

Ecology of the Ringed Seal (Phoca hispida Schreber) in the
Fast-ice of Barrow Strait, Northwest Territories.

by

Michael O. Hammill

A thesis submitted to the Faculty of Graduate Studies
and Research of McGill University in partial fulfillment
of the requirements for the degree of Doctor of Philosophy.

Wildlife Biology
Department of Renewable Resources
Macdonald College of McGill University
Montreal, Quebec

November 1987 ©

Permission has been granted to the National Library of Canada to microfilm this thesis and to lend or sell copies of the film.

The author (copyright owner) has reserved other publication rights, and neither the thesis nor extensive extracts from it may be printed or otherwise reproduced without his/her written permission.

L'autorisation a été accordée à la Bibliothèque nationale du Canada de microfilmer cette thèse et de prêter ou de vendre des exemplaires du film.

L'auteur (titulaire du droit d'auteur) se réserve les autres droits de publication; ni la thèse ni de longs extraits de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation écrite.

ISBN 0-315-45990-5

Suggested short title:

Ecology of the Ringed Seal

ABSTRACT

The number of breathing holes in thirty-two study plots located in Barrow Strait was used as an index of ringed seal (Phoca hispida) abundance. During March to June, 1984-1986 densities were estimated from a combination of dog searches and a modified removal sampling technique. To achieve precision of 30% or better, 80% of the estimated number of seal holes must be located and the probability of hole detection must be greater than 0.3.

Birth lairs were not seen before 4 April, but were found more frequently as the season progressed. Male structures were evident in late March, but were not found after mid-May. In 1986, density of seal holes was correlated with both date of ice consolidation and snow depth. Similar results were not obtained in 1984 or 1985. The plots surveyed in these years were located too close together in ice that consolidated at the same time.

Juvenile animals were under-represented in a shot sample of seals. The mean reproductive rate for females >7 years old was 0.64. The mean date of pupping in Barrow Strait falls in the fourth week of April. Lactation lasts for 41-48 days.

In spring, ringed seals depend on stored reserves to supply 44% of their daily energy requirements. In adult seals no differences in body condition were detected, but juvenile animals collected in 1986 were in significantly better condition than juveniles collected in 1984 and 1985.

Le nombre de trous de respiration dans 32 parcelles d'études situées dans le Détroit de Barrow a été utilisé comme index d'abondance des phoques annelés (Phoca hispida). De Mars à Juin 1984-1986, les densités de trous ont été déterminées par une combinaison de recherche par chiens et de modification de la méthode d'échantillonnage par enlèvement. Pour obtenir une précision de 30% ou plus, 80% des trous de phoques estimés doivent être localisés et la probabilité de détection doit être supérieure à 0.3.

Les repères de naissance n'étaient visibles qu'à partir du 4 Avril; l'incidence de ces structures augmentait au cours de la saison. Les repères utilisés par les mâles en rut étaient présents à la fin Mars, mais disparaissaient après mi-Mai. En 1986, la densité des trous de phoques était corrélée à la fois à la date de consolidation de la glace et à l'épaisseur de neige. Des résultats semblables n'ont pas été obtenus en 1984 ou 1985. Ces années-là, les parcelles d'études ont été définies trop proches les unes des autres dans la glace et se sont toutes solidifiées en même temps.

Les animaux juvéniles étaient sous-représentés de l'échantillon de phoques. Le taux de reproduction majeure des femelles >7 ans était de 0.64. La date approximative de la mis-bas dans le Détroit de Barrow se situe dans la 4ième semaine d'Avril. L'allaitement dure de 41-48 jours.

Au printemps, les phoques annelés dépendent de leur réserve pour fournir 44% de leurs besoins énergétiques journaliers. Chez les adultes, aucune différence de l'état physique n'a été détectée mais les animaux juvéniles collectés en 1986 étaient significativement en meilleure condition physique que ceux collectés en 1984 et 1985.

RESUME

Le nombre de trous de respiration dans 32 parcelles d'études situées dans le Détroit de Barrow a été utilisé comme index d'abondance des phoques annelés (Phoca hispida). De Mars à Juin 1984-1986, les densités de trous ont été déterminées par une combinaison de recherche par chiens et de modification de la méthode d'échantillonnage par enlèvement. Pour obtenir une précision de 30% ou plus, 80% des trous de phoques estimés doivent être localisés et la probabilité de détection doit être supérieure à 0.3.

Les repères de naissance n'étaient visibles qu'à partir du 4 Avril; l'incidence de ces structures augmentait au cours de la saison. Les repères utilisés par les mâles en rut étaient présents à la fin Mars, mais disparaissaient après mi-Mai. En 1986, la densité des trous de phoques était corrélée à la fois à la date de consolidation de la glace et à l'épaisseur de neige. Des résultats semblables n'ont pas été obtenus en 1984 ou 1985. Ces années-là, les parcelles d'études ont été définies trop proches les unes des autres dans la glace et se sont toutes solidifiées en même temps.

Les animaux juvéniles étaient sous-représentés de l'échantillon de phoques. Le taux de reproduction majeure des femelles 7 ans était de 0.64. La date approximative de la mis-bas dans le Détroit de Barrow se situe dans la 4ième semaine d'Avril. L'allaitement dure de 41-48 jours.

Au printemps, les phoques annelés dépendent de leur réserve pour fournir 44% de leurs besoins énergétiques journaliers. Chez les adultes, aucune différence de l'état physique n'a été détectée mais les animaux juvéniles collectés en 1986 étaient significativement en meilleure condition physique que ceux collectés en 1984 et 1985.

TABLE OF CONTENTS

	Page
LIST OF TABLES	i
LIST OF FIGURES	v
ACKNOWLEDGEMENTS	vii
PREFACE	ix
REFERENCES	xii
THESIS OFFICE STATEMENT	xviii
 SECTION I. Removal sampling used to estimate densities of ringed seals in Barrow Strait, Northwest Territories	 1
Introduction	2
Materials and Methods	3
Results	8
Discussion	12
References	17
Tables	19
Figures	22
 CONNECTING STATEMENT	 25
 SECTION II. Factors affecting the abundance of ringed seals in their fast-ice breeding habitat	 26

Introduction	27
Materials and Methods	29
Results	35
Discussion	43
References	50
Tables	54
Figures	63
CONNECTING STATEMENT	65
SECTION III. Biology of the ringed seal in Barrow Strait, Northwest Territories	66
Introduction	67
Materials and Methods	68
Results	72
Discussion	78
References	85
Tables	89
Figures	103
SUMMARY AND GENERAL CONCLUSIONS	106

LIST OF TABLES

PAGE

SECTION I

Table 1. Mean number of searches per plot, precision of population estimates, proportion of population located, number of dogs used in the surveys and average area of study plots searched during 1984 to 1986. 19

Table 2. Hole to seal ratios calculated from this study, and values reported in the literature. The value from Smith and Hammill (1981) has been multiplied by 0.8 to correct for the proportion of the population hauled out on the ice. 20

Table 3. Comparisons between seal densities (seals/km²) obtained from dog surveys and estimates obtained from aerial surveys of hauled out animals. Standard errors are in parentheses. Seal densities from the present study were obtained by dividing the density of seal holes by 3.38. 21

SECTION II

Table 1. Mean wind direction, speed, temperature, snow depth, total snowfall and days of blowing snow recorded at Resolute Bay, Northwest Territories, from September to May 1984 to 1986. (Monthly Record, Atmospheric Environment Service, Environment Canada, Toronto, Ont.) 54

Table 2. Mean snow depths, ice thickness, water depth, amount of pressure ridging, height and thickness of pieces of rough ice measured in the study plots. 55

Table 3.	Correlations between the various habitat features examined. Pearson correlation coefficients lie above the diagonal. Partial correlation coefficients lie below the diagonal. * denotes significance at $p < 0.05$.	56
Table 4.	Mean values of habitat features measured at the different types of subnivean structures of the ringed seal.	57
Table 5.	Mean total snow depths measured at seal structures in Barrow Strait and from other areas.	58
Table 6.	Mean habitat values for densities of seal holes grouped by frequency class. Standard errors are in brackets.	59
Table 7.	Correlations between density of seal holes (holes/km ²) and habitat variables for the 1986 data. Pearson correlation coefficients lie above the diagonal. Partial correlation coefficients lie below the diagonal.	60
Table 8.	Observed and expected frequencies of birth lairs and male structures. Plots surveyed before mid-April and after mid-May are excluded. * denotes significance at $p < 0.05$.	61
Table 9.	Correlations between density of birth lairs and undefined structures, and the habitat variables, snow depth and date of ice consolidation. Pearson correlation coefficients lie above the diagonal. Partial correlation coefficients lie below the diagonal.	62

SECTION III

Table 1.	Sex ratios of animals collected in Barrow Strait between March and June, 1984 to 1986.	89
Table 2.	Percent monthly changes in age composition of harvest. N is number of animals. Age is in years.	90

Table 3.	Chapman-Robson (Robson and Chapman 1961) and Heinke (1913) survivorship estimates to test representation of age classes in sample. * is significant at $p < 0.05$. n.s. = not significant.	91
Table 4.	Number of pregnant and lactating ringed seals shot in early spring.	92
Table 5.	Age specific ovulation rates for females collected in 1984, 1985 and 1986.	93
Table 6.	Age specific reproductive rates. The presence of a fetus or evidence of lactation was used to indicate pregnancy. Smoothed age specific reproductive rates were estimated from the regression for all years combined. Arc sine (pregnancy rate) = $0.0657 (\text{age})$, ($F=64.5$, $df=1,17$).	94
Table 7.	Morphometrics of neonates collected in the spring. All animals had silver jar pelage.	95
Table 8.	Estimated parameters and standard errors from von Bertalanffy growth curves calculated for three populations of ringed seals. B_0 is asymptotic length (cm), B_1 is growth rate (cm yr^{-1}), and B_2 is the age (years), when length is 0 if growth continued as described by the equation.	96
Table 9.	Regression equations to predict weights (g) of different body components from girth and length (cm) data.	97
Table 10.	Age, sex, weights of different body components and body fat composition of 31 seals.	98
Table 11.	Pearson correlation coefficients and probability levels, between percent body fat ($\text{g fat body wt.}^{-1}$) and indices of condition.	99
Table 12.	Mean condition of adults and juvenile seals collected in 1984, 1985, and 1986 using the index; sculp weight maximum girth ⁻² .	100

Table 13.

Mean reproductive rates of female ringed seals from different populations. Amundsen Gulf data excludes low years (Smith 1987). Average reproductive rates of ringed seals from different populations.

101

Table 14.

Asymptotic lengths of ringed seals from different populations.

102

LIST OF FIGURES

PAGE

SECTION I.

Figure 1. Location of study plots surveyed during March to May, 1984 to 1986. Plots 1 to 9 were surveyed in 1984 and 1985. The remaining plots were surveyed in 1986. The dotted line represents the extent of the fast ice edge in 1986. 22

Figure 2a. Relationship between probability of the dog detecting a seal hole and survey precision. Precision is represented by the coefficient of variation. 23

Figure 2b. Relationship between proportion of the population located during ground surveys and survey precision. Precision is represented by the coefficient of variation, 24

SECTION II

Figure 1. Location of study plots surveyed during March to May, 1984 to 1986. Plots 1 to 9 were surveyed in 1984 and 1985. The remaining plots were surveyed in 1986. The dotted line represents the extent of the fast ice edge in 1986. 63

Figure 2. General pattern of ice consolidation in Barrow Strait. Areas denoted by A consolidate first. Areas denoted by F consolidate last. 64

SECTION III

Figure 1. Map of study area showing locations of main hunting effort. 103

Figure 2. Age frequencies of seals collected
between March and June, 1984 to 1986 in
Barrow Strait.

104

Figure 3. Changes in body condition of ringed seals
in Barrow Strait between March and June.

105

ACKNOWLEDGEMENTS

This study could not have been completed without assistance from many individuals and groups.

I thank my supervisor, Dr. T.G. Smith, for the opportunities and support he has provided over the last few years enabling me to work in the north. I thank Hakgagiak and Memogana for sharing with me their knowledge of seals and winter travel. D.W. Doidge, M.C.S. Kingsley and H.E. Welch shared my interest in the north and marine mammals in general. Throughout this project they extended their hospitality, provided lively discussion and constructive criticism, all of which is greatly appreciated.

Much of the data collection for this study would not have been possible without the hard work of the survey dogs "Beau" and "Shuba". Unlike some equipment, they never broke down and after many kilometres of survey work their enthusiasm for finding "birds" never diminished.

B. Alikarialik, H. Cleator, S. Idlout, P. Manik, R. Memogana, and J. Nungaq helped with the winter surveys and in the collecting and processing of samples. G. Benoit, B. Hough and F. Hunt, Polar Continental Shelf Project, Resolute Bay, NWT, G. Horonowitsch, and G.A. Sleno, Arctic Biological Station, Ste. Anne de Bellevue Que. provided logistic support. I thank J.L. Atkinson and J.W. Hilton, Department of Nutrition, University of Guelph for allowing me to use their

laboratory facilities for the proximate analyses. Various sections of this thesis were reviewed by D. W. Doidge, W.G. Halina, M.C.S. Kingsley, I.A. McLaren and D. Roff. Their comments and criticisms are appreciated. I also thank G.A. Sleno for preparing the figures. the abstract.

Financial support was provided by Petro-Canada Ltd., Calgary Alta., the Polar Continental Shelf Project, Energy, Mines and Resources, Ottawa Ont., the Northern Oil and Gas Action Plan, the Arctic Biological Station, Ste. Anne de Bellevue, Que., a University Research grant from Imperial Oil to T.G. Smith and Northern Travel Fellowships, from the Centre for Northern Studies, McGill University, Montreal, Que.

Finally, I would like to thank W.G. Halina for her patience and continued support throughout this project.

PREFACE

The ringed seal (Phoca hispida) is the most abundant marine mammal found year round in northern waters (King 1983). It is an important resource for the people living in northern coastal regions (Maxwell 1979; Wenzel 1978; Malouf 1986), the primary food of the polar bear (Ursus maritimus) (Stirling and McEwen 1975; Stirling and Archibald 1977; Smith 1980; Gjertz and Lydersen 1986) and in some areas forms a major component in the diet of the Arctic fox (Alopex lagopus) (Smith 1976; Lydersen and Gjertz 1986). Because of their importance to the northern economy and the northern ecosystem, ringed seals have been the subject of considerable study.

Aerial surveys of seals during the spring haul-out period have provided minimum population estimates, and documented the species distribution in Canada (Smith 1973; 1975; Stirling et al. 1977; Smith et al. 1979; Finley et al. 1983; Kingsley 1984, 1985; Kingsley et al. 1985), Alaska (Burns and Harbo 1972; Lentfer 1972; Burns and Kelly 1982), Finland (Helle 1980), and the Soviet Union (Fedoseev 1971, 1975). Reproductive biology, growth and population dynamics have been studied extensively (McLaren 1958; Fedoseev 1964; 1975; Nazarenko 1965; Johnson et al. 1966; Smith 1973; 1987; Helle 1978, 1979, 1980). Feeding ecology has also been investigated

(Dunbar 1941; McLaren 1958; Johnson et al. 1966; Nazarenko 1967; Lowry et al. 1980; Gjertz and Lydersen 1986; Smith 1987). Parsons (1977) studied ringed seal energetics in captive animals and Taugbol (1982) has examined the thermal tolerances of neonates. Information is available on haematology, plasma constituents and physiological responses to stress (Geraci and Smith 1975; St. Aubin and Geraci 1977; Geraci et al. 1979; St. Aubin and Geraci 1986). Organochlorine and mercury levels have been examined in tissues from the Canadian Arctic (Addison and Smith 1974; Smith and Armstrong 1978; Addison et al. 1986) and recent work in Finland has suggested that high levels of PCB's found in the Baltic Sea might be responsible for lowered reproductive success in female ringed seals from that area (Helle 1978, 1980). The effects of oil immersion and the ingestion of crude oil on ringed seals have also been examined (Geraci and Smith 1976; Englehardt et al. 1977). Underwater vocalizations have been described (Stirling 1973) and their application to monitoring the distribution of ringed seals under the fast ice has been investigated (Stirling et al. 1983; Calvert and Stirling 1985).

During the winter, ringed seals maintain breathing holes in the ice and excavate haul-out lairs under the snow which are used for resting and as pupping sites (McLaren 1958). Descriptions of the different types of subnivean structures, their function, variation in relative abundance, and qualitative assessments of ringed seal habitat have been

published in Canada (Smith and Stirling 1975; 1978; Smith et al. 1978; Smith and Hammill 1980), Spitzbergen (Lydersen and Gjertz 1986) and in the Soviet Union (Lukin and Potelov 1978). A natural extension of this work is the need to quantify the habitat features chosen by ringed seals for building subnivean structures and to determine the association between these features and seal distribution. The present study was initiated in 1984 to examine this relationship.

As permitted by the Faculty of Graduate Studies this thesis includes the texts of two manuscripts, one to be submitted to the Canadian Journal of Fisheries and Aquatic Sciences and the second to the Canadian Journal of Zoology with Dr. I.G. Smith as co-author. I carried out the collection of data, analysis and writing of the manuscripts herein. The thesis consists of three sections. The first section describes the method used to measure seal abundance in the fast ice. The second section relates seal abundance to features of their fast ice habitat. The findings from both of these sections are new. The third section deals with reproductive rates, growth and condition of animals collected in Barrow Strait. Portions of this section will be combined with data from other areas before being published.

REFERENCES

- 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. PCB's have declined more than DDT-group residues in arctic ringed seals (Phoca hispida) between 1972 and 1981. *Environ. Sci. Technol.* 20: 253-256.
- 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: RU#232, 57 p. (unpublished report).
- Calvert, W. and I. Stirling. 1985. Winter distribution of ringed seals (Phoca hispida) in the Barrow Strait area, Northwest Territories, determined by underwater vocalizations. *Can. J. Fish. Aquat. Sci.* 42: 1238-1243.
- Dunbar, M. 1941. On the food of seals in the Canadian eastern arctic. *Canadian J. Research, D.* 19: 150-155.
- 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.
- Fedoseev, G.A. 1964. On the embryonic and postembryonic growth and sexual maturity of Okhotsk ringed seal. *Zool. Zh.* 43: 1228-1235. (Trans. from Russian. *Can. Trans. Fish Aquat. Sci.* No. 5277: 14 p. 1986).
- 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. 199: 23 p., 1966).
- Fedoseev, G.A. 1971. The distribution and numbers of seals on whelping and moulting patches in the sea of Ochotsk. In K.K. Chapskii and E.S. Mil'chenko (ed.) *Atlanticheskii Nauchno- Issledovatel'skii Institut Rybnogo Khozyaistva i Okeanografii* 39: 87-99. (Trans. from Russian by Fish. and Mar. Serv. Transl. Ser. No. 3185: 135-158. 1974).

Fedoseev, G.A. 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. Reun. Cons. Int. Explor. Mer. 169: 156-160.

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.

Frost, K.J. and L.F. Lowry. 1981. Ringed, Baikal and Caspian seals-Phoca hispida, Phoca sibirica and Phoca caspica. p. 29-53. In S.H. Ridgway and R.J. Harrison (ed.) Handbook of marine mammals. Vol. 2. Academic Press. Toronto, Ont. 359 p.

Geraci, J.R., D. J. St. Aubin and T.G. Smith. 1979.. Influence of age, condition, sampling time and method on plasma chemical constituents in free-ranging seals. J. Fish. Res. Board Can. 36: 1278-1282.

Geraci, J.R. and T.G. Smith. 1975. Functional haematology of ringed seals (Phoca hispida) in the Canadian arctic. J. Fish. Res. Board Can. 32: 2559-2564.

Geraci, J.R. and T.G. Smith. 1976. Direct and indirect effects of oil on ringed seals (Phoca hispida) of the Beaufort Sea. J. Fish. Res. Board Can. 33: 1976-1984.

Gjertzt, I. and C. Lydersen. 1986. Polar bear predation on ringed seals in the fast-ice of Hornsund, Svalbard. Polar Research 4: 65-68.

Gjertzt, I. and C. Lydersen. 1986. The ringed seal (Phoca hispida) spring diet in northwestern Spitsbergen, Svalbard. Polar Research 4: 53-56.

Helle, E. 1978. 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.

Helle, E. 1979. Growth and size of the ringed seal, Phoca (Pusa) hispida Schreber, in the Bothnian Bay, Baltic. 1979. Sonderdruck aus Z.f. Saugetierkunde Bd. 44: 208-220.

- Helle, E. 1980. Lowered reproductive capacity in female ringed seals (Phoca hispida) in the Bothnian Bay, northern Baltic Sea, with special reference to uterine occlusions. Ann. Zool. Fennica 17:147-158.
- 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 Thompson region, Alaska. U.S. Atom. Energy Comm., Div. Tech. Inf. Ext., Oak Ridge, TN. 1250 p.
- King, J.E. 1983. Seals of the World. 2nd edition. Oxford University Press. Oxford, 240 p.
- Kingsley, M.C.S. 1984. The abundance of ringed seals in the Beaufort Sea and Amundsen Gulf, 1983. Can. Manuscr. Rep. Fish. Aquat. Sci. 1778 : iv + 8p.
- Kingsley, M.C.S. 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.
- Kingsley, M.C.S., I. Stirling and W. Calvert. 1985. The distribution and abundance of seals in the High Arctic, 1980-82. Can. J. Fish. Aquat. Sci. 42: 1189-1210.
- Lentfer, J.W. 1972. Alaska polar bear research and management. Proc. of the 3rd Working Meeting of the Polar Bear Specialist Group; Survival Service Commission of IUCN. Publ. by N.Y. Zool. Soc. and Conserv. Found., Suppl. No. 35.
- 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. 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. 1986. Studies of the ringed seal (Phoca hispida) in its breeding habitat in Kongsfjorden, Svalbard. Polar Research 4: 57-63.
- Malouf, A. 1986. Seals and sealing in Canada: Report of the Royal Commission. Vol. 2. Minister of Supply and Services Canada. Ottawa, Ont. 622 p.
- Mansfield, A.W. 1967. Seals of arctic and eastern Canada. Bull. Fish. Res. Board Can. 137: 35 p.

Maxwell, M.S. 1979. The Lake Harbour region: Ecological equilibrium in sea coast adaptations. Nat. Museum of Man. Mercury Ser. 88: 76-88.

McLaren, I.A. 1958. The biology of the ringed seal (Phoca hispida) in the eastern Canadian Arctic. Bull. Fish. Res. Board Can. 118: 97 p.

McLaren, I.A. 1963. Population dynamics and exploitation of seals in the eastern Canadian Arctic. In E.D. LeCren and M.W. Holdgate (ed) The exploitation of natural animal populations. John Wiley and Sons, New York.

Nazarenko, Y.I. 1965. Contributions to the study of the reproduction of the ringed seal, Phoca hispida, of the Choska Inlet. Morskoe Mlekop. Akad. Nauk SSR, P. 171-75 (Transl. from Russian by Fish. Res. Board Can. Transl. Ser. No. 1461: 10 p., 1970).

Nazarenko, Y.I. 1967. Feeding of the ringed seal of the European north of the USSR. Tr. Polyarn. Nauchno-Issled. Proektn. Inst. Morsk. Rybn. Khoz. Okeanogr. 21: 81-85. (Transl. from Russian. Can. Transl Fish. Aquat. Sci. No. 5166: 9 p., 1985).

Parsons, J.L. 1977. Metabolic studies on ringed seals Phoca hispida. Unpublished M.Sc. thesis, University of Guelph, Guelph, Ont. 82 p.

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. and J.R.Geraci. 1986. Adrenocortical function in pinniped hyponatremia. Marine Mammal Science 2: 243-250.

Smith, T.G. 1973. Population dynamics of the ringed seal in the Canadian eastern Arctic. Bull. Fish. Res. Bd. Canada. 181. 55 p.

Smith, T.G. 1975. Ringed seals in James Bay and Hudson Bay: Population estimates and catch statistics. Arctic 28: 170-182.

Smith, T.G. 1976. Predation of ringed seal pups (Phoca hispida) by the arctic fox (Alopex lagopus). Can. J. Zool. 54: 1610-1616.

- Smith, T.G. 1980. Polar bear predation of ringed and bearded seals in the land-fast sea ice habitat. *Can. J. Zool.* 58: 2201-2209.
- Smith, T.G. 1987. The ringed seal, Phoca hispida, of the Canadian western arctic. *Can. Bull. Fish. Aquat. Sci.* 216: 81 p.
- Smith, T.G. and F.A.J. Armstrong. 1978. Mercury and selenium in ringed and bearded seal tissues from Arctic Canada. *Arctic* 31: 175-184.
- Smith, T.G. and M.O. Hammill. 1980. A survey of the breeding habitat of ringed seals and a study of their behaviour during the spring hauling-out period on south-eastern Baffin Island. *Can. Ms. Rep. Fish. Aquat. Sci.* 1561: 23 p.
- Smith, T.G. and M.O. Hammill. 1981. Ecology of the ringed seal, Phoca hispida, in its fast ice breeding habitat. *Can. J. Zool.* 59: 966-981.
- Smith, T.G., K. Hay, D. Taylor, and R. Greendale. 1978. Ringed seal breeding habitat in Viscount Melville Sound, Barrow Strait and Peel Sound. ESCOM Report No. AI-22. Department of Indian and Northern Affairs, Ottawa, Ont. K1A 0H4. 85p.
- Smith, T.G., G.A. Sleno and D. Taylor. 1979. An aerial survey of the marine mammals in the region north of Cornwallis Island, N.W.T. *Fish. and Mar. Serv. Tech. Rep.* 837: 14 p.
- Smith, T.G. and I. Stirling. 1975. The breeding habitat of the ringed seal (Phoca hispida). The birth lair and associated structures. *Can. J. Zool.* 53: 1297-1305.
- Smith, T.G. and I. Stirling. 1978. Variation in the density of ringed seal (Phoca hispida) birth lairs in the Amundsen Gulf, Northwest Territories. *Can. J. Zool.* 56: 1066-1070.
- Stirling, I. 1977. Vocalization in the ringed seal (Phoca hispida). *J. Fish. Res. Board Can.* 30: 1592-1594.
- Stirling, I. 1977. Adaptations of Weddell and ringed seals to exploit the polar fast-ice habitat in the absence or presence of surface predators. In G.A. Llano (ed.) *Adaptations within Antarctic ecosystems. Third Symp. Antarctic Biol.* Smithsonian Institute, Washington, D.C.
- Stirling, I. and W.R. Archibald. 1977. Aspects of polar bear predation. *J. Fish. Res. Bd. Can.* 34: 1126-1129.

Stirling, I., W.R. Archibald and D. DeMaster. 1977. Distribution and abundance of seals in the eastern Beaufort Sea. J. Fish. Res. Board Can. 34:976-988.

Stirling, I., W. Calvert and H. Cleator. 1983. Underwater vocalizations as a tool for studying the distribution and relative abundance of wintering pinnipeds in the High Arctic. Arctic 36: 262-274.

Stirling, I., H. Cleator and T.G. Smith. 1981. Marine Mammals. In: Stirling, I., and H. Cleator. (eds.). Polynyas in the Canadian Arctic. Ottawa: Can. Wildl. Serv. Occas. Pap. 45: 45-48.

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.

Taugbøl, G. 1982. Ringed seal thermoregulation, energy balance and development in early life, a study on Pusa hispida in Kongsfj., Svalbard. Thesis, Zoofysiologisk Institutt, Univ. of Oslo, Norway. 102p. (Transl. Fish. and Aquat. Sci. No. 5090: 109 p., 1984)

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

THESIS OFFICE STATEMENT

The Candidate has the option, subject to the approval of the Department, of including as part of the thesis the text of an original paper, or papers, suitable for submission to learned journals for publication. In this case the thesis must still conform to all other requirements explained in this document, and additional material (e.g. experimental data, details of equipment and experimental design) may need to be provided. In any case abstract, full introduction and conclusion must be included, and where more than one manuscript appears, connecting texts and common abstract introduction and conclusion are required. A mere collection of manuscripts is not acceptable; nor can reprints of published papers be accepted.

While the inclusion of manuscripts co-authored by the Candidate and others is not prohibited for a test period, the Candidate is warned to make an explicit statement on who contributed to such work and to what extent, and supervisors and others will have to bear witness to the accuracy of such claims before the Oral Committee. It should also be noted that the task of the External Examiner is much more difficult in such cases.

SECTION I

Removal Sampling Used to Estimate Densities of Ringed Seals
in the Fast-Ice of Barrow Strait, Northwest Territories

INTRODUCTION

Attempts to census ringed seal (Phoca hispida) populations in the fast-ice are hampered by the inaccessibility of northern regions and by the ringed seal's use of subnivean lairs (McLaren 1958). One approach has been to fly aerial surveys after the lairs have melted and count the number of seals hauled out on the ice (Kingsley 1984, 1986; Kingsley et al. 1985). An advantage to aerial surveys is that they cover large areas in a relatively short time. However, because not all seals in the population are hauled out on the ice at the same time, counts from aerial surveys underestimate population size. A further disadvantage is that the proportion of the seal population hauled out on the ice may vary daily from 20% to 80% as a result of weather, seasonal or diurnal factors (Smith and Hammill 1981). Therefore, unless transects are flown under identical conditions; major changes in population size may reflect differences in the proportion of hauled-out seals, and not real changes in population size.

An alternative to aerial surveys has been to conduct ground surveys using seal holes as an index of seal abundance. In these surveys, conducted during the March to May whelping period, trained dogs have been used to locate the subnivean holes of the ringed seal (Smith and Stirling 1975, 1978). Seal abundance has been expressed as the number of minutes spent

searching per seal hole located. This method is simple and easily applied. It provides additional information on pup production and mortality due to predation (Smith 1976; Smith et al. 1978; Smith 1987), but it only provides an index of hole abundance, which is still only an index of seal abundance; it assumes that the hole to seal ratio is constant and it also assumes that the ability of the dog to find seal holes does not change under variable survey conditions.

Although the dog survey method has been used extensively as part of ongoing studies into the fast-ice ecology of the ringed seal, these assumptions have never been examined. In this paper, I investigate the potential shortcomings of the dog survey technique. I also examine the feasibility of using a catch per unit of effort model called the removal method (Moran 1951; Zippin 1956, 1958; Seber 1982) combined with hole to seal ratios to estimate ringed seal density in Barrow Strait.

MATERIALS AND METHODS

The initial study site encompassed a 3100 km² area of Barrow Strait lying between Lowther and Griffith Islands in the north and Russell and Somerset Islands in the south (Fig. 1.). Normally this area is covered by first year fast ice which begins to form in November and remains in place until breakup in July. There is however, considerable year to year

variation in the amount and pattern of ice formation in the area (Lindsay 1975, 1977). In 1984, fast ice extended from the western edge of the study area with its eastern boundary against unconsolidated pack ice located off Bylot Island in Lancaster Sound. In 1985, the fast ice boundary formed much further west, along a line joining Devon Island to Prince Leopold Island. In 1986, our study area did not freeze over during the winter. This obliged us to extend the study area northwards to McDougall Sound and south into Peel Sound resulting in a new study area of 3400 km² excluding that portion of Barrow Strait that remained ice-free during the winter (Fig.1).

Seal hole densities were determined by searching either 2.25 or 4.0 km² plots (N=32) with trained dogs (Smith and Stirling 1975) during March-May, 1984-1986. Plots were selected randomly prior to the 1984 field season. The same sites searched in 1984 and 1985 were relocated on the sea ice using a satellite navigation system (Magnavox Model MX4102, Torrance, California USA), which has a precision of ± 100 m. The same sites could not be searched in 1986 because of the absence of ice cover. Plots that year, were selected to provide a range of water depths, ice topography and distances from the open water in order to test the effects of these variables on the density of seal holes (Fig. 1).

In 1984, two trained labrador retrievers, a 25 kg female and a 35 kg male, were used in the surveys. Each dog searched

the same plot separately for 40 to 70 min periods. In 1985 and 1986 only the female was used. This dog ran twice daily for 30 to 40 minutes or until the snowmobile following the dog had travelled a distance of 6-10 km. Search effort measured by time spent searching or distance covered, was allowed to vary between plots, but was kept constant within plots. In order to provide the dog with the greatest exposure to all holes, it was run perpendicular to the wind direction, beginning from the downwind side of the plot. All seal structures located by the dog were marked with numbered stakes.

Two additional plots, situated near plot 10, were searched by the dog in June 1985 when most of the snow had melted and seal holes were exposed at the surface. After these searches had been completed, the plots were visually searched by observers on snowmobiles, who scanned 25m wide transects until the whole plot had been covered.

Temperature and windspeed were recorded at the beginning of each search. Snow depths were measured to the nearest cm at 16, 100 and 54 points, spaced equally throughout the plot starting along the east side from the southeast corner in 1984, 1985 and 1986 respectively. Each point measurement represented an average of six snow depths taken at three metre intervals using a steel probe. Ice topography in each plot was assessed by aerial photographs taken from a helicopter at an altitude of 300-350 m with a 6.0 x 6.0 cm format camera. Photographs were then covered by a grid-square overlay.

consisting of 121 grids per frame from which the frequency occurrence of pressure ridges and rough ice was recorded.

Hole:seal ratios were determined in March and April by killing a seal at a breathing hole. I then counted the number of holes in the vicinity that were subsequently found covered by a thin layer of ice indicating that they were no longer being used.

Data Analysis

Data were analysed using the maximum likelihood removal model proposed by Moran (1951) and discussed in detail by Zippin (1956, 1958). The removal model was originally devised for small mammal trapping studies where the animal was captured and permanently removed from the population. In my application of the model the number of seal holes located by the dog constituted a catch. Each time the dog located a new hole it was marked with a numbered stake and treated as a removal from the population. If the population is closed, the probability of detecting a hole in a population is equal and independent of other detections, the probability of detection remains constant throughout the experiment and search effort is constant, then the total number of seal holes in the study plot (N) can be estimated from;

$$N=Y \cdot (1-q^k)^{-1} \quad (1)$$

where Y is the total number of holes located, q is the probability of a hole not being detected, and k is the number of search sessions. The probability of a hole not being detected (q) is determined by solving through iteration the equation;

$$q \cdot p^{-1} - (k \cdot q^k) (1 - q^k) = \sum_{i=1}^k (i-1) \cdot y_i \cdot Y^{-1} \quad (2)$$

where $p = (1-q)$ is the probability that a hole will be located and y_i is the number of holes located for the first time during the i th search, $i = 1, 2, 3 \dots k$.

The maximum likelihood function assumes that a major proportion of the population of seal holes is located and removed during each survey of the plot (Otis et al. 1978). If subsequent surveys of a plot do not show a decline in numbers of holes located for each unit of survey effort then the left and right sides of equation 2 do not converge and the experiment fails. Conditions for the experiment to fail are given by;

$$\sum_{i=1}^k (k+1-2 \cdot i) \cdot y_i < 0 \quad (\text{Seber 1982}) \quad (3)$$

The variance of N is estimated by ;

$$V(N) = N \cdot (1 - q^k) \cdot [N \cdot (-F') (1 - q^k) - (k \cdot p)^2]^{-1} \quad (4)$$

where

(5)

$$F' = 1 \cdot [N \cdot (1 - q^k) (q^k - (1 - q^{2k})) (2 \cdot N \cdot q^{2k} + (1 - q^{3k})) (6 \cdot N^2 \cdot q^{3k})]^{-1}$$

The 95% confidence limits for N are estimated by $\pm 1.96 (V(N))^{0.5}$.

The assumption of equal probability of capture between search sessions was tested by;

$$\chi^2 = \sum_{i=1}^k (y_i - N \cdot p \cdot q^{i-1})^2 / (N \cdot p \cdot q^{i-1} - 1) \quad (\text{Zippin 1956}) \quad (6)$$

with k-2 degrees of freedom.

RESULTS

Detection of a seal hole was indicated by a sudden turn upwind by the dog. Detection distances normally ranged from 10 to 100 m, however one hole was detected from a distance of 1.5 km.

In June 1985, a combination of very low snow cover and a rapid melt with very little water accumulation on the ice, provided an opportunity to ground-truth the removal model at two locations. In the two plots, 32 and 17 holes were located by the dog. The removal model estimated, with 95% confidence limits in brackets, 33 (29-38) and 17 (17-17) holes, while a

total of 34 and 9 holes respectively were located by the visual ground searches from snowmobiles. In the second plot a large crack opened up in the plot after the dog surveys had been completed, but before the plot could be ground-truthed. Since some of the holes located by the dog were situated on this crack they would not have been included in the ground search.

The ground truthing allowed us to conclude that the removal model can be used to estimate the number of seal holes within an area. Applying the model to the results from the other plots which were searched by dogs gave estimates for the number of seal holes present in 31 of 32 plots. Estimates were not obtained for one plot, (plot 9 in 1984), because the search results did not satisfy the failure criterion given by equation (3). When this plot was surveyed the temperatures were close to 0°C and the snow was very deep making it difficult for both dogs, but especially for the smaller female, to run across the soft snow. This could have resulted in a variable search effort and violated the assumption of constant probability of hole detection between searches. The assumption of equal probability of capture was tested in the remaining plots using a chi-square goodness of fit test. None of the chi-square values were significant ($p > 0.05$).

A major difficulty in population surveys is to obtain estimates of sufficient precision to detect differences in population size. Survey precision expressed as the coefficient

of variation of the population estimate (N), improved from 1984 to 1986 (Table 1). Precision was affected by both the probability of a hole being detected (p) and by the proportion of the estimated population of holes located during the searches (Fig.2a,b). The probability of detecting a hole ranged from 0.21 to 1.0 ($\bar{x}=0.45$ SE=0.03 N=33). This means that during each search of a plot the dog missed 0% to 80% of the structures it passed. Significant improvements in the probability of detecting a seal hole were observed when the search area was reduced from 4 km² to 2.25 km² (F=4.4, df=1,32, p=0.04) and when only one dog was used during the survey of a plot (F=7.6, df=1,32; p=0.009)(Table 1). The proportion of the plot covered by pressure ridges had a negative effect on probability of hole detection (p) as shown by the regression: $p=0.595-0.010 (\% \text{ ridge})$, ($R^2=0.34$, F=15.4, df=1,30, p=0.0005). Temperature, windspeed, search time, the amount of rest for the dog between searches and snow depth did not have any significant effect on p. The mean time required for the dogs to run a one km distance averaged 5.1 min (SE=0.2, N=7) for the two dogs combined in 1984, and for a single dog, 4.5 min (SE=0.1, N=8) in 1985 and 6.4 min (SE=0.1, N=14) in 1986. Differences were significant between years (F=51.8, df=2,26; p=0.0001).

Hole densities were highest in 1986 with an average of 7.94 holes/km² (SE=0.98, N=14), followed by 1984 with a mean density of 5.89 holes/km² (SE=0.95 N=9). The 1984 estimate

includes the number of holes found by the dog in plot 9, rather than the estimated number of holes located because the removal model did not work for this plot. This likely results in an underestimate of the 1984 hole density. The 1985 density estimates were the lowest at an average of 5.15 holes/km² (SE=0.63, N=11).

Hole to seal ratios could only be determined in March and April when cold temperatures insured that a hole would freeze if it had not been attended by a seal within the previous 12 hrs. Hole to seal ratios were obtained from holes that froze after we killed five female and three male ringed seals. Two of the females were immature; three were pregnant or lactating. All males were adults. The adult seals maintained an average of 3.5 (SE=0.22, N=6) holes per seal, the immature animals each maintained 3.0 holes per seal. Since the number of holes maintained by immature seals lay within the 95% confidence interval for adults, the results from the two groups were pooled to obtain an average ratio of 3.38 (SE=0.18, N=8) holes per seal.

Seal densities were calculated by dividing hole densities by 3.38. Densities ranged from a high of 2.35 seals/km² in 1986, followed by 1.74 seals/km² in 1984 and 1.53 seals/km² in 1985 (Table 3).

DISCUSSION

The differences in survey precision observed between plots and the year to year changes in time required by the dogs to travel a one km distance show that the dog's performance does vary with survey conditions. Therefore changes in time spent searching per seal hole located may only reflect changes in the dog's ability to detect seal holes, not changes in seal abundance. These difficulties may be overcome by combining the dog survey technique with removal sampling to obtain estimates of the total number of seal holes in a plot.

The removal method assumes that the population under study is closed. However, the tests for closure are often based on the assumption that the probability of capture remains constant throughout the survey. Although seal holes do not move, the closure assumption may be violated if seal holes are abandoned due to continued disturbance from our survey activities or new holes in the fast ice might be created. To avoid possible violations of this assumption, multiple searches of each plot were completed in as short a time as possible (Otis et al. 1978), usually within two to three days whenever weather permitted.

The removal method also assumes that the probability of capture remains constant. I tested for constant probability of capture using a chi-square goodness of fit test (Zippin 1956),

but these tests appear to be very insensitive to changes in capture probabilities (Roff 1973), especially at the low population sizes observed in my plots (< 40 holes). During the surveys, the dog showed much more interest in birth lairs than in structures maintained by male seals. Variable detection rates likely result in the initial surveys locating more seal holes than expected and later surveys locating fewer holes than expected. Population estimates obtained from the removal method under these conditions underestimate the total number of seal holes in the plot. However, I do not believe that variable capture rates will result in major underestimates of population size provided the conditions required by equation 3 given in the methods are satisfied, and reasonable coefficients of variation (precision), of 30% or lower are obtained.

Survey precision was affected by the probability of a hole being found and the proportion of the estimated number of holes in the plot detected during the searches (Zippin 1956). Precision levels of 30% or better were not obtained unless the probability of detecting a hole exceeded 0.35 and at least 80% of the seal structures had been located. Increased pressure ridging interfered with the dog's ability to locate seal holes. Pressure ridges either made travel over the ice more difficult for the dog, or increased air turbulence near the ridge interfered with the dog's ability to home in on a scent. The use of one dog per plot and searching a plot of reduced

size contributed significantly to improvements in the probability of detecting a seal hole. Plot size should be selected to contain at least one seal in a majority of plots (Greig-Smith 1964), which suggests a minimum size of 0.6 km^2 for the areas surveyed in this study. Use of the removal method did not result in any reduction in survey effort. In order to locate 80% or more of the population a minimum of four searches were required. At two searches per day this involves 2.6 hrs or 32 km of searching per plot by the dog. I examined the possibility of using mark-recapture and mark-removal estimators which are more efficient than removal techniques (Seber 1982; Skalski and Robson 1982; Skalski et al. 1984), but the assumption of constant probability of detection of marked and unmarked holes was not satisfied.

The average hole to seal ratio of 3.38 that I obtained is lower than the ratio of 4.8 holes per seal reported by Smith and Hammill (1981) for seals occupying breeding habitat in a south-east Baffin Island fjord. However, if their ratio is corrected to account for a maximum of 80% of the estimated population which they saw on the ice at one time; then their ratio is reduced to 3.8 holes per seal, similar to the present estimate. These ratios fall within the range of two to four holes per seal reported from radio-tagging and behaviour studies indicating that seal holes are a valid, but not yet clearly defined index of seal abundance (Table 2).

A comparison of seal densities obtained using the dog

search and removal method, with densities obtained from aerial surveys of Barrow Strait, indicate that ringed seal populations may be two to three times higher than previously thought (Table 3). These comparisons do not include estimates for the number of pups produced in the study area during the three years of surveys with the dog. Assuming one birth lair per pup, then the densities obtained from the dog surveys in 1984 and 1986 could be increased by up to 40% and the estimates obtained from 1985 by up to 20% (Hamill Section II). These estimates may still underestimate population size because juvenile animals are often excluded from the areas covered by the breeding habitat surveys, towards the ice edge and open water areas (McLaren 1958; Smith 1973, 1987).

The use of trained dogs is presently the only method available for examining ringed seal distribution during the winter and spring months. Capital costs are low, and the method provides otherwise unavailable information on population composition, production and predation rates of seals in their breeding habitat (Smith 1976; Smith and Stirling 1975, 1978). When combined with the removal model, survey quality can be assessed and changes in population size can be detected. Application of the model permits between study comparisons of ringed seal density irrespective of the dog used and conditions encountered. However, this method is labour intensive and limited in the amount of area that can be surveyed. Sample sizes could be increased, possibly doubled by

a sharp reduction in plot size, but the method is still not suitable for surveying large areas. Perhaps the most effective strategy for monitoring ringed seal populations is to combine aerial surveys with the dog search/removal method, using results from the ground surveys to correct aerial survey estimates for seals not hauled-out on the ice.

REFERENCES

- Finley, K. 1979. Haul-out behaviour and densities of ringed seals (Phoca hispida) in the Barrow Strait area, NWT. Can. J. Zool. 57: 1985-1997.
- Greig-Smith, P. 1964. Quantitative plant ecology. 2nd ed. Butterworth & Co. Ltd. London. 256 p.
- Kelly, B. 1985. Dependence by ringed seals on subnivean lairs. Abstracts. Sixth Biennial Conference on the Biology of Marine Mammals. Nov. 22-26, 1985. Vancouver, B.C.
- Kingsley, M.C.S., 1984. The abundance of ringed seals in the Beaufort Sea and Amundsen Gulf, 1983. Can. Manuscr. Rep. Fish. Aquat. Sci. 1778: iv + 8p.
- Kingsley, M.C. S. 1986. Distribution and abundance of seals in the Beaufort Sea, Amundsen Gulf, and Prince Albert Sound, 1984. Environmental Studies Revolving Funds Report, No. 025, Ottawa. 16 p.
- Kingsley, M.C.S., I. Stirling and W. Calvert. 1985. The distribution and abundance of seals in the Canadian high Arctic. Can. J. Fish. Aquat. Sci. 42: 1189-1210.
- Lindsay, D.G. 1975. Sea ice atlas of Arctic Canada, 1961-1968. Department of Energy, Mines and Resources, Ottawa, Ontario. 213 p.
- Lindsay, D.G. 1977. Sea ice atlas of Arctic Canada, 1969-1974. Department of Energy, Mines and Resources, Ottawa, Ontario. 219 p.
- McLaren, I.A. 1958. The biology of the ringed seal (Phoca hispida Schreber) in the eastern Canadian Arctic. Fish. Res. Board Can. Bull. 118: 97 p.
- Moran, P.A.P. 1951. A mathematical theory of animal trapping. Biometrika 38: 307-311.
- Otis, D.L., K.P. Burnham, G.C. White and D.R. Anderson. 1978. Statistical inference from capture data on closed animal populations. Wildl. Mon. No. 62. 135 p.
- Rooff, D.A. 1973. An examination of some statistical tests used in the analysis of mark-recapture data. Oecologia (Berl.) 12: 35-54.

- Seber, G.A.F. 1982. The estimation of animal abundance. 2nd ed. Macmillan Publ. Co. New York, NY. 654 p.
- Skalski, J.R., and D.S. Robson. 1982. A mark and removal procedure for estimating population abundance. J. Wildl. Manage. 46: 741-751.
- Skalski, J.R., M.A. Simmons and D. S. Robson. 1984. The use of removal sampling in comparative censuses. Ecology 65: 1006-1015.
- Smith, T.G. 1976. Predation of ringed seal pups (Phoca hispida) by the arctic fox (Alopex lagopus). Can. J. Zool. 54: 1610-1616.
- Smith, T.G. and M.O. Hammill. 1981. Ecology of the ringed seal, Phoca hispida, in its fast ice breeding habitat. Can. J. Zool. 59: 966-981.
- Smith, T.G., K. Hay, D. Taylor and R. Greendale. 1978. Ringed seal breeding habitat in Viscount Melville Sound, Barrow Strait and Peel Sound. INA Publ. No. QS-8160-022-EE-A1, ESCOM Rep. No. AI-22. 85 p.
- Smith, T.G. and I. Stirling. 1975. The breeding habitat of the ringed seal. The birth lair and associated structures. Can. J. Zool. 53: 1297-1305.
- Smith, T.G. and I. Stirling. 1978. Variation in the density of ringed seal (Phoca hispida) birth lairs in the Amundsen Gulf, Northwest Territories. Can. J. Zool. 56: 1066-1071.
- Zippin, C. 1956. An evaluation of the removal method of estimating animal populations. Biometrics 12: 163-169.
- Zippin, C. 1958. The removal method of population estimation. J. Wildl. Manage. 22: 82-90.

Table 1. Mean number of searches per plot, precision of population estimates, proportion of the population located, number of dogs used in the surveys and average area of study plots during 1984 to 1986.

Year	Mean Number Searches Per Plot			Precision of Estimates (%) Per Plot		Proportion of Estimated Population Located (%)		Probability of Hole Detection Per Plot		Number of Dogs	Area Searched (4km ²)	Total Search Effort (hrs)
	#Plots	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE			
1984	8	4	0.1	48.0	15.7	81.7	4.8	.329	.043	2	4	30
1985	11	5	0.3	20.1	6.0	92.4	2.0	.454	.068	1	4	36
1986	14	4	0.3	15.6	5.7	94.5	1.8	.523	.045	1	2.25	54

Table 2. Hole to seal ratios calculated from this study, and values reported in the literature. The value from Smith and Hammill (1981) has been multiplied by 0.8 to correct for the proportion of the population hauled out on the ice.

Hole to Seal Ratio	Method	Source
3.38:1	Frozen holes	Present study
3.8:1	Behaviour	Smith & Hammill 1981
0.3 - 2.6:1	Behaviour	Finley 1979
4:1	Behaviour	Finley 1979
2:1	Radio tagging	Burns & Kelly 1982 ¹
2-4:1	Radio tagging	Kelly 1985

¹ Burns, J.J. and B. Kelly. 1982. Studies of ringed seals in the Alaskan Beaufort Sea during winter: Impacts of Seismic Exploration. Unpublished Rep. RU # 232 to Outer Continental Shelf Environmental Assessment Programs, Juneau, Alaska, 57 p.

Table 3. Comparisons between seal densities (seals/km²) obtained from dog surveys and estimates obtained from aerial surveys of hauled out animals. Standard errors are in parentheses. Seal densities from the present study were obtained by dividing the density of seal holes by 3.38.

This Study		Aerial Surveys	
Density	Year	Density	Source
2.35 (0.29)	1986	1.17 (0.05)	Kingsley unpublished data, ¹ Barrow Strait transects lying between 95°W and 98°W
1.53 (0.19)	1985	1.07 (0.05)	
1.74 (0.28)	1984	1.07 (0.05)	
	1982	0.90 (0.08)	Kingsley et al. 1985. Stratum 6
	1981	1.16 (0.21)	
	1980	0.85 (0.09)	
	1975	0.69 .	Smith et al. 1978
	1975	0.82 .	Finley (1976) ² average from Smith et al. 1978

¹ M.C.S. Kingsley, Freshwater Institute, Dept. Fisheries and Oceans, Winnipeg, Manitoba, R3T 2N6.

² Finley, K. 1976. Studies of the status of marine mammals in the central District of Franklin, N.W.T. June-August, 1975. Unpubl. rep. prep. by LGL Ltd. Polar Gas Project, Toronto, Ont. 183 p.

Figure 1. Location of study plots surveyed during March to May, 1984 to 1986. Plots 1 to 9 were surveyed in 1984 and 1985. The remaining plots were surveyed in 1986. The dotted line represents the extent of the fast ice edge in 1986.

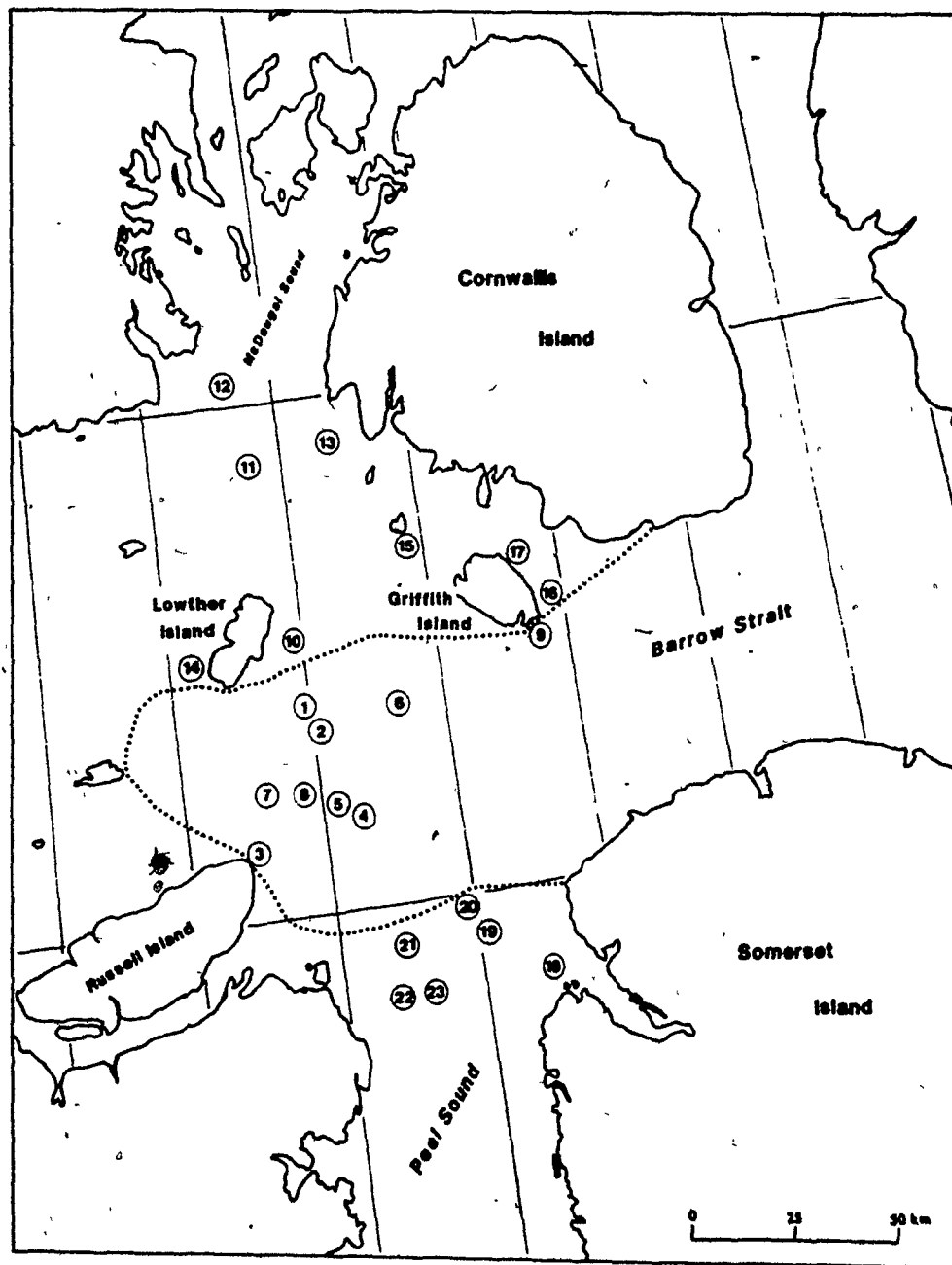


Figure 2a. Relationship between probability of the dog detecting a seal hole and survey precision. Precision is represented by the coefficient of variation.

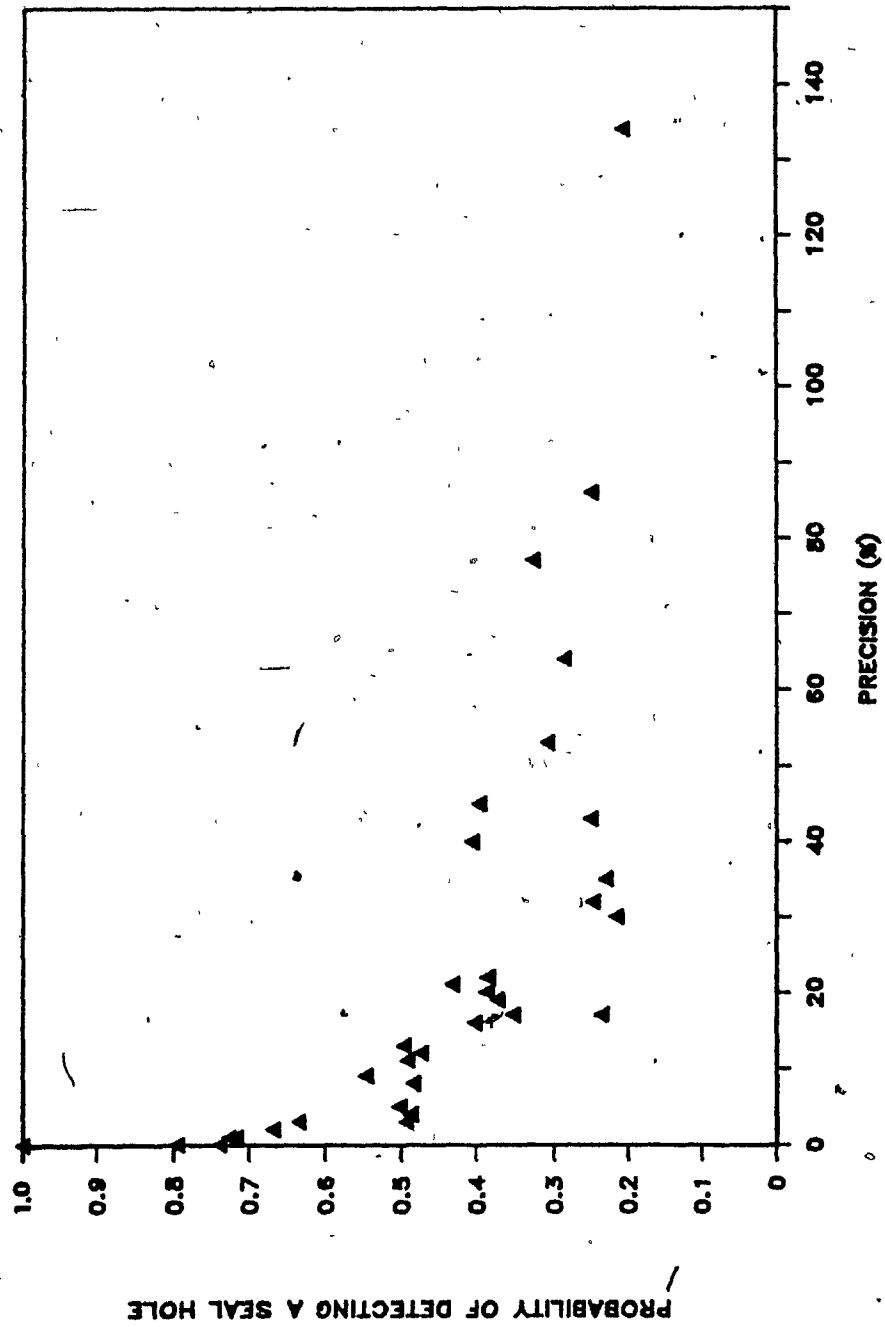
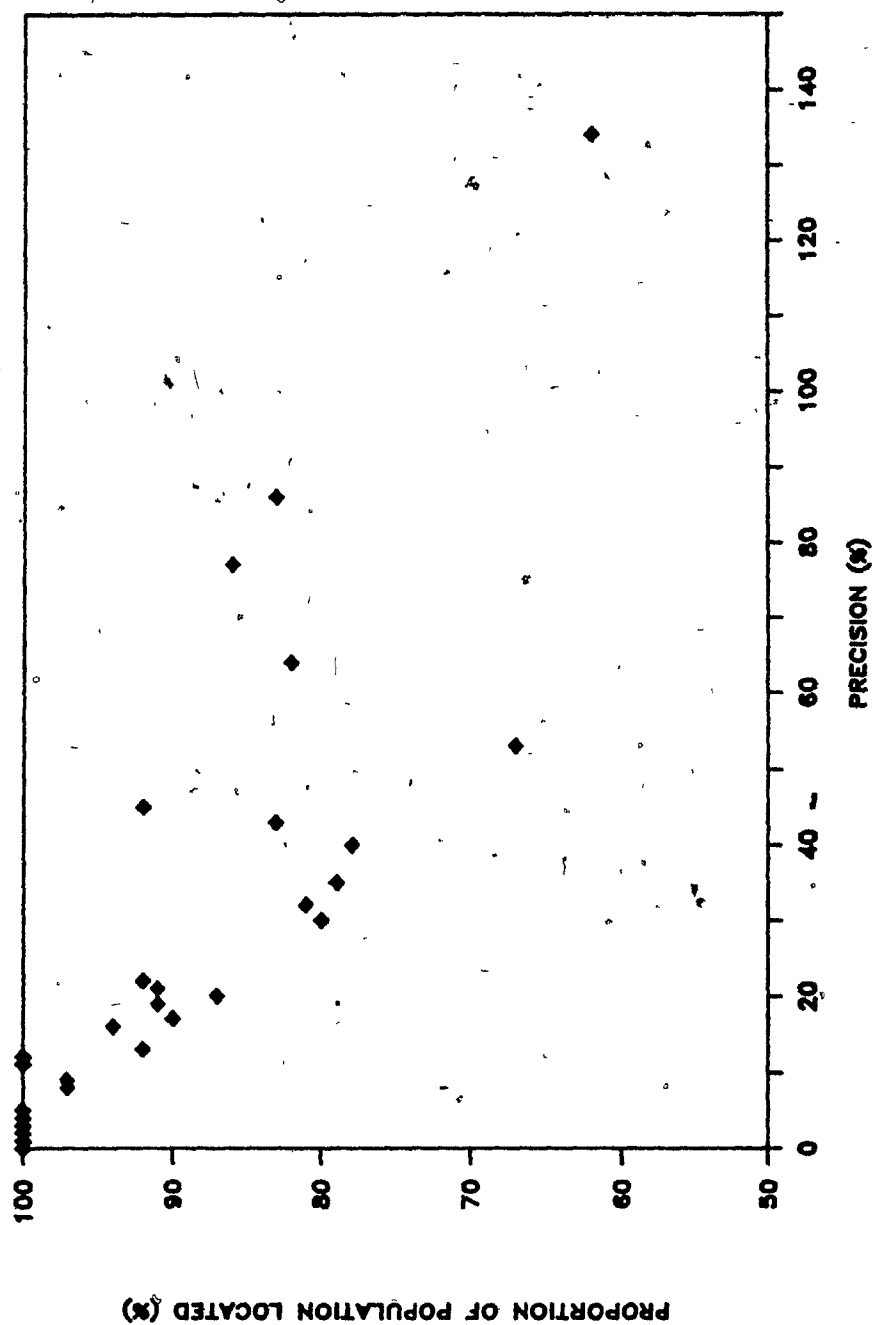


Figure 2b Relationship between proportion of the population located during ground surveys and survey precision. Precision is represented by the coefficient of variation.



CONNECTING STATEMENT

It was necessary to develop a reliable method of measuring seal abundance in the fast ice before factors affecting the distribution of animals could be assessed. In Section II population estimates derived from the breeding habitat surveys were used to determine the relationship between the distribution of seals and features of their fast ice habitat.

SECTION II

Factors Affecting the Abundance of Ringed Seals
in their Fast-Ice Breeding Habitat

INTRODUCTION

At the time of freeze-up, in autumn or early winter, ringed seals are thought to maintain underwater territories around two to four breathing holes (McLaren 1958, Smith and Stirling 1975; Smith and Hammill 1981). In areas of sufficient snow accumulation, seals dig haul-out lairs, which are used for resting, or as pupping sites during March to May. These subnivean structures provide protection from predators and shelter from cold temperatures (McLaren 1958, 1963; Smith and Stirling 1975; Smith 1976, 1980; Taugbol 1982; Smith 1987).

The amount of habitat available for breeding is generally considered to be a major factor limiting ringed seal population size (McLaren 1958). Suitable habitat has been described as stable annually forming land-fast ice that has undergone sufficient deformation to encourage snowdrift formation (McLaren 1958; Smith and Stirling 1975). Smith (1980, 1987) described hummocky ice as the most productive habitat in the Amundsen Gulf, and on southeast Baffin Island, followed by pressure ridges and snow covered refrozen cracks in the deep bays along the eastern Baffin Island coast. In the high Arctic the greatest number of subnivean structures are

associated with pressure ridges in the inter-island channels and at the entrances to large bays. The number of structures inside the bays are thought to be much lower, because of insufficient snow (Smith et al. 1978; Stirling et al. 1981).

Much of the earlier research was concerned with the qualitative description of habitat features and the structures used by ringed seals. Recently, aerial surveys, flown in early summer, have quantified the importance of annual fast ice. These surveys have identified a preference by ringed seals for waters 50 m to 175 m deep (Kingsley et al. 1985), and fast ice with deformation of 10% to 20% of the total ice cover (Burns and Kelly 1982). However, aerial surveys are conducted late in the spring to coincide with the peak of haul-out, well after breeding has been completed. At this time, the postulated underwater territories have broken down and animals have redistributed themselves in the fast ice (Finley 1979; Smith and Hammill 1981; Smith 1987). Aerial survey results are also difficult to interpret because of weather and seasonal effects on the timing and pattern of haul-out (Smith 1973; Smith and Hammill 1981; Kingsley 1984).

In order to test the hypothesis that ringed seals are limited by the availability of suitable habitat, it is necessary to assess both habitat conditions and the distribution of seals in the fast-ice during the whelping period. In this paper, I examine factors affecting ringed seal abundance in Barrow Strait, NWT during March to May, 1984 to

1986 and relate changes in seal distribution to quantifiable features of their fast-ice habitat.

MATERIALS AND METHODS

Study Area

Research was conducted in Barrow Strait near Resolute Bay, NWT (Fig. 1). This area is characterized by mean January temperatures of -33°C and annual precipitation of 125 mm to 150 mm (Maxwell 1981). Water depths are moderate ranging from 50 m to 300 m. Net current flow is eastward: water of Arctic Ocean origin flows into Barrow Strait from the adjoining channels and empties through Lancaster Sound into Baffin Bay and Davis Strait (Collin and Dunbar 1964). Total annual primary production in Resolute Bay is estimated at $45 \text{ gC m}^{-2} \text{ yr}^{-1}$ (Welch and Kalff 1975).

The ice cover consists of first-year fast-ice with occasional pieces of second-year or multi-year ice that has drifted into the strait from Viscount Melville Sound to the west or through McDougall Sound from the north. Normally the fast-ice extends from Viscount Melville Sound towards the east into Lancaster Sound. Its eastern edge varies in position from year to year (Lindsay 1975, 1977; Marko 1982). In 1984 the fast-ice edge formed off Bylot Island ($80^{\circ} 00' \text{ W}$ longitude),

in 1985 at Maxwell Bay on Devon Island ($89^{\circ} 00'$ W longitude), and in 1986 west of Lowther Island ($98^{\circ} 00'$ W longitude). Ice formation begins in September covering the larger bays and smaller channels with fast-ice up to 70 cm thick by mid to late November. Peel and McDougall Sounds consolidate next in late November and early December, with maximum ice thicknesses of 70 cm at this time. This is followed by consolidation in the northern half of Resolute Passage between Cornwallis Island and Griffith Island in December to February (Fig. 2). At the same time, the ice in the area surrounded by Lowther, Bathurst, Cornwallis and Griffith Islands consolidates. Consolidation in this area may be complete as early as December or as late as the beginning of March. In some years continued ice movement results in the formation of an unstable pressure ridge or a persistent lead along the south shore of Bathurst Island, extending across McDougall Sound to Cornwallis Island. Barrow Strait and the northern portion of Peel Sound consolidate last because the newly formed ice is constantly broken up by wind action and exported to Lancaster Sound. During the winter, floes up to 10 km across, consisting of ice up to 70 cm thick, may cover 90% of the strait. Barrow Strait usually consolidates from west to east in late January to March. Ice breakup begins in late June. Clearing of Barrow Strait depends on the position of the fast-ice edge, spring temperatures and the prevailing winds. Normally open-water conditions exist in this area by early to mid-August (Lindsay

1975, 1977; Marko 1982).

Data Collection

Habitat and seal abundance were assessed in two to four km^2 plots ($N=32$) between 19 March and 23 May, 1984 to 1986 (Fig. 1). Plots 1 to 9 were surveyed in 1984 and 1985. These were established randomly prior to the 1984 season and were located on the ice using a satellite navigation system (Magnavox MX4102, Torrance, California USA). In 1986, fast-ice did not form in the main study area. Instead, this area was covered by pack ice varying in concentration from 0 to 7/10 depending on the prevailing winds. Selection of plots to be surveyed in 1986 was subjective. Areas were chosen before the surveys began to determine the effects of date of ice consolidation and water depth on seal abundance. The actual site was established based on rough ice conditions and snow cover. These areas were located 0 to 60 km away from the open water, over water depths of 40 to 260 m, with 0% to 40% rough ice and mean snow depths of 2.0 to 25 cm. The survey plots were reduced from 4 km^2 to 2.25 km^2 in order to increase our sample size. A total of 14 plots, numbered 10 to 23 were surveyed (Fig. 1).

Habitat was described by the variables; snow depth, rough-ice thickness and height, ice thickness, water depth, and ice topography, distance from open water and date of ice con-

solidation. Snow depth in each plot was measured to the nearest cm at 16, 100 and 54 equally spaced points in 1984, 1985 and 1986 respectively, beginning from the southeast corner and moving north along the east border of the plot. Each point measurement represented an average of six snow depths taken at three metre intervals with a steel rod. Rough ice thickness and rough ice height were recorded only in 1985 and 1986. The total thickness and height of any piece of rough ice within one metre of a snow depth measurement was measured to the nearest cm. The thickness of the fast-ice cover in 1984 and 1985, was measured at the four corners of each plot after drilling a hole through the ice with a 10 cm diameter ice auger. In 1986, fast-ice thickness was recorded at 16 equally spaced points beginning along the east border from the southeast corner. Water depth was measured to the nearest metre in 1986 by echo-sounding using the holes drilled for the ice thickness measurements ($N=16$). Water depths for the plots surveyed in 1984 and 1985 were extracted from a hydrographic chart with a coverage of four soundings per km^2 (unpublished chart file # 3182, Bayfield Laboratory, Burlington Ontario). Ice surface topography was assessed by aerial photographs taken from an altitude of 300 to 350 m with a 6.0 cm x 6.0 cm format camera. The photographs were covered with an overlay containing 121 squares per frame. The presence of pressure ridges and rough ice in each square was recorded and expressed as a percentage of the total number of squares per plot. In

plots that were not photographed, the amount of pressure ridging was estimated subjectively. Information on date of ice consolidation was obtained for each year, from NOAA infra-red satellite imagery (Canadian Centre for Remote Sensing, Prince Albert, Saskatchewan). An area was considered to have consolidated if it consisted of gray or white ice, did not contain any black coloured ice, indicative of open water or very thin ice, and showed no signs of movement between consecutive photographs. The resolution of this imagery is one km. Date of ice formation was determined from the equation :

$$I = -25 + ((25 + I_1)^2 + 8(FDD))^{0.5} \quad (\text{Zubov 1938})$$

where I = ice thickness in cm, I_1 = the last measured ice thickness and FDD = freezing degree days, which equals the mean daily temperature below 0°C . Solving for FDD and subtracting from this figure the number of freezing degree days from the date of sampling gave the date of ice formation. Information on freezing degree days was obtained from published meteorological data for Resolute Bay (Monthly Record, Atmospheric Environment Service, Environment Canada, Ottawa, Ontario).

The density of seal holes in each plot was used as a measure of seal abundance. Estimates were obtained by applying the removal method (Zippin 1956) to the number of seal holes located by survey dogs during searches of fixed effort (Smith and Stirling 1975; Hammill Section I). In 1984, two Labrador Retriever dogs were used for the surveys; a 25 kg female and a

35 kg male. In 1985 and 1986 only the female was used for the surveys. All subnivean seal structures located by the dog were identified as either a breathing hole, a male breathing hole, a haul-out lair, a male haul-out lair or a birth lair (Smith and Stirling 1975). These were classified as active if the breathing hole or access hole was ice free, or abandoned if the hole was covered by a layer of ice and showed no signs of predation. Each structure was examined for evidence of predation (Smith and Stirling 1975; Smith 1976, 1980) and then several measurements were made: total snow depth, measured beside the breathing hole and average snow depth where two snow depths were measured to the nearest cm, 5 m and 10 m away from the breathing hole, on the north, north-east, east, south, southwest and west side of the breathing hole for a total of 12 measurements. These measurements plus the total snow depth measurement were then averaged. Average snow depth was not recorded in 1984. In 1986 ice thickness and water depth beside the breathing hole were also measured. Ice thickness was measured to the nearest cm by drilling a hole 2 m to 5 m away from the breathing hole parallel to the feature the seal structure was located on. Water depth at the structure was recorded by lowering the depth sounder transponder down the drilled hole.

Data Analysis

In plot 16, 25 of 27 structures were located in the northern half of the plot. This area consisted of ice 116 cm thick and had a mean snow depth of 14 cm. The southern half of the plot consisted of ice 40 cm thick and was covered by 2 cm of snow. Because the two areas were so different we decided to divide the plot in half, and created a new plot (plot 24), with an area of 1.12 km².

Differences between sample means were tested using Student's t-test. Homogeneity of variances was checked using a $F_{\max}$ test (Snedecor and Cochran 1980). In cases where the variances were unequal, differences between means were examined using a t-test for unequal variances and are denoted by t' (Snedecor and Cochran 1980). The relationship between the habitat variables and seal abundance was examined using path analysis (Legendre and Legendre 1983). Pearson and partial correlation coefficients were calculated using the Corr and GLM procedures of PC-SAS (SAS Institute 1985).

RESULTS

Habitat

In 1984, the mean September to May wind direction was from the north at an average speed of 20 km/hr. The mean

temperature was -20°C and total snowfall for the winter was 82 cm (Table 1). Ice in the study area consolidated in February. All plots consisted of first-year ice except for plot 1 which contained 20% second-year ice. Habitat conditions were characterized by thick ice, a very irregular surface topography and deep snow cover (Table 2).

In 1985, the predominant winds were east north-east at an average speed of 19 km/hr. The mean temperature of -23°C , was 3°C lower than 1984 primarily due to lower autumn temperatures (Table 1). The fast-ice in the study area consolidated in March, one month later than 1984. The ice consolidated quickly resulting in a very smooth ice surface (Table 2). Total snowfall was 35 cm, 45% of the 1984 value. Average snow depth on the ice in the survey plots was 7.9 cm, 42 % less than 1984 (Table 2).

In 1986, windspeeds were the highest of all three years, averaging 21 km/hr from the north. The mean temperature was -21°C , similar to the temperature in 1984, but temperatures between December and February averaged -28°C , 4°C warmer than the same period during the two previous years (Table 1). A solid ice sheet did not form over the initial study area forcing us to survey areas on either side of the open water (Fig. 1). In the areas we examined, the ice consolidated between late November and mid-April; from north to south in the McDougall Sound and Intrepid Passage area and from south to north in Peel Sound. All plots consisted of first-year ice

except for plot 14 which had some multi-year ice forming 1% of the total cover. Mean ice thickness and surface topography were similar to 1985 values (Table 2). However, the pieces of ice forming the pressure ridges were larger in 1986 than in 1985. This combined with greater precipitation and a greater number of days with blowing snow between March and May, resulted in snow depths similar to 1984 (Table 1).

We examined the relationship between the different habitat variables by pooling the data from all years (Table 3). Snow depth was positively correlated with thick, early consolidating ice and the amount of pressure ridging in the plot. The amount of pressure ridging was greater in areas of shallow water and in areas of late consolidating ice. The significant correlation between date of ice consolidation and distance from shore ($r=0.43$, $p=0.02$) indicates that the ice consolidates later as distance from shore increases. We also found a significant partial correlation between snow depth and water depth ($r=0.422$, $p=0.02$) but this appears to be a spurious relationship resulting from our Peel Sound surveys. This area contained the deepest water of all areas examined (200 to 260 m). It also contained thick ice which consolidated early in the winter.

Seal Abundance

Seal structures were located primarily along pressure

ridges approximately one to three metres away from the ridge. Some structures were associated with pieces of rough ice or along refrozen cracks. The density of seal structures was highest in 1986 ($\bar{x}=7.94 \text{ km}^{-2}$, $SE=1.0$, $N=14$), followed by 1984 ($\bar{x}=5.89 \text{ km}^{-2}$, $SE=1.0$, $N=9$), and finally 1985 with the lowest densities ($\bar{x}=4.83 \text{ km}^{-2}$, $SE=0.7$, $N=9$). In 1984, 72% ($SE=5.0$, $N=9$) of the structures located by the dog were lairs as opposed to simple breathing holes. This proportion declined to 54% ($SE=8.0$, $N=9$) in 1985, and increased slightly to 60% ($SE=4.5$, $N=14$) in 1986.

Habitat Immediately Adjacent to Seal Structures

A single observation shows lair formation can occur quite rapidly. A breathing hole located in 1985 became a haul-out lair within 24 hrs after the formation of a snow drift over the hole during a storm.

There is limited indirect evidence suggesting that ringed seals can dig new holes through the fast-ice. In late April and in early May 1986, two lairs located by the dog had small access holes approximately 15 cm in diameter. These holes had smooth sides and were wide at the top indicating they were haul-out holes and not breathing holes. Because of their size these holes could only have been made by pups. One hole had been formed inside the rim of a larger, refrozen adult sized hole that was covered by a layer of ice 15 cm thick. At the

second structure, the ice beside the small access hole was 91 cm thick. In late April, 1986 an adult seal was observed hauled out on flat grey ice, 34 cm thick, in an area free of snow. This area had been searched the previous day during which no hole had been detected by ourselves or the dog.

Snow depths at the different types of structures were greatest in 1984 and 1986 and lowest in 1985 (Table 4). The largest declines in average snow depth, a measure of snowdrift size, were observed at undefined haul-out lairs and male haul-out lairs (Table 4). Snowdrifts at these structures were smaller by 42% and 32% respectively in 1985 compared to 1986, while snowdrifts at birth lairs only decreased by 18%. The decrease resulted from the lower snowfall in 1985 (Table 1) and lower ice hummocks adjacent to the seal structures (Table 4). Except for the 1985 data, total snow depth at the different types of structures were similar to depths found in other areas of the Canadian Arctic and Spitzbergen (Table 5).

Ice thicknesses measured beside the subnivean structures were compared to the mean ice thickness of the fast-ice cover. Breathing holes, male breathing holes, haul-out lairs and male haul-out lairs were located in ice that was significantly thinner than the surrounding fast-ice ($t'=3.6$ $df=50$, $t=4.2$ $df=239$, $t'=3.8$ $df=52$, and $t=3.95$ $df=213$ respectively; $p<0.05$). Little difference was observed between ice thicknesses at birth lairs and the surrounding ice (Table 4). Birth lairs were located in the thickest ice of all structures, but this

difference was not significant between types of lairs.

Water depths at birth lairs were significantly deeper than water depths measured at haul-out lairs ($t' = 2.99$, $df = 52$, $p < 0.05$), but were similar to depths recorded at other structures (Table 4).

Relationship between Seal Abundance and Habitat

During each year of the study we observed high densities of seal holes under a very wide range of habitat conditions. The highest densities were associated with plots that consolidated between January and March. They contained ice in the form of large ice pans or a fast-ice edge, which formed two to four months prior to consolidation. These plots had an average snow depth of 10 cm or greater, with 10 to 40% of the ice surface consisting of pressure ridges and water depths of 90 to 170 m (Table 6).

In 1986, density increased and the percentage of abandoned structures decreased with an increase of pressure ridging and late consolidating ice. Density appeared to be related to the amount of pressure ridging in the plot, but the correlation was not quite significant ($r = 0.460$, $p = 0.08$). However, the effects of rough ice were thought to represent a linear combination of snow cover and date of ice consolidation, based on the relationships identified earlier between the habitat variables (Table 3). Significant partial

correlations between density of seal holes and both snow depth and date of ice consolidation were found, but not between density and rough ice (Table 7).

The results from 1984 and 1985 were examined next to determine whether the same factors were affecting the distribution of seals. The data from 1984, suggested that densities increased with date of consolidation (Table 6). There was a strong correlation between fast-ice thickness and density ($r=0.792$, $p=0.01$, $N=9$), but with no other habitat variable. Partial correlations between density, snow depth and date of ice consolidation were not significant. In 1985, no relationship between density and any of the habitat variables was found.

No birth lairs were observed before April 4. In Barrow Strait the mean pupping date falls in the fourth week of April (Hammill Section III). The proportion of birth lairs in plots surveyed after mid-April was 40% ($SE=8.4$, $N=7$) in 1984; 20% ($SE=6.2$, $N=5$) in 1985; and 40% ($SE=5.3$, $N=10$) in 1986. Male structures were identified early in the season during surveys conducted in March, but were not evident after mid-May. Excluding plots surveyed during the last two weeks in May, male structures made up 18% ($SE=4.1$, $N=8$) in 1984; 38% ($SE=8.1$, $N=8$) in 1985; and 26% ($SE=5.4$, $N=11$) of all structures in a plot in 1986.

I compared the frequency of female structures (birth lairs) to the frequency of male structures to see if the ratio

differed from 1:1. Structures used by males included both haul-out lairs and breathing holes. Females can only be identified by the presence of a birth lair in the plot even though they maintain other structures as part of the birth lair complex (Smith and Stirling 1975). Therefore, I expected the ratio to differ significantly from 1:1 in favour of males. In 1985, the ratio of male structures to birth lairs did not differ significantly from unity. In 1984 and 1986, there were significantly more birth lairs than male structures in the plots indicating segregation of sexes in the fast ice (Table 8). In 1984 and in 1985, plot 9, which was one of the last areas to consolidate in both years, appeared to contain large numbers of non-breeding animals. In 1984, 14% and 22% of 36 holes were birth lairs and male structures respectively. This area was covered by deep snow and thick ice, but had an unstable crack running through the eastern side of the plot. In 1985, plot 9 had very little snow cover (Table 6) and had an unstable pressure ridge along its western boundary. No birth lairs were located in the plot. All seal structures located by the dog were extremely small in size and were situated on the unstable ridge. These structures are thought to have been made by small immature seals. In 1986, only plot 12 did not contain any birth lairs or male structures, indicating the presence of non-breeding animals. This plot was located in southern McDougall Sound near a region of unstable ice (Fig. 1,2). The remaining plots all had male structures

or birth lairs.

In 1986, date of ice consolidation and mean snow depth were found to be the most important factors affecting the distribution of birth lairs and undefined structures, which includes both haul out lairs and breathing holes (Table 9). No relationship was found between any of the habitat variables and the distribution of male structures. We did not examine the results from 1984 and 1985 because of the small sample sizes.

DISCUSSION

The fast-ice in Barrow Strait shows considerable year to year variability in snow cover, ice topography and chronology of ice consolidation. Snow depth is tied to precipitation, ice thickness, and the amount of pressure ridging. The older the ice and the earlier it consolidates, the longer it provides a stable platform for snow accumulation. Pressure ridging acts like a snow fence catching blowing snow and encouraging snow drift formation. The large variation we observed in habitat conditions is likely related to year to year changes in atmospheric circulation patterns. Ice freeze-up and breakup, have been related to synoptic circulation patterns in the western arctic, Davis Strait and Baffin Bay (Keen 1977; Rogers 1978; Hammill 1987).

Lair formation can occur quite rapidly over existing holes after snowdrift formation. We also have limited evidence that suggests seals search for suitable snow drifts for haul-out lairs and then possibly dig new holes through the ice under these drifts. Drifts could be located by the differential penetration of light through the ice between snowdrift covered and snow-free areas. By maintaining several holes or lairs (Smith and Stirling 1975; Smith and Hammill 1981; Burns and Kelly 1981 ; Hammill Section I) and forming new structures when necessary, ringed seals reduce their exposure to predators. In 1986, the thinnest ice containing lairs was 75 cm thick. Most seal holes were associated with ice 10 to 30 cm thinner than the surrounding ice. By digging through cracks parallel to the ridge that appeared at the time of ridge formation, seals would be digging through ice 45 to 65 cm thick and not the maximum 75 cm.

Birth lairs were found in the largest drifts. It is possible these sites are occupied at the time of ice formation, but this assumes a female occupying a site in January can predict if sufficient snow will accumulate in time for pupping in April. Instead, I propose that after a female occupies an area, she searches for a large drift, digs a new hole through the ice under the drift and scratches out a lair. This new hole would be located near other holes used by the female which later form the birth lair complex (Smith and Stirling 1975).

A major difficulty with this study is the small sample size of surveyed plots. The dog search method is the only technique available to study ringed seal populations in their breeding habitat. This method is very labour intensive. In the final year of our study the dog covered over 510 km of sea ice surveying a total of 14 plots. A reduction in plot size from 2.25 km² to 0.6 km² would permit an increase in sample size to about 20 plots per season (Hammill Section I). I have also assumed that a constant relationship exists between density of seal holes and the density of seals. Seal holes are a valid index of seal abundance, but there is some variability in the number of holes maintained by different segments of the population (Hammill Section I). This variability would tend to obscure any relationships between habitat and seal abundance.

High densities of seal structures were observed in a wide range of habitat conditions, indicating a very flexible response to local features. Densities were lower in 1985 than in any other year possibly because of the reduced snow depths in the areas we surveyed, but a longer time series of data are required to confirm or reject this hypothesis.

The decrease in abandonment rates of breathing holes and lairs and increase in density with date of ice consolidation, observed in 1986, shows that seals were following the advancing ice edge and were not necessarily remaining in the same areas they first occupied during the fall months. Preference for late consolidating ice may be in response to

increased food availability at the ice edge (Bradstreet and Cross 1982) or increased mobility because the animals are not restricted by the need to maintain access to a breathing hole. Very few structures were located immediately adjacent to the open water (Table 4). Instead lairs and breathing holes were usually found 0.5 to 1 km away from the ice edge in thicker icepans or in fast-ice that had formed two to four months prior to the consolidation of ice in the plot. This ice was more stable and contained suitable snow drifts for haul-out lairs. In 1984 and 1985, Barrow Strait was completely covered by fast-ice. Date of ice consolidation was not identified as an important factor during these two years because the areas covered by the surveys were close together and were located in ice that had consolidated at the same time (Fig. 1,2; Table 4). I used NOAA satellite infra-red imagery to determine the date of ice consolidation, which provided large scale coverage and has a resolution of one km. In future studies the application of more advanced imagery, such as thematic mapping, which has a resolution of 100 m in the infra-red band, may permit a more precise determination of the date of ice consolidation.

In other studies examining ringed seal distribution in the high arctic, low densities of ringed seals were associated with the early consolidating ice of McDougall and Viscount Melville Sounds and increased towards the late consolidating ice of Barrow Strait (Kingsley, et al. 1985; Fig. 4). Low

densities of seals have also been reported inside the bays in the high Arctic, apparently because of insufficient snow cover for lairs (Smith et al. 1978; Stirling et al. 1983), but more recent work indicates that there is more snow cover inside the bays than in the channels (Calvert and Stirling 1985). These areas are also among the first to freeze early in the fall, which makes them less attractive to seals. Densities are higher at the entrances to large bays because they consolidate later and provide a stable ice edge for snow to accumulate on, near the more unstable ice in the channels.

Some of the variation observed in population composition of the plots can be attributed to seasonal effects, such as the appearance of birth lairs, and the decline in numbers of male structures. Within the fast-ice habitat immature animals are excluded from the most suitable habitat to areas of unstable ice or little snow cover (McLaren 1958; Smith and Hammill 1981; Smith 1987). Birth lairs were associated with thick stable ice and deep snow cover in late consolidating ice, but no relationship was identified between the distribution of male structures and any of the habitat variables examined. During the spring mature males are thought to defend underwater territories (Stirling 1977; Smith and Stirling 1975; Smith and Hammill 1981). Defense of underwater territories has not been observed directly in this species, but the low number of male structures in areas where females are abundant, combined with the increase in the incidence of

fresh cuts on males and the pungent odour associated with mature males in the spring support this hypothesis (McLaren 1958; Smith and Stirling 1978; Smith et al. 1978; Smith and Hammill 1981; Smith 1987). I believe that the underwater territories are not established or at least not rigorously defended until after parturition. At this time the movements of the female under the ice are restricted because of the care required by the pup. After mating and weaning of the pup, ringed seals haul out on the ice to moult, the underwater territories start to break down and seals redistribute themselves in the fast-ice (Finley 1979; Smith and Hammill 1981).

Ringed seal populations are regulated by a combination of habitat availability (McLaren 1958, 1963; Smith and Stirling 1975), social factors (Stirling 1977; Smith and Hammill 1981), and predation (Stirling and McEwen 1975; Smith 1976; Stirling and Archibald 1978; Smith 1987). Recently the availability of food and its subsequent effects on condition and reproduction has also been suggested as a factor limiting ringed seal numbers (Lowry et al. 1980; Smith and Hammill 1981; Smith 1987). During the winter, ringed seals feed primarily but not exclusively on arctic cod (Boreogadus saida) (Lowry et al. 1980; Smith 1987). Very little is known about the winter biology of these fish. They appear to be very mobile and patchy in distribution (Bradstreet et al. 1986). The preference by seals for late consolidating stable ice suggests

that access to food provides the initial attraction for seals to an area. If this is the case, one would expect ringed seal condition to be lower in years when the mobility of animals is reduced by thick, early consolidating ice, and higher in years of thin, late consolidating ice. This hypothesis could be tested by long term studies monitoring changes in population age structure, condition and productivity along with changes in fast-ice conditions.

REFERENCES

- Bradstreet, M.S.W. and W.E. Cross. 1982. Trophic relationships at High Arctic ice edges. *Arctic* 35: 1-12.
- Bradstreet, M.S.W., K.J. Finley, A.D. Sekerak, W.B. Griffiths, C.R. Evans, M.F. Fabijan and H.E. Stallard. 1986. Aspects of the biology of Arctic Cod (Boreogadus saida) and its importance in Arctic marine food chains. *Can. Tech. Rep. Fish. Aquat. Sci.* 1491. 193 p.
- Burns, J.J. and B.P. Kelly. 1982. Studies of ringed seals in the Alaskan Beaufort Sea during the winter: Impacts of seismic exploration. Unpublished report RU#232 to Outer Continental Shelf Environmental Assessment Program, Juneau, Ak. 57 p.
- Calvert, W. and I. Stirling. 1985. Winter distribution of ringed seals (Phoca hispida) in the Barrow Strait area, Northwest Territories, determined by underwater vocalizations. *Can. J. Fish. Aquat. Sci.* 42: 1238-1243.
- Collin, A.E. and M.J. Dunbar. 1964. Physical oceanography in Arctic Canada. *Oceanogr. Mar. Biol. Annu. Rev.* 2:45-75.
- 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.
- Hammill, M.O. 1987. The effects of weather on ice conditions in the Amundsen Gulf, N.W.T. *Can. Manuscr. Rep. Fish. and Aquat. Sci.* 1900. 10p.
- Keen, R.A. 1977. The response of Baffin Bay ice conditions to changes in atmospheric circulation patterns. In Muggeridge, D.B. (ed) 4th International Conference on Port and Ocean Engineering under Arctic Conditions, II: 963-971.
- Kingsley, M.C.S. 1984. The abundance of ringed seals in the Beaufort Sea and Amundsen Gulf, 1983. *Can. Manuscr. Rep. Fish. Aquat. Sci.* 1778 : iv + 8p.
- Kingsley, M.C.S., I. Stirling and W. Calvert. 1985. The distribution and abundance of seals in the High Arctic, 1980-82. *Can. J. Fish. Aquat. Sci.* 42: 1189-1210.

- Legendre, L. and P. Legendre. 1983. Numerical ecology. Elsevier Scientific Publishing Co., New York. 419p.
- Lindsay, D.G. 1975. Sea ice atlas of Arctic Canada, 1961-1968. Dept. Energy, Mines and Resources, Ottawa, Ont. 213p.
- Lindsay, D.G. 1977. Sea ice atlas of Arctic Canada, 1969-1974. Dept. Energy, Mines and Resources, Ottawa, Ont. 219 p.
- 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.
- Lydersen, C. and I. Gjertz. 1986. Studies of the ringed seal (Phoca hispida) in its breeding habitat in Kongsfjorden, Svalbard. Polar Research 4: 57-63.
- Marko, J.R. 1982. The ice environment of eastern Lancaster Sound and northern Baffin Bay. Indian and Northern Affairs. Northern Affairs Program. Environmental Studies No. 26. 215p.
- Maxwell, J.B. 1981. Climatic regions of the Canadian Arctic islands. Arctic 34: 225-240.
- McLaren, I.A. 1958. The biology of the ringed seal (Phoca hispida Schreber) in the eastern Canadian Arctic. Fish. Res. Bd. Canada Bull 118. 97p.
- McLaren, I.A. 1963. Population dynamics and exploitation of seals in the eastern Canadian Arctic. In E.D. LeCren and M.W. Holdgate (ed) The exploitation of natural animal populations. John Wiley and Sons, New York.
- Rogers, J.C. 1978. Meteorological factors affecting interannual variability of summer time ice extent in the Beaufort Sea. Monthly Weather Review 6: 890-897.
- SAS Institute Inc. 1985. SAS/STAT Guide for personal computers, Version 6 edition. Cary, NC, USA. 378p.
- Smith, T.G. 1973. Population dynamics of the ringed seal in the Canadian eastern Arctic. Bull. Fish. Res. Bd. Canada. 181. 55p.
- Smith, T.G. 1976. Predation of ringed seal pups (Phoca hispida) by the arctic fox (Alopex lagopus). Can. J. Zool. 54: 1610-1616.
- Smith, T.G. 1980. Polar bear predation of ringed and bearded

seals in the land-fast sea ice habitat. Can. J. Zool. 58: 2201-2209.

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

Smith, T.G. and M.O. Hammill. 1981. Ecology of the ringed seal, Phoca hispida, in its fast-ice breeding habitat. Can. J. Zool. 59: 966-981.

Smith, T.G., K. Hay, D. Taylor, and R. Greendale. 1978. Ringed seal breeding habitat in Viscount Melville Sound, Barrow Strait and Peel Sound. ESCOM Report No. AI-22. Department of Indian and Northern Affairs, Ottawa, Ont. K1A 0H4. 85p.

Smith, T.G. and I. Stirling. 1975. The breeding habitat of the ringed seal (Phoca hispida). The birth lair and associated structures. Can. J. Zool. 53: 1297-1305.

Smith, T.G. and I. Stirling. 1978. Variation in the density of ringed seal (Phoca hispida) birth lairs in the Amundsen Gulf, Northwest Territories. Can. J. Zool. 56: 1066-1070.

Snedecor, G.W. and W.G. Cochran. 1980. Statistical methods. 7th edition. Iowa State University Press. Ames, Iowa. 507p.

Stirling, I. 1977. Adaptations of Weddell and ringed seals to exploit the polar fast-ice habitat in the absence or presence of surface predators. In G.A. Llano (ed.) Adaptations within Antarctic ecosystems. Third Symp. Antarctic Biol. Smithsonian Institute, Washington, D.C.

Stirling, I., W. Calvert and H. Cleator. 1983. Underwater vocalizations as a tool for studying the distribution and relative abundance of wintering pinnipeds in the High Arctic. Arctic 36: 262-274.

Stirling, I., H. Cleator and T.G. Smith. 1981. Marine Mammals. In: Stirling, I., and H. Cleator. (eds.) Polynyas in the Canadian Arctic. Ottawa: Can. Wildl. Serv. Occas. Pap. 45: 45-48.

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

Welch, H.E. and J. Kalff. 1975. Marine metabolism at Resolute Bay, Northwest Territories. Sect. II pp 67-76. In

Circumpolar Conf. on North Ecol. Nat. Res. Counc.
Ottawa.

Zipin, C. 1956. An evaluation of the removal method of
estimating animal populations. Biometrics 12: 163-169.

Zubov, N.N.. 1938: On the maximum thickness of sea ice of many
years growth. Meteorologiya i Gidrologiya 4:123-131.

Table 1. Mean wind direction, speed, temperature, snow depth, total snowfall and days of blowing snow recorded at Resolute Bay, Northwest Territories from September to May 1984-1986. Data from Monthly Record, Atmospheric Environment Service, Environment Canada, Toronto, Ontario.

Year	Mean Wind Direction	Mean Windspeed (km/hr)	Mean Temperature (°C)	Total Snowfall (cm)	Mean Snow Depth (cm)	Days of Blowing Snow
1984						
Sept.-Nov.	N	23	-6	34	9	20
Dec.-Feb.	N	19	-32	18	25	27
Mar.-May	NNE	18	-22	30	30	17
1985						
Sept.-Nov.	NE	25	-14	24	10	35
Dec.-Feb.	NE	18	-32	7	16	37
Mar.-May	E	15	-22	4.4	12	17
1986						
Sept.-Nov.	N	28	-14	59	23	27
Dec.-Feb.	NE	23	-28	11	28	37
Mar.-May	NNW	23	-22	25	29	30

Table 2. Mean snow depths, ice thickness, water depth, amount of pressure ridging and height and thickness of pieces of rough ice measured in the study plots.

	1984			1985			1986		
	N	$\bar{X}$	SE	N	$\bar{X}$	SE	N	$\bar{X}$	SE
Snow Depth (cm)	143	23.2	1.3	907	10.3	0.3	750	20.2	0.6
Ice Thickness (cm)	28	176	5.3	33	156.3	3.6	209	154.5	3.2
Water Depth (m)	88	105.5	2.6	-	-	-	203	163.0	4.8
Thickness of Rough Ice	-	-	-	94	17.0	2.3	116	23.4	4.1
Height of Rough Ice	-	-	-	92	31.5	2.4	113	56.7	3.7
Amount of Pressure Ridging (%)	9	24.4	4.4	9	12.3	1.9	15	13.6	3.2

Table 3. Correlations between the various habitat features examined between 1984 and 1986 in 32 study plots. Pearson correlation coefficients lie above the diagonal. Partial correlation coefficients lie below the diagonal. * denotes significance at $p < 0.05$.

	Pressure Ridging (%)	Ice Thickness (cm)	Distance to Land (km)	Water Depth (m)	Date of Ice Consolidation	Snow Depth (cm)
Pressure Ridging	1	0.2899 $p=0.102$	0.1086 $p=0.548$	-0.4518* $p=0.008$	0.0519 $p=0.774$	0.4439* $p=0.01$
Ice Thickness	-0.1413 $p=0.465$	1	0.2398 $p=0.179$	0.0109 $p=0.952$	-0.4461* $p=0.009$	0.7949* $p=0.0001$
Distance to Land	-0.0166 $p=0.932$	0.3098 $p=0.102$	1	0.1486 $p=0.409$	0.3096 $p=0.080$	0.0802 $p=0.657$
Water Depth	-0.5979* $p=0.001$	-0.1859 $p=0.334$	0.1518 $p=0.432$	1	-0.0632 $p=0.727$	0.0764 $p=0.673$
Date of Ice Consoli- dation	0.4856* $p=0.008$	-0.0548 $p=0.778$	0.4298* $p=0.018$	0.2104 $p=0.273$	1	-0.6065* $p=0.0002$
Snow Depth	0.6395* $p=0.0002$	0.5546* $p=0.002$	0.0662 $p=0.733$	0.4225* $p=0.022$	-0.6023* $p=0.0006$	1

Table 4. Mean values of habitat features measured at the different types of subnivean structures of the ringed seal.

	Year	Breathing Hole			Male Breathing Hole			Haulout Lair			Male Haulout Lair			Birth Lair		
		N	$\bar{X}$	SE	N	$\bar{X}$	SE	N	$\bar{X}$	SE	N	$\bar{X}$	SE	N	$\bar{X}$	SE
Average Snow Depth (cm)	1985	25	30.1	3.3	26	24.4	3.1	22	34.9	2.8	10	38.6	2.9	6	50.6	4.1
	1986	32	41.8	2.9	25	43.2	3.9	36	59.5	2.6	6	58.6	7.6	43	71.9	12.1
Height of Rough Ice Pieces (cm)	1985	10	48.9	6.5	8	51.9	8.4	15	93.6	9.5	5	70.6	12.7	4	76.5	21.2
	1986	13	85.5	7.8	12	79.4	10.9	19	114.6	10.5	2	98.0	80.0	10	111.0	19.7
Thickness of Rough Ice Pieces (cm)	1985	10	10.3	1.3	8	14.0	3.1	15	12.6	1.5	5	12.0	1.0	4	23.7	16.1
	1986	13	20.7	4.4	12	20.3	5.1	19	25.7	3.4	2	43.0	16.0	10	16.6	2.5
Fast Ice Thickness (cm)	1986	30	127.3	5.7	26	124.2	7.4	31	129.1	5.9	4	122.2	12.1	39	143.5	6.4
Water Depth (m)	1986	30	163.2	12.2	26	160.2	11.0	33	136.0	11.4	4	139.0	30.2	35	174.5	9.4

Table 5. Mean total snow depths measured at seal structures in Barrow Strait and from other areas.

Area	Year	Breathing Holes			Male Breathing Hole			Haulout Lair			Male Haulout Lair			Birth Lair			Source
		N	$\bar{X}$	SE	N	$\bar{X}$	SE	N	$\bar{X}$	SE	N	$\bar{X}$	SE	N	$\bar{X}$	SE	
Barrow St.	1984	31	52.8	4.3	15	57.1	2.8	41	66.7	2.8	17	67.9	2.7	51	79.1	3.3	This study
Barrow St.	1985	28	37.0	3.8	34	29.9	3.1	38	34.9	2.1	17	50.5	3.7	12	50.7	2.9	This study
Barrow St.	1986	50	48.0	3.0	31	44.7	3.9	40	69.9	3.1	6	69.3	7.2	52	76.7	3.3	This study
Amundsen Gulf	.	.	.	.	.	.	.	154	59.8	1.7	17	70.2	4.7	112	64.6	2.3	Smith and Stirling 1975
Kingsfjorden Spitzbergen	.	.	.	.	.	.	.	40	91.0	3.8	22	75.0	3.4	28	89	2.8	Lydersen and Gjertz 1986
Bridport Inlet, NWT	1980	1	35.0	.	3	28.0	3.9	2	55.0	.	8	64.0	8.9	6	91	9.3	Smith, unpublished data
Southeast Baffin Is.	1979	30	30.0	2.9	12	30.0	4.1	17	59.0	5.2	15	57.0	7.0	60	75	3.0	Smith, unpublished data

Table 6. Mean habitat values for densities of seal holes grouped by frequency class. Standard errors are in brackets.

Freq. Class (holes/ km ²)	Number of Plots	Mean Density (holes/km ²)	Mean Number Birthlair (holes/km ²)	Mean Pressure Ridging (%)	Mean Ice Thickness (cm)	Mean Snow Depth (cm)	Mean Water Depth (cm)	Number Abandoned Structures	Date Ice Consoli- dation	Date Ice Formation	Plots
<u>> 10</u>											
1986	4	14 (2)	7 (1)	21 (7)	134 (21)	15 (4)	172 (28)	2 (1)	4 Mar. (12)	6 Jan.	14,16,19,21
1984	1	11	6	19	189	19	119	13	22 Feb.	18 Oct.	5
<u>7-10</u>											
1986	5	8 (1)	2 (1)	12 (4)	155 (14)	18 (3)	157 (27)	8 (4)	11 Jan. (23)	14 Dec.	11,15,17,18,20
1985	2	7 (0)	2 (0)	20 (0)	182 (5)	10 (1)	115 (11)	2 (2)	6 Mar. (4)	1 Dec.	6,8
	1	8	0	38	124	2	67	0	9 Mar.	2 Feb.	9
1984	4	7 (0)	2 (1)	30 (7)	186 (6)	19 (1)	96 (11)	7 (4)	17 Feb. (2)	20 Oct.	2,4,6,8,9
<u>3-6</u>											
1986	5	4 (1)	1 (1)	11 (7)	169 (14)	18 (2)	146 (44)	31 (7)	17 Dec. (6)	24 Nov.	10,12,13,22,23
1985	5	4 (0)	1 (0)	11 (2)	160 (4)	9 (1)	112 (11)	4 (2)	8 Mar. (1)	7 Dec.	2,3,4,5,7
1984	3	3 (0)	1 (0)	12 (2)	169 (7)	16 (1)	128 (13)	0	24 Feb. (8)	1 Dec.	3,7

Table 6. Continued.

Freq. Class (holes/km ²)	Number of Plots	Mean Density (holes/km ²)	Mean Number Birthlair (holes/km ²)	Mean Pressure Ridging (%)	Mean Ice Thickness (cm)	Mean Snow Depth (cm)	Mean Water Depth (cm)	Number Abandoned Structures	Date Ice Consolidation	Date Ice Formation	Plots
< 2											
1986	1	1	0	0	39	2	113	0	7 Apr.	7 Apr.	24
1985	1	1	0	10	136	7	85	0	9 Mar.	14 Dec.	1
1984	1	2	0	27	137	23	85	0	8 Feb.	26 Jan.	1

Table 7. Correlations between density of seal holes (holes/km²) and habitat variables for the 1986 data. Pearson correlation coefficients lie above the diagonal. Partial correlation coefficients lie below the diagonal.

	Density	Snow Depth	Pressure Ridging	Date of Consolidation
Density	1	0.2204 p=0.430	0.4605 p=0.084	0.3691 p=0.176
Snow Depth	0.6488 p=0.016	1	0.3712 p=0.173	-0.7117 p=0.003
Pressure Ridging	0.0456 p=0.8825	0.4270 p=0.1456	1	0.0700 p=0.804
Date of Consolidation	0.7092 p=0.006	0.8873 p=0.0001	0.3284 p=0.273	1

Table 8. Observed and expected frequencies of birth lairs and male structures. Plots surveyed before mid-April and after mid-May are excluded. * denotes significance at $p < 0.05$

Year	Structure	Observed Frequency	Expected Frequency	Chi-square value
1986	Birth Lair	48	33	13.6*
	Male Structures	18	33	
1985	Birth Lair	12	14.5	0.9
	Male Structures	17	14.5	
1984	Birth Lair	51	38	8.9*
	Male Structures	25	38	

Table 9. Correlations between density of birth lairs and undefined structures and the habitat variables, snow depth and date of ice consolidation. Pearson correlation coefficients lie above the diagonal. Partial correlation coefficients lie below the diagonal.

	Birth Lairs	Snow Depth	Date of Consolidation		Undefined Structures	Snow Depth	Date of Consolidation
Birth Lairs	1	0.2938 p=0.381	0.2463 p=0.465	Undefined Structures	1	0.1928 p=0.570	0.3502 p=0.291
Snow Depth	0.6869 p=0.0282	1	-0.7102 p=0.014	Snow Depth	0.6696 p=0.034	1	-0.7102 p=0.014
Date of Consolidation	0.676 p=0.0319	-0.4727 p=0.088	1	Date of Consolidation	0.705 p=0.023	-0.5439 p=0.044	1

Figure 1. Location of study plots surveyed during March to May, 1984 to 1986. Plots 1 to 9 were surveyed in 1984 and 1985. The remaining plots were surveyed in 1986. The dotted line represents the extent of the fast ice edge in 1986.

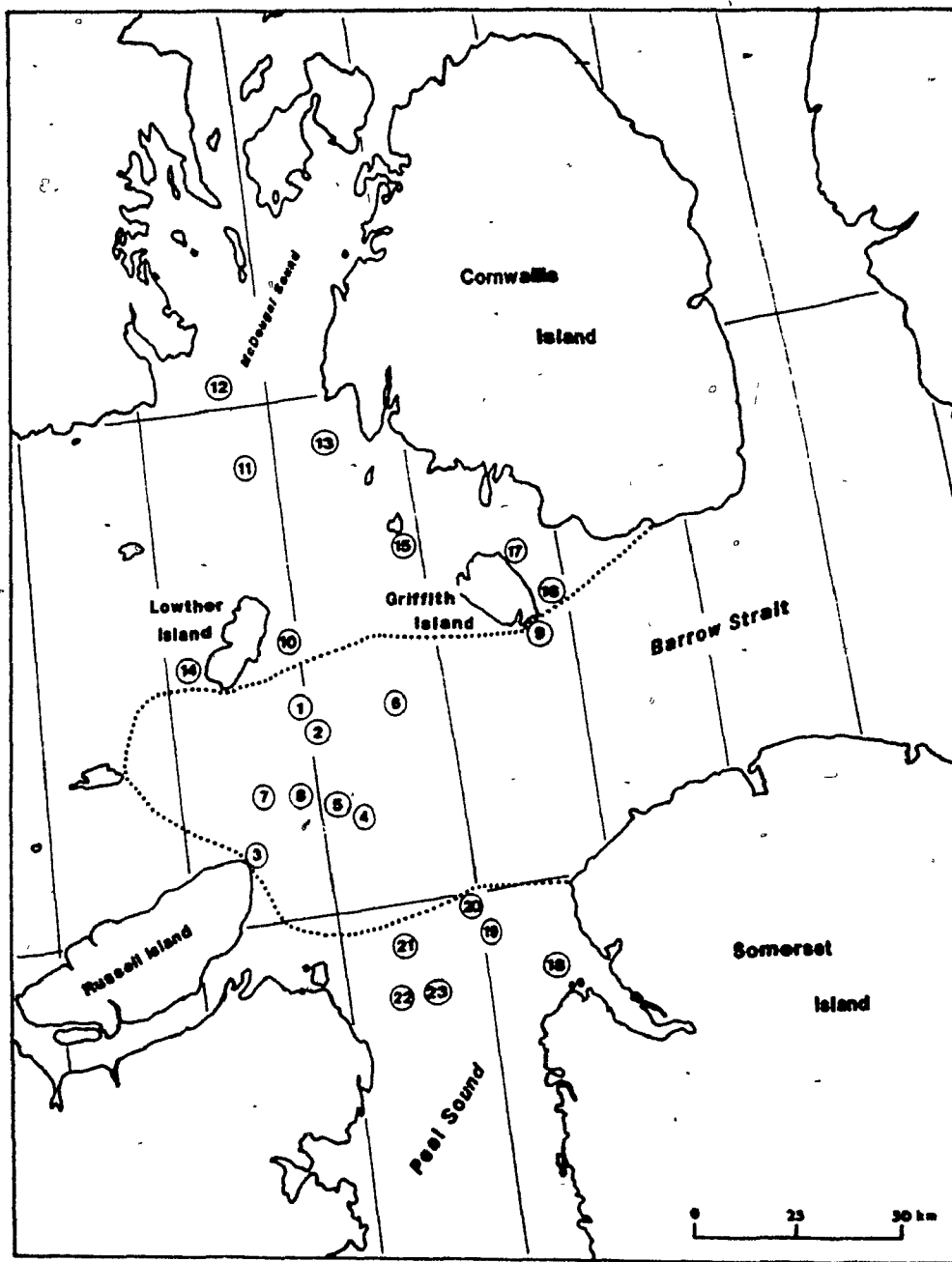
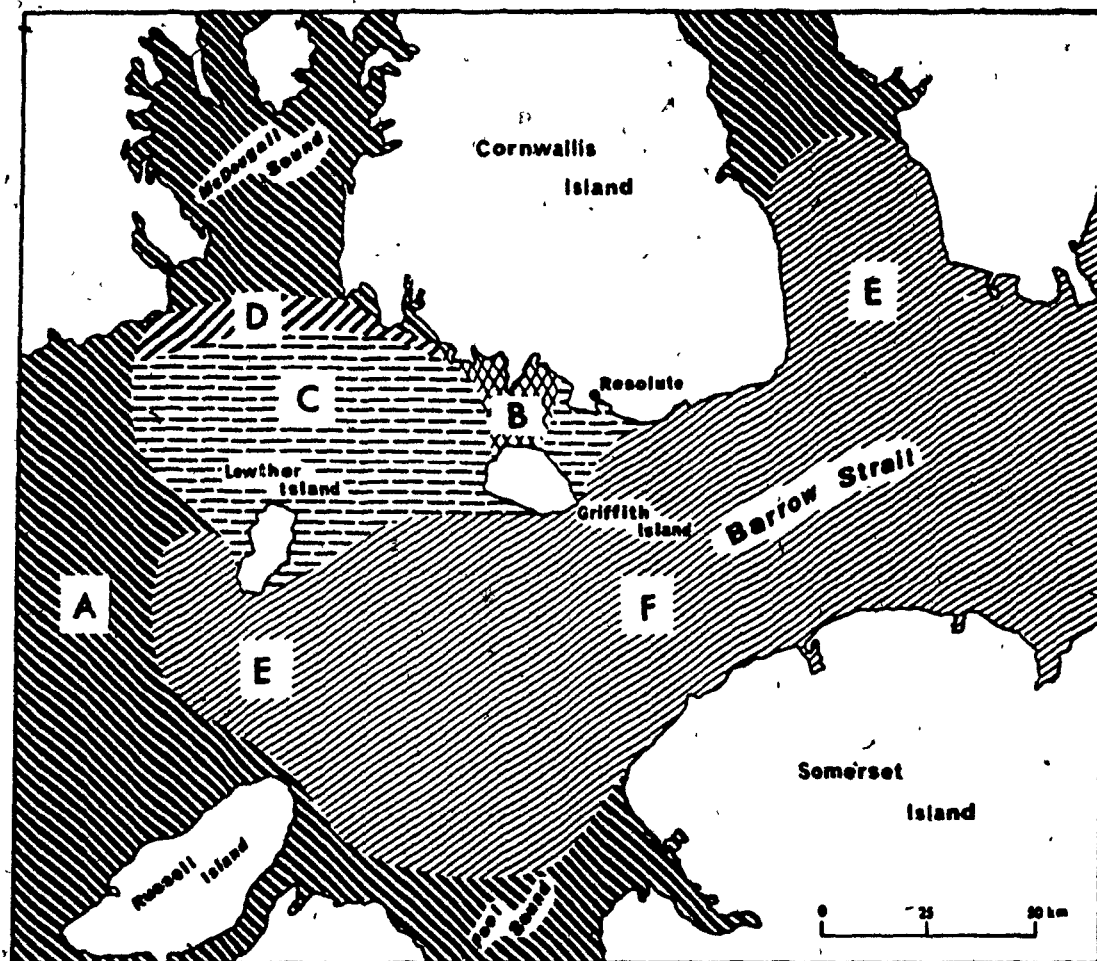


Figure 2. General pattern of ice consolidation in Barrow Strait. Areas denoted by A consolidate first. Areas denoted by F consolidate last.



CONNECTING STATEMENT

In Section II, factors affecting the distribution of ringed seals in the fast ice were identified. Information was obtained on the association between different segments of the population and habitat features. Section III examines the age structure, reproductive rates and body condition of ringed seals occupying the fast ice between March and June.

SECTION III
Biology of the Ringed Seal in Barrow Strait,
Northwest Territories

INTRODUCTION

In winter, ringed seals occupy the fast-ice, where they maintain breathing holes and dig lairs under the snow (McLaren 1958). At that time of year they feed primarily on Arctic cod (Boreogadus saida). Very little is known about the winter biology of this fish. They appear to be very mobile and have a patchy distribution under the ice (Bradstreet et al. 1986). Although, the availability of food resources under the fast ice is poorly understood, if conditions are analagous to observations of the antarctic Weddell seal (Leptonychotes weddelli) (Testa et al. 1983), then ringed seals may either deplete food resources around their breathing holes, or their prey might actively avoid areas occupied by seals. During the 1970's major fluctuations in age specific reproductive rates, body condition and numbers of ringed seals were documented in the Canadian western Arctic (Stirling et al. 1977; Smith 1987). Changes in these parameters were attributed to annual changes in the availability of food resources, possibly mediated by winter ice conditions (Stirling et al. 1977; Smith 1987), but this has not been investigated in any detail.

In section II, I proposed that ringed seals occupying the fast-ice have reduced access to food resources. To test this hypothesis I collected ringed seals throughout the spring in

each year of the study. This collection program also enabled me to obtain information on timing of reproduction, population age structure and age-specific reproductive rates.

In this paper, I examine the hypothesis that ringed seals in the fast-ice have reduced access to food resources, by monitoring annual changes in body condition. I also present information on population parameters as baseline data for ringed seals in the high arctic and compare these parameters with results obtained from other studies (McLaren 1958; Smith 1973, 1987).

MATERIALS AND METHODS

The study area was located in Barrow Strait between Lowther Island and Resolute Bay in the north and Russell and Somerset Islands in the south (Fig. 1). Water depths are moderate, ranging from 50 m to 300 m. Ice cover consists of first year ice which extends from Viscount Melville Sound towards Lancaster Sound in the east. The eastern edge of the first year fast-ice varies in position from year to year (Marko 1982). In 1984 the fast-ice edge formed off Bylot Island; in 1985 at Maxwell Bay and in 1986 west of Lowther Island. The chronology of ice consolidation is also quite variable. Generally the ice solidifies between January and March in Barrow Strait, but begins as early as September in the bays and adjoining channels. In 1986 the ice consolidated

one to two months later than in the two previous years. Ice breakup begins in early July and open water conditions normally exist in this area by early to mid-August (Marko 1982).

Seals were collected by shooting at the breathing hole or on the ice with a high-powered rifle. Collections between March and May were opportunistic because surveys of the breeding habitat took place at this time (Hamill Section II). After mid-May all the effort went into the collecting of seals. Hunting was concentrated along the east and south sides of Lowther Island and Griffith Islands up to 16 km offshore (Fig. 1).

Standard length, axillary girth, sternum blubber thickness and body weight were measured on each animal (American Society of Mammalogists 1967). Body weight was not corrected for loss of fluids. Maximum girth, and blubber weight with the skin attached (sculp) were also recorded. Blubber was removed from 27 skins and the skins weighed. These weights do not correct for oil retained by the pelt. All linear measurements were recorded to the nearest 0.5 cm except blubber thickness which was measured to the nearest 0.1 cm. Weights were measured to the nearest 200 g.

Ages were assigned by counting the number of dentinal annuli in thin cross-sections of lower canine teeth, under transmitted light (McLaren 1958a; Smith 1973). Each tooth was read three times on separate occasions and the results

averaged to obtain a final estimate.

Female reproductive tracts were preserved in 10% formalin. Ovaries were sectioned by hand and examined for the presence of follicles > 5 mm. in diameter and active corpora lutea (Smith 1973).

The growth of animals > 1 year was described using the von Bertalanffy growth curve: $\text{Standard Length} = B_0 (1 - e^{-(B_1 \cdot x + B_2)})$ where B_0 is the asymptotic length, B_1 is a growth rate constant (cm/yr), x is age in years and B_2 is the age at which seals had zero length if they had always grown in the manner described by the equation (Von Bertalanffy 1934). Computations for the growth curves were carried out using the non-linear procedure in the Statistical Analysis Systems package (SAS Institute Inc. 1982).

Predictive equations of the form $Y = aX_1^c \cdot X_2^d$ were calculated for body weight, sculp weight and skin weight using standard length, and maximum girth as the independent variables (Usher and Church 1969).

Fat content was determined on 31 animals. Half of the carcass sectioned longitudinally minus the sculp, and all of the viscera were shipped frozen to Montreal. Carcass and viscera samples were ground in a large animal grinder (Model 801B, Autio Co., Astoria Oreg.), freeze dried (Model 50 SRC, The Virtus Co., Gardiner, N.Y.) and reground in a Thomas-Wiley mill (Model 4, Wiley Co.) Philadelphia, P.). Total lipid content of the half carcass and viscera was determined

separately following extraction (chloroform:methanol, 2:1 by volume) for four hours in a microsoxhlet apparatus (Giese 1967). The crude extract was washed with 0.9% sodium chloride (Folch et al. 1957). Blubber weight was determined by subtracting the weight of the skin, from the sculp. Skin weights were estimated from skin weight-body length relationships presented in the results. Total lipid content (fat weight (g) x 100/ wet weight of seal carcass (g)) was estimated from the equation: %Fat = (carcass fat + viscera fat + fat content of blubber)/ (carcass weight + viscera weight + blubber weight). Blubber was assumed to have a total lipid content of 94% (Worthy and Lavigne 1983).

The mean age at sexual maturity and mean age of first reproduction was determined from the proportion of females with an active corpus luteum or follicle > 5 mm in diameter (DeMaster 1978) and the proportion of pregnant or lactating females (DeMaster 1981).

The mean ovulation and end of lactation dates were calculated by regressing the proportion of ovulating females and proportion of females which had finished lactation respectively on date of collection (Caughley 1977).

Catch curves were used to test the sample for over-representation or under-representation of different age classes in the sample by comparing Chapman-Robson survivorship values with survivorship values calculated from Heinke (1913) using a Chi-square test. Younger age classes are under

represented in the sample if the Chapman-Robson survivorship value is significantly less than the Heinke value. If the reverse is true then the youngest age group in the class interval is over-represented relative to the older age groups. (Robson and Chapman 1961; Smith 1973).

Equality of variances was tested using an $F_{\max}$ test (Snedecor and Cochran 1980). Differences between means were tested using a Student's t -test. Comparisons between means with unequal variances were examined using a modified t -test (Snedecor and Cochran) and are denoted by t' . All statistical analyses were completed using the Statistical Analysis System (SAS Institute Inc. 1982).

RESULTS

Sex ratios of yearlings, subadults (2-7+) and adults were 1:1 (Table 1). Adults (>7+ years old) comprised 46, 68 and 79 % of the catch in 1984, 1985, and 1986 respectively (Fig. 2). The proportion of immature animals varied with month of sampling, but the results were inconsistent. Since the location of hunting activity also varied with month, this change reflects spatial segregation of age groups rather than a seasonal effect (Table 2). In May 1984, 11 juveniles were obtained near Cheyne Point on the south-east side of Griffith Island. All animals were hauled out along an unstable crack

running in a southerly direction from the island. These animals were reluctant to enter the water when approached and readily returned to the ice surface after being disturbed. In 1985 there were more cracks running south from the southern end of the island in May and June than in the previous year. Juveniles again appeared to be concentrated in this area, but not to the same extent as in 1984. The same area was not hunted in 1986 because of the lack of ice. Seals were hunted along the east side of Griffith Island, but no groups of juveniles were seen. Analysis of catch curves from each year indicates that juveniles and young adult animals are under-represented in the samples from 1985 and 1986 and over-represented in the 1984 sample (Table 3).

Direct evidence on timing of birth and development of pups is difficult to obtain because the pups are hidden by the subnivean lairs and females transport their pups to alternative lairs when disturbed. Surveys for subnivean lairs began as early as mid-March, but no birth lairs were detected before 4 April. A lactating female was collected on 3 April 1984 but the majority of females collected in early April were pregnant. Pupping appears to peak in the fourth week of April based on a limited sample of 19 adult females (Table 4). Three neonates collected on 27 April, 8 May 1984 and 16 April 1985, had standard lengths of 60.5 cm, 66 cm and 60 cm respectively. Assuming a standard length at birth of 57.8 cm and a growth rate 0.61 cm/day (Smith 1987), the mean date of birth for this

sample would be 20 April. However, seven full term fetuses collected in late March and early April had a mean standard length of 63.6 cm, which indicates that the calculated length at birth of 57.8 cm is an underestimate. Using the same rate of growth as above with the longer length at birth results in a mean pupping date of 27 April.

Lactation continued into June. A pup with milk in its stomach was collected on 10 June and a lactating female was obtained on 18 June 1986, the last day of hunting. The mean date for the end of lactation based on the proportion of females that had finished lactation in May and June was 7 June (SE=3.5). This indicates a lactation period of 41-48 days assuming that pupping occurs between 20-27 April.

The mean date of ovulation based on the proportion of reproductive tracts collected after 20 April with an active corpus luteum or follicle > 5 mm was estimated as 31 May (SE=5.3) one week before end of lactation.

Mean age of maturity using the presence of a large follicle or an active corpus luteum in the ovary to indicate ovulation, was 7.0 years. The mean age at first reproduction based on lactating or pregnant females was 8.6 years. Age specific ovulation rates were calculated from reproductive tracts collected after 20 April. The unweighted mean ovulation rate for adult females ($> 7+$ years) were 0.889 (N=2), 0.847 (SE=0.10, N=6) and 1.0 (SE=0.0, N=5) for 1984, 1985 and 1986 respectively and 0.922 (SE=0.05, N=6) for all years combined

(Table 5). Reproductive rates calculated using pregnant or lactating females were lower than the rates estimated from the ovarian evidence. The unweighted mean reproductive rates for adult animals were 0.583 (SE=0.300 N=3), 0.698 (SE=0.135 N=5) and 0.724 (SE=0.116, N=6) for 1984, 1985 and 1986 respectively and 0.634 (SE=0.081, N=6) for all years combined (Table 6).

Seven full-term fetuses collected between 11 March and 9 April had a mean standard length of 63.6 cm (SE=1.2) and a mean weight of 4900 g (SE=219). The three neonates discussed earlier had a mean length of 62.2 cm (SE=1.9) and weighed 5900 g (SE=223). Nine pups which had moulted into the silver jar pelage (McLaren 1958a) were shot on the ice in May and June (Table 7). The study of pup growth was not examined further because of the low sample size and difficulties in ascertaining birth date and pup age.

Growth curves were fitted to the data from Barrow Strait, Amundsen Gulf (Smith 1987) and Baffin Island (McLaren 1958a). In all localities males were longer than females (Table 8). Male ringed seals from Barrow Strait were longer than males from the Amundsen Gulf, but were similar in size to those from Baffin Island. Female ringed seals were largest in Barrow Strait, intermediate in size from the Amundsen Gulf and smallest from Baffin Island.

Predictive equations were developed for body weight, sculp weight and skin weight (Table 9).

No differences in body weight or sculp weight were found

between juvenile (1+ - 7+ yrs) males and females. For the lumped sample adult male ringed seals were significantly heavier ($\bar{x}=70.7$ kg, $SE=1.4$, $N=94$) than females ($\bar{x}=62.4$ kg, $SE=1.7$, $N=88$, $t=3.8$, $df=182$, $p<0.0001$). In females the sculp formed 44.7 % ($SE=1.0$ $N=88$) of the total body weight which was slightly greater than in males where the sculp comprised 40.6% ($SE=0.4$ $N=94$) of the total body weight. Body and sculp weights of adult seals declined throughout the spring. An analysis of covariance showed that females were significantly heavier than males when collections began in late March ($F=16.6$ $p<0.0001$). The changes in body weight with date expressed as week of collection were described by the regressions; Male Body Weight (g) = $99999.0 - 1427.7$ (Week); ($F=11.3$, $df=1,92$, $R^2=0.11$, $p=0.001$); Female Body Weight (g) = $111044.0 - 2304.4$ (Week); ($F=20.0$, $df=1,86$, $R^2=0.19$, $p<0.0001$). The decline in sculp weight was described by the regression equations; Male Sculp Weight (g) = $49925 - 1029.7$ (Week); ($F=28.0$, $df=1,92$, $R^2=0.23$, $p<0.0001$); Female Sculp Weight (g) = $64527 - 1728.5$ (Week); ($F=34.3$, $df=1,86$, $R^2=0.28$, $p<0.0001$). Weight loss by pregnant females was described by the regression; Body Weight (g) = $133253 - 3266.8$ (week); ($F=27.2$, $df=1,43$, $p<0.0001$ $R^2=0.39$) and Sculp Weight (g) = $76387 - 2228.6$ (week); ($F=39.7$, $df=1,43$, $p<0.0001$, $R^2=0.48$).

Fat content was measured in 31 seals. Body fat increased with age, but no difference was seen between males and females (Table 10). Strong positive correlations were observed between

percent body fat and the condition indices; sculp weight maximum girth⁻², sculp weight standard length⁻², and body weight standard length⁻² (Table 11). Sometimes it is not possible to obtain sculp or body weight, but body measurements may still be recorded. Strong positive correlations were also observed between percent body fat and the condition indices; maximum girth² standard length⁻¹, and blubber thickness² standard length⁻¹ (Table 11).

The index sculp weight maximum girth⁻² was selected to examine seasonal changes in condition. In adults (>7 yrs old) no differences in condition were found between sexes or between years. Body condition declined from March to June, but considerable scatter was observed in the weekly condition values (Fig. 3). In females, no differences in condition were seen between pregnant and barren animals ($t=0.4$ $df=40$, $p=0.4$). Adult females collected after the mean pupping date of 20 April were examined for differences in condition between ovulating and non-ovulating animals. No differences were observed in 1984 ($t=1.2$, $df=29$, $p=0.17$) and 1986 ($t=0.9$, $df=67$, $p=0.37$), but in 1985 females showing evidence of ovulation were in significantly better condition ($\bar{x}=2.51$, $SE=0.08$, $t=3.1$, $df=62$, $p=0.003$) than were non-ovulating females ($\bar{x}=2.26$ $SE=0.04$).

Adults were in significantly better condition than were juveniles in each year of the study (Table 12). No differences in the condition of juveniles were found between 1984 and 1985

($t=0.8$, $df=73$, $p=0.4$) but juveniles in both years were in significantly poorer condition than juveniles collected in 1986 ($t=4.3$ $df=85$ $p<0.0001$ and $t=4.9$ $df=74$, $p<0.0001$ for 1984 and 1985 respectively) (Table 12).

DISCUSSION

The sex ratio of the shot sample did not differ significantly from unity. This contrasts with results from surveys of the breeding habitat which indicate that males are outnumbered by females or males form small aggregations (Smith and Stirling 1978; Smith et al. 1978; Smith and Hammill 1981; Hammill Section II). I believe the differences between the two samples reflects a bias in sampling. Male seals seem to be less wary than females and are therefore easier to collect. Mature males have a brown face during the spring months which can be used to distinguish them from females and immature seals. The possibility of hunting bias could be tested by visual surveys of the fast ice and monitoring approach distances to determine which group is more sensitive to hunting activity.

McLaren (1958b) and Smith (1973) examined the dynamics of ringed seal populations by constructing static life tables which assume the population has a stationary age distribution (Caughley 1977). This approach was not followed in this study. Variation in annual recruitment over large areas has been

shown to occur elsewhere (Smith 1987) and in this study under-representation of the juvenile age classes, variation in predation rates and changes in ice conditions make it unlikely that the assumption of a stationary population was satisfied.

Pupping in ringed seals appears to follow a latitudinal gradient. In Barrow Strait, the mean pupping date lies in the fourth week of April, one week later than in the Amundsen Gulf (Smith 1987) and three weeks later than in southern Baffin Island and Alaska (McLaren 1958a; Johnson et al. 1966). Lactation lasts for 41 to 48 days. Ovulation occurs approximately one week before the end of lactation (Smith 1987), not shortly after parturition as previously thought (McLaren 1958; Smith 1973).

The mean age of sexual maturity in Barrow Strait ringed seals was seven years old which is the same as estimated for ringed seals in the Okhotsk Sea (Fedoseev 1964), but one to two years older than the five to six years estimated for Baffin Island, Amundsen Gulf and Alaskan populations (McLaren 1958a; Smith 1973; 1987; Johnson et al. 1966). I believe the higher age of sexual maturity in seals from Barrow Strait results from a combination of differences between studies in age determination and under-representation of the younger age classes (McLaren and Smith 1985) in the fast ice, rather than ecological factors.

Ringed seals in Barrow Strait had lower reproductive rates than reported elsewhere (McLaren 1958b; Johnson et al.

1966; Smith 1987) with the exception of ringed seals in the Baltic Sea (Table 14), where high PCB levels might have interfered with reproduction (Helle 1980). Segregation of age classes and different methods make comparisons of reproductive rates between studies difficult (Smith 1987). Juveniles were under-represented in my samples. I recalculated reproductive rates from published sources excluding animals < 8 years old (Table 13). I also used the presence of a full term fetus or lactation as evidence of pregnancy. Most other studies have used ovulation, the presence of a blastocyst chamber or early term fetus to calculate pregnancy rates (McLaren 1958b; Smith 1973; Helle 1978; Smith 1987). These methods overestimate pregnancy rates because of reproductive failure between the time of ovulation and parturition. In humans it has been estimated that over 50% of pregnancies fail between conception and parturition (Shepard and Fantel 1979). In pinnipeds postimplantation failure may range from 5% to 34% (Bigg 1969; Pitcher and Calkins 1981; Fay 1982). Evidence of reproductive failure is hard to detect, but may be quite variable between years. Comparison of pregnancy rates with ovulation rates from samples collected the previous year provides some indication of the year to year changes in the incidence of reproductive failure.

Male ringed seals are about 5% longer than females. At sexual maturity females in Barrow Strait have reached 85.8% of their asymptotic length which agrees with the generalization

for pinnipeds given by Laws (1959).

McLaren (1958) suggested that body size increased with latitude. The growth curves I constructed support this hypothesis for females, but males from southern Baffin Island had an asymptotic length similar to male seals in Barrow Strait. McLaren's (1958a) estimate of 135 cm and 138 cm for females and males respectively are also similar to the asymptotic lengths of the High Arctic population. Large differences in body size are also seen between seals from the Okhotsk Sea, Alaska, Baffin Island and the Baltic Sea, yet all three areas lie at the same latitude as southern Baffin Island. Body size may also be tied to stability of the fast ice (McLaren 1958a; Helle 1979). Ringed seals in the Okhotsk Sea occupy the unstable pack ice and are generally smaller than other populations with the exception of seals in Alaska which are found in the fast ice. This comparison of body size between areas is not completely valid since different methods were used to calculate asymptotic lengths. However, much more information on morphometrics of ringed seals is now available than when McLaren (1958a) first proposed his hypotheses. Given the discrepancies identified above a re-examination of these hypotheses appears warranted.

Body condition of both male and female ringed seals declined throughout the spring months. At the beginning of hunting in March female ringed seals were heavier than males, but lost weight at a higher rate. Male seals lost 204 g day^{-1}

with 72% of this weight being lost from the blubber. Assuming a caloric value of 8.77 kcal g^{-1} (Worthy 1982), males would lose $1789 \text{ kcal day}^{-1}$. The average daily metabolic rate (ADMR) of an adult male seal weighing 83 kg in late March would be approximated by ; $\text{ADMR} = 2 \cdot (70 W^{0.75})$ where W is body weight in kg (Stewart and Lavigne 1984). This results in an ADMR of 3850 kcal, with 46% of this energy being derived from stored reserves. The ADMR of an adult female weighing 89kg at the start of lactation would be 4057 kcal. The cost of lactation can be estimated from $\text{MP} = ((G + (2 \times 70 W^{0.75})) E^{-1})$ where MP is milk production (kcal), G is the growth increment (kcal) and E is the proportion of energy in the milk available to the pup as net energy (Lavigne et al. 1982). I assumed a daily weight gain of 0.44 kg day^{-1} based on a birth weight of 5 kg, a weaning weight of 25 kg (Table 7), a lactation period of 45 days and a caloric value for the weight gain of 5.25 kcal g^{-1} (Stirling and McEwen 1975). E was assumed to be 0.85 (Anderson and Fedak 1987). Daily milk production costs the female $3962 \text{ kcal} \times 1.4$ (Anderson and Fedak 1987) resulting in a total daily energy requirement of 9603 kcal. Females lose an average of 467 g day^{-1} or $4093 \text{ kcal day}^{-1}$ which would supply 43% of their estimated daily requirements. After a lactation period of 45 days females have lost 21 kg or 24% of their body weight. This is similar to the estimated 16% to 22% weight loss reported for hooded seals (Cystophora cristata) (Bowen et al. 1987) and harp seals (Phoca groenlandica) (Stewart and

Lavigne 1984), but is much lower than the figure of 46% reported for the Weddell seals (Leptonychotes weddelli) (Tedman and Green 1987), which occupy the antarctic fast-ice. The accuracy of these calculations depends on the assumption that all females give birth at the same time. In ringed seals the pupping season extends from early April until mid-May and it is not possible to determine how long animals have been lactating. Therefore, it is likely that the above calculations underestimate the actual rate of weight loss (Anderson and Fedak 1987).

Although ringed seals do feed under the fast ice, it is apparent that they depend on stored body reserves to supply much of their daily energy requirements. After the pups are weaned, the adults continue to lose weight in the spring since much of their time is spent hauled out on the ice for the moult (McLaren 1958a; Smith and Hammill 1981). Intensive feeding resumes in the summer just after breakup. The improvement in condition documented during the fall and early winter (McLaren 1958a; Smith 1987) may be crucial to reproductive success (Smith 1987), because of its possible effects on implantation in the early fall and ovarian function in the subsequent spring. Foraging activity in the fall depends on both overall food abundance and access to food resources. I proposed in section II- that condition will be higher in years when the ice consolidates late in the season because foraging would not be limited by the need to maintain

breathing holes. In 1986, the ice consolidated one to two months later than in the previous two years and in some areas open water or loose pack ice persisted throughout the winter. In adults, no differences in body condition were observed between years, but seal densities in the study areas were lower in 1984 and 1985 than in 1986. Smith and Hammill (1981) proposed that females defend small territories around the birth lair complex, within territories maintained by males. Adults may respond to reduced availability of food by increasing the spacing between individual seals resulting in lower seal densities. Juvenile seals collected in 1986 were in significantly better condition than juveniles collected in the previous two years. This provides some support for the above hypothesis, but a larger data set is required before it can be adequately tested.

REFERENCES

- American Society of Mammalogists. 1967. Standard measurements of seals. J. Mammal. 48: 459-462.
- Anderson, S.S. and M. A. Fedak. 1987. Grey seal, Halichoerus grypus, energetics: females invest more energy in male offspring. J. Zool., Lond. 211:667-679.
- Bertalanffy, L. von. 1934. Untersuchungen ubber die Gesetzlichkiet des Wachstums. I. Roux Archiv. 131: 613.
- Bigg, M.A. 1969. The harbor seal in British Columbia. Bull. Fish. Res. Board Can. 172:1-33.
- Bowen, W.D., D.J. Boness and O.T. Oftedal. 1987. Mass transfer from mother to pup and subsequent mass loss by the weaned pup in the hooded seal, Cystophora cristata. Can. J. Zool. 65:1-8.
- Bradstreet, M.S.W., K.J. Finley, A.D. Sekerak, W.B. Griffiths, C.R. Evans, M.F. Fabijan and H.E. Stallard. 1986. Aspects of the biology of Arctic Cod (Boreogadus saida) and its importance in Arctic marine food chains. Can. Tech. Rep. Fish. Aquat. Sci. 1491. 193 p.
- Caughley, G. 1977. Analysis of vertebrate populations. John Wiley and Sons. Toronto, Ont. 234 p.
- DeMaster, D.P. 1978. Calculation of the average age of sexual maturity in marine mammals. J. Fish. Res. Board Can. 35: 912-915.
- DeMaster, D.P. 1981. Estimating the average age of first birth in marine mammals. Can. J. Fish. Aquat. Sci. 38:237-239.
- Fay, F.H. 1982. Ecology and biology of the Pacific walrus, Odobenus rosmarus divergens Illiger. North American Fauna No. 74. U.S. Dept. of the Interior, Washington, DC.
- Fedoseev, G.A. 1964. On the embryonic and postembryonic growth and sexual maturity of Okhotsk ringed seal. Zool. Zh. 43: 1228-1235. (Trans. from Russian. Can. Trans. Fish Aquat. Sci. No. 5277: 14 p. 1986.
- Folch, J., M. Lees and G.H. Scoane-Stanley. 1957. A simple method for the isolation and purification of total lipids from animal tissues. J. Biol. Chem. 226: 497-509.

- Frost, K.J. and L.F. Lowry. 1981. Ringed, Baikal and Caspian seals-Phoca hispida, Phoca sibirica, and Phoca caspica. p. 29-53. In S.H. Ridgway and R.J. Harrison (ed.) Handbook of marine mammals. Vol. 2. Academic Press. Toronto, Ont. 359 p.
- Giese, A.C. 1967. Some methods for the study of the biological constitution of marine invertebrates. Oceanogr. Mar. Biol. Ann. Rev. 5: 159-186.
- Heincke, F. 1913. Investigations on the plaice. General report. I. The plaice fishery and protective measures. Preliminary brief summary of the most important points of the report. Rapp. Proces-Verbaux Reunions Cons. Perma. Int. Explor. Mer 16: 67 p.
- Helle, E. 1978. 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.
- Helle, E. 1979. Growth and size of the ringed seal, Phoca (Pusa) hispida Schreber, in the Bothnian Bay, Baltic. 1979. Sonderdruck aus Z.f. Säugetierkunde Bd. 44: 208-220.
- Helle, E. 1980. Lowered reproductive capacity in female ringed seals (Phoca hispida) in the Bothnian Bay, northern Baltic Sea, with special reference to uterine occlusions. Ann. Zool. Fennici 17:147-158.
- 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 Thompson region, Alaska. U.S. At. Energy Comm., Div. Tech. Inf. Ext., Oak Ridge, TN. 1250 p.
- Lavigne, D.M., W.W. Barchard, S. Innes and N.A. Oritsland. 1982. Pinniped bioenergetics. FAO Fisheries Series No. 5. 4:191-235.
- Laws, R.M. 1959. Accelerated growth in seals, with special reference to the Phocidae. Hvalfangst-Tidende 9: 425-452.
- Marko, J.R. 1982. The ice environment of eastern Lancaster Sound and northern Baffin Bay. Indian and Northern Affairs Program. Environmental Studies No. 26. 215 p.
- McLaren, I.A. 1958. The biology of the ringed seal (Phoca hispida) in the eastern Canadian Arctic. Bull. Fish. Res. Board Can. 118: 97 p.

- McLaren, I.A. 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. Marine Mammal Science 1:54-83.
- Pitcher, K.P. and D.G. Calkins. 1981. Reproductive biology of Steller sea lions in the Gulf of Alaska. J. Mammal. 62:599-605.
- Robson, D.S. and D.G. Chapman. 1961. Catch curves and mortality rates. Trans. Amer. Fish. Soc., 91:181-189.
- SAS Institute Inc. 1982. SAS user's guide: Statistics, 1982 edition. Cary, NC. 584p.
- Shepard, T.H. and A.G. Fantel. 1979. Embryonic and early fetal loss. Clin. Perinatol. 6: 219-243.
- Smith, T.G. 1973. Population dynamics of the ringed seal in the Canadian eastern Arctic. Bull. Fish. Res. Board Can. 181: 55p.
- Smith, T.G. 1987. The ringed seal, Phoca hispida of the Canadian western Arctic. Can. Bull. Fish. Aquat. Sci. 216: 81 p.
- Smith, T.G. and M.O. Hammill. 1981. Ecology of the ringed seal, Phoca hispida, in its fast ice breeding habitat. Can. J. Zool. 59: 966-981.
- Smith, T.G., K. Hay, D. Taylor and R. Greendale. 1978. Ringed seal breeding habitat in Viscount Melville Sound, Barrow Strait and Peel Sound. ESCOM Report No. AI-22. Department of Indian and Northern Affairs, Ottawa, Ont. 85 p.
- Smith, T.G. and I. Stirling. 1978. Variation in the density of ringed seal (Phoca hispida) birth lairs in the Amundsen Gulf, Northwest Territories. Can. J. Zool. 56: 1066-1071.
- Snedecor, G.W. and W.G. Cochran. 1980. Statistical methods. 7th edition. Iowa State University Press. Ames, Iowa. 507 p.
- Stewart, R.E.A. and D.M. Lavigne. 1984. Energy transfer and female condition in nursing harp seals Phoca groenlandica. Holarct. Ecol. 7: 182-194.

- 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., 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.
- Tedman, R. and B. Green. 1987. Water and sodium fluxes and lactational energetics in suckling pups of Weddell seals (Leptonychotes weddelli). J. Zool., Lond. 212: 29-42.
- Testa, J.W., D.B. Siniff, M.J. Ross and J.D. Winter. 1985. Weddell seal-antarctic cod interactions in McMurdo Sound, Antarctica. p. 561-565. In W.R. Siegfried, P.R. Condy and R.M. Laws (ed.) Antarctic nutrient cycles and food webs. Springer-Verlag, Berlin.
- Usher, P.J. and M. Church. 1969. On the relationship of weight, length and girth of the ringed seal (Pusa hispida) of the Canadian arctic. Arctic 22: 120-129.
- Worthy, G.A.J. 1982. Energy sources of harp seals, Phoca groenlandica, during the post-weaning period. M.Sc. thesis, University of Guelph, Guelph, Ont. 100 p.
- Worthy, G.A.J. and D.M. Lavigne. 1983. Energetics of fasting and subsequent growth in weaned harp seal pups, Phoca groenlandica. Can. J. Zool. 61: 447-456.

Table 1. Sex ratios of animals collected in Barrow Strait between March and June 1984 to 1986.

Age (years)	1984 M:F	1985 M:F	1986 M:F
1+	3:1	5:3	2:2
1+ - 7+	18:15	11:6	3:4
> 7+	21:15	38:29	20:32

Table 2. Percent monthly changes in age composition of harvest. N is number of animals. Age is in years.

		Percent Age Composition			
	N	0+	1+	1-7+	7+
1984					
APR	10	10	-	20.0	70.0
MAY	33	3.0	9.1	69.7	18.2
JUNE	32	9.4	3.1	21.9	65.6
1985					
APR	6	16.7	0	0	83.3
MAY	51	0	15.7	11.8	72.5
JUNE	40	7.5	5.0	27.5	60.00
1986					
APR	4	0	0	25	75
MAY	14	7.1	0	7.2	85.7
JUNE	47	4.3	8.5	10.6	87.2

Table 3. Chapman-Robson (Robson and Chapman 1961) and Heinke (1913) survivorship estimates to test representation of age classes in sample. * is significant at $p < 0.05$. n.s. = not significant.

Year	Age	Robson-Chapman $\bar{X} \pm SD$	Heinke	χ^2	Psig.
1984	0-20	0.881 $\pm$ 0.013	0.935	2.42	n.s.
	1-20	0.874 $\pm$ 0.014	0.944	3.72	n.s.
	2-20	0.864 $\pm$ 0.016	0.721	13.66	*
	3-20	0.887 $\pm$ 0.015	0.959	2.90	n.s.
	4-20	0.877 $\pm$ 0.017	0.936	1.74	n.s.
	9-20	0.833 $\pm$ 0.026	0.943	3.63	n.s.
	10-20	0.811 $\pm$ 0.030	0.909	2.57	n.s.
	12-20	0.755 $\pm$ 0.042	0.963	8.41	*
1985	0-20	0.899 $\pm$ 0.010	0.959	4.35	*
	1-20	0.892 $\pm$ 0.011	0.894	0.002	n.s.
	3-20	0.892 $\pm$ 0.012	0.973	5.79	*
	4-20	0.882 $\pm$ 0.013	0.986	8.68	*
	5-20	0.868 $\pm$ 0.015	0.986	10.16	*
	7-20	0.849 $\pm$ 0.017	0.943	5.83	*
	8-20	0.832 $\pm$ 0.019	0.955	8.75	*
	9-20	0.807 $\pm$ 0.022	0.953	10.91	*
	10-20	0.774 $\pm$ 0.026	0.867	3.81	n.s.
1986	0-20	0.909 $\pm$ 0.011	0.954	1.74	n.s.
	1-20	0.904 $\pm$ 0.012	0.935	0.77	n.s.
	2-20	0.901 $\pm$ 0.012	0.983	4.82	*
	5-20	0.883 $\pm$ 0.015	0.982	5.90	*
	6-20	0.869 $\pm$ 0.017	0.963	4.79	*
	7-20	0.855 $\pm$ 0.019	0.981	7.75	*
	8-20	0.833 $\pm$ 0.022	0.863	0.38	n.s.
	11-20	0.788 $\pm$ 0.032	0.917	4.54	*

Table 4. Number of pregnant and lactating females shot in early spring.

Date	Number pregnant	Number lactating
Before 22 March	2	0
23 Mar - 2 Apr	2	0
3 Apr - 13 Apr	1	1
14 Apr - 24 Apr	2	2
25 Apr - 5 May	.	.
6 May - 16 May	0	2
17 May - 27 May	0	7

Table 5. Age specific ovulation rates for females collected in 1984, 1985 and 1986.

Age	1984		1985		1986		All years combined	
	N	Proportion	N	Proportion	N	Proportion	N	Proportion
1	2	0.0	4	0.0	1	0.0	7	0.0
2	8	0.12	1	0.0	-	-	9	0.11
3	2	0.0	-	-	-	-	2	0.0
4	-	-	1	0.0	-	-	1	0.0
5	3	0.0	1	0.0	-	-	4	0.0
6	3	0.0	-	0.0	-	-	3	0.0
7	-	-	-	0.0	1	1.0	1	1.0
8	-	-	2	0.5	2	1.0	4	0.75
9	1	1.0	2	1.0	4	1.0	7	1.0
10	-	-	1	1.0	2	1.0	3	1.0
11	-	-	1	1.0	-	-	1	1.0
12	-	-	3	1.0	5	1.0	8	1.0
>12	9	0.78	12	0.58	11	1.0	32	0.78

Table 6. Age specific reproductive rates. The presence of a fetus or evidence of lactation was used to indicate pregnancy. Smoothed age specific reproductive rates were estimated from the regression for all years combined. Arc sine (pregnancy rate) = $0.066 (\text{age})$; ($F = 64.5$, $df = 1,17$).

Age	1984		1985		1986		Smoothed reproductive rates
	N	Proportion pregnant	N	Proportion pregnant	N	Proportion pregnant	
4	2	0.0	1	0.0	1	0.0	0.260
5	2	0.0	1	0.0	1	0.0	0.323
6	3	0.0	-	-	-	-	0.384
7	-	-	1	0.0	1	0.0	0.444
8	-	-	2	0.5	5	0.4	0.502
9	-	-	2	0.0	4	1.0	0.557
10	2	0.0	3	1.0	2	0.5	0.611
11	1	1.0	3	1.0	1	1.0	0.661
12	-	-	4	0.67	4	0.5	0.709
>12	7	0.75	14	0.32	13	0.945	0.914

Table 7. Morphometrics of neonates collected in the spring. All animals had silver jar pelage.

Specimen number	Date	Sex	Standard length (cm)	Blubber thickness (cm)	Body weight (g)	Remarks
8619	18 May 86	F	88	3.4	20000.0	Shot beside female
2634	3 Jun 86	M	79	1.6	12045.0	Empty stomach
8664	8 Jun 86	F	91	4.0	22727.0	Milk in stomach
8565	6 Jun 85	M	82	3.2	19091.0	Milk in stomach
8569	10 Jun 85	M	91	3.3	23182.0	Milk in stomach
8583	13 Jun 85	M	75	1.4	9545.0	Mysids in stomach
8479	18 Jun 84	M	81	2.0	12045.0	Empty stomach
8480	23 Jun 84	M	83	2.2	16590.0	Empty stomach
8482	23 Jun 84	M	85	2.4	22045.0	Empty stomach

Table 8. Estimated parameters and standard errors from von Bertalanffy growth curves calculated for three populations of ringed seals. B_0 is asymptotic length (cm), B_1 is a growth rate constant (cm/yr), and B_2 is the age (years) when length is 0 if growth continued as described by the equation.

	Barrow Strait		Baffin Island		Amundsen Gulf	
	Males N=114	Females N=106	Males N=54	Females N=33	Males N=629	Females N=725
B_0	141.86 ±3.47	135.63 ±3.76	141.05 ±9.40	120.46 ±5.13	130.10 ±2.32	123.24 ±1.14
B_1	0.17 ±0.03	0.17 ±0.04	0.11 ±0.05	0.25 ±0.12	0.18 ±0.04	0.25 ±0.04
B_2	-0.76 ±0.05	-0.87 ±0.07	-1.04 ±.11	-1.16 ±0.16	-1.11 ±0.06	-1.14 ±0.08

Table 9. Regression equations to predict weights of different body components from girth and length data. Weights are in g, girth and length are in cm.

Body Weight (g)	= 0.1509 • Maximum Girth	2.0527	Standard Length	0.6891
$R^2 = 0.98, df = 2,268, F = 5296$				
Sculp Weight (g)	= 0.0251 • Maximum Girth	2.9764	$R^2 = 0.92$ $df = 1,265$	$F = 3268$
Skin Weight (g)	= Standard Length	1.7545	$df = 1,25$	$F = 70503$

Table 10. Age, sex, weights of different body components and body fat composition of 31 seals.

Age	Sex	N	Body Weight kg		Sculp Weight kg		Percent Body Fat		Percent Carcass Fat		Percent Blubber		Percent Viscera Fat	
			$\bar{X}$	Range	$\bar{X}$	Range	$\bar{X}$	Range	$\bar{X}$	Range	$\bar{X}$	Range	$\bar{X}$	Range
1	F	1	6.4		4.8		14.6		6.8		7.4		0.4	
1	M	1	12.5		4.3		20.2		3.1		16.7		0.4	
2	F	3	16.1	14.3-17.5	6.1	5.4- 6.4	24.4	19.3-28.8	2.8	2.4-3.1	21.2	16.0-25.3	0.3	0.2-0.5
2	M	2	18.8	18.4-19.1	7.6	6.4- 8.9	27.9	18.9-36.8	2.4	2.2-2.6	25.2	16.4-33.9	0.3	0.2-0.3
5	F	1	28.6		12.3		33.0		5.2		27.6		0.3	
7	M	1	45.9		23.2		53.7		3.1		50.4		0.2	
≥ 8	F	11	65.4	44.3-86.8	28.2	15.0-38.6	45.1	28.5-53.7	3.1	1.7-5.0	41.8	25.6-51.0	0.3	0.2-0.3
≥ 8	M	11	63.8	48.6-82.7	25.5	21.6-32.5	40.9	37.8-46.1	3.4	1.9-5.4	37.2	35.0-42.2	0.3	0.2-0.4

Table 11. Pearson correlation coefficients and probability levels, between percent body fat (g fat . g body wt.⁻¹) and indices of condition.

Condition Index	Pearson correlation coefficient
<u>Sculp weight</u>	0.9421
<u>Maximum girth²</u>	0.0001
<u>Sculp weight</u>	0.936
<u>Standard length²</u>	0.0001
<u>Body weight</u>	0.875
<u>Standard length²</u>	0.0001
<u>Maximum girth²</u>	0.890
<u>Standard length</u>	0.0001
<u>Blubber thickness²</u>	0.8000
<u>Standard length</u>	0.0001*
<u>Axillary girth²</u>	0.392
<u>Standard length</u>	0.030

Table 12. Mean condition of adults and juvenile seals collected in 1984, 1985 and 1986 using the index sculp weight $\cdot$ (maximum girth) $^{-2}$

	N	Mean	Standard error
Adults			
1986	75	2.38	0.04
1985	69	2.36	0.04
1984	38	2.45	0.05
Juveniles			
1986	18	2.02	0.13
1985	26	1.61	0.09
1984	37	1.69	0.07

Table 13. Mean reproductive rates of female ringed seals from different populations. Amundsen Gulf data excludes low years (Smith 1987).

All age groups	Reproductive Rates	Reproductive Rates Animals $\geq$ 8 years old
Barrow Strait all ages	0.45	0.634
Amundsen Gulf (Smith 1987)	0.54	0.747
Baffin Island (Smith 1987)	0.62	0.774
Baffin Island (McLaren 1958b)	0.779	0.810
Alaska (Johnson <u>et al.</u> 1966)	0.857	-
Baltic Sea (Helle 1977)	0.261	0.300

Figure 1. Map of study area showing locations of main hunting effort.

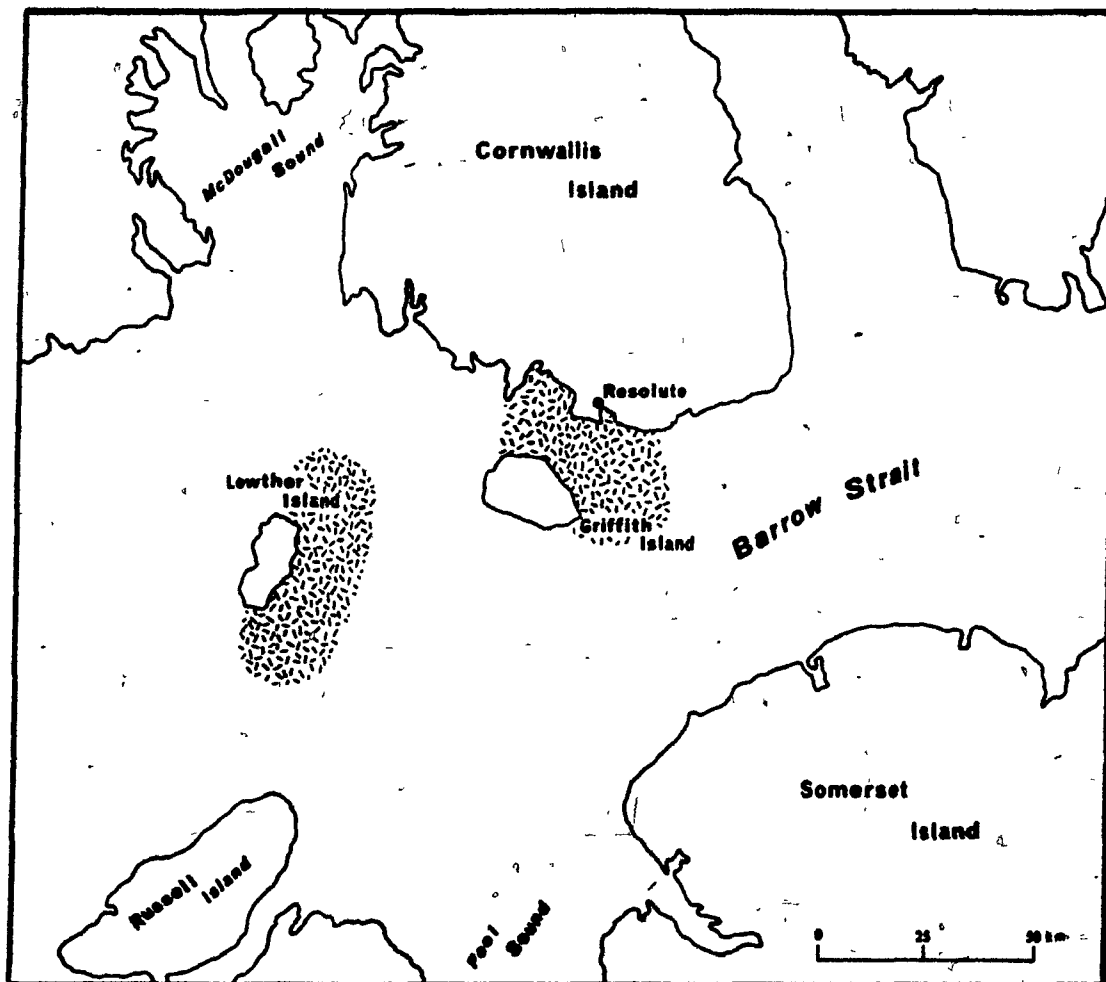


Figure 2.

Age frequencies of seals collected between March and June, 1984 to 1986 in Barrow Strait.

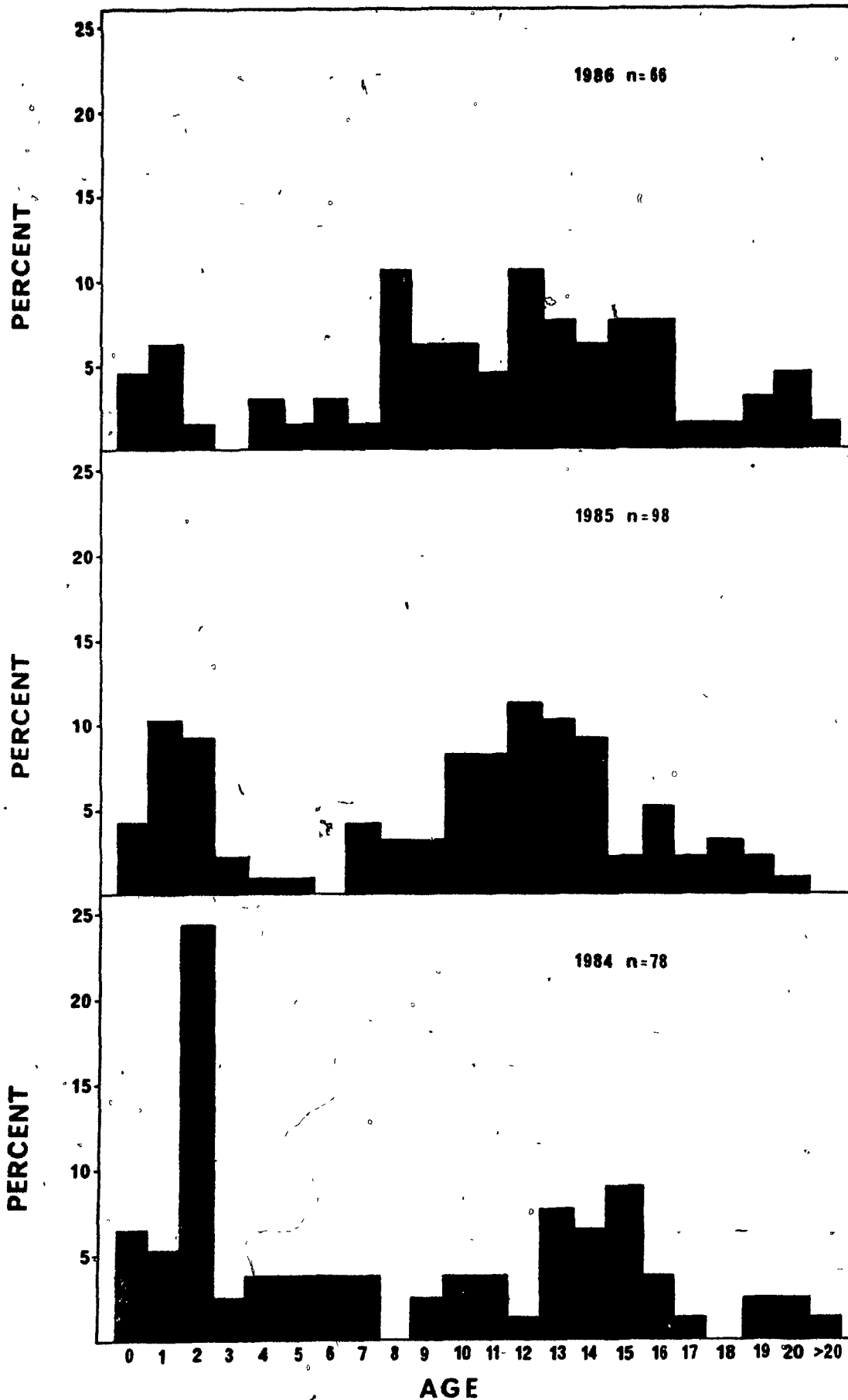
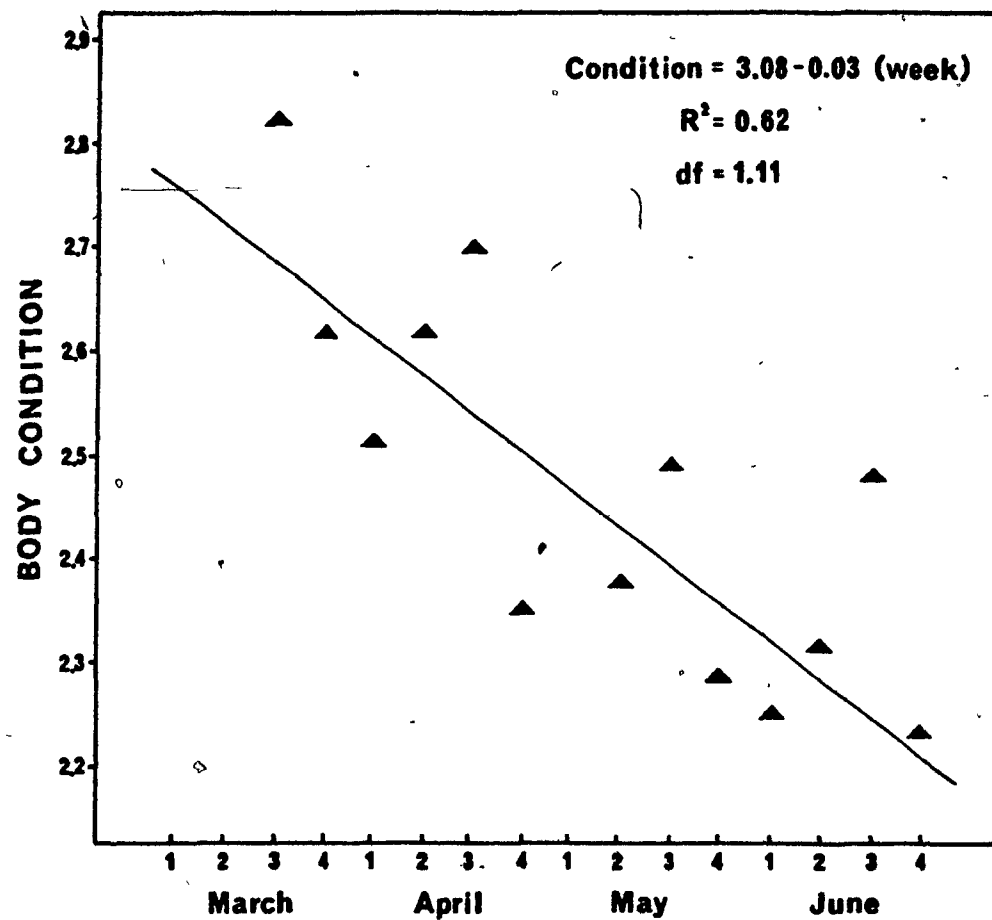


Figure 3.

Changes in body condition of ringed seals
in Barrow Strait between March and June.



SUMMARY AND GENERAL CONCLUSIONS

At the present time, surveys using dogs to locate the subnivean structures of the ringed seal are the only means of studying its distribution and abundance in the fast ice. The information presented in Section I represents the first detailed examination of the dog survey method and its shortcomings. The results show that seal holes are a valid index of seal abundance, but the ability of the dog to detect lairs varies with local conditions. The combination of removal sampling and the dog survey technique provides a means of estimating seal hole density. This method also provides a measure of survey quality which is essential if comparisons are to be made between different studies.

In Section II, it was shown that the fast ice is a very heterogeneous habitat subject to marked year to year changes in ice and snow conditions. By occupying this habitat the ringed seal has increased its exposure to terrestrial predators. The utilization of multiple breathing holes or haul-out lairs and the ability to scratch new holes in the ice are a direct response to predation pressure.

The strong positive correlation observed between seal abundance and the habitat features; late consolidating ice and deep snow cover was the most significant finding in Section II. This provides some support for the hypothesis that the

amount of habitat suitable for breeding is an important factor limiting ringed seal populations, but it also suggests that access to adequate food resources before freeze-up is an important consideration in the early winter months. Habitat conditions had an important effect on the distribution of female seals in the fast ice, but social factors may control the distribution of male and juvenile animals. It has been proposed in previous studies that males maintain underwater territories from which other males and juvenile seals are excluded. It is unlikely that these territories would be established until after the ice had consolidated and reached a thickness at which seals would be reluctant to dig new holes. At this time the movement of seals underneath the ice would be limited by their access to breathing holes. Defense of territories would not begin in earnest until after parturition, when the movements of the female are restricted by the demands of the pup and would last until mating which takes place in late May, five to six weeks after parturition.

The age composition, age specific reproductive rates and body condition of ringed seals occupying the fast ice were examined in Section III. The results from this section support the findings in Section II and previous studies that juvenile animals are excluded from the breeding habitat.

Age specific reproductive rates for ringed seals in Barrow Strait were lower than reported for ringed seal populations from other areas. These differences are thought to result from

the different methods used in other studies to calculate these rates. Previous studies have used evidence of ovulation, a blastocyst chamber or a small fetus to indicate pregnancy. These methods overestimate reproductive rates because reproductive failure can occur at any stage between ovulation and parturition .

Ringed seals depend heavily on body reserves accumulated during the autumn months to carry them through the winter and spring. Foraging in the fall and early winter will be affected by both food abundance and access to food resources. Early consolidating ice interferes with foraging because seal activity is restricted by the need to maintain breathing holes. In order to test this hypothesis long-term studies monitoring reproductive rates, body condition and habitat conditions are required.