 45% (27/60) for the seals 1 SD below the mean of their age class. This is compared to a mean ovulation rate of 0.89 for all years except the low recruitment years of 1973–75 (see section on Reproduction). Only two virgin seals of greater than 8 years of age were found indicating that permanent sterility was not strongly associated with conditions causing stunting. Most of the seals, which did show inactive ovaries were shot in 1974 and 1975, when reduced body condition was positively correlated with reduced reproductive activity in all seals (see section on Reproduction).

## Discussion

It appears from the regression analysis that growth after weaning continues only for approximately 37 days, that is, until about the end of June (Table 20). At that point there appears to be a lowering of the physical condition of pups which reaches a low in late June and does not improve until about mid-September. Other phocids are known to lose condition after weaning (Boulva and McLaren 1979; Stewart and Lavigne 1980; Innes et al. 1981). Harp seals, *Phoca groenlandicus*, a pack ice species, are weaned after only 2 weeks and can undergo fasting for up to 6 weeks before feeding commences (Worthy and Lavigne 1983). Weaned ringed seals do not appear to fast, but depending on the date of their birth and the time of ice break up, there could be a varying amount of food available to them.

The pattern of adult growth is similar to that seen in other phocid species. The attainment of sexual maturity at 86% of adult size agrees well with the generalization by Laws (1959). Adult asymptotic lengths of 131 cm for males and 127 cm for females are slightly longer than those estimated for southeastern Baffin Island (McLaren 1958a).

The occurrence of significantly smaller or stunted seals is a phenomenon which is widely known among the Inuit hunters and which has drawn comment from several researchers (McLaren 1958a; Fedoseev 1975). Stunting has been thought to result from pups being born in peripheral breeding habitats, such as offshore areas of unstable ice (Finley et al. 1983). It has been postulated that in these situations, the period of parental care and nourishment of

TABLE 20. Summary of growth statistics for both sexes of western arctic ringed seal pups from conception to the end of the first year.

| Period | Duration | Standard length at end | Growth rate $\cdot d^{-1}$ |
|---|---|---|---|
| Foetal growth | 241 days | 57.8 cm | 2.8 mm |
| Birth to weaning | 37 days | 85.8 cm | 6.1 mm |
| Birth to asymptotic length | 74 days | 93.9 cm | 2.2 mm |
| Weaning to end of first year | 328 days | 93.9 cm | 0.02 mm |

the pups would be cut short and thus result in retarded growth. My data, largely from stable coastal ice, indicates that there might be a different cause. The natural spread in birth dates and apparently restricted time of growth in the first year of life seems to result in a normal distribution of the standard lengths of pups with a slight negative skew. The smallest pups, which are possibly the last born, are also in poor physical condition, with the stunted animals in the oldest age classes varying from low to normal condition. This indicates that stunting likely results from poor nourishment during the suckling and immediate post weaning period, a cause similar to that found by Bryden (1968) for the elephant seal, *Mirounga leonina*. The largest of the pups also seem to remain later in the autumn in the Holman area than do their smaller sized cohort members which migrate west along the mainland coast. It is possible that these large pups which can possibly compete with older seals will benefit even more in growth by feeding on the coastal concentrations of cod present at that time.

The large variation in annual condition also indicates that changes in food availability from year to year might result in retarded growth of certain cohorts. The extreme decrease in condition in 1974–75 documented in this study in fact did not produce this result because the actual pup production was reduced by the failure of females to ovulate. The possibility of reduced survivorship of stunted seals also would make it difficult to detect such affected cohorts if, in fact, they do exist. There is a slight indication that such an effect might have been felt by the 1966–69 cohorts as shown in Fig. 20. There is also the possibility that such stunted seals are, or become, spatially segregated from the main population, which would also make their detection difficult. Fedoseev (1975) and Finley et al. (1983) suggest offshore seals form a separate ecotype. It is not at all clear whether these seals are born in such areas or are segregated to such areas because of competition with the larger seals maintaining territories in the stable inshore ice.

Even after resolving the problems of the lack of standardization of measurements and methods of data analysis (McLaren and Smith 1985) studies of growth in seals from shot

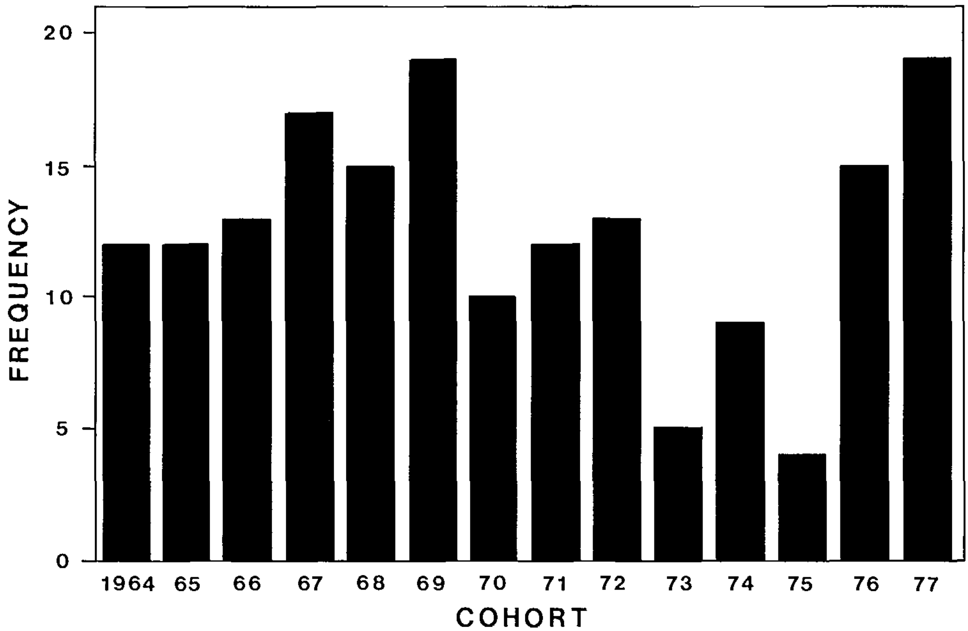



FIG. 20. Frequencies of ringed seals below one standard deviation (SD) of the mean size of their age class, by cohort from 1964 to 1977.

samples suffer greatly from not knowing the exact age of the specimens. More accurate and precise techniques of age determination would be of great value especially for the first few age classes where development is rapid and errors can greatly affect the growth curves. Advances in the understanding of how growth is controlled and the effect on the survivorship of cohorts will only be made when individual seals can be followed through a season. Emphasis should be placed on energetic studies with free-ranging individuals using the technology now available to track seals and document their time-energy budgets.

## Feeding Ecology

### Species and Types of Prey

Thirty six food species have been identified in the stomach contents of 519 ringed seals taken in the Coronation Gulf, Amundsen Gulf and southeastern Beaufort Sea (Table 21). Crustaceans, which formed the majority of items, were represented by two types: pelagic forms of which *Parathemisto libellula* and *Thysanoessa raschii* were dominant, and nectobenthonic types in which *Mysis oculata* was the most important species. Only a small number of hyperbenthic organisms such as decapods, polychaetes, gastropods and isopods were found. Of the fish identified in stomach contents, *Boreogadus saida* was the most important, but in some localities at certain times, sculpins, *Myoxocephalus* sp., were also well represented. one squid species, *Rossia* (*pacificus*?) was frequently found in the food of adult ringed seals occupying the winter breeding habitat near Iluvilik in Prince Albert Sound.

Of the crustacea, *M. oculata* was the most consistently dominant prey, appearing in 55% of stomachs from all areas, followed by *P. libelula* (26%); and copepods, mainly *Calanus hyperboreus*, and various amphipods in 4 to 5% of the stomachs. Only minor differences occurred in the composition of the prey species in different areas, the dominant prey remaining the same. At Brown's Harbour the amphipod *Anonyx nugax* was locally abundant. There, ringed seals also fed on the decapods *Lebbeus polaris* and *L. groenlandicus*. At Herschel Island the isopod *Mesidotea entemon*, was a common prey item and was noticed to be locally abundant in the Pauline Cove area near where the seals were caught. In this area the amphipod *Ophesura glacialis* also figured prominently in stomachs.

It was most common to find one (31%) to two (30%) prey items in the stomach contents, usually a crustacean species and arctic cod (Fig. 21). There was some indication of differences between years (1971–76). In 1974, 50% of the seals had only one prey item, Arctic cod, and this was significantly higher than the overall mean value for all year of 30% ($\chi^2 = 3.84$, $P < 0.05$). In the years 1974, 1975, and 1976, compared with the totals for all years, a significantly greater proportion of seals had two food items ($\chi^2 = 19.0$, $P < 0.001$).

Single-species food was found more frequently in the stomachs of pups (39%) than in adults ($\chi^2 = 6.72$, $P < 0.01$) or adolescents ($\chi^2 = 3.26$, $P < 0.05$) (Fig. 22). The diversity of food items in the stomachs of all age classes increased slightly from the ice-covered to the open-water season (Fig. 23).

### Age-Specific and Seasonal Differences in Food

Pups eat significantly more invertebrates than do adolescents ($\chi^2 = 11.7$, $P < 0.001$), but not more than adults ($\chi^2 = 1.39$, $P < 0.05$). They also eat significantly less fish than either adolescents ($\chi^2 = 18.0$, $P < 0.001$) or adults ($\chi^2 = 4.6$, $P < 0.05$). Adolescents feed more on fish than do the adults ($\chi^2 = 8.3$, $P < 0.01$), who feed equally on invertebrates and fish (Fig. 24). Pups have smaller mean volumes (79 cc) and weights (64 g) of stomach contents

TABLE 21. Food species and percent occurrence (+ = < 1%) in the stomach contents of 519 ringed seals from Amundsen Gulf and adjacent waters.

| Food species | Amundsen Gulf (*n* = 471) | Coronation Gulf (*n* = 16) | Brown's Hbr. (*n* = 25) | Herschel Is. (*n* = 7) |
|---|---|---|---|---|
| Nemertinea (unidentified) | + | | | |
| Polychaeta (unidentified) | + | | | |
| Gastropoda (unidentified) | + | | | |
| Cephalopoda | | | | |
| *Rossia* sp. | 1.5 | | | |
| Copepoda (unidentified) | 5.2 | | | |
| *Metridia longa* | + | | | |
| *Calanus hyperboreus* | 4.5 | | | |
| *Euchaeta glacialis* | + | | | |
| Misidacea | | | | |
| *Mysis oculata* | 30.0 | 62.5 | 43.4 | 85.0 |
| Isopoda | | | | |
| *Mesidotea entomon* | + | | | + |
| Amphipoda | 17.0 | | | |
| *Weypechtia pinguis* | + | + | | |
| *Gammarus oceanicus* | + | | | |
| *Gammarus wilkitzki* | + | | | + |
| *Gammarocanthus loricatus* | + | | | + |
| *Onisimus littoralis* | + | | | |
| *Onisimus glacialis* | + | | | |
| *Anonyx nugax* | 4.0 | | 34.7 | |
| *Anonyx sarsi* | + | | + | |
| *Stegocephalus inflatus* | + | | | |
| *Isdyrocerus sp.* | + | + | | |
| *Opherusa glacialis* | + | | | 42.0 |
| *Parthemisto libellula* | 28.0 | 25.0 | + | |
| *Parathemisto abyssorum* | + | | + | |
| Euphausiacea | | | | |
| *Thysanoessa raschii* | + | 25.0 | | + |
| *Thysanoessa inermis* | + | | | |
| Decapoda | | | | |
| *Argis dentata* | + | | | |
| *Sabinea septemcarinata* | + | + | + | |
| *Lebbeus polaris* | + | | 26.0 | |
| *Lebbeus groenlandicus* | | | 13.0 | |
| Ostracoda | | | | |
| *Philomedes globosus* | + | | | |
| Fish | | | | |
| Gadidae (unidentified) | | | | |
| *Boreogadus saida* | 43.0 | 38.0 | 44.0 | 23.0 |
| *Eliginus gracilis* | + | | | |
| *Arctogadus glacialis* | + | | | |
| Cottidae (unidentified) | + | | 16.0 | |
| Anarhicadidae | + | | | |
| Agonidae | + | | | |

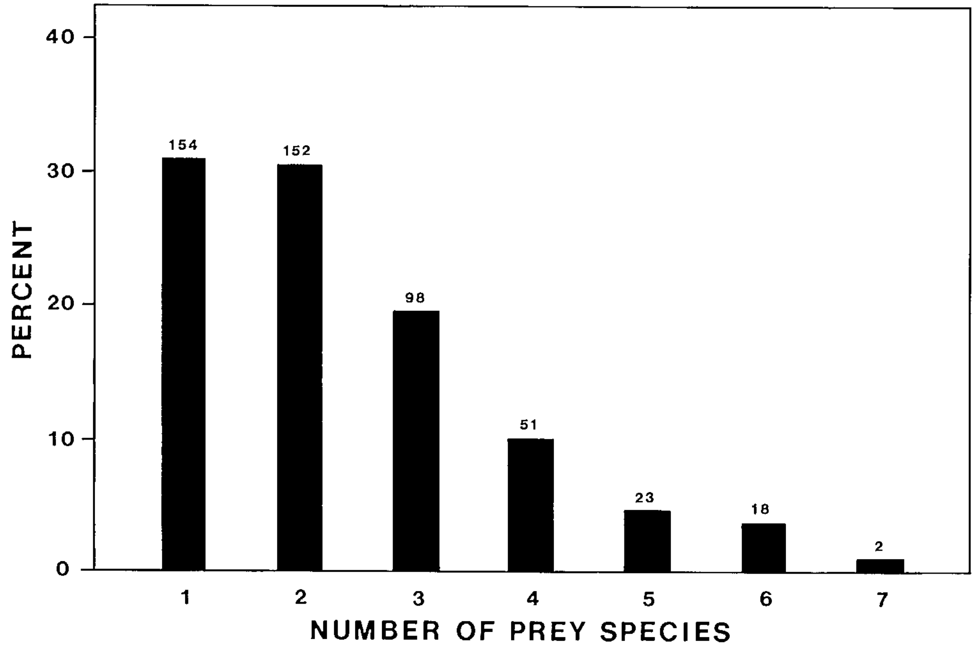



FIG. 21. Number of food items in the stomach contents of ringed seals collected from the Amundsen Gulf area during 1971–76.

than either adolescents (134 cc, 100 g) or adults (128 cc, 109 g); but there is no difference in these quantities between adolescents and adults. Benthic food ranges from 4 to 7% of stomach contents by weight in all age classes.

Fish are the most important food items for all age classes during the ice-covered months (Fig. 25). In the open-water period (July–October) invertebrates are dominant in the stomachs of pups and adults, but fish are slightly more important in the diet of adolescent ringed seals. The amount of food eaten appears to be about the same between the two periods for pups and adolescents, but increases markedly for adults from mean stomach weights of 95–119 g. This increase is also indicated in Fig. 26, which shows the lowest number of adult stomachs containing food in May and June, increasing gradually through the summer to a maximum (87%) in September. This is also reflected by the change in body condition of adult seals which undergo a considerable weight loss in the early summer (see section on Growth and Condition).

## Feeding Behaviour

There appears to be a definite diel pattern of feeding. All age classes have the least amount of food in their stomachs during the 06:00 to 12:00 period (Fig. 27). Maximum weights of food are found in the stomachs of pups and adults shot between 18:00 to 24:00; while adolescents show peak stomach weights from 12:00 to 18:00. In adults the peak weight of the stomach contents in the evening and early night are correlated with the lowest percentage of digested food (33%).

Intact arctic cod, of up to 20 cm long, have been found in the stomachs of ringed seals. During our netting and live-capture programs we have kept ringed seals in sea water holding pens for up to 3 weeks hand-feeding them with small Arctic char, *Salvelinus alpinus*. Char of 15–20 cm long were swallowed whole by the captive adult seals. They would approach the fish from behind and quickly extend their necks to capture the fish. As the vibrissae of

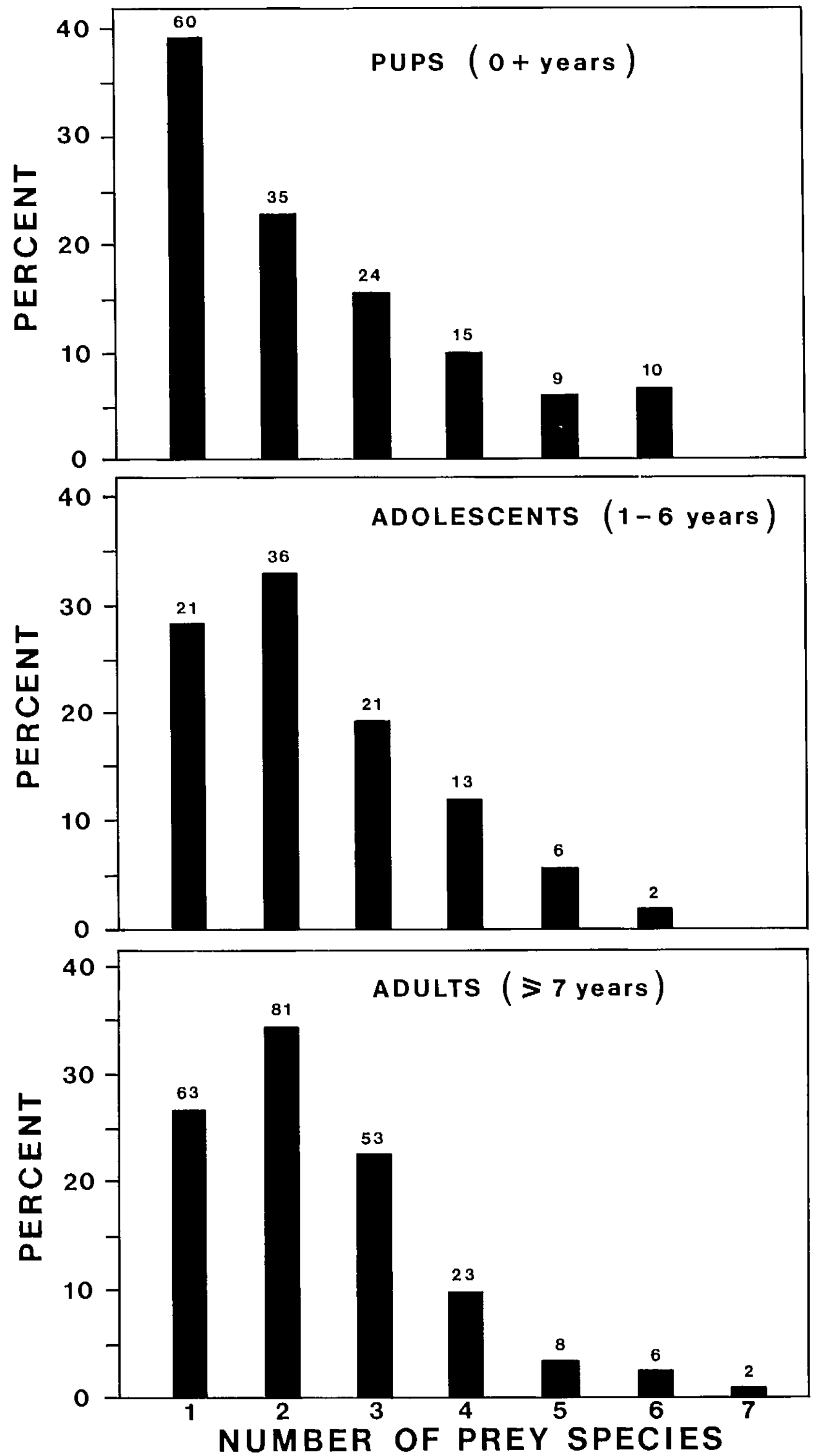



FIG. 22. Number of food items found in the stomachs of pup (0+), adolescent (1+ to 6+) and adult (≥7) ringed seals in Amundsen Gulf, N.W.T.

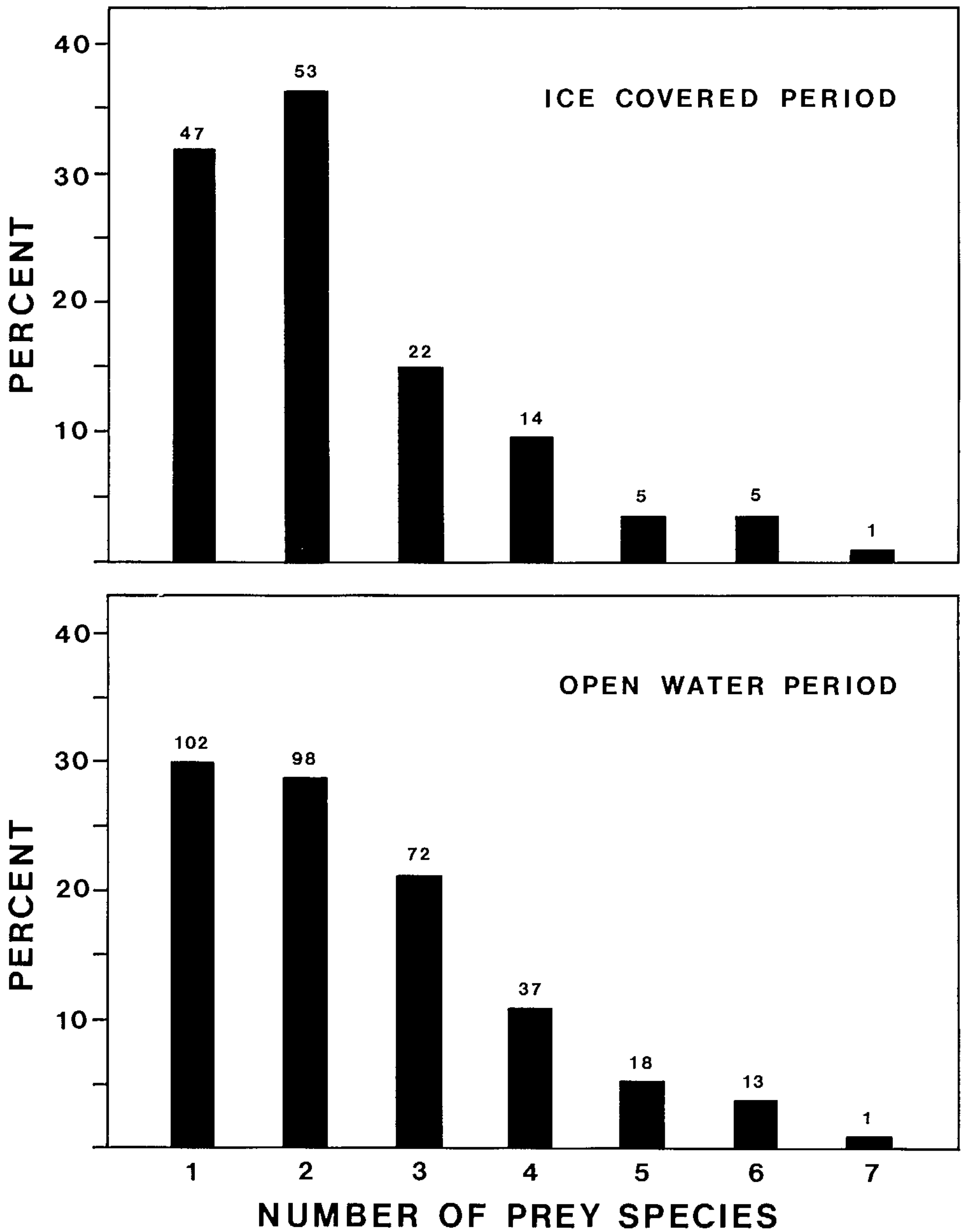



FIG. 23. Number of food items in the stomach contents of all age classes of ringed seals collected during the ice-covered (to 30 June) and open-water (July–October) seasons in Amundsen Gulf, N.W.T.

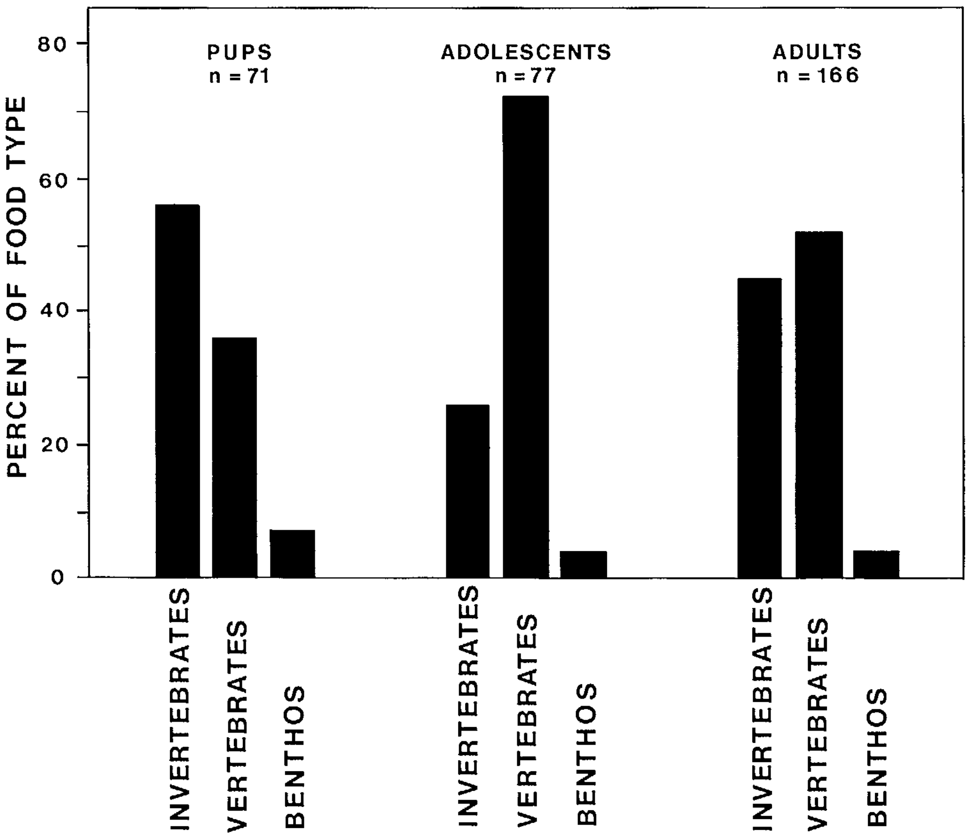



FIG. 24. Types of food in the stomach contents of three age-classes of ringed seals from Amundsen Gulf, N.W.T. during the ice-covered period (March to end June).

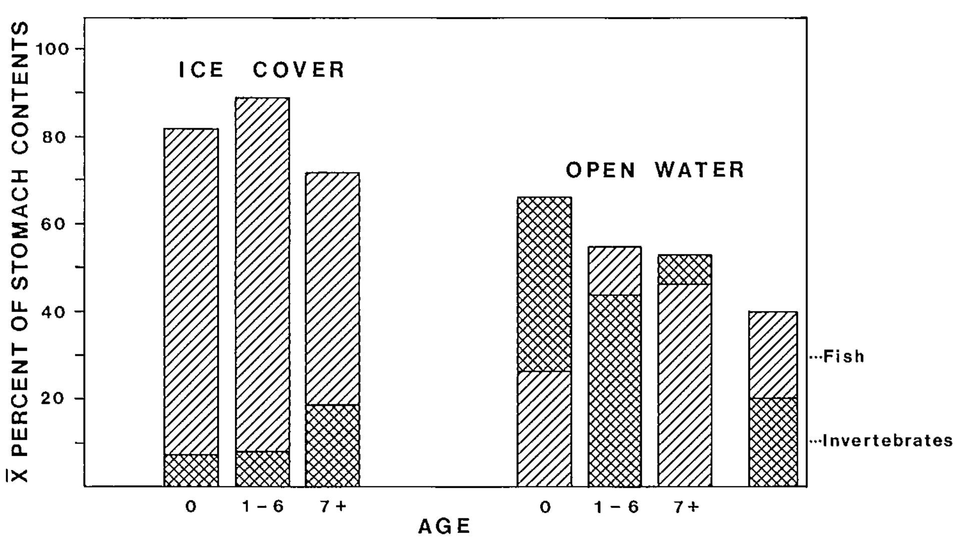



FIG. 25. Seasonal changes in consumption of invertebrates and fish by three age-classes of ringed seals in Amundsen Gulf, N.W.T.

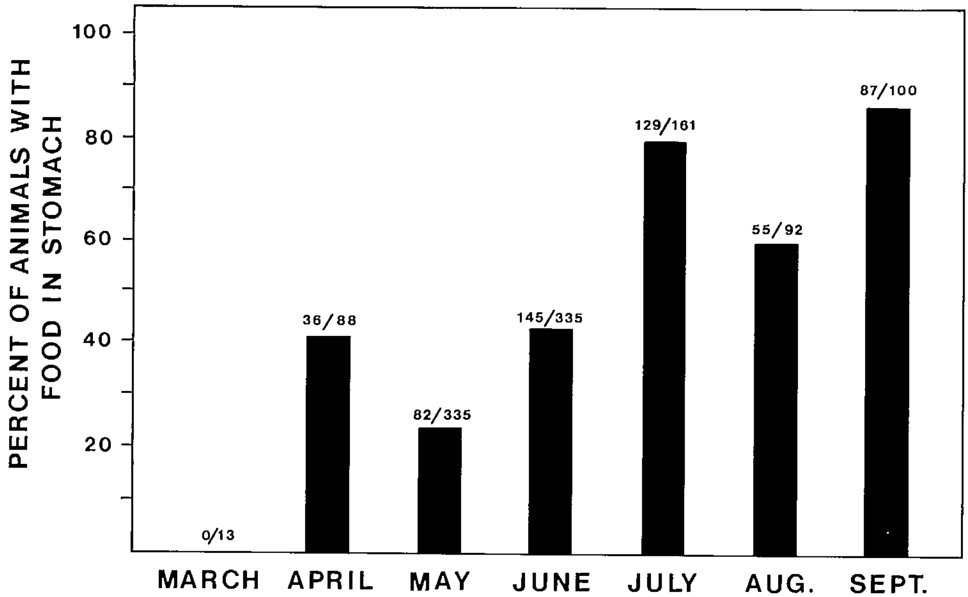



FIG. 26. Seasonal variation in the percentage of ringed seals with remains of food in their stomachs.

the seal made contact with their prey, they would catch the fish by sucking them into their mouth. This was immediatly followed by swallowing. Vibrissal contact appears to be important for ringed seals in identifying objects under water. They would frequently investigate the hands and feet of their handlers by gently pushing their vibrissae against our boots and hands.

Several large live char (50–67 cm long) were fed to captive adult seals in the confines of their holding pens. One adult seal took 22 minutes to kill a 67 cm long, 7.7 kg char. It swam behind the fish and repeatedly struck it in the head and gill region until the head was completely bitten off. Half of another large live char was consumed by an adult ringed seal in 37 min. The seal held the prey in its mouth and tore bites of flesh from it while pushing with its foreflippers. A large (13.6 kg) wolfish, *Anarichas sp.* was apparently killed by a medium sized ringed seal. It was found floating in the breathing hole of the seal (Smith 1977). The fish had been bitten in the head and gill region and bore marks on its body from the claws of the seal.

One observation of a ringed seal ingesting small stones from the bottom of its holding pen, might be of significance in explaining the occasional pebbles found in the stomach contents of pinnipeds. An emaciated pup was captured in our nets and kept in captivity until it eventually died after 3 weeks when its stomach was found to be full of small pebbles. We had not been able to capture any fish with which to feed this seal, during its period of captivity. We interpreted the behaviour as having been triggered by extreme hunger over a considerable period of time.

Ringed seals are seen to feed in groups only during the autumn. In the nearshore area of Prince Albert Sound groups of ringed seals numbering from 2 to 30 individuals are commonly seen to be feeding on schools of small arctic cod during the months of September and October. Such seal groups are usually revealed by associated flocks of birds, either Glaucous gulls, *Larus hyperboreus*, or Thayer's gulls, *L. thayerii*. This has been observed previously in the Amundsen Gulf and Beaufort Sea (Ryder 1956). Closer examination of these feeding associations revealed that kleptoparasitism or piracy (Ingolfsson 1969; Evans 1982) was in fact occurring. Both Glaucous and Thayer's gulls were seen to land among the

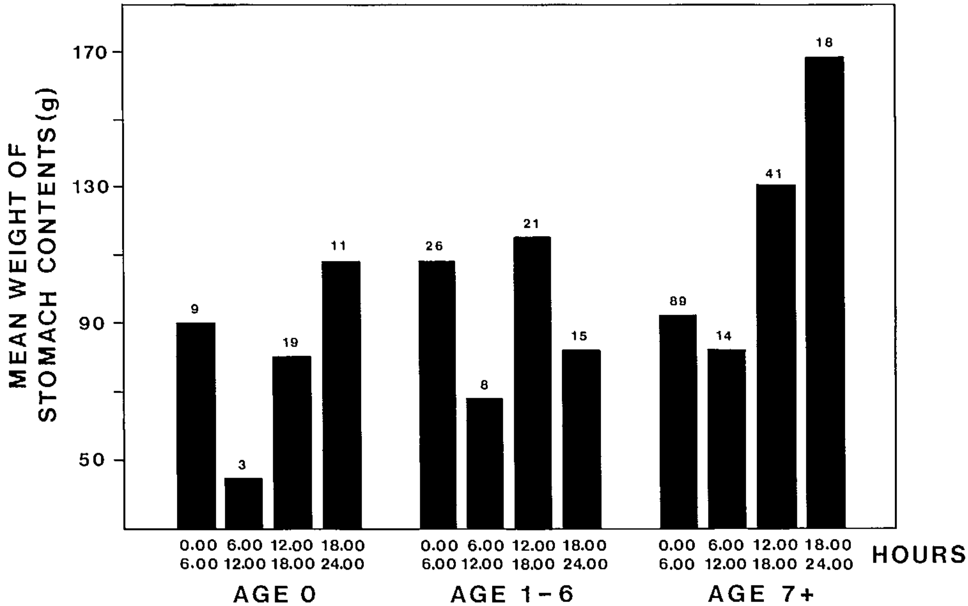



FIG. 27. Diurnal changes in the mean weight of stomach contents of ringed seal pups (0+), adolescents (1+ to 6+) and adults (≥7).

surfacing seals, lunging and pecking at their heads, causing them to drop their fish. Gulls collected in these situations were indeed seen to have fed on *B. saida*. Both the seals and gulls were actively following the moving schools of fish, making it necessary for us to travel at a significant pace in order to keep up with them. In calm weather it was usual to contact 20–30 such feeding groups per day during September and October 1971 and 1973.

Seals in such aggregations were of both sexes and almost exclusively older adults; the average age was 14.7 years ($n = 100$). Stomachs contained up to 400 *B. saida* measuring from 3 to 5 cm. The maximum stomach weight was 319 g. Most stomachs contained fish only, but a few also contained a small quantity of *Mysis oculata*.

## Quantity of Food Ingested

No direct measurements of the daily quantity of food ingested are possible from collections of stomach contents. Boulva and McLaren (1979) attempted to calculate meal size as a percent of body weight, using data on stomach contents of less than 30% digested, regressed on the body weight of the seal. A similar calculation with the present data yielded the equation:

$$\text{stomach contents (g)} = 5.89 - \text{weight of seal (kg)}^{0.85}$$

this gave similar results to theirs, predicting that meal size is some 3–4% of the body weight. The high asymptotic standard error of both terms in the equation (5.89, SE = 6.82; 0.85, SE = 0.29) makes the predictive value of this equation somewhat suspect.

## Discussion

Ringed seals of Amundsen Gulf show similar food preferences to those of the Beaufort Sea (Lowry et al, 1980) and Davis Strait (McLaren 1958a). Fish, mainly Arctic cod, were the dominant food item during the period of ice-cover for all age classes including pups, which began feeding on them just after weaning in May. In the summer, fish are slightly more important in the diet of adolescent (1+ to 6+ years) seals than for either pups or adults, which feed mainly on crustaceans, such as *M. oculata*, *P. libellula* and *C. hyperboreus*. This might indicate a partitioning of the nearshore feeding niche through competition between adults and sexually immature seals. A further indication of such competition is shown by the difference between adults and adolescents in their peak feeding times.

In 1974, ringed seals appeared to shift to squid and benthic food during the spring in their fast-ice breeding habitat and there was a reduction in the mean weights of stomach contents (Table 22). These changes were significant, even though the sample size was quite small, and might reflect decreases in fish during the 1974 winter. It was during this year that the mean body condition of ringed seals first dropped significantly and was correlated with reduced ovulation rates.

The autumn aggregations of ringed seals eating *B. saida* point to the importance of this fish in the annual energy budgets and seasonal distribution of seals within their habitat. Possible direct competition with adult seals for these nearshore food supplies, is the proximate factor causing the autumn offshore and westward movement of pups and adolescent ringed seals. The eventual occupation and maintenance of territories, in what will later in the season become breeding habitat, might be heavily influenced by the presence and distribution of Arctic cod in the autumn and early winter, when adult seals appear to replace their much depleted blubber reserves. It is possible that, after the burst of feeding in the autumn, winter feeding under solid ice merely maintains the seals. Other ice breeding phocids, such as the Weddell seal, *Leptonechotes weddelli*, are extremely energy efficient in their dives, during which time they search out low density fish prey (Dearborn 1965; Calhaem and Christofell 1969; Kooyman 1981). A similar situation might exist with ringed seals occupying fast-ice breeding areas in the winter.

Stomach contents do not appear adequate to provide data necessary to quantitatively assess either the seasonal changes in feeding or the calculation of daily energy budgets. Clearance rates of the stomach and intestines are quite rapid (Parsons 1977; Helm 1983), in the order of 4 to 5 hours and dependant on the water content of the food ingested. Captive ringed seals, fed on a constant diet throughout the year, showed a natural weight loss in April and May (Parsons 1977). This could indicate that ringed seals continue to feed throughout the year in the wild and that the loss of blubber reserves are more directly related to endogenous physiological changes. Empty stomachs of seals shot on the ice during the spring thus would not indicate complete fasting, but clearing of the digestive tract during the long periods spent on the ice by individuals at that time of year (Smith and Hammill 1981).

Prediction of meal size by the body weight of seals (Boulva and McLaren 1979) yields an estimate of 3–4% of the body weight of the seal in food per day, as a maintenance requirement. Using 1408 kcal·kg$^{-1}$ wet weight for Arctic cod (Lowry et al. 1980), this level of feeding (3% of body weight of a 45 kg seal) would provide 1905 kcal·day$^{-1}$. This is

TABLE 22. Annual changes in the quantity and type of food in the stomachs of adult ($\geq$ 7 years) ringed seals from Amundsen Gulf, N.W.T.

| Year | Percent food type | | | Mean weight | Mean volume | Max. weight | *n* |
|---|---|---|---|---|---|---|---|
| | Invertebrate | Fish | Benthos | | | | |
| 1971 | 25 | 72 | 5 | 118 g | 150 cc | 404 g | 52 |
| 1973 | 49 | 51 | 1 | 91 g | 101 cc | 302 g | 38 |
| 1974 | 35 | 50 | 8 | 36 g | 43 cc | 92 g | 14 |
| 1975 | 68 | 32 | 1 | 139 g | 156 cc | 541 g | 33 |

slightly higher than the maintenance energy level of 35 kcal·kg$^{-1}$·day$^{-1}$ calculated for adult captive ringed seals by Parsons (1977). These data suggest that ringed seals could maintain themselves with only one fish meal and possibly only a few crustacean meals each day and not the 7 to 12 stomachs full postulated by Lowry et al. (1980).

More detailed energy budgets could be constructed for free-ranging ringed seals from activity budgets of radio-tagged seals and by respirometry studies conducted at the breathing hole. The possibility should also be considered, that large prey, such as polar cod. *Arctogadus borisovi*, and wolffish, *Anarhichas denticulatus*, could provide maintenance energy for several days. Evidence of this from stomach contents could be missed, because otoliths would often not be ingested, since these fish are not eaten whole.

The possibility that food might be limiting to ringed seal populations has been denied (McLaren 1958) and postulated (Lowry et al. 1980; Smith and Hammill 1981). The importance of autumn and winter feeding should be studied in more detail. Detailed studies of the fish and crustaceans present in areas consistently occupied by ringed seals are required to shed more light on the role of food in controlling ringed seal numbers. This study strongly suggests that major decreases in recruitment during the years 1974 and 1975 were somehow related to a decrease in food which probably occurred in the autumn–winter period of 1973–74.

## Demographic Parameters

### Age Frequency Distribution 1971–81

I have Smith (1973b) commented on the various biases in catch curves for ringed seals associated with seasonal segregation of different age classes and the increased catchability of the 0+ and adolescent age classes. I indicated that the least biased catch curves could be obtained from seals shot during the summer open water period when all age classes were equally represented in the hunting areas. The shaded areas of the unsmoothed age frequencies of the sample shot in the open water around Holman for the years 1971 to 1981 (Table 23) highlight the effect of reduced pup production and increased pup mortality during the years 1973 to 1975. The effects are clearly evident in the succeeding 1975 to 1978 age frequency distributions, but virtually disappear thereafter. The marked reduction in pup production during the mid 1970's is shown in the various seasonally divided catches from both Holman and Brown's Harbour (Fig. 28). Unfortunately, I did not obtain samples of seals in either 1973 or 1974 during the open water season at Holman. The reduction in the proportion of pups in those years is evident however from the complete lack of 0+ seals in the 1973 and 1974 Holman spring catches, and further supported by the much reduced proportion of 0+ seals caught in the 1974 autumn net catch at Brown's Harbour, which in most years took from 77 to 100% 0+ aged seals. The 1975 reduction in pups was very real and quite drastic as no 0+ animals were taken in 271 seals shot during the summer at Holman, and only 22% (7/32) pups were caught in the nets at Brown's Harbour that summer.

A further examination of the change in cohort strength was made by calculating the mean percentage frequency $f_x/n$ of each year-class from 1971 to 1980 (Table 24). This statistic was multiplied by the square root of the number of years of data to weight it for the decreased frequencies caused by annual mortality in the older cohorts. The 1973–75 year classes are significantly weaker (Fig. 29); the 1973 and 1974 cohort might be somewhat under-represented since no data were available for their 0+ class frequency.

TABLE 23. Unsmoothed age frequencies from the catch in the open water (1 July to end September) from the Holman area. Shaded area highlights the effect of reduced recruitment in 1974 and 1975.

| Age | YEARS | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1971 | 1972 | 1973 | 1974 | 1975 | 1976 | 1977 | 1978 | 1979 | 1980 | 1981 |
| 0+ | 115 | 129 | | | 1 | 61 | 79 | 174 | 30 | 195 | 118 |
| 1 | 36 | 23 | N | N | 1 | 2 | 5 | 40 | 6 | 61 | 87 |
| 2 | 42 | 11 | O | O | 0 | 1 | 1 | 31 | 9 | 26 | 89 |
| 3 | 46 | 24 | | | 4 | 1 | 0 | 19 | 12 | 59 | 82 |
| 4 | 21 | 24 | D | D | 8 | 2 | 1 | 4 | 12 | 13 | 73 |
| 5 | 12 | 11 | A | A | 20 | 19 | 4 | 12 | 6 | 32 | 57 |
| 6 | 6 | 12 | T | T | 18 | 46 | 23 | 42 | 7 | 21 | 52 |
| 7 | 5 | 11 | A | A | 25 | 41 | 28 | 55 | 7 | 8 | 15 |
| 8 | 4 | 4 | | | 38 | 55 | 30 | 62 | 7 | 8 | 10 |
| 9 | 7 | 3 | | | 55 | 46 | 22 | 48 | 17 | 28 | 16 |
| 10 | 12 | 5 | | | 53 | 44 | 20 | 17 | 9 | 24 | 17 |
| 11 | 21 | 6 | | | 46 | 49 | 20 | 18 | 7 | 19 | 11 |
| 12 | 7 | 4 | | | 39 | 36 | 19 | 17 | 3 | 10 | 13 |
| 13 | 7 | 4 | | | 29 | 32 | 21 | 10 | 6 | 16 | 11 |
| 14 | 9 | 8 | | | 17 | 22 | 19 | 6 | 3 | 15 | 15 |
| 15 | 14 | 6 | | | 18 | 17 | 9 | 7 | 5 | 10 | 16 |
| 16 | 12 | 6 | | | 8 | 5 | 5 | 3 | 3 | 6 | 6 |
| 17 | 9 | 4 | | | 5 | 8 | 4 | 3 | 0 | 4 | 7 |
| 18 | 8 | 5 | | | 3 | 1 | 5 | 6 | 2 | 2 | 4 |
| 19 | 8 | 4 | | | 1 | 1 | 2 | 4 | 1 | 1 | 7 |
| 20 | 2 | 1 | | | 2 | 1 | 2 | 2 | 0 | 3 | 4 |
| Totals | 403 | 305 | | | 391 | 490 | 319 | 580 | 152 | 561 | 710 |

## Parameters for an Assumed Stationary Population

Catch curves for 1971–72, 1980–81 were combined since they appeared free of the effects of reduced recruitment seen during the years 1973–78. Smoothing of the age classes 1+ to 20+ was done by regression of log frequencies on age where $\log f_x = 2.32 - 0.06_x$ ($R^2 = 0.81$) (Table 24). The frequency for age class 0+ was generated from the age specific reproductive values ($m_x$) given in Table 15. Total pup survivorship $P_x$ is calculated as 0.84 from the smoothed and adjusted lumped age frequencies.

In this study recruitment was greatly affected by reduced ovulation in 1973–75 and by increased mortality from foxes in 1973 and 1974. To calculate the part played by increased natural mortality only, it was assumed that the only significant source of natural mortality for the 0+ age class was from fox predation. This was known to be 0.10 for most years and increasing to 0.37 for 1974 and 1975. The relation, $\hat{a} = H + N - HN$ where: $\hat{a}$ = total mortality; $H$ = hunting mortality; and $N$ = natural mortality (fox predation), was used to calculate the decreased recruitment attributed to increased natural mortality only. In normal years mortality of the first year-class was 0.16 (from Table 25) therefore: $0.16 = H + 0.10 - 0.10H$ and $H = 0.07$. If $N$ is increased to 0.37 as seen in 1973–74 then: $\hat{a} = 0.07 + 0.37 - (0.37)(0.07) = 0.41$.

Fluctuations in percentage of females ovulating was quite marked during the years 1971 to 1980 ranging from 1.0 to 0.386. The mean proportion of females ovulating in the years 1971–72, 1976–80 was 0.89 which was significantly different from the reduced mean percentage of 0.49 during the years 1973–75 ($\chi^2 = 259.7$ $P < 0.01$). The effect of the reduced percentage of ovulation on $m_x$ values is detailed in Table 26.

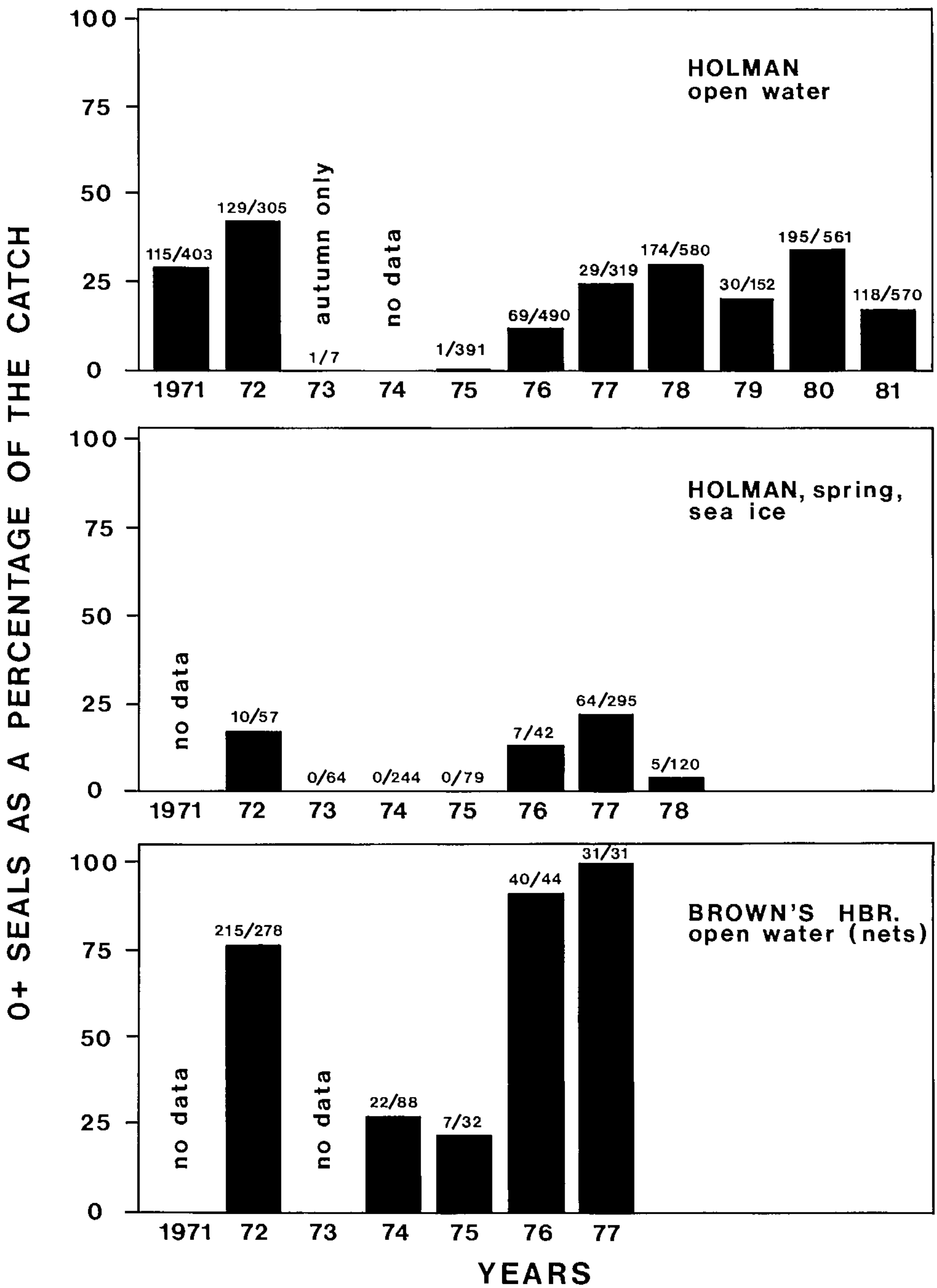



FIG. 28. Ringed seal pups (0 + age) as a percentage of the catch in the spring and summer shot sample at Holman and the autumn net catch at Brown's Harbour, N.W.T. for the years 1971 to 1981. Sample size is shown above the histogram.

TABLE 24. Percentage age frequencies (*%fx*) from the catch in the open water (1 July to end September) from the Holman area.

| Age | %fx | | | | | | | | | | | $\bar{x}$ %fx · √No. Cohort Yr. | Cohort Year |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1971 | 1972 | 1973 | 1974 | 1975 | 1976 | 1977 | 1978 | 1979 | 1980 | 1981 | | |
| 0+ | 0.285 | 0.422 | | | 0.002 | 0.124 | 0.247 | 0.300 | 0.197 | 0.347 | 0.166 | | |
| 1 | | 0.075 | | | 0.002 | 0.004 | 0.015 | 0.069 | 0.039 | 0.108 | 0.122 | 0.331 | 1980 |
| 2 | | | N | N | 0 | 0.002 | 0.003 | 0.053 | 0.059 | 0.046 | 0.125 | 0.248 | 1979 |
| 3 | | | O | O | 0.010 | 0.002 | 0 | 0.032 | 0.078 | 0.105 | 0.115 | 0.250 | 1978 |
| 4 | | | | | 0.020 | 0.004 | 0.003 | 0.006 | 0.078 | 0.023 | 0.102 | 0.260 | 1977 |
| 5 | | | D | D | | 0.038 | 0.012 | 0.020 | 0.039 | 0.057 | 0.080 | 0.152 | 1976 |
| 6 | | | A | A | | | 0.072 | 0.072 | 0.046 | 0.037 | 0.073 | 0.082 | 1975 |
| 7 | | | T | T | | | | 0.094 | 0.046 | 0.014 | 0.021 | 0.040 | 1974 |
| 8 | | | A | A | | | | | 0.046 | 0.014 | 0.014 | 0.037 | 1973 |
| 9 | | | | | | | | | | 0.049 | 0.022 | 0.212 | 1972 |
| 10 | | | | | | | | | | | 0.023 | 0.234 | 1971 |
| Total specimens | 403 | 305 | 0 | 0 | 391 | 490 | 319 | 580 | 152 | 561 | 710 | | |

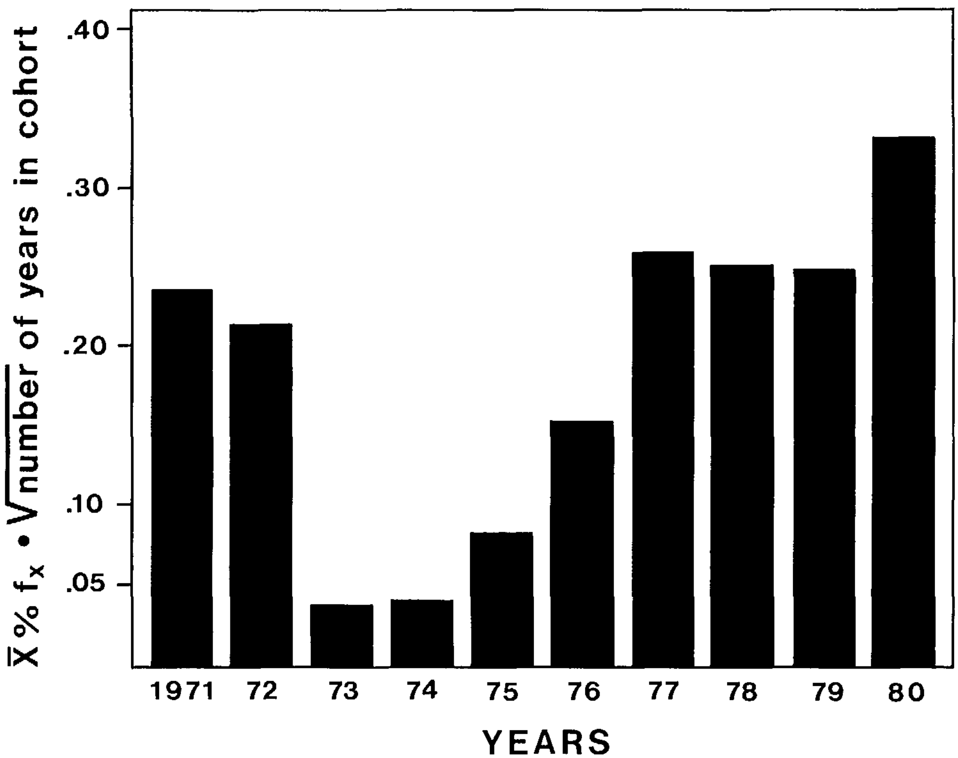



FIG. 29. Index of cohort strength from the statistic $\bar{x}\%fx \cdot \sqrt{\text{number}}$ of cohort years for the open-water catch of ringed seals in the Holman area from 1971 to 1980.

TABLE 25. Smoothed age-frequency distribution from the Holman open water catch 1971–72, 1980–81. The adjusted 0+ frequency 'a' is from age-specific reproductive rates in Table 15a.

| Age | Lumped 1971–72, 1980–81 *fx* | Smoothed *fx* | Smoothed Proportion Pregnant (Table 15a) | $m_x$ | $P_x$ |
|---|---|---|---|---|---|
| 0 | 557 | 257[a] | | | 0.840 |
| 1 | 207 | 216 | | | 0.861 |
| 2 | 168 | 186 | | | 0.860 |
| 3 | 211 | 160 | | | 0.856 |
| 4 | 161 | 137 | 0.196 | 0.098 | 0.861 |
| 5 | 112 | 118 | 0.288 | 0.144 | 0.864 |
| 6 | 91 | 102 | 0.390 | 0.195 | 0.863 |
| 7 | 39 | 88 | 0.494 | 0.247 | 0.852 |
| 8 | 26 | 75 | 0.604 | 0.302 | 0.867 |
| 9 | 94 | 65 | 0.706 | 0.353 | 0.862 |
| 10 | 58 | 56 | 0.802 | 0.401 | 0.857 |
| 11 | 57 | 48 | 0.877 | 0.438 | 0.854 |
| 12 | 34 | 41 | | | |
| 13 | 38 | 36 | | | |
| 14 | 47 | 31 | | | |
| 15 | 46 | 26 | | | |
| 16 | 30 | 23 | | | |
| 17 | 24 | 20 | | | |
| 18 | 19 | 17 | | | |
| 19 | 20 | 14 | | | |
| 20 | 10 | 12 | | | |

## Discussion

With the ringed seal all population parameters have been derived from specimens taken from the Inuit hunt. The possibility does not exist for a tag–recapture study of sufficient sample size to permit estimates from cohort analysis. Caughley (1966) has commented on the weakness of the static life table analysis which has as its basic assumption that the population is stable and stationary. Evidence presented here on varying rates of fox induced pup mortality and decreased reproduction show that these assumptions do not hold for the western arctic ringed seal population. Even with these assumptions satisfied, population parameters based on large samples of distributions of long-lived animals often give totally unrealistic survival rates because of sampling variance and correlation of estimated survival rates between successive age classes (Spinage 1974; Polacheck 1985).

For the years where fox predation appeared to be fairly constant at about 0.10 and where ovulation and age specific reproductive rates were fairly high there still remains the problem of arriving at a measure of unbiased mortality estimates especially for the first few year classes. Increased catchability of the 0+ age class makes it necessary to generate its age frequency by the use of $m_x$ values. These in themselves are probably underestimates because of social segregation (McLaren and Smith 1985) which would tend to cause the youngest of the sexually mature females to be under-represented in the sample. The representativeness of the 1+ age class which is the numerator in the equation yielding the mortality estimate of the 0+ group cannot be tested independantly and is suspect. The

TABLE 26. Changes in age-specific fecundities during the years 1973 to 1975 in the ringed seals from Holman, N.W.T. caused by reduced ovulations.

| Age | $m_x$ from 1971–72, 76–80 | $m_x$ 1973 | $m_x$ 1974 | $m_x$ 1975 |
|---|---|---|---|---|
| 0 | | | | |
| 1 | | | | |
| 2 | | | | |
| 3 | | | | |
| 4 | 0.098 | 0.085 | 0.046 | 0.042 |
| 5 | 0.144 | 0.125 | 0.067 | 0.062 |
| 6 | 0.195 | 0.169 | 0.091 | 0.084 |
| 7 | 0.247 | 0.214 | 0.115 | 0.107 |
| 8 | 0.302 | 0.262 | 0.141 | 0.130 |
| 9 | 0.353 | 0.306 | 0.165 | 0.152 |
| 10 | 0.401 | 0.348 | 0.161 | 0.173 |
| 11 | 0.438 | 0.380 | 0.205 | 0.189 |

smoothing operations, violated assumptions and biases involved in the estimates make the calculation of exact population parameters an exercise of questionable significance and limited usefulness. The discrepancy between the estimated survivorship of the 0+ age class in this study of 0.84 and of 0.59 in east Baffin (Smith 1973a) where conditions appear similar, reinforces this conclusion.

The large-scale reduction in recruitment and increase in pup mortality during the years 1973–75 were discovered only because of fairly labor intensive birth lair surveys and by collecting a large number of sexually mature females during the early spring, summer and autumn months. It would have been extremely difficult to establish the exact cause of reduced recruitment had I only been able to examine the age-frequency distribution. It appears that a marked reduction in ovulation associated with decreased physical condition of females plus increased pup mortality from arctic foxes both had marked negative impacts on the recruitment of the 1974–75 cohorts. The significant changes in age structure of 1974–75 had almost disappeared from the age frequency distributions by 1978, only three seasons after the extreme low, pointing out the insensitivity of the single season cross-sectional life table approach in monitoring changes in the vital parameters of populations. Errors in age determination are probably also involved in obscuring real differences. It appears that in the absence of other data on body condition, reproductive output and occupation of breeding habitat, it would be impossible to distinguish between real changes and differences caused by sampling error.

The demonstrated potential for ringed seals to move long distances and perhaps to shift their distribution to more favourable wintering and feeding areas in response to unfavourable conditions or depleted resources, makes it extremelly difficult to apply traditional population methods for documenting the magnitude and causes of the changes on local stocks. More emphasis must be placed on studying how a few individuals behave, feed and maintain themselves throughout the arctic year. The measurement of quantitative indicators of ringed seal condition and a knowledge of the factors affecting the production of their seasonally important marine food species are required. Instrumentation of free-ranging ringed seals with telemetric devices and dive time recorders combined with new techniques to calculate energy expenditure such as the double labelled water method (Costa and Gentry 1986) will lead to major advances in understanding the factors affecting the populations of top carnivores in the arctic marine ecosystem.

## Present and Future Considerations

Over the past 30 years there has been substantial change in the lives of the people in the Canadian arctic. The Inuit have moved from a subsistence economy, dependent on sea and terrestrial mammals, to a cash livelihood based on fur trading. They are now entering the wage economy of modern society. Studies of ringed seal populations were originally initiated to determine the sustainable yields from local stocks (McLaren 1958b). The final centralization of the Inuit into villages, which was completed by the mid-1960's, made this necessary. The higher number of people, hunting in more restricted hunting areas, opened the possibility of overexploitation at the local level (Smith 1973a). The replacement of the dog team in the early 1970's by motorized transportation had, as its net result the decrease in need for seal meat, but an increased dependence on the sale of seal pelts. Ironically, as the demand for protein decreased the cost of hunting using snowmobiles increased, putting the Inuit firmly into a cash economy (Smith 1980b). Prices of seal skins rose to a high in the mid-1970's, resulting in an increased harvest of ringed seals. Since 1977, prices have dropped drastically, primarily because of the strong European anti-sealing campaign, which has now effectively destroyed the market for all types of seal pelts (Wenzel 1978). This, coupled with the corresponding rapid rise in the cost of hunting during the inflationary early 1980's, has had the effect of drastically reducing seal harvests throughout the Canadian arctic.

The advent of offshore hydrocarbon exploration in the early 1970's also brought forth new problems for wildlife managers. Much of the recent research conducted on arctic marine mammals and their predators has been directed at attempting to predict the possible impact of offshore industrial activities and accidents (Stirling and Calvert 1983). Since seals, whales and polar bears are the most visible species and probably the best studied members of the arctic ecosystems, with a direct importance to the Inuit people, large amounts of money have been allocated to such studies. In most cases the research has been site-specific and usually of short duration (Stirling et al. 1979). A few of these studies have benefited from the insights gained in longer-term work, conducted outside of the context of impact-related research. Most studies have not directly or experimentally attempted to measure the effect of a particular impact, but instead were of the reconnaissance or census type, or consisted of bibliographic reviews e.g. Johnson (1983); Richardson et al. (1983). In most reports, predictions about particular impacts were based mainly on opinion rather than on empirical evidence. Also most studies remain unpublished, often with restricted or limited circulation, either in the hands of government agencies or consulting firms hired by the proponents of industrial development. Yet major decisions may be made on the strength of their content.

### Effects of Industrial Development on Ringed Seals of the Western Arctic

Two major arctic non-renewable resources, petroleum and minerals, have attracted the attention of industry in the last 20 years. In the Beaufort Sea, considerable reserves of gas and oil have been discovered in offshore waters (Pimlott et al. 1976). Current hydrocarbon development plans call for offshore oil and gas production on a year-round basis in the relatively near future (Dome Petroleum Ltd., Esso Resources Canada Ltd., and Gulf Canada Resources Inc. 1982). No commercially exploitable ore deposits have yet been identified for development in the southeastern Beaufort Sea or Amundsen Gulf region, but are being developed elsewhere at even higher latitudes (Keith et al. 1981; Stirling and Calvert 1983).

Oil spills are possible, either during production (Milne 1977; Milne and Herlinveaux 1977), or during transportation (Johnson 1983). Offshore petroleum developments could affect ringed seals directly, in the case of oil spills by contact, inhalation, or ingestion; and indirectly by affecting their food species (Blood 1977). Other effects of industrial activities, such as tanker traffic and pipelines, are more difficult to envisage. Year-round traverses by ice-breaking tankers, now thought to be feasible for transporting gas and oil to the southern markets (Science Council of Canada 1977), could directly kill ringed seals in the fast-ice breeding habitat. There could be an even more widespread effect from the destabilizing of ice edges. The noisy, high-powered ships have the potential of causing widespread disturbance and acoustic interference with intraspecific communication in sea mammals. Underwater pipelines would be less disturbing once they were built but, because of the cost, are less frequently being considered for long distance transportation of arctic petroleum products.

The direct effect of immersion in crude oil and ingestion of small quantities was evaluated during the 1974–75 Beaufort Sea Program. Six ringed seals placed for 24 hours in a sea water pen, with a 1 cm thick slick of Norman Wells light crude oil, absorbed volatile fractions of oil through their lungs (Englehardt et al. 1977). Eye irritation and corneal lesions were seen and kidney lesions resulted from the excretion of the inhaled fractions of oil. Neither the eye nor kidney damage was severe enough to incapacitate the six experimental ringed seals and all seemed to recover fully from the short exposure to floating oil (Geraci and Smith 1976a).

Coating of harp seal white-coat pups, with the same light crude oil, had no effect on thermoregulation (Smith and Geraci 1975). An in vitro experiment, using an adult ringed seal pelt, showed that Norman Wells crude oil, did not significantly change its insulating values in air at varying wind speeds (Øritsland 1975, *in* Smith and Geraci 1975).

Three ringed seals taken to a southern research facility, died within 71 minutes of exposure to a water pool covered with Norman Wells crude oil. Their death was triggered by exposure to oil added to the already considerable stress of captivity and handling (Geraci and Smith 1976a, b, 1977).

Ingestion of up to 75 mL of crude oil per day was judged not permanently harmful to ringed seals. In their exposure to floating crude oil the ringed seals did not appear to accidentally ingest any significant amounts of oil. Seals do not groom themselves and are thus not exposed to ingesting large amounts of oil. Oil ingested because of excessive grooming behaviour, has been shown to be fatal in polar bears (Øritsland et al. 1981).

It is not known how ringed seals would react to an offshore oil spill. Recently, bottlenose dolphins, *Tursiops truncatus*, have been shown to be able to visually detect oil floating on water (Geraci et al. 1983). Under experimental conditions it was also demonstrated that the dolphins could avoid areas of oil-coated water, even down to the very low concentrations of an oil sheen (Smith et al. 1983; Geraci et al. 1985). Part of the avoidance behaviour was reinforced by a few brief tactile contacts with the oil slick. It might be reasonable to assume that ringed seals would have similar capabilities and be able to avoid oil in open-water situations.

Oil spills which spread into the fast-ice breeding habitat of the ringed seals would likely have the greatest impact. Newborn ringed seal pups have been found to have lower critical temperatures of −20°C to −25°C in air, but only a few degrees below 0°C when wet (Taugbol 1984). If oil spills caused female seals to move their pups, thus exposing them to the stress of oil and water immersion resulting in hypothermia, neonate mortality could be quite high.

In open water situations, the effect of oil spills on the food of ringed seals might be minimal. Arctic cod and their fry are generally found at depths below 10 m and thus would not be affected (Johnson 1983). This also applies to the other pelagic food organisms of the ringed seal. Adult fish, which are fed upon in the winter (Lowry et al. 1980), might be associated with the crustacean fauna on the underside of the ice and are often found in cracks and leads during the spring. Under-ice oil spills might thus have a more serious impact on the winter and spring food supplies. These could then have a signficant effect on local concentrations of breeding ringed seals, which live in the fast-ice with their neonates, until just prior to break-up in early July.

Ice-breaking oil and liquified natural gas (L.N.G.) tankers could soon be a common sight in the arctic. Projections by industry indicate that 50 ice breakers each month will pass through Amundsen Gulf at the peak of offshore oil production in the Beaufort Sea (Dome Petroleum Ltd., Esso Resources Ltd. and Gulf Resources Canada Inc. 1982). Since the ships will tend to stay in a fixed navigation lane mostly in the offshore ice where birth lair densities are low, mortality of newborn ringed seals from this source may not be significant. Of more concern is the possible destabilization of ice edges by ice breakers, which could change the ice cover and climatic conditions over a large region. The total extent and location of open water during the winter in the southeastern Beaufort Sea and Amundsen Gulf are quite variable (Lindsay 1975). Prevailing barometric pressure patterns and wind direction are the major influences on dates of freeze-up and break-up of ice. Areas of open water such as the large Bathurst polynya in the southeastern Beaufort Sea and Amundsen Gulf are known to be important areas for overwintering marine mammals (Stirling 1980; Stirling and Cleator 1981). Significant vertical mixing occurs in such situations (Kupetskii 1959, 1962; Szekielda 1974), which might explain the productivity of areas in the vicinity of polynyas (Dunbar 1981). There is some concern that the frequent impact of ice-breaking ships might cause the collapse of the Bathurst polynya, which would directly affect the distribution of the youngest age classes of ringed seals living there in the winter. This might also reduce the current annual marine productivity of the region. While such a change is still considered a possibility by some, the general concensus among ice experts is that the magnitude of the forces maintaining polynyas is so much greater than the impact possible from ice-breakers, that large-scale destabilization is unlikely.

Acoustic interference and disturbance from tanker noise might produce some of the most significant adverse effects on marine mammals. Baleen whales appear to depend on low frequency sounds for long distance communication (Payne and Webb 1971); and odontocetes on echolocation for navigation and food finding. The masking of such acoustic signals by loud ice-breakers could have significant adverse effects. Both species of arctic seals, the ringed seal (Stirling 1973) and the bearded seal (Dubrovskii 1933; Freuchen 1937; Poulter 1968; Ray et al. 1969; Stirling et al. 1983), vocalize underwater. Of the two species, the ringed seal is the quietest, but at certain times of the year it can be quite vocal. Ringed seals are territorial in their fast-ice breeding habitat (Smith and Hammill 1981) and the greatest number of vocalizations are recorded during the period prior to reproduction. It is thought that the majority of these calls, in the 2–5 kHz range, such as barks and growls, are aggressive displays, involved with the maintenance of territory (Stirling 1973; Stirling et al. 1983).

Audiograms have been made of ringed seals in captivity. The underwater tests showed a uniform sensitivity in the frequency range 1–45 kHz and that ringed seals are able to discriminate between frequencies of up to 60 kHz (Terhune and Ronald 1975a, b, 1976). At 5 kHz, which appears to be the frequency level of many ringed seal vocalizations (Stirling 1973), the hearing threshold is approximately 70 $dB/(1 \mu Pa)^2/Hz$.

Richardson et al. (1983) constructed a model to delimit the zone of influence of a ship, with a sound source level at 1 m of 138 $dB/(1 \mu Pa)^2/Hz$, which would be representative of a class 7 ice-breaking tanker. Ambient noises were assumed to be 40 dB. Using propagation loss estimates based on Verrall (1981), they concluded that ringed seals would be able to detect the ship at a distance of 50 km. Further, assuming that sounds relevant to seals are normally 20 dB above auditory threshold, the zone of masking and potential disturbance would be within 5 km of the ship. They concluded that since most industrial noise would be of low frequency and that the auditory thresholds of seals are high in this range, there would be minimal effects on seals. Other models disagree with these conclusions. The existence of sound channels (Payne and Webb 1971) would greatly increase the propagation of ship noise and alter the impact on the receiving animals. Mohl (1980) pointed out, that the coastal region enhancement effect, might be relevant in many areas of the arctic. Clearly, while many of the physical properties of sound transmission are known, there is still much divergent opinion about the possible quantitative and behavioural effects of industrial noise, on arctic marine mammals (Mansfield 1983).

Industrial activity in the arctic might lead to the release of contaminants into the marine ecosystem. Apart from oil released by accident, drilling muds containing toxic heavy metals, are potentially the most harmful contaminants likely to be released by the petroleum industry. Since these are accumulated through the ecosystem and can reach high concentrations in the top consumers, a knowledge of the naturally occurring levels already present is important. This is especially so, because all arctic marine mammals are used as food by the Inuit.

It is known that mercury occurs in high concentrations in the livers of ringed seals and bearded seals (Smith and Armstrong 1975). High mercury levels are found in the liver and muscle of seals from Amundsen Gulf (Smith and Armstrong 1978) and the western Beaufort Sea (Galster 1971, 1974, 1976; Galster and Burns 1972), as well as from other Canadian arctic locations (Eaton 1979). Polar bears reflect the high mercury content of their main prey species, the ringed seal (Eaton and Farant 1982). Seals appear able to convert methylated mercury, accumulated from the sediments through the food chain, to the inorganic form. This appears to take place in the liver, which in the Amundsen Gulf ringed seals, contains a mean of 27 ppm Hg, 95–97% of which is in the inorganic form. Selenium, which occurs in a 1:1 molar concentration with the mercury, might be involved in the detoxification process (Smith and Armstrong 1978). No evidence of health problems, associated with heavy Hg loads, were found in any of the seals collected.

Elevated mercury levels in the blood of some Canadian arctic Inuit have led to concern about their high seal consumption (Hendzel et al. 1974; Wheatley 1979). An experiment on two groups of cats, one fed on seal livers containing an average of 27 ppm naturally occurring mercury and the other on a diet of beef liver with the added equivalent amounts of methyl mercury chloride, showed mercury intoxication to occur only from the artificially added mercury (Eaton et al. 1980). A further experiment with cats clearly showed a reduced toxicity of added methyl mercury, when it was fed along with selenium (Eaton and Hewitt 1981). They concluded that the high mercury levels in the blood of indigenous people of the arctic should not be taken as an indication of a health hazard.

In view of the high mercury level present in various components of the arctic ecosystem, it appears unlikely that the minor local additions from sources such as drilling muds would be of much consequence. Wagemann and Muir (1981) review concentrations of other heavy metals in marine mammals of northern waters. For these there was not enough information to establish patterns of accumulation with age nor assess the effect of the heavy metal loads on the health status of the species involved.

Hydrocarbons of the chlorinated form have been found in the lipids of most arctic and antarctic marine mammals (Holden 1978). Throughout the Canadian arctic *p′,p′*-DDE, *p′,p′*-DDT and PCB residues are present at low levels in the blubber of ringed seals (Table 27). Addison and Smith (1974) showed that there was a definite accumulation of DDT in male ringed seals with age, but not in females; nor was the relationship present for PCBs. Addison and Brodie (1977) showed that the female DDT burden in grey seals, was reduced by transferring it through their milk during suckling. More recently, evidence has shown that PCBs have declined significantly in the lipids of arctic ringed seals over the last 10 years; but that DDT levels have not decreased (Addison et al. 1986). The reduction of PCB used in Canada during the 1970's (Addison 1983) probably accounts for the reduced levels in ringed seals. The source of the continuing influx of DDT into the Canadian arctic, where its use has been banned since 1970, is not known. It may be from the Far East, where it was in use until 1981 (Wang 1981).

In Canada no clinical or pathological effects, of chlorinated hydrocarbons have been observed in ringed seals, but adverse effects have been documented elsewhere in several pinniped species (Gilmartin et al. 1976; Newby 1978). The much greater levels of DDT and

TABLE 27. Chlorinated hydrocarbons (ppm) in the blubber of ringed seals from Holman, N.W.T., from other Canadian arctic locations and from the Gulf of Bothnia.

| Location | References | Sex | Σ DDT | $p'p'$ DDE | $p'p'$ DDT | PCB |
|---|---|---|---|---|---|---|
| Study area (1972) (Amundsen Gulf N.W.T.) | Addisson and Smith (1974) | Males | 1.10 | 0.63 | 0.47 | 3.69 |
| | | Females | 0.55 | 0.28 | 0.27 | 1.83 |
| Study area (1981) (Amundsen Gulf N.W.T.) | Addisson et al. (1986) | Males | 0.78 | 0.39 | 0.38 | 1.29 |
| | | Females | 0.33 | 0.14 | 0.19 | 0.58 |
| Grise fiord Lancaster Sound, Canada | Bowes and Jonkel (1975) | Males | | 0.41 | 0.28 | 0.87 |
| Gulf of Bothnia | Helle et al. (1976) | Pregnant females | 88.0 | | | 73.0 |
| | | Non-reproducing females | 130.0 | | | 110.0 |

PCB residues in the Gulf of Bothnia ringed seals (Table 27) appear to have had a major effect on their reproduction rates (Olsson 1977; Olsson et al. 1974). Helle et al. (1976a, b) documented a condition called uterine stenosis, which was positively correlated with the high levels of DDT and PCB levels in ringed seals. While the proximate cause of the reproductive failures was not directly identified, they felt that PCBs were the likely causative agents. Reproduction rates of northern Baltic seals averaged 0.28 and there was a strong indication of a further decrease during the period 1974–79 (Helle 1980a, b). These are the lowest reproductive rates yet documented for this species (see section on Reproduction).

## Ringed Seals in the Inuit Culture and Economy

The long and intimate association of the Inuit culture with the ringed seal has been well-documented. Boas (1888), in a study of winter settlement patterns of the Inuit, described the degree of dependance of the northern aboriginals on the ringed seal. Stefansson (1913a) described the living habits of the people of the Victoria Island area, who subsisted almost entirely on ringed seals during the winter. Ethnographers (Rasmussen 1931; Van de Velde 1956; Damas 1972; Wenzel 1978, 1979) have studied the complex behaviour and social structure involved in the distribution and sharing of seal meat, the main staple of the Inuit subsistence economy.

Ringed seals have provided a consistently available and high quality source of food for the Inuit since their first occupation of the arctic. Nutritional studies emphasize the importance of sea mammals in the modern Inuit diet (Stefansson 1946; Schaeffer 1971; Draper 1977; Geraci and Smith 1979).

The best data on ringed seal harvests come from the fur records of the Hudson Bay Company (H.B.C.), the largest and oldest, but not the only trading company (Usher 1971), in the Canadian arctic. Trade in seal pelts began in the eastern Arctic in the 1940's. From 1941 to 1959 an average of about 70 000 hair seal pelts were bought annually by the H.B.C. (SD = 3 414), mostly from settlements in the Eastern Arctic, including Hudson Bay and Foxe Basin. Table 28 details the annual numbers of hair seal pelts purchased for the period 1960–78, according to the reporting source and area of harvest. Smith and Taylor (1977) identified the most important seal hunting communities in northern Canada in an analysis of game reports from several different sources. They indicated that potential maximum annual

TABLE 28. Record of ringed seal pelts[a] traded at Holman, N.W.T., and for 31 other arctic and northern Quebec, Hudson Bay posts for the years 1960 to 1978. (Includes a maximum of 7% harp seal pelts from the eastern arctic).

| Year | Holman harvest | Western arctic | Central arctic | Eastern arctic | Total |
|---|---|---|---|---|---|
| 1960 | 301 | 626 | 1051 | 11,689 | 13,366 |
| 1961 | 758 | 1521 | 1815 | 14,989 | 18,325 |
| 1962 | 679 | 1354 | 1121 | 16,376 | 18,845 |
| 1963 | 2309 | 6471 | 6147 | 36,909 | 49,520 |
| 1964 | 4922 | 14390 | 9471 | 43,213 | 67,074 |
| 1965 | 3900 | 16514 | 9207 | 46,595 | 72,316 |
| 1966 | 2704 | 9087 | 5415 | 37,384 | 51,946 |
| 1967 | 1346 | 4713 | 3880 | 23,485 | 32,078 |
| 1968 | 1740 | 2838 | 1589 | 19,351 | 23,778 |
| 1969 | 2372 | 7829 | 6840 | 35,281 | 49,950 |
| 1970 | 1567 | 6923 | 4228 | 27,262 | 38,413 |
| 1971 | 3614 | 7592 | 3993 | 25,885 | 37,439 |
| 1972 | 1975 | 5495 | 3516 | 20,129 | 29,140 |
| 1973 | 3251 | 5814 | 4143 | 25,214 | 35,171 |
| 1974 | 2798 | 5362 | 3935 | 28,693 | 37,990 |
| 1975 | 2071 | 3486 | 3770 | 34,809 | 42,065 |
| 1976 | 1646 | 2897 | 2284 | 29,408 | 34,589 |
| 1977 | 1180 | 2068 | 1350 | 28,987 | 32,405 |
| 1978 | 2337 | 3230 | 1846 | 21,327 | 26,403 |

[a] From Hudson Bay Co. fur records, N.W.T. Department of Fish and Game fur records and Royal Canadian Mounted Police, G Division annual game reports.

takes, based on the highest catches recorded for any year in each community could reach 84 000 ringed seals (their table 1, p. 20). Not included in this total are an additional nine communities along the northern Quebec coasts, with estimated annual harvests of 8 477 ringed seals for the years 1973–74, 1974–75 (James Bay and N. Quebec N.H.C. 1979). Adding these to the above total would bring the maximum annual ringed seal harvest up to approximately 92 500 animals.

The seasonal distribution for the harvest of ringed seals at Holman for 6 years of catches and the proportion of the catch for each month lost by sinking is shown in Fig. 30. A total of approximately 0.199 of the harvest is lost each year by sinking, which indicates maximum annual total kills for the Canadian arctic could be as high as 115 000 ringed seals. This could still be an underestimate, since records of pelts traded are known to be low. Some pelts are used for domestic purposes, but a more serious source of error in recent years is that a significant number are sold either at southern fur auctions, or privately and are missed by the fur record keepers. A further small number will be lost by wounding, but this is not considered a serious source of error.

The number of ringed seals killed each year is highly correlated to the price paid for pelts (Smith 1973a). The largest annual harvest recorded by the H.B.C. was in 1965. This occurred when prices for seal pelts were averaging $14.85 Can. (Foote 1967). After 1965 the market was depressed for several years as a result of anti-seal hunt protests in Canada and Europe. Prices again rose to reach a high in 1975 and 1976, but a renewed and more determined anti-sealing movement has severely depressed the seal pelt market since 1977.

Centralization of the Inuit into villages, which was virtually completed by 1965, has been one of the major influences on their economy. The change from dog traction to snowmobiles, which occurred at about the same time, increased the cost of transportation significantly (Usher 1970; Hall 1971). At the same time it reduced the need for large

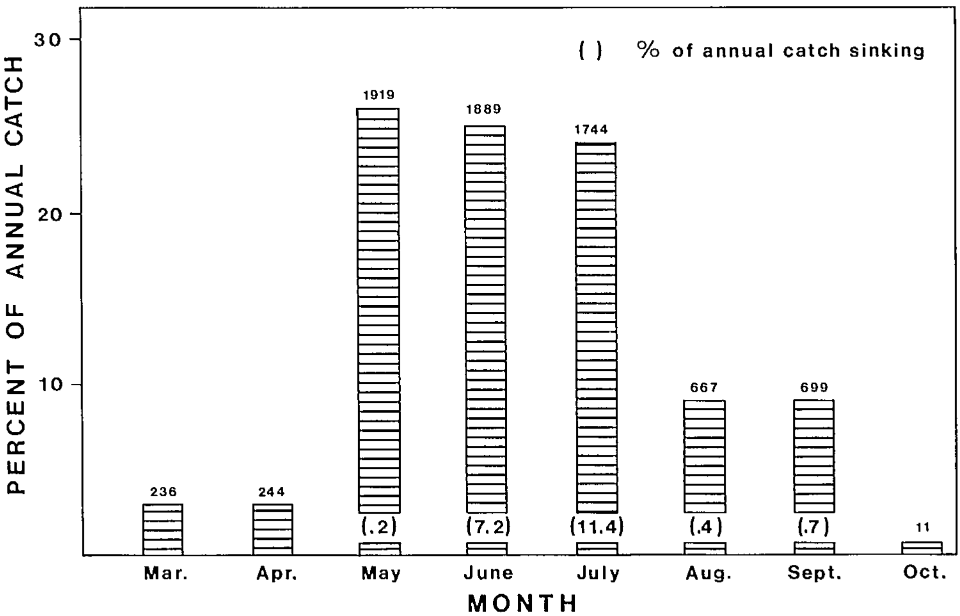



FIG. 30. Seasonal distribution of the Inuit catch of ringed seals from Holman, N.W.T. Proportion lost is shown in parentheses ( ) and sample size per month is shown above the histogram.

quantities of ringed seal meat used to feed the high numbers of dogs formerly maintained by a hunting community. The immediate effect was that of an increase in ringed seal harvests for pelts, which lasted through to approximately 1976. Subsequently, the combined high price of snowmobile operation and depressed seal prices led to significantly reduced harvests.

Smith (1980b) analysed the cost of hunting at Holman and underlined the importance of the role of the hunter, who remains the provider of almost all the food consumed by the arctic communities. In 1978 when the data were gathered, the Inuit of Holman were able, largely through their seal hunting and fox trapping, to make a slight cash profit after paying for their hunting equipment and operating costs. The considerable value of the food they produced for the community concurrently with their fur harvesting, is certainly the most important benefit derived from hunting. Recalculation of the average substitution value of food (Usher 1977) using a weighted average of $10.22/kg shows that approximately $6,321 of food, per average household of 4.5 people, is provided by full-time Inuit hunters of Holman N.W.T. (Smith and Wright, unpublished data).

In recent years, more and more full-time hunters have had to turn to any wage-earning opportunity available, to finance the cost of the equipment used in hunting. In addition to the increased costs of such items as snowmobiles and boats, hunters have recently added all-terrain motorcycles and increasingly more powerful snowmobiles and boat motors to their stores of hunting equipment. The large increase in cost and horsepower of the equipment, has not resulted in larger harvests, but allowed the village dwelling Inuit to continue to feed their families and spend less time at hunting. The increased amount of time away from hunting is spent at wage-earning either in or away from their home village. There is evidence from other communities, such as Coppermine, that rotational wage earning opportunities in the oil industry have not resulted in a reduced food or fur harvest (Hobart 1981). There are, in fact, some slight indications that these harvests have actually increased.

Fuller (1981) indicated that the rapidly growing 13 000 strong Canadian Inuit population, will increase to 37 500 by the year 2001. His view was that it was unlikely that a human population of twice the size now present in the Northwest Territories, could be supported on the fish and wildlife available to them at their present rate of consumption. One of the major underutilized sources of protein, at present, is the ringed seal. Even during the period of maximum harvest in the mid-1960's, only a small proportion of the total meat harvested was used for human consumption. It can be expected that there will be increased pressure brought upon this species in the future, when the more popular native food species, such as caribou, *Rangifer tarandus*, become limited either through increased hunting or natural decline.

Two fur bearers of direct economic importance to the Inuit, the polar bear and arctic fox, feed on ringed seals. Polar bears, which currently are worth $189,000 annually to the Inuit of the Northwest Territories, prey predominantly on the ringed seal (Stirling and McEwan 1975; Stirling and Archibald 1977; Smith 1980a). The survivorship and production of polar bears in the western arctic has been shown to be directly linked to availability of ringed seals during the winter months (Stirling and Archibald 1977; Stirling et al. 1982). Arctic fox, which are the single most important cash-fur for Inuit trappers (Tinling 1982), in some years kill a large proportion of ringed seal pups (Smith 1976a). This is thought to play an important role in maintaining physical condition in foxes and thus directly influences their reproductive success (Hammill 1983).

## Recommendations for Future Research and Management

More is known about the ringed seal and its main predator, the polar bear, than about most of the other organisms in the arctic marine ecosystem. The variability in annual recruitment of ringed seals documented in the western arctic, underlines the importance of long-term studies, which should seek to describe the mechanisms of population control and identify the important limiting factors. In the present study the response of lowered recruitment, correlated with reduced body condition was identified, but the causative factors are still unknown. Heavy ice conditions are possibly directly responsible for reduced marine productivity, but the magnitude of the changes and where in the trophic chain they occur, remain to be determined. Even though there was a marked effect on the ringed seal and polar bear populations of the western arctic, we still do not know the proximate causes.

It is only through detailed quantitative studies designed to monitor population parameters, physical conditions, habitat quality and ringed seal behaviour, that the processes involved in population changes will be elucidated. Such studies are now possible and new techniques can be brought to bear on problems which have been difficult to solve in the past. The choice of the study site(s) is important, since such research must be carried out over a considerable span of years. The Holman–Amundsen Gulf area was considered to be an ideal site for the present study because of the high ringed seal harvest, the large scale variability in ice cover from year to year, and the presence of two good seal-netting sites along the mainland coast. Because of the established research facilities and background knowledge, studies in this area should be continued to include annual age-structure samples of the Inuit seal catch, along with a subsample of female reproductive tracts and accurate indices of physical condition. Trained collectors in the area will make this easy to implement and very cost effective. More information on feeding during the winter and spring are also needed. This would be especially important to document during periods of high variation in the total ice cover. Studies on ringed seals using radio tags, time-depth recorders, and respirometers in subnivean lairs to document foraging time and metabolic effort, would yield data needed to understand their energy budgets. This research, combined with an oceanographic and fish sampling program, could provide useful insights into the trophic constraints on ringed seal populations. Data are especially needed on the winter distribution of arctic cod and on such features as under-ice aggregations of plants or invertebrates which might influence fish populations. Little is yet known of the characteristics of the sea-bed topography which might also directly influence the density and winter distribution of invertebrates and fish used as food by ringed seals. Sampling over several years in the same area is needed to understand the variability in the system. Significant progress, in understanding the factors controlling seal, whale and polar bear populations, cannot be made in the absence of an increased effort in research on primary and secondary productivity. Close coordination of such research conducted from the ice platform, during the winter and spring months and in the same areas as marine mammal studies, would be most desirable.

A study basic to further ringed seal research, would be a detailed analysis of the precision of the age determination methods used for this species. Ringed seal teeth are especially difficult to interpret. Within and between observer variation in readings from dentinal and cementum tissues and for a variety of preparations should be documented. The effect of the estimated experimental error should then be determined for the population parameters estimated from age-specific data. The meaning of adventitious growth lines should also be investigated by careful documentation of necropsy results from collected animals, including detailed examination of the reproductive history from microscopic analyses of ovarian tissues. Short and long term studies of captive animals injected with tetracyclene, or other markers of hard tissue, might eventually serve to validate the age determination techniques.

The ability to live-capture and maintain large numbers of ringed seals in field situations and in southern research facilities, offers a unique opportunity to do many different biological, behavioural and physiological experiments (Smith and Geraci 1975). Established field facilities could be used to study the role and effect of parasitism and disease, to expand the study of impact related stress and to conduct behavioural research on ringed seals in large ocean enclosures.

Recently we have initiated a long term study of ringed seals in the high arctic because of the imminent probability of ice-breaking ship traffic through Parry Channel and the interest of the petroleum industry in assessing their impact on ringed seal populations. This study seeks to relate changes in ringed seal population parameters, including numbers, physical condition and behaviour to large scale changes in the quality and quantity of ice in Lancaster Sound and Barrow Strait. Standardized quantification of breeding habitat using trained dogs to search the same study plots, over a period of years, has begun. Aerial surveys yielding confidence limits of the population estimates (Stirling et al. 1977; Stirling et al. 1982; Kingsley 1985) will also be flown in the same way each year of the study. Winter studies of the foraging and resting behaviour of ringed seals, which are tagged with radio transmitters and whose subnivean lairs are monitored with activity recorders, are being conducted and the whole of these data will be used in the quantitative evaluation of habitat. The quality and quantity of sea ice is being evaluated using remote imagery (Digby 1984), aerial photography and measurments of snow and ice thickness taken during the breeding habitat surveys.

Ringed seals figure prominently in any discussion concerning environmental impacts and have been considered in all arctic environmental assessment reviews as a species of primary importance to the Inuit inhabitants. Yet, in general, wildlife managers have not felt that the ringed seal is seriously threatened, either by overexploitation or by any proposed industrial development. This is because the ringed seal is widely dispersed throughout the arctic and is abundant even in areas far away from any exploitation. It is true that there are no immediate management problems with this species. Future industrial developments resulting in large-scale disturbance and the increased need for seal meat to feed a rapidly expanding human population, could well cause problems with availability and overexploitation at the local level. There is, therefore, a management requirement to anticipate the problem areas, to estimate the potential required yields of ringed seals from these localities, and to initiate programs aimed at evaluating the causes and consequences of changes in levels of local stocks. Management research aimed at improving harvest statistics, including measurements of hunting effort, costs and economic benefit, should be initiated in the major seal hunting communities. The opportunity to obtain this information using local Inuit researchers now exists, and should be used. In areas where large scale disturbance to local hunting territories is anticipated, annual surveys and documentation of existing sources of disturbance should be made. The effect of future impacts might be completely obscured by the disturbance already present from local traffic in certain areas (Bradley 1970; Beaubier et al. 1970).

Of all the arctic species the ringed seal best demonstrates the importance and characteristics of the renewable resources harvested by the Inuit. It would be a serious mistake to become complacent about management and research on this species, simply because of the current reduced harvests and the lack of an immediate threat to the populations. The future role of ringed seals as a cash crop cannot be reliably predicted, but as a food source it will undoubtedy be very important. The identity of the Inuit culture is tightly bound to this ice-breeding species. Proper management, based on forward-looking research rather than crisis response will ensure its conservation.

## Summary

This study was based on research spanning the years 1971 to 1983 in Amundsen Gulf and southeastern Beaufort Sea regions of the western Canadian arctic. Most ringed seal specimens (8 483) were collected from the Holman area (70°43′N, 117°43′W) on western Victoria Island. Breeding habitat studies were concentrated in Prince Albert Sound, in the same area.

The greatest densities of ringed seals (2.83/km$^2$) are found in Prince Albert Sound. There is some evidence of annual variation in densities in Amundsen Gulf corresponding to similar changes documented in the adjacent southeastern Beaufort Sea. A seasonal segregation of age classes occurs similar to that seen in other studies. Older seals occupy the fast-ice breeding habitats in the autumn and the adolescent and neonate age classes disperse offshore and west along the mainland coast.

Movements of ringed seals were studied by capturing them in nets situated at Brown's Harbour (Cape Parry; 70°05′N, 124°22′W) and Herschel Island (69°30′N, 139°00′W). Autumn movements consisted primarily of young-of-the-year and adolescent age classes moving west towards the Beaufort and Bering Seas. The few recoveries of tagged seals (4 of 229 released) showed that seals could move as far west as Injun, Chukotskiy Peninsula, Siberia.

Prime breeding habitat is found in stable first-year ice where ice hummocks and pressure ridges allow snow accumulation. Several types of subnivean structures can be identified including haul-out (resting) lairs; lairs used by rutting males; and birth lairs. Several birth lairs are usually found in close proximity which are part of a complex maintained by a single female. These are used to provide escape from predators and also thermal shelter for neonates that have a high critical temperature when they are wet. Seals are territorial in their breeding habitat. Prime breeding habitat is occupied by older, larger seals. Males appear to maintain territories around several females, who in turn appear to be territorial in the vicinity of their birth lair complex. Searches of the Prince Albert Sound area revealed a significant reduction in the number of birth lairs found during 1974 and 1975. In 1975 there was also a significant reduction in the number of lairs occupied by rutting males.

Arctic fox predation of neonate seals in birth lairs is quite significant, reaching levels of up to 37% in 1973. The years 1973 and 1974 showed the highest fox predation, which corresponded to peak fox numbers seen from the fox trapping harvest in 1974.

The peak of births occurs in mid-April with the mean date of ovulation on 21 May several weeks prior to the end of lactation. Foetuses implant on average 18 August, after a delay of 89 days. Females are sexually mature at 5.61 years and first reproduce at 7.67 years. Neonate sex ratio is unity. Ovulation rates were reduced in 1974 and 1975 to 0.41 and 0.38, respectively down from a mean of 0.89 in the 8 other years. Body condition of adult and

adolescent ringed seals collected in 1974–75 was also significantly lower. Excluding the years of reduced ovulation a mean reproductive rate of 0.56 was estimated.

Foetal growth rates of 2.8 $mm \cdot d^{-1}$ were estimated with a predicted standard length (STL) at birth of 57.8 cm. Pre-weaning growth rates were estimated as 6.1 $mm \cdot d^{-1}$ and 0.76 $kg \cdot d^{-1}$. Most of post-weaning growth appears to take place before July or approximately 4–5 weeks after weaning. An asymptotic length of 93.9 cm is reached for the 0+ age class. Physical condition of pups is highest during suckling, much reduced during the summer months after weaning and improves in September.

Adult males reach asymptotic lengths of 131.2 cm and females 126.9 cm with asymptotic weights of 63.4 and 61.1 kg, respectively. Mean indicators of body condition also undergo a seasonal low in mid summer. In 1974 and 1975 condition indices for both adolescents and adults were significantly lower than in other years. A small proportion (2%) of seals were significantly shorter than the mean size of their respective age classes. Pups in this category had low indices of body condition. It is thought that nutritional deprivation during suckling and shortly after weaning can result in stunting of seals.

Thirty-six prey species were found in ringed seal stomachs. *Boreogadus saida* was the most important food of all age classes during the ice-covered period. The crustaceans *Mysis oculata, Parathemisto libellula* and *Thysanoessa raschii* were dominant. Existence of competition in feeding between adolescents and adults was indicated from different diurnal regimes and slightly different diets. Ringed seals probably consume 3.4% of their body weight in food daily. Feeding on *Boreogadus saida* in the autumn is intensive and it is the only time that ringed seals are seen in groups. These are almost all old adults. It is possible that territorial exclusion of younger animals, because of feeding competition, is the proximate cause of the autumn migrations and segregation of age classes.

The way of life of the Canadian Inuit has changed drastically in the last 20 years. Marine mammals which formed the basis of the subsistence economy became an important source of cash revenue needed to purchase modern hunting equipment. Recent anti-seal hunting sentiments have seriously reduced their income. Modern hunters provide most of the food for the arctic villages, but need a cash revenue to support the hunt.

Impacts from northern industrial development have been a subject of study in Canada since about 1970. Seals are seen to be able to survive immersion in crude oil and ingestion of small amounts. Therefore oil spills are not perceived to be as serious a threat as was once thought. The effects of disruption of breeding habitat by ice-breaking tankers and disturbance from underwater noise is not yet evaluated. Contaminants such as heavy metals and chlorinated hydrocarbons are not a serious threat to Canadian arctic seals.

Future research should concentrate on defining the role of the ringed seal in the arctic ecosystem and evaluating the effects of changes in production at lower trophic levels on marine mammal populations. Energy budgets using instrumentation on free-ranging seals, annual documentation of body condition and reproductive status are the most sensitive and effective ways of monitoring seal populations.

The ringed seal is intimately bound to the Inuit culture. Northern human populations are rapidly expanding, which will result in a greater dependence on ringed seals as a source of food. There is a need to anticipate and implement the types of management and research programmes required to conserve such important renewable resources.

# РЕЗЮМЕ

Настоящая работа основана на результатах исследований, проводившихся с 1971 по 1983 год в заливе Амундсена и в юго-восточных районах моря Бофорта на западе Канадской Арктики. Большинство экземпляров кольчатой нерпы (8483) было получено в районе поселения Холмен (70°43′ с.ш., 117°43′ з.д.) в западной части острова Виктория. Изучение щенних залежок производилось в том же районе на побережье залива Принс-Альберт.

Наиболее высокая плотность популяции кольчатой нерпы (2,83/км$^2$) наблюдается в заливе Принс-Альберт. Имеются указания на годичные колебания плотности популяции в заливе Амундсена, совпадающие с аналогичными колебаниями, зафиксированными в прилегающих юго-восточных районах моря бофорта. Как и в других областях обитания кольчатой нерпы, в обследованных районах отмечается сезонное разделение возрастных классов. Осенью взрослые особи занимают залежки на припае, в то время как сеголетки и молодые нерпы мигрируют в сторону открытого моря и на запад вдоль побережья материка.

Миграции кольчатой нерпы изучались путем отлова ее сетями, установленными в бухте брауна (мыс Парри; 70°05′ с.ш., 124°22′ З.Д.) и у острова Хершел (69°30′ с.ш, 139° З.Д.) вблизи континентального побережья моря Бофорта. Осенние миграции заключались в основном в перемещении сеголеток и молодых нерп на запад в сторону моря Бофорта и Беренгового моря. Немногочисленные случаи отлова меченых нерп (4 из выпущенных 229) показывают, что в ходе миграции нерпы могут достигать таких далеких мест, как поселение Инчоун на Чукотском полуострове.

Наиболее благоприятные условия для размножения отмечаются на устойчивых отнолетних ледяных полях, где между торосами и гребнями, образовавшимися в результате бокового давления льда, накапливается достаточное количество снега. Выделяется несколько типов отрываемых в снегу нор: лежбишные норы, норы самцов в состоянии половоц охоты и щенные норы. Очень часто несколько расположенных рядом щенных нор образуют комплекс, занимаемый одной самкой. Такие норы служат убежищем от хищников, а также обеспечивают тепловую защиту мокрым новорожденным щенкам, имеющим высокую критическую температуру тела. В залежках для нерпы характерно территориальное поведение. Залежки с наиболее благоприятными условиями занимают более старые и крупные животные. Самцы охраняют территорию вокруг нескольких самок, а те в свою очередь охраняют участки, прилегающие к их щенным норам. Наблюдения в районе залива принсАлберт показали, что в 1974 и 1975 годах число щенных нор кольчатой нерпы значительно сократилось по сравнению с предшествующими годами. В 1975 году наблюдалось также заметное уменьшение числа нор, занимаемых самцами, находящимися в состоянии половой охоты.

Количество новорожденных щенков, похищаемых из щенных нор песцами, весьма значительно. В 1973 году потери щенков по этой причине составили 37 %. В 1973 и 1974 годах охотничья активность песцов была особенно высокой. Это обьясняется тем, что, судя по результатам промысла песцов 1974 года, на этот период приходится пик численности их популяцин.

Число рождений достигает максимальной величины в середине апреля, а овуляция наступает в среднем 21 мая — за несколько недель до окончания лактации. Имплантация зародыша происходит в среднем 18 августа,

т.е. через 89 дня после оплодотворения. Самки достигают половой зрелости в возрасте 5,61 лет и впервые производят потомство в возрасте 7,67 лет. Численное соотношение полов среди новорожденных детенышей равно единице. В 1974 и 1975 годах показатель овуляции снизился со средней величины 0,89 за предшествующие восемь лет до 0,41 и 0,38 соответственно. физическое состояние взрослых и молодых кольчатых нерп, отловленных в 1974–1975 годах, также оказалось значительно хуже обычного. За вычетом лет, в течение которых наблюдалосв существенное понижение уровня овуляции, средний показатель воспроизведения составил 0,56.

Темпы роста плода составляют по произведенным оценкам 22 мм/д$^{-1}$, а предполагаемая нормальная длина тела при рождении - 63,2 см. Темпы роста до отбивки оцениваются в 6,1 мм/д$^{-1}$. После отбивки щенки продолжают расти в основном до июля, или в течение примерно 4-5 недель. Щенки возрастного класса 0+ достигают асимптотической длины 93,9 см. Физическое состояние щенков, найлучшее в молочный период, значительно ухудшается в летние месяцы после отбивки, но затем вновь нормализуется в сентябре.

Взрослые самцы достигают асимптотической длины 131,2 см, а самки — 126,9 см. Асимптотический вес самцов и самок равен 63,4 и 61,1 кг соответственно. Средние показатели физического состояния также претерпевают сезонное понижение в середине лета. В 1974 и 1975 годах показатели физического состояния как молодых, так и взрослых нерп были значительно более низкими, чем в другие годы. Небольшая часть нерп (2 %) оказалась заметно короче средней длины своего возрастного класса. Щенки в этой группе нерп характеризовались низкими показателями физического состояния. По-видимому, недостаточно хорошее питание в молочный период и в течение короткого времени после отбивки может привести к остановке в росте молодых нерп.

В желудках кольчатой нерпы обнаружено тридцать шесть видов употребляемых ею в пищу организмов. В период, когда море было покрыто льдом, основной пищей для всех возрастных классов служила **Boreogadus saida**. Важную роль в питании нерпы играют также рачки **Mysis oculata, Parathemisto libellula** и **Thysanoessa raschii**. Между молодыми и взрослыми нерпами существует пищевая конкуренция, о чем свидетельствуют несовпадение их дневных режимов и некоторые различия в составе их питания. Общий вес пищи, поглащаемый кольчатой нерпой в течение суток, составляет по произведенным оценкам 3,4 % от веса ее тела. Осенью кольчатая нерпа интенсивно питается полярной треской **Boreogadus saida**, и это единственное время года, когда отдельные особи обьединяются в группы. Эти группы состоят почти исключительно из старых нерп. Вполне возможно, что вытеснение молодых животных вследствие пищевой конкуренции является непосредственной причиной осенних миграций и разделния возрастных групп.

За последние 20 лет уклад жизни канадских эскимосов претерпел очень большие изменения. Охота на морских млекопитающих, которая составляла в прошлом основу их натурального хозяйства, стала позднее важным источником денежных поступлений, необходимых для приобретения современных орудий и средств промысла. Недавние протесты общественности против охоты на нерпу привели к существенному сокращению доходов эскимосов. В наше время охотники по-прежнему добывают большую часть пищи, потребляемой в арктических поселениях, но для успешного ведения промысла им необходимы определенные денежные поступления.

Начиная примерно с 1970 года в канаде ведется изучение влияния промышленного развития на экологию Севера. Специалисты считают, что нерпы могут переносить погружение в сырую нефть и даже поглашать ее в небольших количествах без катастрофических последствий для себя. Поэтому разлив нефти и образование нефтяных пятен на поверхности морей и океанов не рассматривается в настоящее время в качестве очень серьезной экологической угрозы. Влияние нарушения экологии зон размножения танкерами-ледоколами, а также воздействие на нерп подводного шума еще полностью не изучены. Загрязняющие вещества, как, например, тяжеллые металлы и хлорированные углеводороды, для канадской полярной нерпы большой опасности не представляют.

В будущем исследователям необходимо сосредоточить свои усилия на определении роли кольчатой нерпы в экосистеме Арктики, а также на оценке того влияния, которое оказывают на популяции морских млекопитающих изменения в продуктивности на более низких трофических уровнях. Измерение энергетического баланса с помощью приборов, закрепленных на свободноплавающих животных, а также ежегодные проверки их физического состояния и способности к размножению являются самыми точными и эффективными методами наблюдения за популяциями кольчатой нерпы.

Кольчатая нерпа занимает очень важное место в культуре эскимосов. В северных районах наблюдается быстрый рост населения, в связи с чем значение кольчатой нерпы в качестве источника пищи должно также существенно возрасти. Необходимо разработать и осуществить научно-исследовательские и хозяйственные программы, способные обеспечить сохранение и восполнение этого важного компонента живых приодных ресурсов.

## Acknowledgements

It is a pleasure to thank the many people, whom over a period of almost 15 years, have helped with this study.

My largest debt is to my old travelling companion and friend, Jimmy Memorana, of Holman, Northwest Territories. He shared his inestimable knowledge and love of the Inuit hunter's way of life with me. *Quana pargonartok, angoon.*

Bug and Beau, working Labradors in the true sense of the word, searched thousands of miles of sea-ice, often in appalling weather, for the subnivean lairs of the ringed seal. I simply could not have done it without them.

My friends and colleagues, Ian Stirling, Joe Geraci and Mike Hammill, shared my interest in the species, and helped with scientific advice, practical ideas, strong backs, good company and inspiration. My assistants, Gary Sleno, Brian Beck, Debbie Taylor and Harold Wright aided throughout with the field and laboratory studies, contributing significantly to the completion of the task. Arthur Mansfield, and Charles Lépine of the Arctic Biological Station (A.B.S.), have been of considerable aid in helping to provide a pleasant atmosphere in which to work. David Burrage, Université du Québec à Montréal (UQUAM), was programming consultant and contributed to the analysis of the data. Ted Grainger and Jay Waycasey (A.B.S.) helped identify invertebrates; Don McAllister, National Museums of Canada, identified the fish.

Considerable logistic support was given by the Polar Continental Shelf Project, Department of Energy, Mines and Resources. I thank George Hobson and his staff for their indispensible professional support of our efforts in the western and high arctic.

This was written while on sabbatical leave at the British Antarctic Survey (B.A.S.), Cambridge, England. I thank the Director, R.M. Laws for his hospitality and support, and Nigel Bonner and John Croxall for helping to make my stay there a pleasant and productive experience.

Ian McLaren, Dalhousie University and Ian Stirling, Canadian Wildlife Service, have provided helpful scientific criticism, detailed critiques of the manuscript, and good advice about the direction in which pinniped research should be going.

Sue Norris (B.A.S.), Lois McMullon and Dora Godard (A.B.S.) aided greatly in the production of the final manuscript. June Currie, our librarian (A.B.S.), has been an important source of information and help throughout. Mimi Breton (D.F.O. Quebec) kindly provided the French translation.

# References


ABRAHAMSON, G. 1963. Tuktoyaktuk-Cape Parry area economic survey. Dep. of Northern Affairs and National Resources, Industrial Div., Ottawa. 109 p.

ABRAHAMSON, G., P. J. GILLESPIE, D. J. MCINTOSH, P. J. USHER, AND H. A. WILLIAMSON. 1964. The Copper Eskimos, an area economic survey 1963. Dep. of Northern Affairs and National Resources, Industrial Div., Ottawa. 194 p.

ADDISON, R. F. 1983. PCB replacements in dielectric fluids: an initial environmental assessment. Environ. Sci. Technol. 17: 486A–494A.

ADDISON, R. F., AND P. F. BRODIE. 1977. Organochlorine residues in maternal blubber, milk and pup blubber from grey seals (*Halichoerus grypus*) from Sable Island, Nova Scotia. J. Fish. Res. Board. Can. 34: 937–941.

ADDISON, R. F., AND T. G. SMITH. 1974. Organochlorine residue levels in arctic ringed seals: variation with age and sex. Oikos 25: 335–337.

ADDISON, R. F. , M. E. ZINCK, AND T. G. SMITH. 1986. PCBs have declined more than DDT-group residues in arctic ringed seals (*Phoca hispida*) between 1972 and 1981. Environ. Sci. Technol. 20: 253–256.

AMERICAN SOCIETY OF MAMMALOGISTS. 1967. Standard measurements of seals. J. Mammal. 48: 459–462.

BANDI, H. G. 1969. Eskimo prehistory. Univ. of Alaska Press, College, AK., 226 p.

BEAUBIER, P. H., M. J. BRADLEY, AND J. G. VESTEY. 1970. Human ecological studies — Igloolik, N.W.T. Final Rep. I.B.P., Human Adaptability Project, Dep. Geogr., McGill. Univ., Montreal, Que. 180 p.

VON BERTALANFFY, L. 1934. Untersuchungen uber die Gesetzlichkiet des Wachtums. I. Roux Archiv. 131: 613.

BLOOD, D. A. 1977. Birds and mammals. The Beaufort Sea and the search for oil. Beaufort Sea Project, Fish. Mar. Serv., Institute of Ocean Sciences, Patricia Bay, B.C. 124 p.

BOAS, F. 1888. The Central Eskimo. Bureau of American Ethology, Wash. D.C. Annual Rep. 6: 409–699.

BOULVA, J., AND I. A. MCLAREN. 1979. Biology of the harbour seal, *Phoca vitulina*, in Eastern Canada. Bull. Fish. Res. Board Can. 200: 24 p.

BOWES, G. W., AND C. J. JONKEL. 1975. Presence and distribution of polychlorinated biphenyls (PCB) in arctic and subarctic food chains. J. Fish. Res. Board Can. 32: 2111–2123.

BOYD, I. L. 1983. Luteal regression, follicle growth and the concentration of some plasma steroids during lactation in grey seals (*Halichoerus grypus*). J. Reprod. Fertil. 69: 157–164.

1984. Development and regression of the corpus luteum in grey seal (*Halichoerus grypus*) ovaries and its use in determining fertility rates. Can. J. Zool. 62: 1095–1100.

BRADLEY, M. 1970. Ringed seal avoidance behaviour in response to Eskimo hunting in Northern Foxe Basin. M. Sci. thesis, Dep. Geogr., McGill Univ., Montreal, Que. 113 p.

BROWN, W. R., J. R. GERACI, B. D. HICKS, AND D. J. ST. AUBIN. 1983. Epidermal cell proliferation in the bottlenose dolphin (*Tursiops truncatus*). Can. J. Zool. 61: 1585–1590.

BROWN, R. G. B., D. I. GILLESPIE, A. R. LOCK, P. D. PEARCE, AND G. H. WATSON. 1973. Bird mortality from oil slicks off eastern Canada. February to April 1970. Can. Field-Nat. 87: 225–234.

BRYDEN, M. M. 1968. Control of growth in two populations of elephant seals. Nature 217: 1106–1108.

BURNS, B. M. 1973. The climate of the Mackenzie Valley–Beaufort Sea. Vol. 2. Environ. Can. Climatol. Study No. 24: 239 p.

BURNS, J. J., AND S. J. HARBO. 1972. An aerial census of ringed seals, northern coast of Alaska. Arctic 25: 279–290.

BURNS, J.J., AND B. P. KELLY. 1982. Studies of ringed seals in the Alaskan Beaufort Sea during winter: Impacts of seismic exploration. Annual report to NOAA Project No: RU#232, 57 p. (Unpublished)

CALHAEM, I., AND D. A. CHRISTOFFEL. 1969. Some observations on the feeding habits of a Weddell Seal and measurements of its prey *Dissostichus mausoni*, at McMurdo Sound, Antarctica. N.Z. J. Mar. Freshw. Res. 3: 181–190.

CANADIAN HYDROGRAPHIC SERVICE. 1984. Canadian tide and currents tables. Government of Canada Fisheries and Oceans, Ottawa, Ont. 51 p.

CAUGHLEY, G. 1966. Mortality patterns in mammals. Ecology 47: 906–918.
1977. Analysis of vertebrate populations. John Wiley and Sons, Toronto, Ont. 234 p.
COLLINS, H. B., AND B. HENRY. 1958. The present status of the Dorset porblem. Proc. 32nd Int. Cong. of Americanists, Copenhagen, 1956. p. 557–560.
COSTA, D. P., AND R. L. GENTRY. 1986. Free-ranging energetics of nothern fur seals, p. 79–101. *In* R. L. Gentry and G. L. Kooyman [ed.]. Fur seals. Maternal strategies on land and at sea. Princetown University Press.291 p.
CRAIG, P. C., W. GRIFFITHS, L. HALDORSOM, AND H. ELDERRY. 1982. Ecological studies of arctic cod, *Boreogadus saida*, in Beaufort Sea coastal waters, Alaska. Can. J. Fish. Aquat. Sci. 39: 395–406.
DAMAS, D. 1972. Central Eskimo systems of food sharing. Ethnology 11: 220–240.
DEARBORN, J. H. 1965. Food of Weddell seals at McMurdo Sound, Antarctica. J. Mammal. 46: 37–43.
DEMASTER, D. P. 1978. Calculation of the average age of sexual maturity in marine mammals. J. Fish. Res. Board Can. 35: 912–915.
DIGBY, S. A. 1984. Remote sensing of drained ice areas around the breathing holes of ice-inhabiting seals. Can. J. Zool. 1011–1014.
DOME PETROLEUM LTD., ESSO RESOURCES CANADA LTD. AND GULF CANADA RESOURCES INC. 1982. Environmental impact statement for hydrocarbon development in the Beaufort Sea–Mackenzie Delta region.Vol. 3a. Beaufort-Delta setting 127 p. Calgary, Alberta.
DRAPER, H. H. 1977. The aboriginal Eskimo diet in modern perspective. Am. Anthrop. 79: 309–316.
DUNBAR, M. J. 1981. *In* I. Stirling and H. Cleator [ed.] Polynyas in the Canadian arctic. Can. Wildl. Serv., Occas. Pap. 45: 73 p.
DUBROVSKII, A. N. 1933. The nuptial cry of the bearded seal (*Erignathus barbatus* Fabr.). 4: 124 (Can. Wildl. Serv, Transl. 1973).
EATON, R. D. P. 1979. High background mercury levels in northern latitudes. Arctic 32: 376–377.
EATON, R. D. P., D. C. SECORD, AND P. HEWITT. 1980. An experimental assessment of the toxic potential of mercury in ringed seal liver for adult laboratory cats. Toxicol. Appl. Pharmacol. 55: 514–521.
EATON, R. D. P., AND M. P. HEWITT. 1981. Protective effect of sodium selenite against methyl mercury toxicity in laboratory cats. Proc. 5th Int. Symp. Circumpolar Health, Copenhagen. Nordic Council for Arctic Medical Research Rep. Ser. 33: 546–553.
EATON, R. D. P., AND J. P. FARANT. 1982. The polar bear as a biological indicator of the environmental mercury burden. Arctic 35: 422–425.
ENGELHARDT, F. R., J. R. GERACI, AND T. G. SMITH. 1977. Uptake and clearance of petroleum hydrocarbons in the ringed seal, *Phoca hispida*. J. Fish Res. Board Can. 34: 1143–1147.
EVANS, P. G. H. 1982. Associations between seabirds and cetaceans: a review. Mammal Rev. 12: 187–206.
FEDOSEEV, G. A. 1965. 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. Mosk. Mlekop., Akad, Nauk SSSR, p. 105–112. (Trans. from Russian by Fish Res. Board Can. Transl. Ser. No. 799: 23 p., 1966).
1975. Ecotypes of the ringed seal (*Phoca hispida* Schreber, 1777) and their reproductive capabilities. *In* K. Ronald and A. W. Mansfield [ed]. Biology of the seal. Rapp. P.-V. Reuni. Cons. Int. Explor. Mer 169: 156–160.
FENCO CONSULTANTS LTD., AND F.F. SLANEY CO. 1978. An arctic atlas: Background information for developing marine oil spill counter-measures. Envir. Protection Serv. 9-EC-78-1: 413 p.
FINLEY, K. J. 1979. Haul-out behaviour and densities of ringed seals (*Phoca hispida*) in the Barrow Strait Area, N.W.T. Can. J. Zool. 57: 1985–1997.
FINLEY, K. J., G. W. MILLER, R. A. DAVIS, AND W. R. KOSKI. 1983. A distinctive large breeding population of ringed seals (*Phoca hispida*) inhabiting the Baffin Bay pack ice. Arctic 36: 162–173.
FOOTE, D. C. 1967. Remarks on Eskimo sealing and the harp seal controversy. Arctic 20: 267–268.
FREUCHEN, P. 1937. Mammals. Part 2. Field notes and biological observations, Vol. 2: 68–278. *In* Report of the fifth Thule expedition 1921–24. Glydendal, Copenhagen.
FROST, K. J., AND L. F. LOWRY. 1981. Trophic importance of some marine gadids in northern Alaska and their body-otolith size relationships. Fish. Bull. 79: 187–192.
FULLER, W. A. 1981. Fish, fur and game in the Northwest Territories: some problems of,

and prospects for, increased harvests, p. 12–29. *In* M. R. Freeman [ed.] Proc. First Int. Symp. on Renewable Resources and Economy of the North, Banff, Alberta. 268 p.

GALSTER, W. A. 1971. Accumulation of mercury in Alaska pinnipeds. (Abstract), Proc. Alaskan Science Conference Alaskan AAAS College, Alaska, 22: 76.

1974. Assessment of the potential health hazard in accumulation of mercury in Alaskan marine mammals, p. 666. *In* R. J. Shephard and S. Itoh [ed.] A commentary in Proceedings of the Third International Symposium on Circumpolar Health, Yellowknife, N.W.T. Univ. Toronto Press, Toronto, Ont. 678 p.

1976. Mercury in Alaskan Eskimo mothers and infants. Environ. Health Perspect. 15: 135–140.

GALSTER, W. A., AND J. J. BURNS. 1972. Accumulation of pesticides in Alaskan marine mammals, p. 23. *In* Alaskan Science Conference, Proc. 23rd Alaskan Sci. Conf., Aug. 1972. Fairbanks, AK.

GERACI, J. R., AND T. G. SMITH. 1976a.Direct and indirect effects of oil on ringed seals (*Phoca hispida*) of the Beaufort Sea. J. Fish. Res. Board. Can. 33: 1976–1984.

1976b. Behaviour and pathophysiology of seals exposed to crude oil, p. 447–462. *In* Sources, effects and sinks of hydrocarbons in the aquatic environment. Am. Inst. Biol. Sci., Wash. DC.

1977. Consequences of oil fouling on marine mammals, p. 399–410. *In* D. C. Malins [ed.] Effects of petroleum on arctic and subarctic marine environments and organisms. Vol. II. Biological Effects. Academic Press Inc., New York, NY. 500 p.

1979. Vitamin C in the diet of Inuit hunters from Holman, Northwest Territories. Arctic 32: 135–139.

GERACI, J. R., AND D. J. ST. AUBIN. 1979. Possible effects of offshore oil and gas development on marine mammals: present status and research recommendations. A report prepared for the Marine Mammal Commission. Wash. DC. 1979, 37 p.

GERACI, J. R., D. J. ST. AUBIN, T. G. SMITH, AND T. G. FREISEN. 1985. How do bottlenose dolphins, *Tursiops truncatus*, react to oil films under different light conditions? Can. J. Fish. Aquat. Sci. 42: 430–436.

GERACI, J. R., D. J. ST. AUBIN, AND R. J. REISMAN. 1983. Bottlenose dolphins, *Tursiops truncatus*, can detect oil. Can. J. Fish. Aquat. Sci. 40: 1516–1522.

GIDDINGS, J. L. 1967. Ancient men of the arctic. A. A. Knopp [ed.]. New York, NY. 391 p.

GILMARTIN, W. G., R. L. DE LONG, A. W. SMITH, L. A. SWEENEY, M. D. DAILY, AND D. B. PEAKALL. 1976. Premature parturition in the California sea lion. J. Wildl. Dis. 12: 104–115.

GRAINGER, E. H. 1965. Zooplankton from the Arctic Ocean and adjacent Canadian waters. J. Fish. Res. Board. Can. 22: 543–564.

1971. Arctic zooplankton. *In* C. T. Shih, A. J. G. Figueira, andE. H. Grainger. A synopsis of Canadian marine zooplankton. Bull. Fish. Res. Board. Can. 176: 189–229.

1974. Nutrients in the Southern Beaufort Sea, p. 589–606. *In* J. C. Reed and J. E. Sater [ed.]. The coast and shelf of the Beaufort Sea. Arctic Inst. N. Am. Arlington, VA, USA.

1975. Biological productivity of the southern Beaufort Sea: the physical-chemical environment and the plankton. Beaufort Sea Project. Beaufort Sea Tech. Rep. No. 12A. Fish. Mar. Serv. Victoria, B.C. 82 p.

GRAINGER, E. H., AND K. GROHE. 1975. Zooplankton data from the Beaufort Sea 1951 to 1975. Fish. Mar. Serv. Tech. Rep. 591: 54 p.

HALL, E. S. 1971. The iron dog in northern Alaska. *In* J. and P. Lotz [ed.], Pilot, not commander: essays in memory of Diamond Jenness. Ottawa 1971. 323 p. Maps, tables, illus. (Anthropologica, v. 13, no. 112, special issue.)

HAMMILL, M. O. 1983. The arctic fox, *Alopex lagopus* as a marine mammal: Physical condition and population age structure. M.Sc. thesis, McGill Univ. Montreal, Que. 72 p.

1987. The effects of weather on ice conditions in the Amundsen Gulf, N.W.T. Can. Tech. Rep. Fish. Aquat. Sci. 1900: 9 p. + 1 Fig.

HARTLEY, H. O. 1961. The modified Gauss-Newton method for the fitting of non-linear regression functions by least-squares. Technometrics 3: 269–280.

HELLE, E. 1977. On the reproductive success in the Bothnian Bay population of the ringed seal and future prospects for the species. Proc. Symp. on the Conservation of Baltic Seals. Finn. Game Res. 37: 32–35.

1980a. Reproduction, size and structure of the Baltic ringed seal population of the Bothnia Bay. Acta Univ. Oulu. Ser. A. Saential Rerum Nat. 106, Biol. 11: 47 p.

1980b. Lowered reproductive capacity in female ringed seals (*Pusa hispida*) in the Bothnian Bay, northern Baltic Sea, with special reference to uterine occlusions. Ann. Zool. Fennici 17: 147–158.

HELLE, E., M. OLSSON, AND S. JENSEN. 1976a. DDT and PCB levels and reproduction in ringed seals from the Bothnia Bay. Ambio 5: 188–189.

1976b. High frequencies of pathological changes in seal uteri correlated with PCB levels. Ambio 5: 261–263.

HELM, R. C. 1983. Rate of digestion in three species of pinnipeds. Can. J. Zool. 62: 1751–1756.

HENDZEL, M., J. E. SAYED, O. SCHAEFER AND J. A. HILDES. 1974. Mercury content of Iglooligmiut hair, p. 608–663. *In* R. J. Shephard and S. Itoh [ed.] Proc. 3rd Int. Symp. on Circumpolar Health, Yellowknife N.W.T., Univ. Toronto Press, Toronto, Ont. 18 + 678 p.

HENRY, R. F. 1975. Storm surges. Project completion Report to the Beaufort Sea Project. Fish. Mar. Serv. Victoria, B.C. 41 p.

HERLINVEAUX, R. H. AND B. R. DE LANGE BOOM. 1975. Physical oceanography of the southeastern Beaufort Sea. Beaufort Sea Project. Beaufort Sea Tech. Rep. 18: Fish Mar. Serv. Victoria, B.C. 97 p.

HOBART, C. W. 1981. Impacts of industrial employment on hunting and trapping among Canadian Inuit, p. 202–218. *In* M. R. Freeman [ed.] Proc. First. Int. Symp. on Renewable Resources and Economy of the North, Banff, Alberta. 268 p.

HOLDEN, A. V. 1978. Pollution and seals—a review. Mammal Rev. 8: 53–66.

HSIAO, S. I. C. 1975. Biological productivity of the southern Beaufort Sea: Phytoplankton and seaweed studies. Beaufort Sea Project. Beaufort Sea Tech. Rep. No. 12C, Fish Mar. Serv. Victoria, B.C. 99 p.

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 Beaufort Sea. Can. J. Bot. 55: 685–694.

HUNTER, J. G. 1979. Abundance and distribution of arctic cod, *Boreogadus saida*, in the southeastern Beaufort Sea. Can. Atl. Fish. Sci. Adv. Comm. Res. Doc. 79/39: 13 p.

INGOLFSSON, A. 1969. Behaviour of gulls robbing eiders. Bird Study 16: 45– 52.

INNES, S., R. E. A. STEWART, AND D. M. LAVIGNE. 1981. Growth in northwest Atlantic harp seals *Phoca groenlandica*. J. Zool. Lond. 194: 11–24.

JAMES BAY AND NORTHERN QUEBEC NATIVE HARVESTING COMMITTEE. 1979. Research to establish present levels of native harvesting: Harvests by the Inuit of northern Quebec. Phase II (yr. 1976) Prepared for the coordinating committee on hunting, fishing and trapping. Montreal, Quebéc. 108 p.

JENNESS, D. 1925. A new Eskimo culture in Hudson Bay. The Geogr. Rev. 15: 428–437.

JOHNSON, L. 1983. Assessment of the effects of oil on arctic marine fish and marine mammals. Can. Tech. Rep. Fish. Aquat. Sci. 1200: 15 p.

JOHNSON, M. L., C. H. FISCUS, B. T. OSTENSON, AND M. L. BARBOUR. 1966. Marine mammals, p. 887–924. *In* N. J. Wilimovsky [ed.] Environment of the Cape Thompson Region, Alaska. U.S. At. Energy Comm., Div. Tech. Inf. Ext., Oak Ridge, TN. 1250 p.

KEITH, R. F., A. KERR, AND R. VLES. 1981. Mining in the north. Northern Perspect. 9: 1–7.

KINGSLEY, M. C. S. 1984. The abundance of ringed seals in the Beaufort Sea and Amundsen Gulf, 1983. Can. MS. Rep. Fish. Aquat. Sci. 1778: iv + 8 p.

1985. Distribution and abundance of seals in the Beaufort Sea, Amundsen Gulf, and Prince Albert Sound, 1984. Environmental Studies Revolving Funds Report 025, Ottawa. Ont. 16 p.

KOOYMAN, G. L. 1981. Weddell seal: consummate diver. Cambridge Univ. Press, Cambridge. 135 p.

KUMLEIN, 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. 15: 179p.

KUPETSKII, W. N. 1959. Atlantic deep waters as a cause of some peculiarities in polar climate. Probl. Arktiki, Sb. State 6: 13–21.

1962. A stationary polynya in the Baffin Bay "North Water". Trans. Dep. Secr. of State Can. 1972. from: Gos i Okeanogr. Inst. Moskva 70: 47–60.

LAWS, R. M. 1959. Accelerated growth in seals, with special reference to the Phocidae. Hvalfangst-Tidende 9: 425–452.

LEAR, W. H. 1979. Distribution, size and sexual maturity of arctic cod (*Boreogadus* *saida*) in the Northwest Atlantic during 1959–1975. CAFSAC Working paper 79/58.

LINDSAY, D. G. 1975. Sea ice atlas of arctic Canada, 1961-1968. Dept. Energy, Mines and Resources, Ottawa. 213 p.

1978. Sea ice atlas of arctic Canada 1975–1978. Supply and Services Canada. 139p.

LOWRY, L. F., K. J. FROST, AND J. J. BURNS. 1980. Variability in the diet of ringed seals, *Phoca hispida*, in Alaska. Can. J. Fish. Aquat. Sci. 37: 2254–2261.

LUKIN, L. R. 1980. Habitat of White Sea ringed seal in the initial period of post-natal development. Tranlated from Biologiya Morya 5: 33–37, Sept. 1980. Plenum Publishing Corp. 1981.

LUKIN, L. R., AND V. A. POTELOV. 1978. Living conditions and distribution of ringed seal in the White Sea in the winter. Translated from Biologiya Morya, 3: 62–69. Plenum Publishing Corp. 1979.

LYDERSEN, C., AND I. GJERTZ. 1984. Studies of the ringed seal (*Phoca hispida* Schreber 1775) in its breeding habitat in Kongsfjorden, Svalbard. Norsk. Polarinstitutt, Rapportserie, No. 19: 46 p.

1986. Studies of the ringed seal (*Phoca hispida* Schreber 1775) in its breeding habitat in Kongsfjorden, Svalbard. Polar Res. 4: 57–63.

MANSFIELD, A. W. 1983. The effects of vessel traffic in the arctic on marine mammals and recommendations for future research. Can. Tech. Rep. Fish. Aquat. Sci. 1186: 97 p.

MARKHAM, W. E. 1975. Ice climatology of the Beaufort Sea. Beaufort Sea Project. Beaufort Sea Tech. Rep. No. 26, Fish. Mar. Serv., Victoria, B.C. 87 p.

MAXWELL, M. S. 1979. The Lake Harbour Region: Ecological equilibrium in sea coast adaptations. Nat. Museum of Man. Mercury Ser. 88: 76–88.

MCGHEE, R. 1974. Current interpretation of Central Canadian arctic prehistory. Internord, Vols. 13–14: 171–180.

MCGHEE, R., AND J. A. TUCK. 1976. Updating the Canadian arctic. In: Eastern arctic prehistory:Palaeoeskimo Problems, M. S. Maxwell [ed.], Soc. Am. Archeol. Mem. 31: 6–14.

MCLAREN, I. A. 1958a. The biology of the ringed seal (*Phoca hispida* Schreber) in the eastern Canadian arctic. Bull. Fish. Res. Board Can. 118: 97 p.

1958b. The economics of seals in the eastern Canadian arctic. Fish. Res. Board Can. Arct. Unit Circ. 1: 94 p.

MCLAREN, I. A., AND T. G. SMITH. 1985. Population ecology of seals: Retrospective and prospective views. J. Mar. Mammal. Sci. 1.: 54–83.

MILNE, A. 1977. Oil, ice and climate change. The Beaufort Sea and the search for oil. Beaufort Sea Project, Fish. Mar. Serv., Institute of Ocean Sciences, Patricia Bay, B.C. 103 p.

MILNE, A., AND R. H. HERLINVEAUX. 1977. Crude oil in cold waters. The Beaufort Sea and search for oil. Beaufort Sea Project, Fish. Mar. Serv., Institute of Ocean Sciences, Patricia Bay, B.C. 119 p.

MOHAMMED, A. A., AND E. H. GRAINGER. 1974. Zooplankton data from the Canadian arctic archipelago, 1962. Fish. Mar. Serv. Tech. Rep. 460: 185 p.

MOHL, B. 1980. Memo on the Arctic Pilot Project, regarding noise pollution in the arctic marine environment. Arctic Seas Bull. 8: 2 p.

NAZARENKO, Y. I. 1965. Contributions to the study of the reproduction of the ringed seal, *Phoca hispida*, of the Choska Inlet. Morskie Mlekop. Akad. Nauk SSSR, p. 171–75 (Transl. from Russian by Fish. Res. Board Can. Transl. Ser. No. 1461: 10 p., 1970).

NETTLESHIP, D. N. 1977. Seabird resources of eastern Canada: Status, problems and prospects, p. 96–108. *In* Proceedings of the Symposium on Canada's Threatened Species and Habitats.

NEWBY, T. G. 1978. Pacific harbour seal, p. 185–191. *In* D. Haley [ed.] Marine mammals of eastern North Pacific and arctic waters. Pacific Search Press, Seattle, WA.

OLSSON, M. 1977. Mercury, DDT and PCB in aquatic test organisms. Baseline and monitoring studies, field studies on biomagnification, metabolism and effects of some bioaccumulating substances harmful to the Swedish environment. Nat. Swed. Environ. Protect. Board, PM 900: 139 p.

OLSSON, M., A. G. JOHNELS, AND R. VAZ. 1974. DDT and PCB levels in seals from Swedish waters. The occurrence of aborted seal pups. Proc. Symp. on the seal in the Baltic. Nat. Swed. Environ. Protect. Board, PM 591: 43–65.

ØRITSLAND, N. A., F. R. ENGLEHARDT, R. A. JUCK, R. A. HURST AND P. D. WATTS. 1981. [released 1982]. Effects of crude oil on polar bears. Environmental studies No. 24, Northern Affairs Program, Dep. Indian

Affairs and Northern Development, Ottawa. 268 p.

PARSONS, J. L. 1977. Metabolic Studies on Ringed Seals *Phoca hispida*. M.Sc. thesis, Dep. of Pathology, University of Guelph, Guelph, Ont. 82 p.

PAYNE, R., AND D. WEBB. 1971. Orientation by means of long range acoustic signaling in baleen whales. Ann. N.Y. Acad. Sci. 188: 110–141.

PIMLOTT, D., D. BROWN, AND K. SAM. 1976. Oil Under the ice. Canadian arctic Resources Committee. Ottawa, Ont. 178 p.

POLACHECK, T. 1985. The sampling distribution of age-specific survival estimates from an age distribution. J. Wildl. Manage. 49: 180–184.

POULTER, T. G. 1968. Underwater vocalization and behaviour of pinnipeds. p. 69–84. *In* R. J. Harrison, R. C. Hubbard, R. S. Peterson, C. E. Rice and R. J. Shusterman. [ed.] The behaviour and physiology of pinnipeds. Appleton-Century-Crofts, New York, NY. 411 p.

QUAST, J. C. 1974. Density distribution of juvenile arctic cod, *Boreogadus saida*, in the eastern Chuckchi Sea in the fall of 1970. Fish. Bull. 72: 1094–1105.

RASMUSSEN, K. 1931. The Netsilik Eskimo: social life and spiritual culture. Rep. Fifth Thule Exp., 1921–1924, Vol. 8, Nos. 1 and 2 Gyldendal, Copenhagen.

RAY, C., W. A. WATKINS, AND J. BURNS. 1969. The underwater song of *Erignathus barbatus* (bearded seal). Zoologica 54: 79–83.

RICHARDSON, W. J., C. R. GREEN, J. P. HICKIE, AND R. A. DAVIS. 1983. Effects of offshore petroleum operation on cold water marine mammals. A literature review. Environ. Affairs Dep. American Petroleum Institute, Wash. D.C. AIPP Rep. No. 4370: 248 p.

RYDER, R. A. 1956. Avian-pinniped feeding associations. Condor 59: 68–69.

SAS INSTITUTE INC. 1985. SAS user's guide: Statistics version 5 edition. Cary, NC. 956 p.

SCHAEFFER, O. 1971. When the Eskimo comes to town. Nutrition Today 6: 8–16.

SCIENCE COUNCIL OF CANADA AND ATLANTIC PROVINCES ECONOMIC COUNCIL. 1977. Seminar on natural gas from the arctic by marine mode: a preliminary assessment. Ottawa SCC-APEC. 254 p.

SEKERAK, A. D. 1982. Young of the year cod (*Boreogadus saida*) in Lancaster Sound. Arctic 35: 75–87.

SHIH, C. T., AND D. R. LAUBITZ. 1978. Zooplankton distribution in the eastern Beaufort Sea and the Northwest passage. Astarte 11: 45–54.

SMITH, T. G. 1970. Computer programs for the analysis of ringed seal population data. Fish. Res. Board Can. Tech. Rep. 224: 45 p.

1973a. Population dynamics of the ringed seal in the Canadian eastern arctic. Bull. Fish. Res. Board Can. 181: 55 p.

1973b. Censusing and estimating the size of ringed seal populations. Fish. Res. Board Can. Tech. Rep. 427: 18 p. + 4 figs.

1976a. Predation of ringed seal pups (*Phoca hispida*) by the arctic fox (*Alopex lagopus*). Can. J. Zool. 54: 1610–1616.

1976b. The icy birthplace and hard life of the Arctic ringed seal. Can. Geog. J. 93: 58–63.

1977. The Wolffish, cf. *Anarhichas denticulatus*, new to the Amundsen Gulf, Northwest Territories, and a probable prey of the ringed seal. Can. Field-Nat. 91: 288.

1980a. Polar bear predation of ringed and bearded seals in the land-fast sea ice habitat. Can. J. Zool. 58: 2201–2209.

1980b. How Inuit trappers make ends meet. Can. Geog. J. 99: 56–61.

SMITH, T. G., AND F. A. J. ARMSTRONG. 1975. Mercury in seals, terrestrial carnivores, and principal food items of the Inuit, from Holman, N.W.T. J. Fish. Res. Board Can. 32: 795–801.

1978. Mercury and selenium in ringed and bearded seal tissues from Arctic Canada. Arctic 31: 175–184.

SMITH, T. G., B. BECK, AND G. A. SLENO. 1973. Capture, handling, and branding of ringed seals. J. Wildl. Manage. 37: 579–583.

SMITH, T. G., AND J. R. GERACI. 1975. The effect of contact and ingestion of crude oil on ringed seals in the Beaufort Sea. Beaufort Sea Project.Beaufort Sea Tech. Rep. 6. Fish. Mar. Serv., Victoria, B.C. 67 p.

SMITH, T. G., J. R. GERACI, AND D. J. ST.AUBIN. 1983. The reaction of bottlenose dolphins, *Tursiops truncatus*, to controlled oil spills. Can. J. Fish. Aquat. Sci. 40: 1522–1526.

SMITH, T. G., M. O. HAMMILL, D. W. DOIDGE, T. CARTIER, AND G. A. SLENO. 1979. Marine mammal studies in southeastern Baffin Island. Final Report to the Eastern

Arctic Marine Environmental Studies (EAMES) Project. Can. MS Rep. Fish. Aquat. Sci. 1552: 70 p.

SMITH, T. G., AND M. O. HAMMILL. 1980a. A survey of the breeding habitat of ringed seals and a study of their behaviour during the spring hauling-out period on southeastern Baffin Island. Can. Tech. Rep. Fish. Aquat. Sci. 1561: 23 p.

1980b. Ringed seal, *Phoca hispida*, breeding habitat survey of Bridport Inlet and adjacent coastal sea ice. Can. Ms. Rep. Fish. Aquat. Sci. 1557: 31 p.

1981. Ecology of the ringed seal, *Phoca hispida* in its fast ice breeding habitat. Can. J. Zool. 59: 966–981.

SMITH, T. G., AND J. MEMOGANA. 1977. Disorientation in ringed and bearded seals. Can. Field-Nat. 91: 181–182.

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.

1978. Variation in the density of ringed seal (*Phoca hispida*) birth lairs in the Amundsen Gulf, Northwest Territories. Can. J. Zool. 56: 1066–1071.

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. Rep. 694: 37 p.

SOKAL, R. F., AND F. J. ROHLF. 1969. Biometry. The principals and practice of statistics in biological research. W. H. Freeman and Co., San Francisco, CA. 776 p.

SPINAGE, C. A. 1972. African Ungulate life tables. Ecology 53: 645–652.

ST. AUBIN, D. J., AND J. R. GERACI. 1977. Tissue distribution and plasma levels of liver enzymes in phocid seals. Can. J. Zool. 55: 1936–1941.

ST. AUBIN, D. J., J. R. GERACI, T. G. SMITH, AND V. I. SMITH. 1978. Blood volume determination in the ringed seal, *Phoca hispida*. Can. J. Zool. 56: 1885–1887.

STEFANSSON, V. 1913a. My life with the Eskimos. Collier Books, Inc., 447 p.

1913b. Victoria Island and the surrounding sea. Amer. Geog. Soc. Bull. 45: 93–106.

1914. The Stefansson-Anderson Expedition. Anthropological papers, Am. Mus. Nat. Hist. 14: 7–379.

1921. The friendly arctic. MacMillan and Co. Ltd., London, 784 p.

1946. Not by bread alone. MacMillan and Co., New York, NY. 339 p.

STEWART, R. E. A., AND D. M. LAVIGNE. 1980. Neonatal growth of northwest Atlantic harp seals, *Pagophilus groenlandicus*. J. Mammal. 61: 670–680.

STIRLING, I. 1973. Vocalization in the ringed seal (*Phoca hispida*). J. Fish. Res. Board Can. 30: 1592–1594.

1974a. Midsummer observations on the behaviour of wild polar bears (*Ursus maritimus*). Can. J. Zool. 52: 1191–1198.

1974b. Adaptations of Weddell and Ringed seals to exploit polar fast-ice habitat in the presence or absence of land predators, p. 741–748. *In* G.A. Llano [ed.]Adaptations within antarctic ecosystems. Third Symp. Antarctic Biol. Wash., DC.

1980. The biological importance of polynyas in the Canadian arctic. Arctic 33: 303–315.

STIRLING, I., AND W. R. ARCHIBALD. 1977. Aspects of polar bear predation. J. Fish. Res. Board Can. 34: 1126–1129.

STIRLING, I., W. R. ARCHIBALD, AND D. DEMASTER. 1977. The distribution and abundance of seals in the eastern Beaufort Sea. J. Fish. Res. Board Can. 34: 976–988.

STIRLING, I., AND W. CALVERT. 1983. Environmental threats to marine mammals in the Canadian arctic. Polar Rec. 21: 433–450.

STIRLING, I., W. CALVERT, AND H. CLEATOR. 1983. Underwater vocalization as a tool for studying the distribution and relative abundance of wintering pinnipeds in the high arctic. Arctic 36: 262–274.

STIRLING, I., AND H. CLEATOR [ED.]. 1981. Polynyas in the Canadian arctic. Can. Wildl. Serv. Occas. Pap. 45. 73 p.

STIRLING, I., M. KINGSLEY, AND W. CALVERT. 1982. The distribution and abundance of seals in the eastern Beaufort Sea, 1974–1979. Can. Wildl. Ser. Occas. Pap. 47: 25 p.

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 behaviour. Can. J. Zool. 53: 1021–1027.

STIRLING, I., R. R. WALLACE, AND G. T. GLAZIER. 1979. An environmental research and management strategy for the eastern arctic region: a discussion. Northern Perspect. 7: 4–9.

SZEKIELDA, H. 1974. Hot spots in the Ross Sea: upwelling during winter-time. Tethys 1964: 105–110.

TAUGBOL, G. 1984. Ringed seal thermoregulation, energy balance and development in early life, a study on *Pusa hispida* in Kongsfd., Svalbard. Thesis, Zoofysiologisk Institutt, Univ. Oslo, Norway, 102 p. 1982. (Translation of Fish. Aquat. Sci. No. 5090).

TERHUNE, J. M., AND K. RONALD. 1975a. Underwater hearing sensitivity of two ringed seals (*Pusa hispida*). Can. J. Zool. 53: 227–231.

1975b. Masked hearing thresholds of ringed seals. J. Acoust. Soc. Am. 58: 515–516.

1976. The upper frequency limit of ringed seal hearing. Can. J. Zool. 54: 1226–1229.

THOMAS, I., AND D. DEMASTER. 1979. Umbilical dropoff as a measure of age in the weddell seal, *Leptonychotes weddelli*. J. Mammal. 60: 436.

TINLING, R. 1982. Northwest Territories fur production 1957–58 to 1978-79. N.W.T. Wildlife Serv. Information report No. 1. Yellowknife, N.W.T. 45 p.

USHER, P. J. 1965a. Economic basis and resource use of the Coppermine— Holman region, N.W.T. Dept. North Affairs Nat. Res., Ind. Div. Area Econ. Surv. Report 65–2: 290 p.

1965b. Banks Island an area economic survey. Dep. North Aff. Nat. Res. Ind. Div. Area Econ. Surv. Report, 65–1, 125 p.

1970. The Bankslanders: Economy and ecology of a frontier trapping community. Vol. 2–Economy and Ecology. Northern Science Research Group: Dep. of Indian Affairs and Northern Development. 169 p.

1971. Fur trade posts of the Northwest Territories 1870-1970. Northern Science Research Group. Dept. Indian Affairs and Northern Development. NSGR 71–4, 180 p.

1977. Evaluating country food in the northern native economy. Arctic 29: 105–120.

USHER, P. J., AND M. CHURCH. 1969a. Field tables for the calculation of ringed seal weights from length and girth measurements. Dep. Indian Affairs and Northern Dev. Tech. Notes 3: 9 p.

1969b. On the relationship of weight, length and girth of the ringed seal (*Pusa hispida*) of the Canadian arctic. Arctic 22: 120–129.

VAN DE VELDE, F. 1956. Rules governing the sharing of seal after the Aglus hunt among the Arvilgjuarmiut. Eskimo 41: 3-6.

VERRALL, R. 1981. Acoustic transmission losses and ambient noise in Parry Channel, p. 220–283. *In* N. M. Peterson [ed.] The question of sound from ice breaker operations: the proceedings of a workshop. Arctic Pilot Project, Petro-Canada, Calgary Alta. 350 p.

WAGEMANN, R., AND D. C. G. MUIR. 1981. Assessment of heavy metals and organochlorine concentrations in marine mammals of northern waters. Int. Cons. Expl. Sea. Marine Env. Quality Comm., Marine Mammal Comm., C.M. 1981/N: 9: 22 p. +14 tables + 10 figs.

WANG, DA-XIANG. 1981. The status of pesticides in China and their future. J. Pesticide Sci. 6: 397–399.

WENZEL, G. 1978. The harp seal controversy and the Inuit economy. Arctic 31: 3–6.

1979. Social organization as an adaptive referent in Inuit cultural ecology: the case of Clyde River and Agvigtiuk. Ph.D. thesis, Dep. Geogr., McGill Univ., Montreal, Que. 298 p.

WHEATLEY, B. 1979. Methylmercury in Canada: exposure of Indian and Inuit residents to methylmercury in the Canadian environment. Dep. National Health and Welfare, Medical Services Branch. Ottawa, Ont. 200 p.

WORTHY, G. A., AND D. M. LAVIGNE. 1983. Energetics of fasting and subsequent growth in weaned harp seal pups, *Phoca groenlandica*. Can. J. Zool. 61: 447–456.

YORK, N. E. 1983. Average age at first reproduction of the northern fur seal (*Callorhinus ursinus*). Can. J. Fish. Aquat. Sci. 40: 121–127.

# DATE DUE
## DATE DE RETOUR

| | | | |
|---|---|---|---|
| ~~29/10~~ | | | |
| 27/03/98 | | | |
| | | | |
| | | | |
| | | | |
| | | | |
| | | | |
| | | | |
| | | | |
| | | | |
| | | | |
| | | | |
| | | | |
| | | | |
| | | | |
| | | | |
| | | | |
| | | | |

Canada