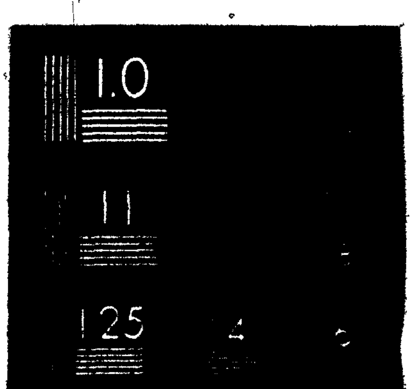
1 OF/DE 2



NATIONAL LIBRARY
OTTAWA

BIBLIOTHÈQUE NATIONALE
OTTAWA

CANADA

NAME OF AUTHOR...Jean Boulva...

TITLE OF THESIS...The harbour seal, Phoca vitulina concolor, in eastern Canada.

UNIVERSITY...Dalhousie...

DEGREE FOR WHICH THESIS WAS PRESENTED...Ph. D....

YEAR THIS DEGREE GRANTED...1973...

Permission is hereby granted to THE NATIONAL LIBRARY OF CANADA to microfilm this thesis and to lend or sell copies of the film.

The author reserves other publication rights, and neither the thesis nor extensive extracts from it may be printed or otherwise reproduced without the author's written permission.

(Signed)...[redacted]...

PERMANENT ADDRESS:

...4040 Wilson...
...Montréal 260,...
...Québec...

DATED...23 July...1973

THE HARBOUR SEAL, PHOCA VITULINA CONCOLOR,

IN EASTERN CANADA

by

Jean Boulva

Submitted in partial fulfillment of the requirements for the Degree of Doctor of Philosophy at Dalhousie University

July 1973

Approved by:

[redacted]

DALHOUSIE UNIVERSITY

Date 23 July 1973

Author Jean Boulva

Title The harbour seal, Phoca vitulina concolor, in eastern Canada.

Department or School Biology

Degree Ph. D. Convocation Fall Year 1973

Permission is herewith granted to Dalhousie University to circulate and to have copied for non-commercial purposes, at its discretion, the above title upon the request of individuals or institutions.

[redacted]

Signature of Author

TABLE OF CONTENTS

	Page
Abstract	viii
List of tables	ix
List of figures	xiii
Introduction	1
Material and methods	4
Collection of samples and field observations	4
Treatment of samples	7
Age determination	7
Reproductive organs	8
Embryos and foetuses	8
Stomach content	8
Population estimates	9
Distribution and abundance	10
Present status	10
Past distribution	14
Natural factors controlling the distribution	14
Growth	20
Prenatal growth	20
Length	20
Weight	21
Growth from birth to weaning	24
Nursed pups	24
Deserted pups	24
Growth after weaning	28
Length	28
Weight	28

	Page
Techniques to estimate weight	28
Length-weight relationship	28
Length-girth-weight relationship	31
Comparison of the two methods	31
Reproduction	34
Age at sexual maturity	34
Males	34
Females	39
Fertility of females	43
Annual reproductive cycle	44
Males	44
Females	46
Annual cycle of the population	52
Winter	52
Spring	57
Movement of seals	57
Whelping	57
Lanugo and umbilicus	61
Preweaning mortality	61
Weaning	64
Mating	66
Summer and fall	67
Moult	67
Predators	67
Regional differences in diurnal activity patterns	68
Population dynamics	71
Sampling	71

Page

Sex ratio 75

Population structure 75

Fourchu 75

Charlotte County 78

Maritimes 82

Population changes in the Maritimes 87

The bounty 87

Population estimates 90

Natural mortality 92

Rate of increase 93

Prediction 96

Case 1: bounty maintained 96

Case 2: bounty discontinued 97

Case 3: sustainable yield 98

Discussion 98

Feeding and production 101

Consumption in nature 101

Foods consumed 101

Changes in feeding with age 104

How is fish eaten 104

Seasonal changes in condition 105

Quantity of food ingested per meal 109

Consumption in captivity 110

Production 113

Population model 113

Description of terms used 114

Energy flow table 116

Page

Energy flow diagram 120

Discussion 120

Acknowledgements 125

References 127

Appendix A: Boulva, 1971 135

Appendix B: Boulva, 1973 140

ABSTRACT

This report on the distribution, numbers and biology of the harbour seal covers the coastal areas of New Brunswick, insular Newfoundland, Nova Scotia, Prince Edward Island, Québec and the French islands of Saint-Pierre et Miquelon. About 13,000 harbour seals occur in eastern Canada and are distributed in small populations. Variations in the numbers of postcanine teeth suggest a restricted genetical exchange between these populations. The abundance of harbour seals in an area seems to be related to the availability of islets or sandbars. Growth rates of pups during nursing are greater than the growth rate of the prenatal seal (0.58 cm/day vs 0.36 cm/day); pups increase their weight on the average from 10 kg at birth to 25 kg at weaning. Fully grown males and females average respectively 159 cm and 145 cm in nose-tail length, and 91 kg and 72 kg in weight. Techniques to estimate weight from length and girth are discussed. Most males become sexually mature at 6 years old while most females ovulate at 4 years old. The age specific fertility rates of females are given. Males are potent from early May to late July, possibly earlier but data are lacking for March and April. Most adult females ovulate around mid-June and implantation is delayed for about 88 days. Active gestation lasts 8 months. In winter, the Sable Island population forms large herds and becomes more pelagic; in cold weather, these seals do not generally haul-out on land at air temperatures below -15°C. The large herds break down just before whelping which starts in mid-May in most areas. The birth season generally lasts one month. Preweaning pup mortality averages 17% during the first month of life on Sable Island. Pups are weaned about 31 days after birth. Moulting takes place during July and August and can be completed in about 20 days for individual seals. On Sable Island, seals generally spend the night at sea, hauling-out during the day, while on the mainland, hauling-out appears more closely related to low tides. Females live older than males (30 vs 25 years old) and constitute 52% of the seals aged 1 year old or more. Life tables for females from a hunted and non-hunted population suggests that the age specific fertility rates of the former do not apply to the latter. The harbour seals in New Brunswick, Nova Scotia and Prince Edward Island were estimated to number 12,000 in 1949 and 4,800 in 1972. These two estimates combined with known hunting mortality and pup production rates permit a calculation of an annual mortality of 0.164 and a realised annual rate of increase of -0.03. The consequences of maintaining or discontinuing the bounty are examined. An annual sustainable yield of 5% of the total postwhelping population could be achieved with the present population. The diet consists mainly of herring, flounder and squid. There is no indication of a decrease in feeding intensity during the summer moult. The drop in the condition index of the seal in spring and summer seems to parallel the drop in condition of a good proportion of the fish eaten at that time. The quantities of food found eaten in nature agree well with feeding rates of captive seals of this species with controlled diets. A 20 kg and a 100 kg harbour seal can live well on a diet of food equivalent respectively to 5% and 2.2% of their body weight per diem. An energy flow table is described for a harbour seal population; it indicates an ecological efficiency of 6% assuming that the seals eat on the average only once a day.

LIST OF TABLES

		Page
Table 1.	Numbers of harbour seals aged one year or more collected for this study, per month and per locality of sampling, for males and females.	5
2.	Variations in the numbers of post-canine teeth (premolars and molars) on the lower jaw of harbour seals in seven areas of eastern Canada.	11
3.	Relation between the total number of pups killed during the years 1951, 1959, 1962-64, 1966-70 and the numbers of islets, 500 yards long or less, counted on hydrographic charts of Nova Scotia.	16
4.	Age at maturity of male and age at maturity with age specific fertility rates of female harbour seals in eastern Canada.	38
5.	Percentage of the follicle luteinized in females collected in June and July in northeastern Nova Scotia.	47
6.	Presence or absence of an implanting blastocyst indicated by the presence or absence of a bulbous swelling on the cornua of harbour seals collected during September and October in northeastern Nova Scotia	50

LIST OF TABLES

		Page
Table 1.	Numbers of harbour seals aged one year or more collected for this study, per month and per locality of sampling, for males and females.	5
2.	Variations in the numbers of post-canine teeth (premolars and molars) on the lower jaw of harbour seals in seven areas of eastern Canada.	11
3.	Relation between the total number of pups killed during the years 1951, 1959, 1962-64, 1966-70 and the numbers of islets, 500 yards long or less, counted on hydrographic charts of Nova Scotia.	16
4.	Age at maturity of male and age at maturity with age specific fertility rates of female harbour seals in eastern Canada.	38
5.	Percentage of the follicle luteinized in females collected in June and July in northeastern Nova Scotia.	47
6.	Presence or absence of an implanting blastocyst indicated by the presence or absence of a bulbous swelling on the cornua of harbour seals collected during September and October in northeastern Nova Scotia	50

		Page
Table 7.	Annual cycle of adult female harbour seals in northeastern Nova Scotia.	51
8.	Numbers of seals hauled out on Sable Island, in winter and weather conditions observed on the mornings of the counts.	54
9.	Details of the 1971 and 1972 whelping seasons of harbour seals on Sable Island.	59
10.	Number of seals reported killed for bounty in the Fourchu area, Cape Breton and in Charlotte County, southern New Brunswick from 1959 to 1971.	72
11.	Life table for the population of harbour seals in Fourchu, Cape Breton.	77
12.	Life table for the population of harbour seals in Charlotte County, New Brunswick.	79
13.	Life table of female harbour seals from data cumulated for the period 1966-1971 and obtained from the bounty kill in the Maritimes.	83
14.	Life table of male harbour seals from data cumulated for the period 1966-1971 and obtained from the bounty kill in the Maritimes.	84

		Page
Table 15.	Calculation of a correction factor to account for adult seals likely killed for bounty but not retrieved, mainly due to sinking.	89
16.	Number of harbour seals killed for bounty in the Maritimes between 1950 and 1971.	91
17.	Calculated changes in numbers of harbour seals in the Maritimes between 1950 and 1971.	95
18.	Percentage of different food items found in 279 harbour seals.	102
19.	Seasonal variations in feeding intensity of harbour seals in eastern Canada.	107
20.	Spawning time of the fish species regularly eaten by the harbour seal in eastern Canada.	108
21.	Feeding rates of harbour seals in captivity.	112
22.	Energy flow table for a population of 1,000 harbour seals in eastern Canada.	117
23.	Water content and calorific values of the edible portion of various fishes eaten by the harbour seal.	118

		Page
Table 24.	Calorific value of three types of meat, raw.	119
25.	Assimilation efficiency in four mammals.	121

LIST OF FIGURES

		Page
Fig. 1.	Harbour seals resting on the beach of Sable Island, Nova Scotia.	2
2.	Map showing location of sampling localities.	6
3.	Map showing areas of abundance of the harbour seal in eastern Canada.	12
4.	Harbour seals haul out mainly on ledges and sand bars exposed at low tide.	17
5.	Relation between the numbers of pups killed for bounty per coastal county in Nova Scotia and the number of islets 50 yards long or less, in the corresponding county.	18
6.	Growth in nose-tail length of harbour seal foetuses in eastern Canada.	22
7.	Growth in weight of harbour seal foetuses in eastern Canada.	23
8.	Growth in length of harbour seal pups on Sable Island.	25

Page

Fig. 9. Growth in weight of male and female harbour seal pups on Sable Island. 26

10. Increase and lost in weight of individual pups, nursed and deserted, on Sable Island. 27

11. Growth in nose-tail length of harbour seals in eastern Canada. 29

12. Growth in weight of harbour seals in eastern Canada. 30

13. Length-weight relationship for harbour seals in eastern Canada. 32

14. Comparison of two techniques for calculating the weight of harbour seals from nose-tail length and from nose-tail length and maximum girth. 33

15. Photomicrographs of male testis and epididymis. 35

16. Increase with age of tubule diameter of testis and epididymis in male harbour seals taken during the breeding season in eastern Canada. 37

17. Sections of left and right ovaries of a four-year-old harbour seal collected on January 18, illustrating

		Page
	the corpus albicans and the corpus luteum.	40
Fig. 18.	Changes in diameter of the corpus luteum and of the corpus albicans of harbour seals in eastern Canada.	41
19.	Total numbers of corpora albicantia found in the two ovaries of harbour seals at various ages.	42
20.	Annual variations in the diameter of the testis and epididymis tubules.	45
21.	Relation between the number of seals hauled out on Sable Island in winter and the corresponding air temperature corrected for windchill.	55
22.	Monthly changes in the number of herds and in the mean number of harbour seals per herd on Sable Island.	56
23.	Six weeks premature pup, healthy and covered with a firm lanugo.	60
24.	Percentage of harbour seal pups born with the lanugo on Sable Island, 1971, retaining it at given ages.	62
25.	Percentage of harbour seal pups with a healed umbilicus at given age, on Sable Island, 1971.	63

Page

Fig. 26. Percentage of harbour seal pups weaned on a given date on Sable Island, 1971. 65

27. Hauling out of harbour seals on Sable Island on mornings when the weather is good. 69

28. Eye-fitted line indicating the changes in sex ratio with age of harbour seals in eastern Canada. 76

29. Smoothed age frequency distribution of harbour seals in an area of low hunting intensity, Fourchu, Cape Breton and in an area of high hunting intensity, Charlotte County, New Brunswick. 81

30. Age-$\log_{10}$ frequency distribution showing survival of males and females. 85

31. Age-$\log_{10}$ frequency distribution of the total bounty kill from 1966 to 1971 in New Brunswick, Nova Scotia and Prince Edward Island. 86

32. Hunting mortality of harbour seals in the three maritime provinces for the period 1950-1971. 94

33. Monthly changes in the condition index (maximum girth x 100)/ nose-tail length, of harbour seals in eastern Canada. 106

		Page
Fig. 34.	Relationship between the estimated stomach content's weight before digestion in nature and the weight of the corresponding harbour seal.	111
35.	Diagram of energy flow in a population of 1,000 harbour seals in eastern Canada.	122

INTRODUCTION

The harbour seal, Phoca vitulina, Linné (Fig. 1), has a wide distribution, occurring in coastal areas of the north Atlantic and of the north Pacific, ranging south to California and north to Ellesmere Island in the Canadian Arctic (Mansfield, 1967a). It is a sedentary species and is generally found year round near its breeding sites.

The first extensive description of the harbour seal in North America was given by Allen (1880) who also reviewed most of the literature then available on this species. Later, studies have been published in Europe and North America on its general biology (Havinga, 1933; Doutt, 1942; Scheffer and Slipp, 1944; Imler and Sarber, 1947; Fisher, 1952 and 1954; Sergeant, 1951) but these were limited by the absence of a proper ageing technique. Mansfield and Fisher (1960) confirmed that this seal could be aged by counting annual layers in the cementum of canine teeth. Since then, three publications (Bishop, MS 1968; Bigg, 1969a; Naito and Nishiwaki, 1972) have presented results of age determination of samples from populations of harbour seals.

There has been no general account published of this species in eastern Canada and eastern United States other than Allen's (1880) extensive description. Information was published on local abundance (Gilpin, 1874; Comeau, 1945; Fisher, MS 1949; Templeman, Squires and Fleming, 1957; Mansfield, 1967b and 1967c; Caldwell and Caldwell, 1969; Boulva, 1971), feeding (Fisher and Mackenzie, 1955; Templeman et al., 1957), pupping season (Bigg, 1969b; Boulva, 1973) and on the importance of these seals as the final host of the codworm (Scott, 1953; Fisher and Mackenzie, 1955; Scott and Fisher, 1958).

Fig. 1. Harbour seals resting on the beach of Sable Island, Nova Scotia.

In Nova Scotia, New Brunswick and Prince Edward Island, here referred to as the Maritimes or the Maritime provinces, a bounty has been in effect on the harbour seal since 1927 and since 1952 the bounty has been extended to Newfoundland and Labrador. Even though the numbers of seals killed for bounty has been recorded from year to year, there has been no publication examining the consequences of this hunt on the population, with the result that little has been known on the numbers of harbour seals left in eastern Canada and on the stability of the population. The present study was initiated in 1971 for the Arctic Biological Station of the Fisheries Research Board of Canada, in an attempt to obtain information on these questions as well as on the general biology of these seals and on their present interactions with man.

MATERIAL AND METHODS

Collection of samples and field observations

This study uses samples collected mainly by the Arctic Biological Station of the Fisheries Research Board of Canada since 1968, either by their own personnel or by trained fishermen. The author added to this collection specimens obtained from the population which he studied from 1969 to 1972 on Sable Island, Nova Scotia.

Table 1 gives the monthly numbers of males and females aged one year old or more collected in each locality of sampling. The localities of sampling are indicated on Fig. 2; the circled numbers on the map refer to the map numbers in Table 1. It can be seen from the table that the sample is strongly biased towards summer and fall months, the few winter samples coming mainly from Sable Island. This is because fishermen generally pull their boat out of the water for the winter and because seals are seldom seen in cold weather on the islets and ledges where they normally haul out, thus making collection of winter samples very difficult.

Information noted in the field consisted of: locality and date of capture, nose-tail length measured in a straight line and not including body curvature, and sex. The following measurements were taken occasionally: blubber thickness measured through a narrow incision over the posterior end of the sternum and not including the skin, the maximum girth and the total weight with no allowance for blood loss. Formaldehyde was added to the stomach content which was generally kept for examination in the laboratory. Ovaries, reproductive tracts and foetuses were preserved in a formaldehyde solution while transverse

Table 1. Numbers of harbour seals aged one year or more, collected for this study, per month and per locality of sampling, for males (M) and females (F). The map numbers refer to the numbers on Fig. 2.

Map		Month →												
		J	F	M	A	M	J	J	A	S	O	N	D	Totals
no.	Locality	M-F	M-F	M-F	M-F	M-F	M-F	M-F	M-F	M-F	M-F	M-F	M-F	M-F
1	Fourchu, N.S.					3-12	7-13	5-11	4-5	8-14	8-6	3-1		38-62
2	Sable Island, N.S.	5-4	3-1		1-3	4-3	11-5	2-1		4-0	0-3	2-5	3-0	35-25
3	Ecum Secum, N.S.					1-1	1-1	2-1	2-0	1-0			0-1	7-4
4	Port Mouton, N.S.						3-1							3-1
5	Grand Manan, N.B.					3-0	2-1	2-6	2-4	7-3	2-0			18-14
6	Gulf of St. Lawrence							1-0	4-7					5-7
7	Escoumins, Qu.						1-10	3-4	2-0	4-1			1-0	12-15
	Totals	5-4	3-1	0-0	1-3	11-16	25-31	15-23	14-16	24-13	10-9	5-6	4-1	118-123

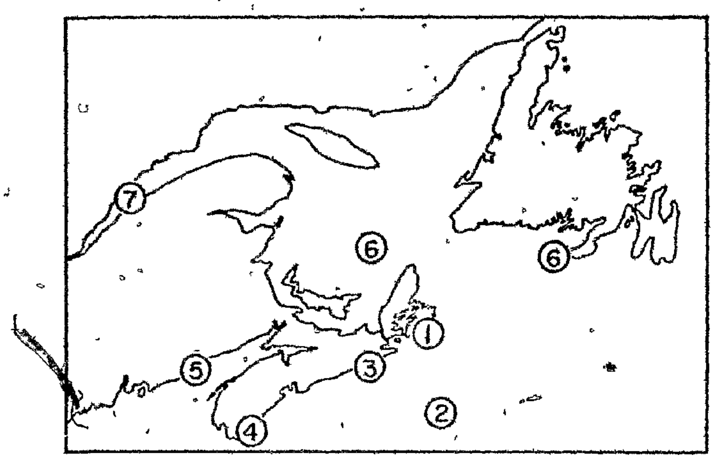


Fig. 2. Sampling localities are 1: Fourchu, Cape Breton; 2: Sable Island; 3: Ecum Secum; 4: Port Mouton; 5: Grand Manan and Blacks Harbour; 6: Magdalen Islands (left) and Saint-Pierre et Miquelon (right) in the Gulf of St. Lawrence; 7: Escoumins.

sections of one testis and epididymis, about 1 cm in thickness, were cut with a scalpel and preserved in Bouin's solution.

Canine teeth were extracted from the boiled lower or upper jaw bone and a note was made of the numbers of postcanine teeth present in some specimens. Data on the numbers of postcanine teeth or tooth sockets were also obtained from the lower jaw bones submitted in support of bounty claim. Canine teeth were also extracted from these jaws and allowed the ageing of the seals killed for bounty.

Information on the seals' activity throughout the year was noted during the numerous field trips on Sable Island. The techniques used for ageing and studying the pups from birth to weaning were described elsewhere (Boulva, 1971 and 1973). Weather data for Sable Island were supplied by Maritime Weather Central of the Department of the Environment of Canada.

Treatment of samples

Age determination - One of the two canines was cut longitudinally to obtain a section about 0.4 mm thick, and the annual lines in the cementum were counted (Mansfield and Fisher, 1960; Bishop, MS 1968; Bigg, 1969a). This technique for ageing harbour seals was validated by Mansfield and Fisher (1960). Each seal was given an age in years and tenths of years. The starting date is May 24 which corresponds to the average birth date for Sable Island harbour seals (Boulva, 1973); because of the absence of adequate information on birth time elsewhere in the area covered by this study and because of the need to age each animal, it is assumed that the other sampled populations whelp at the same time as the Sable Island Seals. A possible exception might be in the estuary of the St. Lawrence River where harbour seals are said to give birth mainly in

June.

Reproductive organs - Sections of the testis and of the epididymis were mounted and examined as described by Smith (MS 1970). Ovaries were hand cut transversely in slices approximately 2 mm thick. For each of the two ovaries, the numbers of follicules, divided in three classes, less than 3 mm, between 3 and 6 mm, and more than 6 mm in diameter were noted as well as the numbers and sizes of the corpora albicantia and of the corpus luteum.

Embryos and foetuses - Preserved prenatal seals were measured as to nose-tail length and weight. The length in small embryos was obtained by drawing a silhouette of the embryo on paper as described by Hewer and Backhouse (1968) for grey seals; the length of the line running from the nose through the eye and following approximately the vertebral column to the tail was used as the nose-tail length.

Stomach contents - The food items found in the stomachs were identified by comparison with skeletons of fish kept in a collection at the Arctic Biological Station. Invertebrates were keyed to species if possible, except for cephalopod remains which were forwarded to the Biological Station in St. Johns, Newfoundland, for identification. Stomach contents which could be identified only as far as family were distributed among the species identified positively, according to the frequency of occurrence of the identified species. For example, if only cod and hake were identified in the stomachsin a ratio of 2 to 1, and if there was 30% unidentified gadids in the stomachs, then 20% and 10% were added respectively to the percentages for cod and hake.

The state of digestion was subjectively coded as follows: 0: stomach empty; 1: 90% digested; 2: 50-90% digested; 3: 10-50% digested and 4: 0-10% digested. The weight of stomach contents given code 3 and 4 was generally noted. The volumetric importance of each food species found in a given stomach was visually assessed and attributed a fraction so that the total amount of food in the stomach would have a value of 1. If only species A was found, it was given a value of 1; if species A and B were found in about equal quantity, they were given each a value of 0.5.

Population estimates

Questionnaires were sent by the Arctic Biological Station to Fisheries Officers in eastern Canada, to obtain information on local abundance, movements, dates of whelping and interference with fishing operations by the grey seals and harbour seals. These questionnaires provided the author with basic information on the distribution and numbers of the harbour seals in eastern Canada. Interviews with fishermen in most fishing communities of Nova Scotia, New Brunswick, Prince Edward Island and Québec provided additional data on numbers and distribution.

These two sources of information were completed by a study of the data supplied by the bounty kill, with the assumption that areas where intense killing occurs correspond to areas where harbour seals are abundant. The Sable Island population was surveyed as described in an earlier paper (Boulvà, 1971).

DISTRIBUTION AND ABUNDANCE.

Present status

The harbour seals in eastern Canada are not grouped in one continuous population, but are rather distributed in numerous small populations apparently isolated one from the other. For example, field counts, colour patterns of the pelage and cranial evidence suggest that the 1,200 to 1,500 harbour seals inhabiting Sable Island, located 90 miles from mainland Nova Scotia, are isolated from the mainland populations with little or no emigration or immigration taking place (Boulva 1973 and McLaren 1973).

The examination of the bounty kill elsewhere in eastern Canada also indicates that the seals killed always come from certain specific areas, while reports of kill are never received from certain other areas also inhabited by fishermen, thus indicating a probable discontinuity in the distribution of these seals. The variation in the numbers of post-canine teeth (premolars and molars) suggests furthermore that harbour seals from one population do not commonly mix with seals of a nearby population. The normal complement of these teeth is 5, varying between 3 and 7 in the lower jaws which I examined. This variation is fairly consistent in certain areas as can be seen in Table 2.

Area no. 1 is geographically closest to area no. 2, with the Bay of Fundy acting as a barrier. No seal with less than 5 post-canine teeth on at least one of the two lower jaws have been found in area 1, while 5% are found in area 2; there is also a 50% decrease (but not significant) from area 1 to area 2 in the number of animals having more

Table 2. Variations in the numbers of post-canine teeth (premolars and molars) on the lower jaw of harbour seals in seven areas of eastern Canada. The area numbers refer to the circled numbers on Fig. 3. There are three classes of teeth in the table: animals having either less than five post-canines on at least one of the two jaw bones; five on both jaw bones; more than five on at least one of the two jaw bones.

Area no.	Area	less than 5 %	5 %	more than 5 %	No. in sample
1	Charlotte Co., N.B.	0	86	14	51
2	Digby to Halifax, N.S.	5	88	7	111
3	Halifax to Louisbourg, N.S.	6	91	3	79
4	Sable Island	39	61	0	36
5	Prince Edward Island	12	88	0	26
6	Insular Newfoundland	24	74	2	38
7	Labrador	5	94	1	114

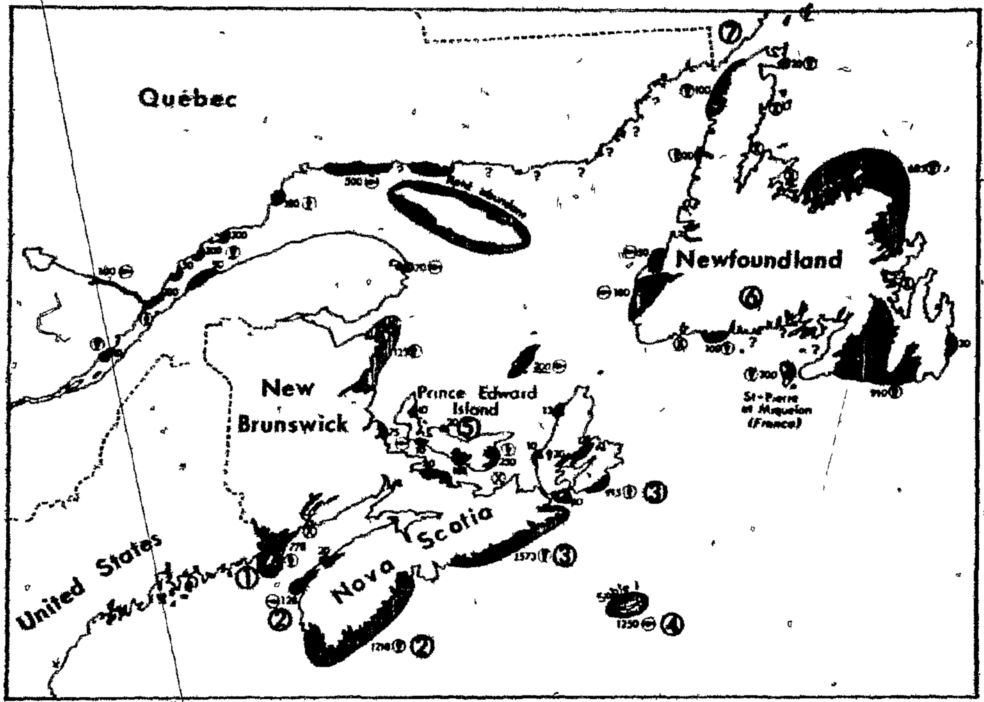


Fig. 3. Areas of abundance of harbour seals* in Eastern Canada, indicated by hatching. The estimated numbers of animals are given with the current trend for each population. The trend is indicated by a circled arrow: pointing down = decreasing; pointing horizontaly = stationary. A circled X indicates an area from which the harbour seal is reported to have disappeared during the last 15 years. Question marks mean absence of information. Circled numbers refer to area numbers in Table 2.

than 5 post-canine teeth.

Similarly, Sable Island is closest to area 3; however, it has six times more seals with less than 5 post-canines (difference significant at the 0.001 level) and no seal with more than 5 post-canines compared to 3% in area 3. Areas 5, 6 and 7 have their own typical variations in numbers of post-canines. Assuming that the number of post-canine teeth is at least partly genetically controlled, these variations suggest that gene exchange between these small populations of harbour seals is somewhat restricted.

An examination of the distribution of seals killed for bounty and of questionnaires returned by Fisheries Officers in eastern Canada, as well as my own conversations with fishermen in all areas covered by this study, with the exception of Newfoundland, Labrador and the north side of the Gulf of St. Lawrence, from Sept-Iles to the Québec-Labrador border, have supplied sufficient information for the preparation of a map showing the distribution and the estimated numbers of seals in each of these populations (Fig. 3). The trend of each population, according to local residents, is also given, whether decreasing or stationary; nowhere are the harbour seals said to be increasing. The disappearance of this species in an area during the last 15 years is indicated by a circled X; absence of information from an area is shown by a question mark.

The estimates of number of seals can be grouped by provinces, providing a total estimate of about 12,700 harbour seals at present in the area covered by this report:

New Brunswick	978

Newfoundland (Labrador excluded)	2015
Nova Scotia (including Sable Island)	5247
Prince Edward Island	478
Saint-Pierre et Miquelon	300
Québec — Areas visited	1380
Québec — Estimate for areas not visited	2300
Total for area covered by this study	12698

Past distribution

It is likely that the present discontinuous distribution of the harbour seal is a consequence of encroaching civilisation combined with many decades of hunting for bounty, the species having survived only in the most favourable areas.

In the last century, for example, their range extended much further west than at present. Harbour seals once occured in lake Ontario and lake Champlain (Allen, 1880). In more recent times, a few have been seen in the Lachine Rapids and in Beauharnois near Montreal (David Sergeant, personal communication).

Since 1960, there has been no report of their presence in areas where they used to be killed for bounty: the lower St. John River in southern New Brunswick, from Pictou to Georges Bay on the north coast of Nova Scotia and from numerous localities of Newfoudland, mainly in the north-eastern regions. In most of the other areas, as mentioned above, they are reported by Fisheries Officers and fisherman to be decreasing in numbers.

Natural factors controlling the distribution

Harbour seals are generally considered to be animals of bays and inlets. Their absence from the north shore of the Gaspé Peninsula could be explained by the lack of bays along that coast; this area is also poor in islets and ledges. These seals also are few in bays which have no ledges or islets. On the other hand, they are found around small offshore islands such as Seal Island in south-western Nova Scotia where there are no bays but where numerous ledges are available at low tide. I have examined the physical characteristics of the areas of Nova Scotia where harbour seals are concentrated and of the areas where they are few. It is assumed that the total abundance of harbour seals in a county is proportional to the number of pups killed in that county, as pups are easily captured and are generaly born in a fixed proportion to the number of adults present (Bigg 1969a and Boulva 1973). The numbers of pups killed per county in 1951, 1959, 1962 to 1964 and 1966 to 1971 were cumulated and a count of the numbers of islets 50 yards in length or shorter per county, was done from nautical charts for the coast of Nova Scotia. The data are summarised in Table 3. The assumption is that areas with numerous islets offer good protection from seal hunters because of the navigation hazards even with small craft and also provide the seals with adequate areas to haul out (Fig. 4).

A regression was made of the number of pups killed on the number of islets per county (Fig. 5). The regression coefficient is highly significant ($P < 0.001$). Most points are relatively close to the line except the point marked A which represents data from Guysborough County; in this case, 138 islets are located in or at the entrance of Canso Harbour where the permanent presence of man and an intense boat traffic help keep the seals away, thus providing very few pups for the number of islets. If point A is moved 138 units to the left on Fig. 5, it comes well in line

Table 3. Relation between the total number of pups killed during the years 1951, 1959, 1962-64, 1966-70 and the numbers of islets, 50 yards long or less, counted on hydrographic charts of Nova Scotia (excluding Sable Island). The data are illustrated on Fig. 5.

County	Number of islets	Number of seal pups killed
Cumberland North	4	20
Colchester North	10	1
Pictou	16	3
Antigonish	17	1
Inverness	56	12
Victoria	91	2
Cape Breton	254	188
Richmond	107	81
Guysborough	664	334
Halifax	691	616
Lunenburg	177	41
Queens	439	321
Shelburne	464	394
Yarmouth	785	677
Digby	219	99
Annapolis	9	17
Kings	5	3
Hunts	5	0
Colchester South	9	0
Cumberland South	4	6

Fig. 4. Harbour seals haul out mainly on ledges and sand bars exposed at low tide.

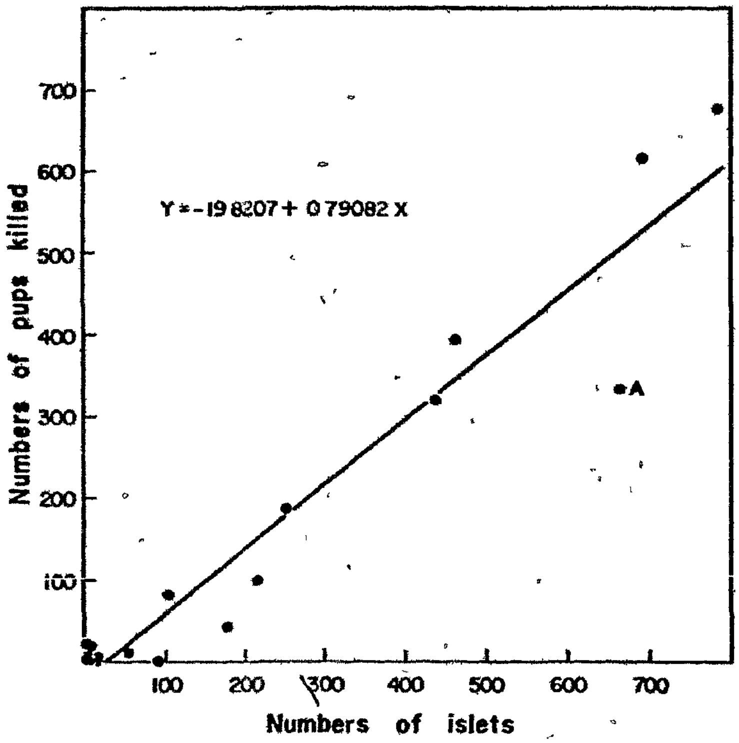


Fig. 5. Relation between the numbers of pups killed for bounty per coastal county in Nova Scotia and the number of islets 50 yards long or less, in the corresponding county, using the data in Table 3. The regression coefficient differs significantly from 0 ($P < 0.001$) while the intercept of the line with the ordinate does not differ significantly from 0 ($P > 0.05$). Point A is data from Guysborough County (see text).

with the other points.

There is therefore a strong relation suggesting that the availability of islets in Nova Scotia might affect the abundance of harbour seals in a given area. In other regions such as the Miramichi estuary in eastern New Brunswick, where rocky islets are fewer, the availability of sand bars might in turn limit the abundance of the harbour seal.

GROWTH

The growth of the harbour seal is well documented for most areas where the species occurs. For the eastern Pacific, growth has been described by Scheffer and Slipp (1944), Fisher (1952), Bishop (MS 1968) and Bigg (1969a); Naito and Nishiwaki (1972) gave an account of the comparative growth of two species of harbour seals, Phoca largha and P. stejnegeri (=kurilensis and insularis) in the western Pacific. Whether these two species are races of P. vitulina is in dispute (McLaren, 1973). For the eastern Atlantic, information on growth is given by Havinga (1933), Venables and Venables (1955) and Harrison (1960 and 1963). For the northwest Atlantic, Boulva (1971 and 1973) has given details on the growth of pups from birth to weaning.

Information is presented here on the growth in size of the harbour seal in eastern Canada during gestation, nursing and after weaning. The age of the embryos and foetuses is calculated in days, the mean weaning date June 24 being taken as day 0 due to lack of accurate data on the mean date of fertilisation of the ovum; this will be dicussed in more details in the section on the annual cycle. Pups were aged when tagged, the age being estimated from the condition of the umbilicus as described in Boulva (1973).

Prenatal growth

Length - Numerous reproductive tracts obtained in August and two in early September, were examined for the presence of embryos but even though a new corpus luteum was observed in most cases, no sign of pregnancy was visible. Three females collected each on different days, September 15, 25 and 26, had an implanting blastocyst located in a swelled knob on the cornu while six out of seven females obtained during the first half of October had a small embryo present, the seventh having a new corpus luteum but showing otherwise no sign of pregnancy. Thus, in eastern Canada, the growth of the embryo begins in mid-September.

The increase in length of embryos and foetuses is illustrated on Fig. 6. The first measurable embryo, 7 mm in length, was found on October 1st. The equation of the regression line for growth in length indicates that the embryo and foetuses increase at a rate of 0.36 cm per day. The regression line intercepts the 0 cm line on day 102 (October 4). The point of intercept with the line of mean birth date on May 24 suggests a mean birth length of about 85 cm. This differs by 9 cm from the mean birth length of 76 cm for live pups (Boulva, 1973); the discrepancy may be accounted for by the fact that live pups contract themselves slightly when measured and by a possible slowdown of growth during the few days preceeding and following birth.

<u>Weight</u> - The increase in weight of the foetus can be related to time with rectilinear regression, if the cubic root of the weight is paired with the age of the foetus (Hugget and Widdas, 1951). The regression line (Fig. 7) intercepts the 0 kg line on day 97 (Sept. 29) and indicates a mean birth weight of 11.7 kg (22.7^3 g). The mean birth weight of live pups on Sable Island has been recorded as 10 kg (Boulva, 1973). The difference between these two birth weights, if not a result of the small number of foetuses available, is likely explained as for the difference in birth lengths between foetuses and live pups, by a slowdown in growth around the time of birth.

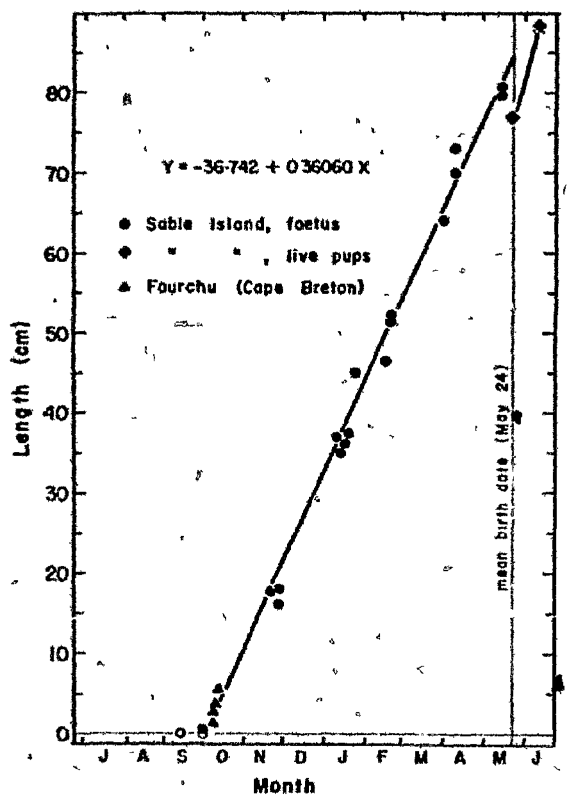


Fig. 6. Growth in nose-tail length of harbour seal foetuses in eastern Canada. The equation for the regression line is given, indicating a growth rate of 0.36 cm per day. The regression line intercepts the 0 cm line 102 days after the mean weaning date (June 24). The diamonds indicate for comparison the growth rate of live pups between birth and weaning.

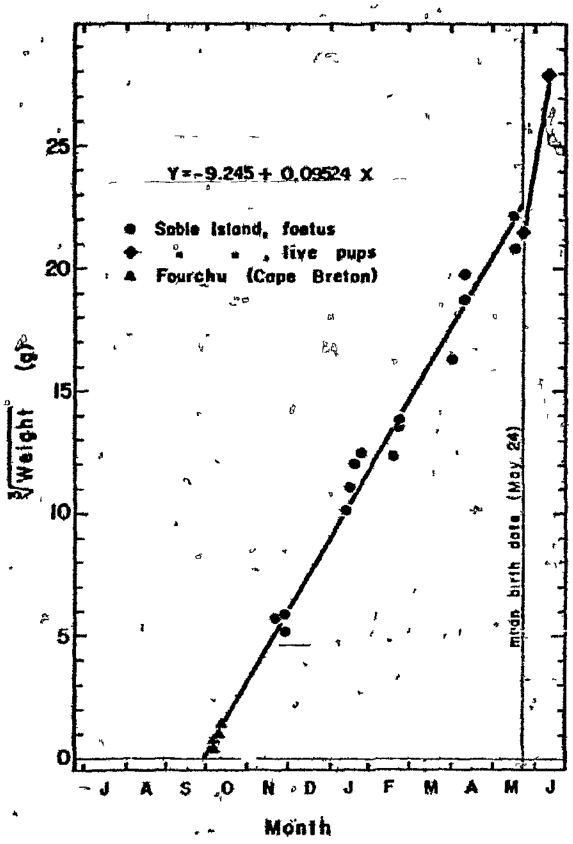


Fig. 7. Growth in weight of harbour seal foetuses in eastern Canada. The regression equation describes the daily increment of the cubic root of the weight. The regression line intercepts the 0 g line on day 97 after the mean weaning date (June 24). The diamonds indicate for comparison the increase in weight of live pups between birth and weaning.

Growth from birth to weaning

Nursed pups - Following birth, the average rate of growth in length increases from the 0.36 cm per day value in utero to 0.58 cm per day during nursing. The differences in mean birth lengths and mean growth rates (Fig. 8) do not differ significantly between sexes ($P > 0.05$). At weaning, both sexes are about 90 cm in length and the end of nursing results in a slowdown in growth at that time.

The increase in weight is correspondingly more rapid from birth to weaning than in utero. During gestation for example, the foetus doubles its weight from 5 to 10 kg in about 55 days; after birth, the nursing pup increases its weight from 10 to 20 kg in less than 18 days (Fig. 9). The weight increases at a fairly constant rate during nursing but drops noticeably at weaning as shown by recaptured tagged pups (Fig. 10).

Deserted pups - It was observed on Sable Island that numerous pups are deserted by the female at an early stage in life. These pups lose weight and death from starvation generally occurs when these starvelings reach a weight of 7 kg, the lowest weight recorded for a live starveling being 5 kg.

Comparison of nursed and deserted pups (Fig. 10) suggests that a minimal weight of about 14 kg must be reached for a pup to survive. This is illustrated by one male which was weaned prematurely at 12 days of age, weighing then 14 kg. His weight dropped to 11 kg on day 21 but had increased to 12 kg on day 31. He had become very active by then and was often seen feeding in calm shallow water close to shore. However, another pup was deserted at 6 days of age, weighing at that time almost 15 kg. He lost weight constantly and died 24 days later. These observations suggest that, possibly, the condition for survival of pups in nature require an

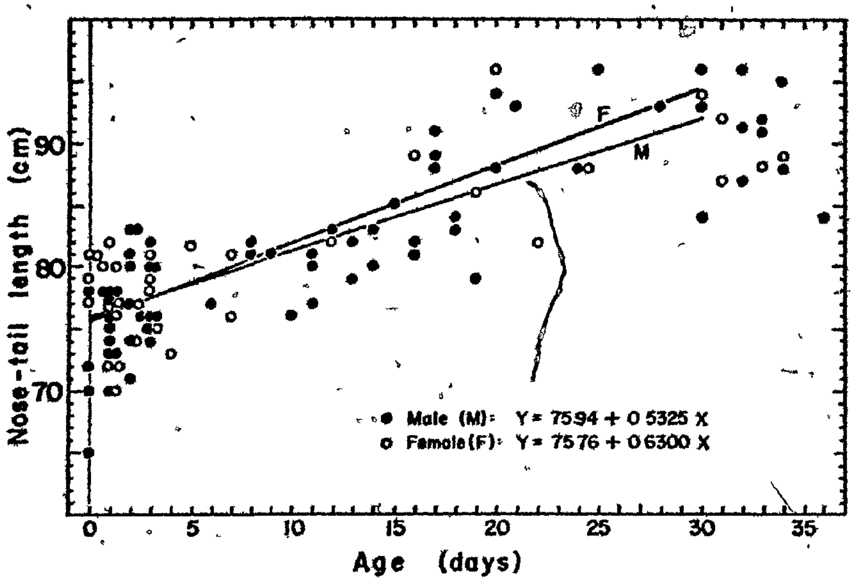


Fig. 8. Growth in length of harbour seal pups on Sable Island. The two regression lines do not differ significantly in slope or position; they include data from day 0 to day 30. Young after day 30 are considered to be weaned.

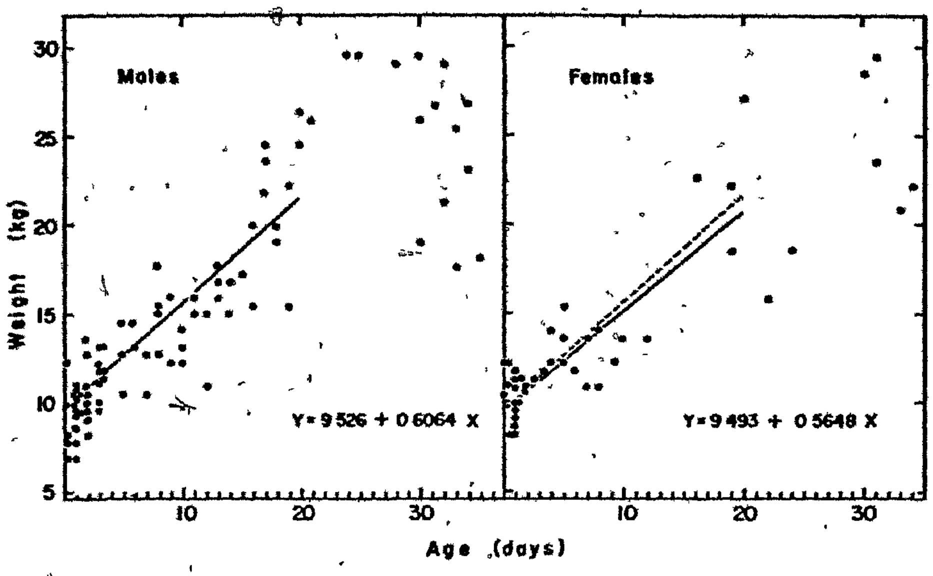


Fig. 9. Growth in weight of male and female harbour seal pups on Sable Island. The regression lines do not differ significantly either in slope or position. The line for males is reproduced as a dotted line in the female section for comparison. Closed circles indicate nursed pups, open circles, weaned pups. The regression line includes data from day 0 to day 30.

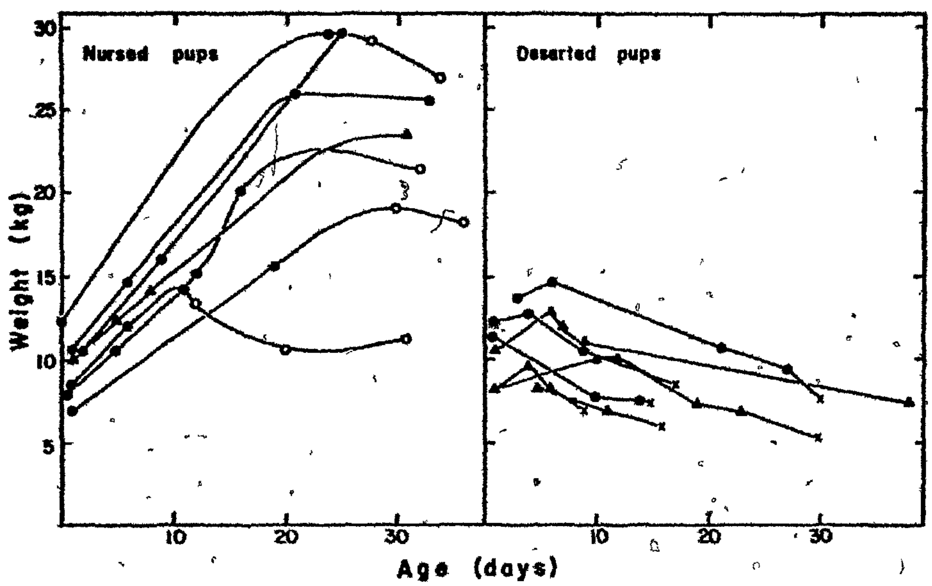


Fig. 10. Increase and loss in weight of individual pups, nursed and deserted, on Sable Island. Circles indicate males, triangles indicate females and X indicate death. In the left portion of the graph, closed symbols are of nursed pups and open symbols of weaned pups.

increase in weight up to about 14 kg combined with a minimum nursing time of about 10 days.

Growth after weaning

Length - From one year of age on, males average longer than females (Fig. 11). Maximum length is reached in males when about seven years old and in females when about five years old. Fully grown males average in nose-tail length 159 cm and females 145 cm.

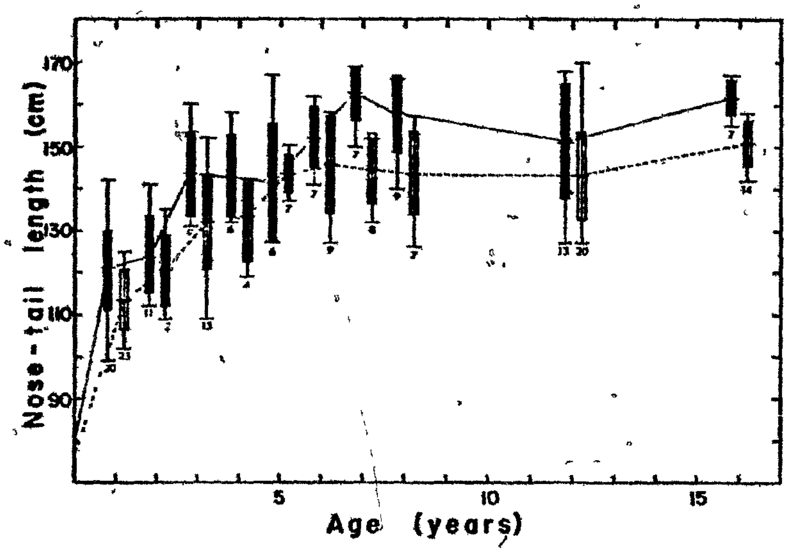
Weight - The increase in weight follows a pattern similar to the growth in length, with males reaching their maximum weight when approximately seven years old, and females when about six years old (Fig. 12). Fully grown males average 91 kg and females 72 kg, the males thus being on average 26% heavier than females.

Bigg (1969a) obtained values for fully grown males of 161 cm and 87 kg and for females, of 148 cm and 65 kg in harbour seals of the northeast Pacific. Naito and Nishiwaki (1972) give averages for fully grown Phoca largha of 170 cm and 161 cm respectively for males and females and for P. stejnegeri (= kurilensis and insularis) of 186 cm and 169 cm respectively for males and females.

Techniques to estimate weight

It is often useful to obtain rapidly weight of seals in the field when scales and means of lifting dead seals are seldom available. During this study, data were collected on the length, maximum girth and weight of 43 seals and these measurements can be related with two equations.

Length-weight relationship - This is a standard technique used in fisheries to obtain weight from fish of known length, using an equation



Fig, 11. Growth in nose-tail length of harbour seals in eastern Canada, The vertical bars, solid for males and open for females, are one standard deviation and the vertical lines are range around the mean (central horizontal line). Numbers of animals in the sample are given below the bar. Data is combined for ages 9-15 and 16 or more years-old.

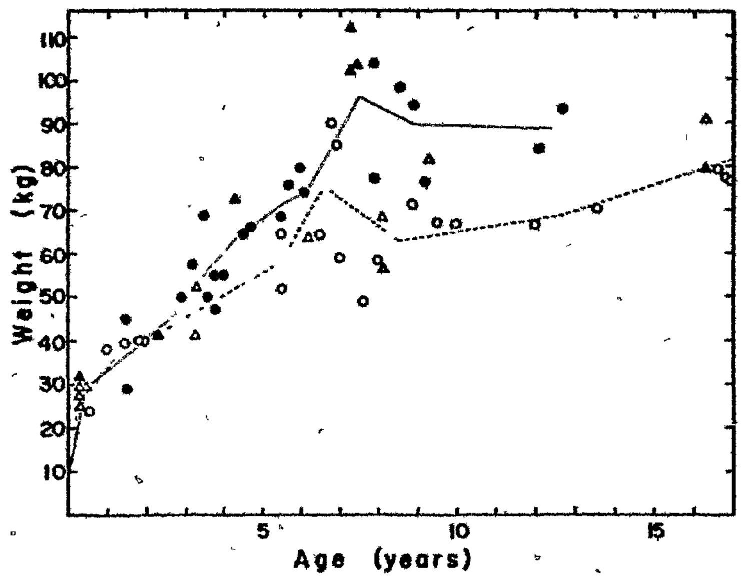


Fig. 12. Growth in weight of harbour seals in eastern Canada. Circles are specimens from Sable Island, triangles from Fourchu, Cape Breton. Closed symbols and solid line indicate males, open and dotted line indicate females. The lines are drawn through the annual averages, 7-9, 12-13 and 16 plus being combined for females, and 8-9 being combined for males.

of the type: $W = aL^b$, a and b being constants determined for each species (Ricker, 1968). The paired weight-length data for harbour seals in eastern Canada were transformed to $\log_{10}$ and linear regression was calculated, giving the constants for the equation:

$$\text{Weight of seal (kg)} = 0.000159 \text{ Length (cm)}^{2.602}$$

The data are plotted on Fig. 13. The equation allows the calculation of an estimate of the weight of a harbour seal when only the nose-tail length is known.

Length-girth-weight relationship - If the maximum girth is known, a more precise estimate of the seal's weight may be obtained, using an equation described by Poulter (MS 1965): $W = (G^2L)/K$, where W is the weight of the seal, G is the maximum girth, L is the nose-tail length and K a constant determined for each species. An equation of this type is also described in more detail by Usher and Church (1969). Data from 22 male and 21 female harbour seals of eastern Canada were used to calculate the constant: K for males is 20.59 cm^3/g and for females is 20.88 cm^3/g. The difference between the two sexes is not significant ($P > 0.05$). The average value of K is 20.735 cm^3/g; these values are converted to $inch^3/lb$ if multiplied by 27.675.

Comparison of the two methods - The calculated weight was compared to the observed weight and a correlation coefficient was calculated for each of the two techniques to find which one provides the best estimate of the seal's weight. The weight calculated from length when compared to the actual weight gives a correlation coefficient of 0.856 while the weight obtained from girth and length gives a correlation coefficient of 0.973 (Fig. 14). The length-girth-weight equation should therefore be used in preference to the length-weight equation when both girth and length are available.

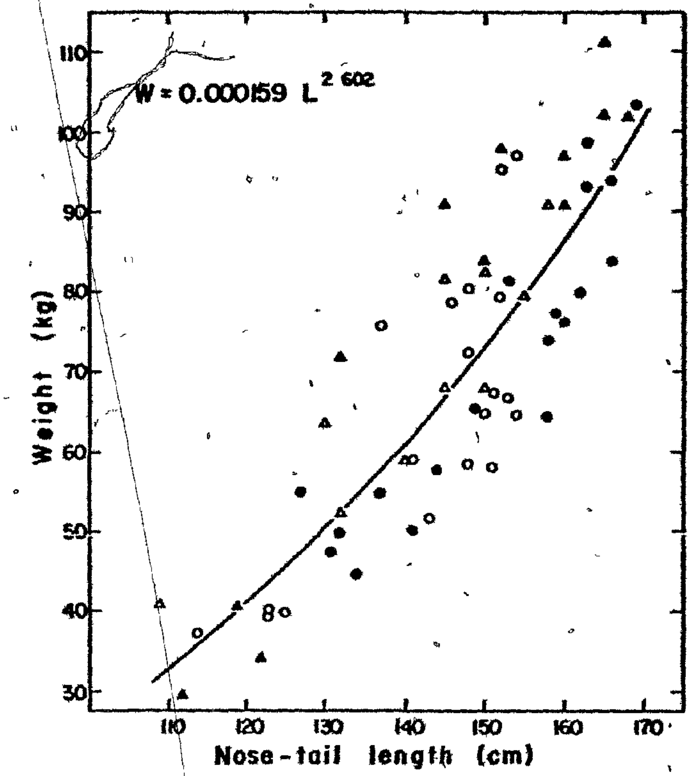


Fig. 13. Length-weight relationship for harbour seals in eastern Canada. W is weight in kg and L is length in cm. Symbols are as in Fig. 12.

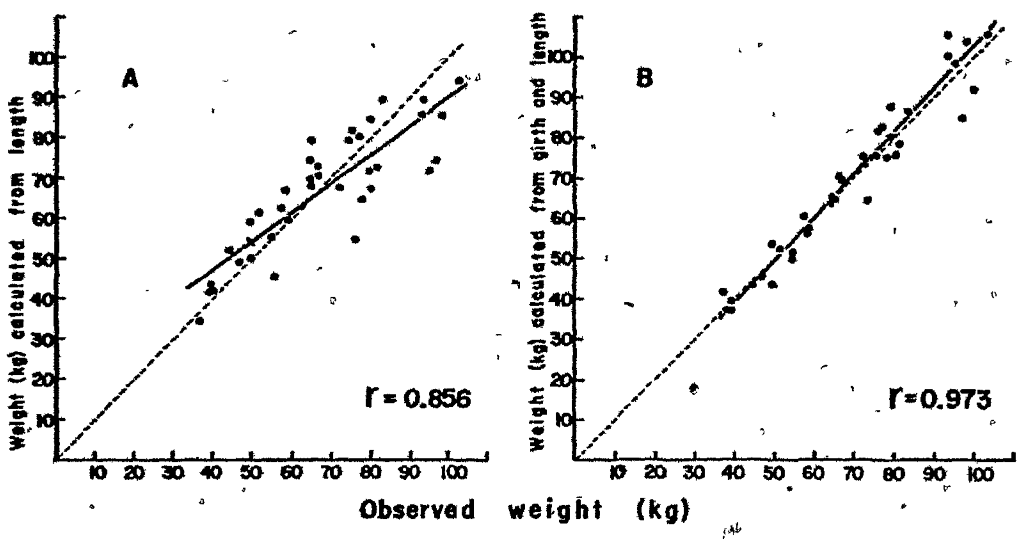


Fig. 14. Comparison of two techniques for calculating the weight of harbour seals from nose-tail length (A) and from nose-tail length and maximum girth (B), using equations described in the text; r is the coefficient of correlation.

REPRODUCTION

Information is given here on the age of sexual maturity of male and female harbour seals in eastern Canada, on the age specific fertility rates of females and on the annual reproductive cycle of both sexes. The structural changes in the reproductive glands of each sex have been found to be generally similar to those described by Bishop (MS 1968) and Bigg (1969a) for the Pacific harbour seal. A detailed description of the macroscopic and microscopic changes of the testis and of the ovary with age and with the seasons is given by McLaren (1958) for the ringed seal, Phoca (Pusa) hispida, and similar changes have been observed in harbour seals collected for this study even though the cycle has a different annual schedule; the reader is referred to the work by McLaren for more details.

Age at sexual maturity

Males - The examination with a microscope of thin sections of seal testis and epididymis yields information on the reproductive condition of the animal from which the samples were obtained. In mammals which have a limited breeding season such as harbour seals, the testes are active only for a limited time during the year. The production of sperm during the breeding season is detected by the presence of sperm visible in the lumen of the testis and epididymis tubules (Fig. 15B) while outside that season the testes are inactive and no sperm is produced (Fig. 15C). Therefore, to find out at what age the male harbour seal becomes sexually mature, samples must be collected

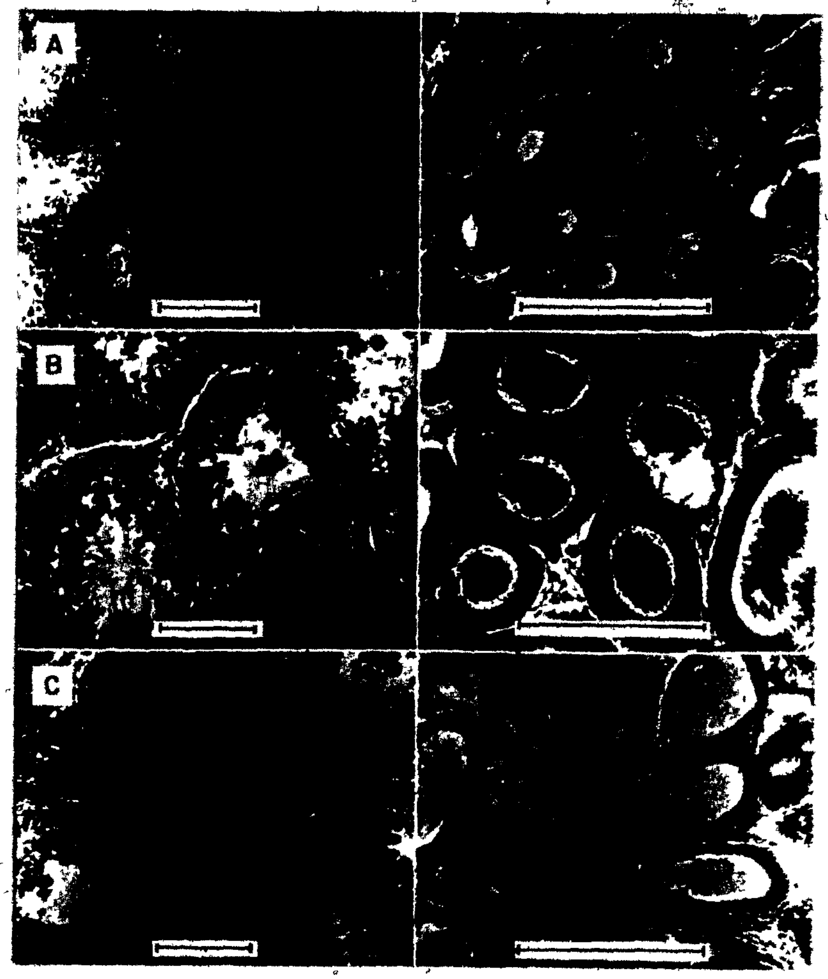


Fig. 15. Photomicrograph of male testis (left) and epididymis (right) from a 3-years-old immature taken on July 3 (A), a 7-years-old adult with sperm present in the tubules of both the testis and the epididymis, taken on June 6 (B) and a 14-years-old adult with numerous spermatogenetic cells in the lumen of the testis and empty tubules in the epididymis, taken on January 22 (C). Horizontal bars represent on the left 0.1 mm and on the right 0.5 mm.

during the breeding season when those seals producing sperm can be distinguished easily from immatures (Fig. 15A).

Male harbour seals in eastern Canada become sexually mature at six years old, as indicated by the presence of sperm in at least one of the ten epididymis tubules examined during the breeding season. The presence or absence of sperm in the epididymis tubules is used as criterion for sexual maturity because this is where sperm complete their maturation (Bishop and Walton, 1962). Of all the samples collected during the breeding season, no sperm were observed in the epididymis of the 13 males aged one to three years old, some was found in a 137 cm long four years old while the four remaining four years olds had no sperm. The three five years olds examined were immature while all animals six or more years old were potent, with the exception of two eight years olds collected, according to the information supplied by the fishermen who shot the seals, near the island of Grand Manan in late May and early June; of these two seals, one shot on 9 June had sperm in only the testis tubules while in the other shot on May 24, no sperm was present. However, a twelve years old collected there on May 29 had its epididymal tubules filled with sperm. An other indication of sexual maturity is obtained if the mean size of the testis and epididymis tubules is calculated for each age group. It is found that there is a very rapid increase in the diameter of these tubules between ages 5 and 6 (Fig. 16); at older ages, the diameter of the tubules remains fairly constant.

This information indicates that generally male harbour seals in eastern Canada reach sexual maturity at six years of age (Table 4). Bishop (MS 1968) and Bigg (1969a) found that harbour seals in the eastern Pacific also become sexually mature at six years old. However, the male

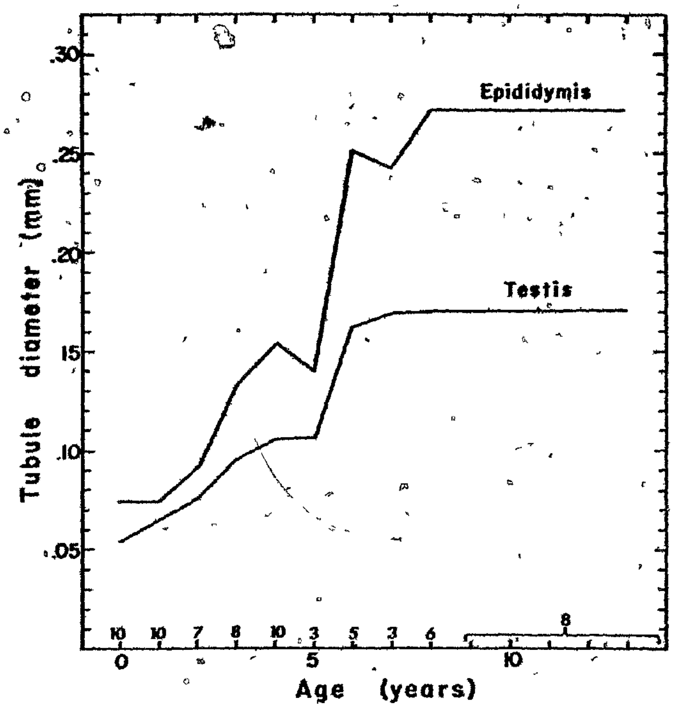


Fig. 16. Increase with age of tubule diameter of testis and epididymis in male harbour seals taken during the breeding season in eastern Canada. The lines are drawn through the annual means; values for animals 9 years old or older are combined. The numbers at the base of the graph are the sample size for each age.

Table 4. Age at maturity of male and age at maturity with age specific fertility rates of female harbour seals in eastern Canada.

Age	Males		Females			
	No. examined	% mature	No. exam.	% mature	No. exam.	% fertile
1	8	0	13	0	27	0
2	3	0	8	0	13	0
3	2	0	10	30	9	0
4	5	20	5	80	13.5	*33.3
5	3	0	7	86	7.38	*59.4
6	4	100	7	100	10.71	*81.3
7	2	100	7	100	7.87	*100
8	7	71	7	100	7.31	*100
9	10	100	24	100	24.98	* 92

*) adjusted for females of unknown ages (see text).

pagophilic harbour seal Phoca largha, appears to reach sexual maturity at three to four years of age (Tikhomirov, 1966; Naito and Nishiwaki, 1972).

Females - Seals like other mammals have in their ovaries follicles which once a year enlarge near time of mating. In mature seals, one of the follicles releases an ovum. The structure of the follicle then changes and it becomes larger and yellowish-tan, taking the name of corpus luteum. This corpus is maintained until the end of lactation when it degenerates and becomes a white scar in the ovary and is then called a corpus albicans (Fig. 17 and 18). It is not known in this species if the corpus luteum persists in the absence of fertilization of the ovum. A corpus luteum will form, whether mating takes place or not, in the guinea-pig and in the pig; this luteal phase is called pseudopregnancy and occurs in most species (Perry, 1971).

In eastern Canada, 30% of the female harbour seals ovulated for the first time at three years of age, 50% at 4, 6% at 5 and 14% at six years of age (Table 4), the evidence for a first ovulation being the presence either of a follicle with a diameter of 6 mm or more, or a corpus luteum and no corpus albicans. However, as the corpus albicans (Fig. 17) is retained generally for at least one year (Fig. 19) and up to 14 years in the case of an eighteen-years-old non pregnant female from Sable Island, the four years olds with one corpus albicans were added to the group ovulating for the first time at three years old while those ovulating for the first time at four years of age were added to the portion of seals not ovulating at three years old. This procedure was not used on five years old females as the corpus albicans of first ovulation might have disappeared by then.

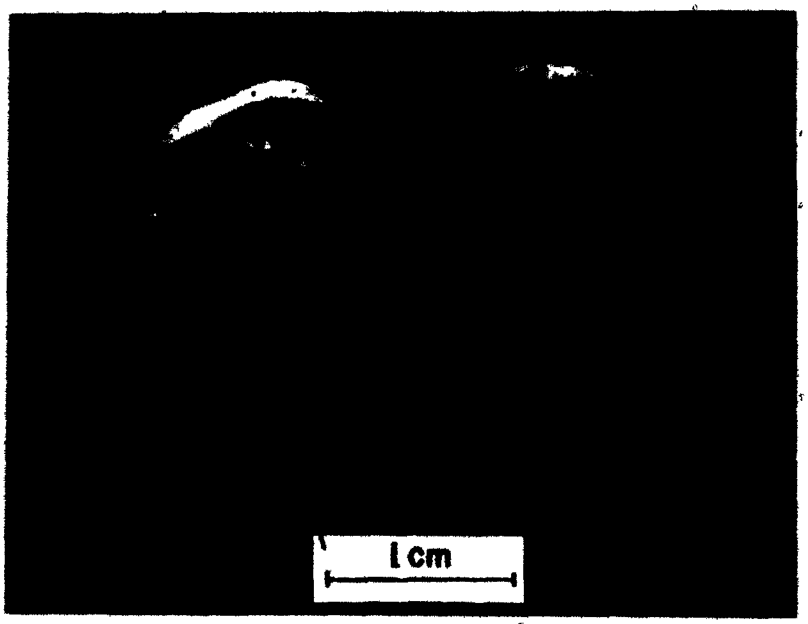


Fig. 17. Sections of left and right ovaries of a four-years-old harbour seal collected on January 18, illustrating the corpus albicans (ca) in the left ovary and the corpus luteum (cl) in the right ovary.

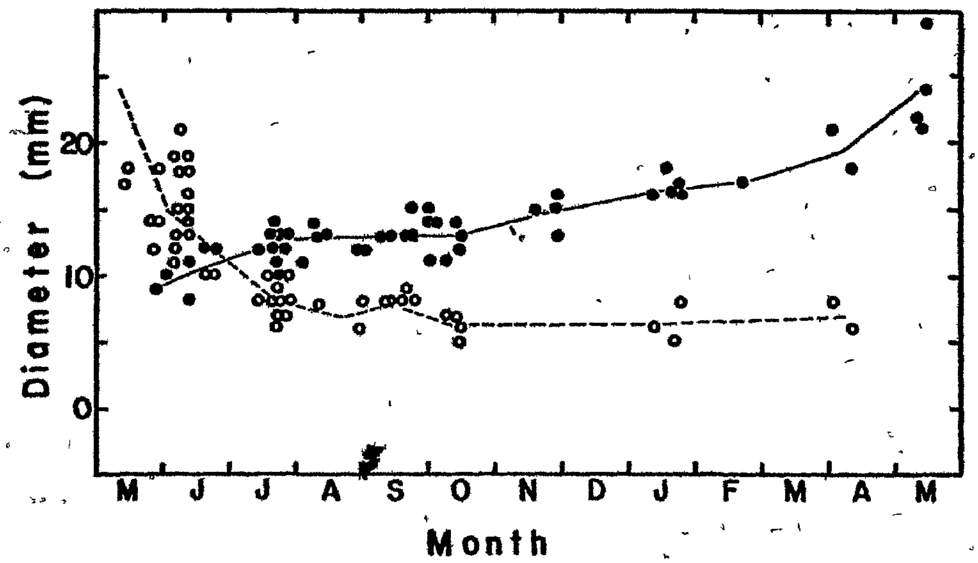


Fig. 18. Changes in diameter of the corpus luteum (closed symbols, solid line) and of the corpus albicans (open symbols, dotted line) of harbour seals in eastern Canada. The lines are drawn through the monthly means. Closed symbols in June are for the largest follicles found.

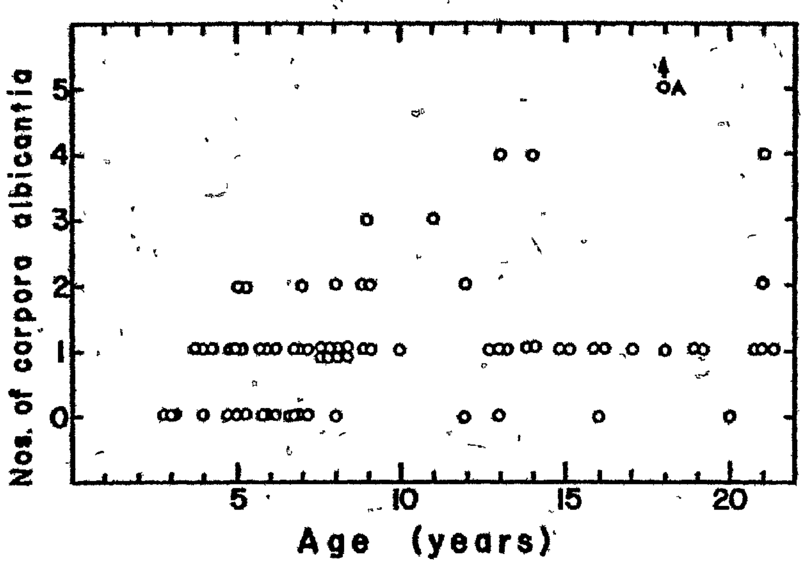


Fig. 19. Total numbers of corpora albicantia found in the two ovaries of harbour seals at various ages. The point marked A refers to an 18-year-old female which had 14 corpora albicantia and which was not pregnant. Generally, corpora albicantia are easily found only for one year after their formation.

Bishop (MS 1968) found that female harbour seals from Alaska mature at 3 to 4 years of age while Bigg's (1969a) results indicate that the majority of females in British Columbia ovulate for the first time at 2 to 4 years of age. In *Phoca largha*, some females ovulate at three while most (93%) are mature at four (Tikhomirov, 1966; Naito and Nishiwaki, 1972).

Fertility of females - It is possible to say whether a seal is pregnant during most of the year, except during the period from ovulation to implantation, when a corpus luteum is present but when the fate of the ovum, whether fertilized or not, is unknown. In harbour seals of eastern Canada, this delay in implantation has been reported to last about 2½ months (Fisher, 1954). Therefore the females collected during this period of delay were not used for the determination of fertility rates of each age group. A problem also arose when teeth used for ageing were accidently destroyed; one nulliparous female with follicles, five primiparous and two multiparous females were without age. Ignoring these eight seals would have introduced a bias, thus underrepresenting the proportion of pregnant females in the total female sample. To avoid the bias, the proportion of nulliparous females with follicles, primiparous and multiparous females in each age group was calculated and the samples without age were distributed in each age group according to these proportions. This explains the values with decimals in Table 4 where the age specific fertility rates are given. It is seen from this table that fertility increases steadily from 33% at age four to 100% at age seven and eight, with the 50% level being reached at five years of age. The average fertility for the 25 seals aged nine or more years in the sample, is 92%. Female harbour seals in British Columbia are fertile about one year younger with the 50% fertile female level being reached at four years of age (Bigg, 1969a).

Annual reproductive cycle

Males - The changes in reproductive condition of the adult male were followed by the examination of the testis and epididymis tubules for presence or absence of sperm, and by measuring the diameter of these tubules. Only seals six-years-old or more were examined here. The results are illustrated on Fig. 20. No data are available for March-April and November-December. The lines joining the monthly means indicate the major trend.

As can be seen, sexual activity is at its lowest level in January but slowly increases afterwards, with sperm first appearing in the testis in late February (closed symbols indicate the presence of sperm). The diameter of the tubules becomes maximal in May-June with sperm then being present in both the testis and the epididymis of most males examined. From mid-July to mid August, sexual activity in the testis is almost completely inhibited. However, in September and October, the testis becomes somewhat active, as indicated by the increase in the diameter of the tubules and by the presence of sperm in one seal. Afterwards, the activity probably decreases until mid-January when the cycle resumes.

It is not known certainly when harbour seals copulate as this is generally accomplished in the water in this species and is therefore very seldom observed. I have seen what was without question "sex play" between two seals as early as April 10 on Sable Island; this is six weeks before the mean whelping date of May 24. Harrison (1963) has

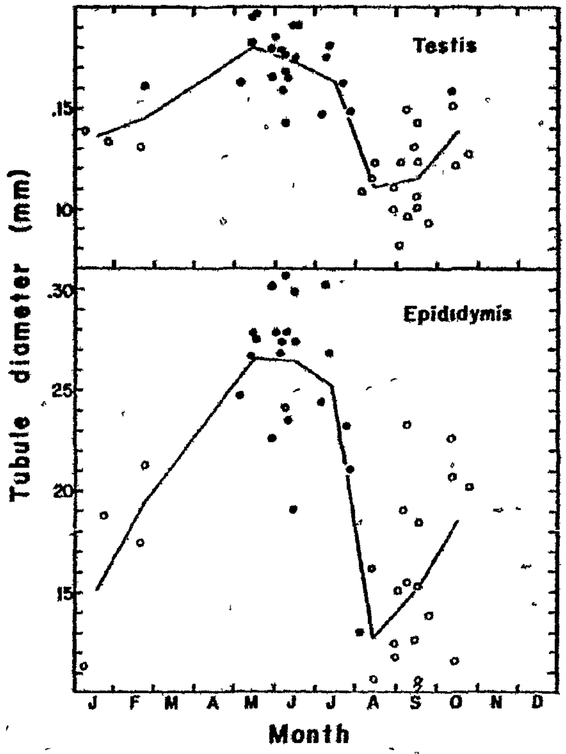


Fig. 20. Annual variations in the diameter of the testis and epididymis tubules. Each point represents the mean of 10 tubules in one seal. Closed symbols are tubules with sperm, open symbols are tubules without sperm. The lines indicating the major trend are drawn through the monthly means.

found that nulliparous females in the Wash, England, can ovulate and have a corpus luteum five to six weeks before parturition so that there likely are some females in oestrus at that time. Mating on land was seen once, by D. Welsh (personnal communication) on July 10, 1972 on Sable Island, half an hour before a total eclipse of the sun; he describes seeing numerous pelvic thrusts of a male laying on a female a few meters from the water's edge. Mating on sand bars is also reported by Harrison (in Venables and Venables, 1957). Because of the scarcity of these sightings, the time when most matings take place remains unknown. On Sable Island, assumed males are seen "courting" assumed females in the water from early April until late July. The increased activity of the testis in September and October described above might explain the renewal of "sex play" noted by seal hunters in August and September in eastern Canada (Fisher, 1954).

Females - The annual cycle of the female is best described starting at the end of the lactation period, which on Sable Island ends about three weeks after birth of the pups. On this island, most births occur around May 24; the mean date for the end of lactation is approximately June 14. A series of 16 ovaries collected from early June to late July on Sable Island and in north-eastern Nova Scotia where, according to local seal hunters, the whelping season occurs at about the same time as on Sable Island, supplies an approximate date of ovulation. The data (Table 5) suggest that most ovulation must take place between June 12 and 25. Mid-June (median, June 19) is likely a good approximation of the mean ovulation time of those females having ovulated in the past. Those ovulating for the first time might do so somewhat earlier in the season, as suggested by specimen PV 107, a nulliparous female with a luteinizing

Table 5. Percentage of the follicle luteinized in females collected in June and July in northeastern Nova Scotia. Percentage obtained from examination of transverse sections.

Sample no. PV-	Date	% luteinized	Remarks
107	2-6	8	first ovulation
86	9-6	0	no mature follicle
441	12-6	0	mature follicle present
402	12-6	5	female with large pup
226	23-6	80	post-partum
227	23-6	90	"
228	23-6	70	"
371	25-6	0	no mature follicle
236	15-7	100	post-partum
135	22-7	80	"
143	23-7	100	nulliparous
158	"	100	post-partum
161	"	100	"
162	"	100	"
239	24-7	100	"
240	25-7	100	"

follicle, captured on June 2. It was mentioned earlier that young females can ovulate before the whelping season as described by Harrison (1963); Venables and Venables (1959) also describe some copulation before whelping in harbour seals found in Shetland, England.

It does appear that in north-eastern Nova Scotia, ovulation (median date: June 19) occurs in parous females soon after the end of lactation (median date: June 14). This is suggested by specimen PV 409, a female still with her pup shot on June 12; in one ovary, a large ruptured follicle just starting to luteinize was found. Unfortunately, the pup escaped and the condition of the mammary gland was not noted; it is thus unknown if the pup was still being nursed or just accompanying the female. One female (PV 371) shot on June 25 had an unruptured mature follicle and no corpus luteum while the latest female (PV 135) without a completely luteinized corpus luteum was collected on July 22; she had probably weaned a pup recently as suggested by the large regressing corpus luteum and had a new corpus luteum 80% luteinized.

These samples, and information published elsewhere refered to above (Venables and Venables, 1959; Harrison, 1963) thus indicate that ovulation can occur during a period extending from a month before parturition for young females, to a month and a half after parturition for older females. In north-eastern Nova Scotia, ovulation appears to take place generally at the end of lactation, in mid-June, or about three weeks to a month after pupping. This agrees with earlier results by Fisher (1954) who studied harbour seals in eastern Canada. Slightly different results were obtained by Harrison (1963) with harbour seals in the Wash, England; he found that ovulation occurs generally two to three weeks after the end of lactation, or six weeks after birth.

After ovulation, the corpus luteum is formed but no sign of pregnancy is noted until about mid-September when a small bulbous swelling becomes noticeable on the cornu. In eastern Canada, such swellings have been found from September 15 onward (Table 6). It is difficult to say from preserved specimens, when the blastocyst does implant in the uterine wall. It is assumed here that implantation takes place when the bulbous swelling becomes noticeable on the cornua. If this assumption is correct, implantation of the blastocyst in north-eastern Nova Scotia is completed around September 15 or on the average three months after ovulation. Fisher (1954) reported a delay of about three months in eastern Canada; Harrison (1963) estimated the delay to last two to three months in the Wash while in British Columbia, Bigg (1969a) found two months. The data available for eastern Canada suggest an active gestatation of eight months. The annual cycle of the adult female harbour seal in north-eastern Nova Scotia is summarized in Table 7.

Table [illegible]. Presence or absence of an implanting blastocyst indicated by the presence or absence of a bulbous swelling on the cornu of harbour seals collected during September and October in northeastern Nova Scotia. Seals without swelled cornua had ovulated earlier in the year as indicated by the presence of a corpus luteum in one of the two ovaries.

Sample no. PV-	Date	Age	Bulbous swelling absent	Bulbous swelling present
177	1-9	13	X	
2[illegible]2	3-9	[illegible]	X	
2[illegible]6	1[illegible]-9	[illegible]		X
58	21-9			X
59	21-9	22		X
291	2[illegible]-9	17		X
292	26-9	-		X
492	29-9	-		X
273	1-10	3	X	
274	1-10	4		X
275	1-10	3		X
294	[illegible]-10	-		X
296	9-10	9		X
301	12-10	-		X
305	14-10	-		X

Table 7. Annual cycle of adult female harbour seal in northeastern Nova Scotia, from data obtained in this study. Values are approximate.

Event	Estimated date	Mean or median	Days after ovulation
Ovulation	June 19	median	0
Implantation	Sept. 15	"	88
Embryo 1 cm long	Oct. 1	mean	104
Birth	May 24	"	339
End of lactation	June 14	median	360
Ovulation	June 19	"	365
Weaning of pups	June 23	mean	369

ANNUAL CYCLE OF THE POPULATION

The activities of the harbour seals in eastern Canada during the year depend largely on the reproductive cycle described previously. Environmental factors such as meteorological conditions, availability of food and presence of predators also modify the behaviour of the seals during the year. Some of the effects of these environmental factors are described in relation to the seasons. Unless otherwise noted, the observations described below were made on Sable Island.

Winter

Numerous reports from fishermen, Fisheries Officers and scientists contributed in the past to the belief that harbour seals disappear from eastern Canada during the winter months, although other works had clearly stated that this species is a permanent resident of the localities which it inhabits (Allen, 1880; Templeman et al., 1957). This belief was based on the rarity of sightings of these seals along the coast during the cold season. Mansfield (1967b) stated that harbour seals disappear from Sable Island in the winter, after seeing only two seals there in January and February of four consecutive years. Since then, more winter counts around the whole island have shown that this species is to be found regularly there during the cold season. From these winter observations, I came to believe that harbour seals would not haul out on the beach if the air temperature was below a certain critical level. Weather data were obtained from the Sable Island weather station for those days when counts were done. The data consisted of the mean air temperature and wind velocities in morning (07:00h. - 12:00h. A.S.T.); by using a formula provided by the Atmospheric Environment Service of Canada, the air temperature was corrected for windchill. The morning data were used as harbour seals on the island generally haul out in early morning. The numbers of seals counted on the beach on winter days, the temperatures and the winds are given in Table 8. These data suggest that when the air temperature corrected for windchill drops below -15°C, harbour seals prefer to stay in the water (Fig. 21). As this temperature often occurs in eastern Canada from December to March, seals would rarely be seen on their normal hauling grounds during these months.

Another factor responsible for the rare sightings of harbour seals in winter is that most bays and inlets which they frequent during spring, summer and fall freeze up during the cold season. As this species does not, like the ringed seal, Pusa hispida, maintain a breathing hole in the ice, the most likely assumption is that they move to areas of open water as they do in the Arctic (Mansfield, 1967a). On mild winter days, they haul out on the ice, as sometimes noted in St. Margarets Bay, Nova Scotia (Dr. E. T. Garside, personal communication). On Sable Island, herds of this species will rest for hours on snow without apparent discomfort from the cold substrate.

The structure of herds is modified during the winter months. The number of seals per herd increases from an average of 30 in June to an average of 160 seals in January while the average number of herds during the same months, decreases from 40 to about 7 (Fig. 22). Often during very cold weather very few seals are seen in the water around

Table 8. Numbers of seals hauled out on Sable Island, in winter, and weather conditions observed on the mornings of the counts. The corrected air temperature (T/W) is calculated from a formula incorporating the observed air temperature in ^{o}F (TA) and the wind velocity in miles per hour (VA):

$$T/W = 91.4 - \left[(0.288\sqrt{VA} + 0.45 - 0.019 \times VA)\,(91.4 - TA)\right].$$

Date	Seals on the beach	Mean morning (0700 - 1200h.) Temp. ^{o}C	Wind m.p.h.	Corrected temp. ^{o}C
26- 1-1962	0 (1)	-1.39	29.3	-16.94
21-12-1967	345 (2)	2.50	26.6	-10.62
19-11-1970	1000+ (3)	5.56	15.0	- 2.03
17- 2-1971	2 (3)	-2.50	28.0	-16.19
22- 1-1972	442 (3)	-0.56	9.1	- 5.45
24- 1-1972	1032 (3)	3.74	10.0	- 1.22
25- 1-1972	1204 (3)	0.28	12.8	- 7.48
28- 1-1972	0 (3)	-9.23	22.5	-25.71
29- 1-1972	9 (3)	-7.69	17.3	-20.94
1- 2-1972	40 (3)	-6.78	19.1	-20.53

(1) Mansfield and Fisher, MS 1962

(2) Mansfield, MS 1968

(3) Author

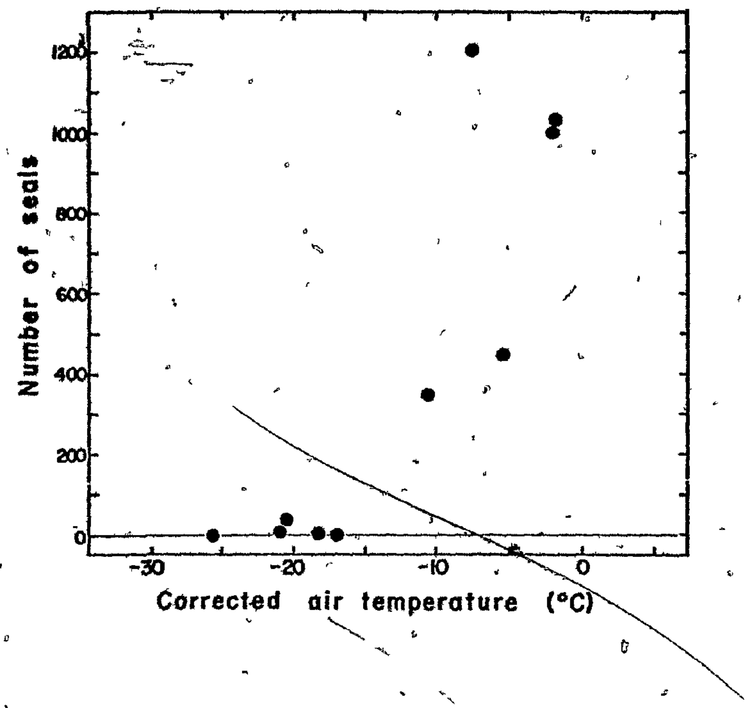


Fig. 21. Relation between the numbers of seals hauled-out on Sable Island in winter and the corresponding air temperature corrected for windchill, from the data in Table 8.

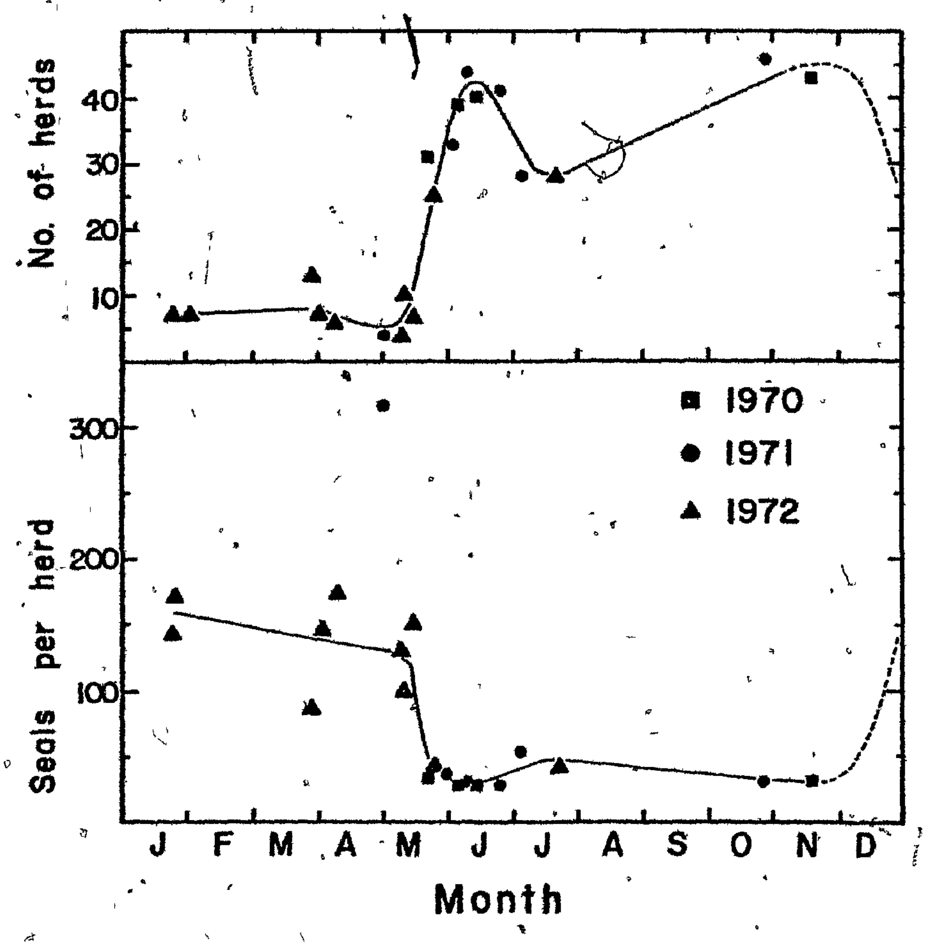


Fig. 22. Monthly changes in the number of herds and in the mean number of harbour seals per herd on Sable Island, from data collected during 1971 - 1972. The eye-fitted lines indicate the trend.

the island. For example, during a complete ground census of Sable Island on a cold January 28, 1972, only 30 harbour seals were counted, all in the water, while 3 days before on a milder day, 1204 seals distributed in seven herds all on the beach, had been counted (Table 8). Probably the seals often move offshore during cold days, possibly to feed on inshore fish which are said to migrate to deeper warmer water during winter months (Havinga, 1933; Leim and Scott, 1966; Sergeant, 1951); also, when avoiding the colder inshore water, the seals would diminish their energy requirement for the maintenance of the body temperature by decreasing the heat loss.

Spring

Movements of seals - As warmer days return to eastern Canada in April and May, the harbour seals appear more often in bays and inlets. Numerous fishermen interviewed stated that the seals disappear in the winter and return in May to have their pup on sand bars and islets at the head of bays.

On Sable Island, the large herds are maintained until early to mid-May when, coincident with the onset of parturition, they break down in numerous small herds (Fig. 22). At the same time, numerous pregnant females cross the south beach of the island to three brackish lakes called the Wallace Lakes, probably seeking the calm waters where they can safely give birth and raise their pup away from the heavy breakers (see also Mansfield, 1967b).

Whelping - Parturition appears to start in mid-May throughout the area covered by this study, with the exception of the St. Lawrence estuary where the first pups are born in late May (David Sergeant, personal communication). The time of birth can also change from year to year in a locality; in 1971 on Sable Island, the mean date of birth was on May 21 while in 1972, it was on May 26 (Table 9).

Abortions occur at times. During a 10 day visit on the island in late February 1971, two aborted foetuses were found, respectively 46 and 51 cm in nose-tail length. The former was still alive when found and died half an hour later while the other one was dead. In each case, a herd of seals on the beach had been scared by my approach and possibly the births were a result of the commotion created by the disturbance. A similar situation occured on April 11, 1972 when a six week premature pup was found. It was fully developed, 70 cm long, but thin and completely covered with a firm white coat called lanugo (Fig. 23); vocalisation was as in the newborn pup. No seal was seen waiting for the pup in the way that females often do during the whelping season. The pup wandered on the island for two days, covering some distance, and was then killed as gulls were attacking it. Newby (1966) obtained by Caesarean section a four week premature, lanugo covered Pacific harbour seal which appeared as healthy as normal newborn pups. Sable Island was also visited by the author for two weeks in late January 1972 but no aborted foetus was found at that time.

The pups can swim at birth but generally do not attempt to escape from approaching humans when newborn. However, some of the females with a pup will adapt to regular disturbance during consecutive years by carrying their pup to sea. After three years of continuous disturbance during pupping on Sable Island, caused mainly by the present study, I saw in the third year, for the first time, females grabbing the pup with

Table 9. Details of the 1971 and 1972 whelping seasons of harbour seals on Sable Island.

Details	1971	1972
Mean birth date (May)	21	26
First birth (May)	11	7
Last birth (June)	7	10
Prewhelping population	1329	1147
Mean birth length (cm)	75.9	77.7
Total pups born	331	359
Pup mortality (1^{st} month), %	21	13
Pups dying before weaning	71	47
Death due to: desertion by mother (%)	79	69
stillbirth (%)	10	29
shark kill (%)	1	0
unknown cause (%)	10	2

Fig. 23. Six weeks premature pup, healthy and covered with a firm lanugo. It survived for two days and was killed as gulls were attacking it.

their mouth either by its fore or hind flipper and towing it in the sea, past the breakers, where the water is calmer and where the newborn pup can swim safely, often riding on the back of its mother. In areas where bounty hunting has been taking place for many years, hunters report that often the female will tow her pup under water in trying to evade them.

Lanugo and umbilicus - On Sable Island, numerous or few pups can be born with a white coat depending on whether the birth season is early or late (Boulva, 1973). In 1971, when the birth season was early, 25% of the pups were born with lanugo. Most of these retained it for nine days after which shedding started (Fig. 24). After the loss of the natal fur, the young pup has a pelage of a gray colour with varying spotted patterns similar to the pelage of the freshly moulted adult. The umbilical cord in newborn pups is generally severed at about 3 cm from the umbilicus. The remains of the cord on the pup dry up and shrink; in nursed pups, the umbilicus can heal completely between four and nine days with an average of six days (Fig. 25). The condition of the umbilicus can be used to estimate the age of the pups until they are about five days old (Boulva, 1973).

Pre-weaning mortality - In a previous paper (Boulva, 1973), I indicated that, apparently, on Sable Island a higher mortality of pups prior to weaning was associated with an earlier mean birth date and that the types of mortality changed slightly with different mean birth dates. The mortality and population size for 1971 and 1972 are given in Table 9. There are three major causes of mortality in pups: desertion by the mother, stillbirth and shark kill. It is difficult to assess what proportion of the desertion should be attributed to human disturbance;

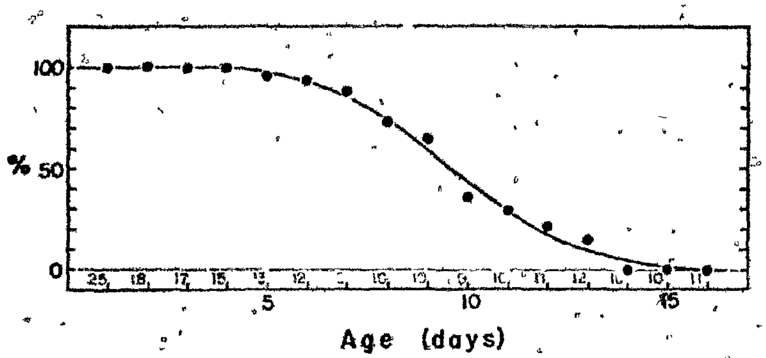


Fig. 24. Percentage of harbour seal pups born with the lanugo on Sable Island, 1971, retaining it at given ages. The sample size for each age is given along the abscissa.

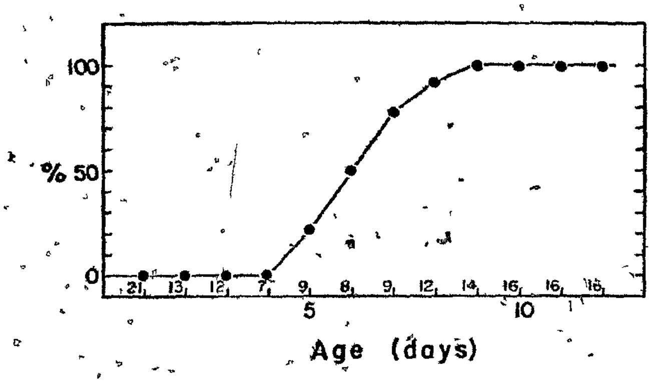


Fig. 25. Percentage of harbour seal pups with a healed umbilicus at given age, on Sable Island, 1971. The sample size for each age is given along the abscissa.

it is assumed however that this disturbance has been constant from year to year during this study. The major difference in mortality patterns between 1971 and 1972 was the almost threefold proportional increase in stillbirths, possibly related to a larger mean size of pups at birth in the latter year (Table 9). However the overall mortality was significantly less ($P < 0.01$) in 1972 (13% vs 21% in 1971) possibly because the pups, being better developed at birth, were able to follow their mother more easily, thus decreasing the mortality due to accidental separation of pup and mother. The toll taken by sharks might be underestimated as most pups attacked are probably entirely eaten; however, it is felt that the cold water in May and June probably keep most sharks away from the area of Sable Island until later in the summer.

Weaning - Weaned pups are first solitary but rapidly associate together forming small herds as the season progresses and are then easily told apart from nursing pups who generally are accompanied by their mother. Most pups are weaned 31 days after birth according to field counts (Fig. 26). The data on the pups' growth in weight (Fig. 9) also suggest that lactation ceases about 10 days before weaning. As can be seen on this figure, there are numerous recaptures of nursed pups from age 0 to 20 days, very few recaptures between ages 21 and 30 days and a substantial increase in recaptures of weaned pups (open circles) older than 30 days. These data combined with my observations of the seals at the time of weaning are interpreted as follows: nursed pups are sleepy when digesting a milk feed and do not wake up rapidly enough to escape with the fleeing female as the observer approaches; pups still with their mother between age 21 and 30 are not as sleepy, having little

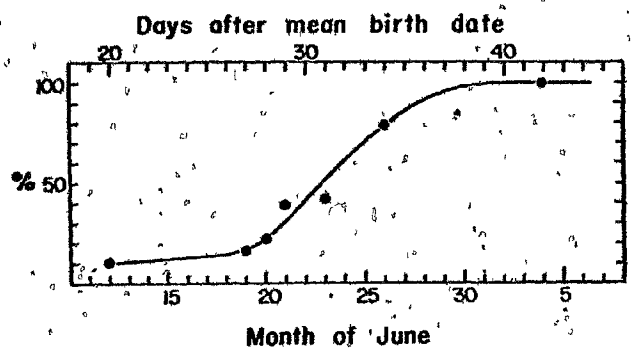


Fig. 26. Percentage of harbour seal pups weaned on a given date on Sable Island, 1971. The assumed rate of weaning is indicated by the eye-fitted line.

or no milk to digest; as soon as the female escapes to the water, the pup follows and is then difficult to catch; when weaned, the pup loses its clue to danger, having no mother to follow, and is more readily caught. It has been seen that 20 days of nursing is sufficient for the average pup to more than double its weight (Fig. 9). This short nursing period is related to the high fat content of the milk of the female, 45% in the harbour seal (Harrison, 1960) as compared to only 3.4% in bovines (Pilson and Kelly, 1962).

Mating - It has been mentioned that ovulation occurs a few days after the end of lactation (Table 7). What the social structure of the population is at that time and whether territoriality and polygyny occur during the breeding season are difficult to ascertain because ...st of the sexual activity of the harbour seal takes place in the water. ...owever, two small points of evidence suggest that adult males may engage ...n some form of territorial behaviour, 1- from early June on, numerous ...les are seen with bleeding cuts on the head and neck, suggesting ...ighting; some of these cuts are quite deep and it seems unlikely that ... were made by females reluctant to copulate, 2- during June and July, ...solated large males often with scarred head and neck are scattered at ...egular intervals, about every half mile, along the beach often in the ...mpany of one or more females with pup or with one or two other smaller ...als of unknown sex. These males may occupy the same area of beach for ... consecutive days, often in places where the seals do not normally ...l out at other times during the year. This suggests a form of ...ritoriality but at this point, one can only speculate on the role of ... scattered large males. Even without direct evidence for polygyny, ... can be noted that the average adult male of this species must mate with almost two females for all to be impregnated. The ratio of mature females to adult males is, in eastern Canada, 1.79 : 1.

Summer and fall

During these two seasons which, because of the maritime climate, tend to be little differentiated in eastern Canada, Sable Island harbour seals appear to live a very quiet life, sunning themselves or sleeping on the beach. They remain in numerous small herds (Fig. 22) often with a few grey seals, Halichoerus grypus, ~~amongst them~~. There is however a small reduction in numbers of herds in mid to late July, possibly associated with moulting which takes place at that time.

Moult - The moult starts in early July on Sable Island. A yearling captured there on July 5 and just starting to moult was fully moulted on July 20. The onset of moulting might start at different times elsewhere as 9 of a sample of 13 harbour seals collected in mid-August on the island of Miquelon, just south of Newfoundland, had moulted. Harbour seals do not appear to change their way of life during this moulting period and seem to feed normally (see section on feeding).

Predators - During late summer and early fall, predation by sharks appears to intensify, possibly due to a greater number of sharks moving northward because of warmer waters. Most kills of harbour seals by sharks on Sable Island take place from late July to late October as evidenced by the greater numbers of dead seals with shark bites found on the beach during these months (B. Beck and D. Welsh, personal communication). Sharks appear to be a regular predator of seals in eastern Canada; Fred Bruemmer (personal communication) examined breeding grey seals on Sable Island in 1972 and found that about 10% of the males had deep crescent shaped scars that were most likely shark bites. Templeman (1963) gives evidences of predation by the white shark, Charcharodon carcharias, on harbour seals in eastern Canada while Sergeant (MS 1961) indicate that the killer whale, Orcinus orca, may occasionally eat seals.

As the weather turns colder in November and December, the harbour seal starts forming large herds and becomes more reluctant to come on the shore. Slowly, its way of life becomes more pelagic as the winter season sets in.

Regional differences in diurnal activity patterns

On Sable Island, harbour seals haul out independently of the tides. Numerous trips on the beaches at night indicate that almost no seals stay out of the water during the dark period, with the exception of some of the females with pup during the whelping season. This was true in winter as well as in summer, suggesting that these animals are more active during the night. The seals haul out at dawn when the weather is favourable. The first seals generally come out of the water some 30 to 50 minutes before sunrise (Fig. 27). Herds on the beach are most often well established two hours after sunrise eventhough numerous seals are seen in the water throughout the day. Except for some warm winter and early spring days, the whole population is never out of the water all at once. An exemple of the exception is on March 26, 1972 when 95% of the population was hauled out on the beaches of Sable Island.

Whether or not most feeding takes place at night is not known; vision is not essential for feeding as healthy blind females with pup have been found in Washington State (Newby et al., 1970). Day feeding

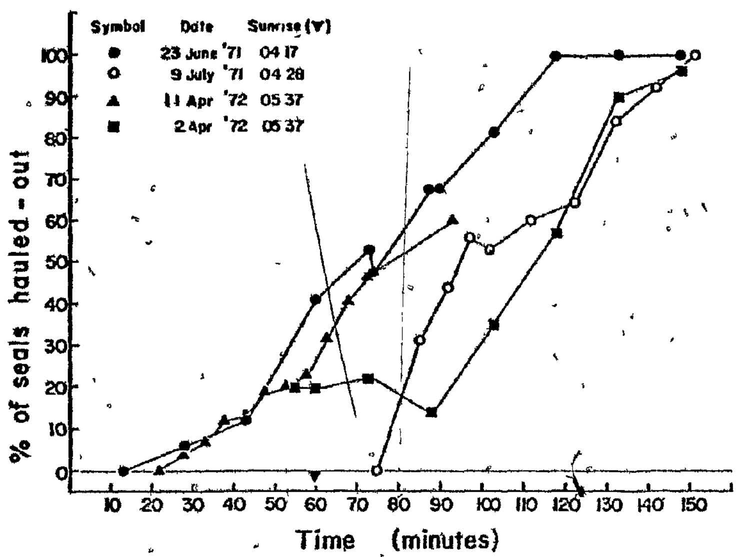


Fig. 27. Hauling out of harbour seals on Sable Island on mornings when the weather is good. Time 0 is 60 minutes before sunrise. The number of seals present on the beach at 150 minutes is taken as 100% for comparison even though more seals might have hauled out later during the day. During bad weather, few or no seals may haul out.

occurs: a large male (PV 409) collected at 13:00h. on July 9, 1971 had a stomach full of freshly ingested flounders and gadids; the seals are often seen in mid-day being very active in shallow waters where terns are taking small fish, and are probably also feeding. However, it is difficult to establish whether most seals feed at night or during the day without an adequate sample from all hours of the day.

Elsewhere in eastern Canada, hauling out is probably related to low tides, as this is when many ledges become exposed for the seals. Under these conditions, seals would be expected to haul out at night to benefit from nocturnal low tides. In numerous areas, fishermen report hearing growls during the night, coming from ledges where harbour seals often haul out during the day; these sounds are attributed by the fishermen to seals spending the night on the ledge.

POPULATION DYNAMICS

In the section on distribution, it was mentioned that the harbour seals in eastern Canada form small discrete populations. Theoretically, separate analysis should be made of each of these groups, but data are not adequate for this. However, it is possible to follow the changes of two typical populations by using data from the bounty returns. One of these populations is located in the Fourchu area in southern Cape Breton and the other in Charlotte County in southern New Brunswick. These two populations differ strongly, the former having been left relatively unharmed until 1968 when sampling for this study was initiated; the latter population has been hunted intensively for bounty during the last ten years and before (Table 10). It will thus be possible to see how constant hunting modifies the age structure of a population of harbour seals. This will be related to the age structure of the overall population of these seals found in Nova Scotia, New Brunswick and Prince Edward Island. Estimates of population size in 1950 and 1971 combined with known hunting mortalities and fertility rates will allow calculation of natural mortality and permit determination of a sustainable yield.

Sampling

The age distributions obtained from shot samples are assumed to represent the age structure of the population at the time of sampling. However as indicated by Caughley (1966), shot samples tend, in most wild mammal populations, to be biased towards the younger age classes which, being less aware of danger, are more easily collected. Furthermore,

Table 10. Number of seals reported killed for bounty in the Fourchu area, Cape Breton and in Charlotte County, southern New Brunswick from 1959 to 1971. There are no data for 1960, 1961 and 1965.

Year	Charlotte County		Fourchu	
	Adults	Pups	Adults	Pups
1959	116	115	8	12
1962	[illegible]	143	1	11
1963	[illegible]	104	2	17
1964	[illegible]	[illegible]	2	11
1966	[illegible]	[illegible]	6	4
1967	12	23	1	4
1968	41	72	16	17
1969	84	112	35	56
1970	74	93	40	56
1971	68	77	[illegible]	35

a population should be sampled at a given time, as the age structure changes during the year because of mortality. If the population is numerically stable from year to year and if the age structure remains the same with time, then a random sample from that population will provide an age distribution which parallels that of a cohort born at a given time. If small samples are taken from such a population at the same time each year, they can be added to provide a better estimate of the actual age composition.

Such a population is rare, but by knowing that the population is not rapidly increasing or decreasing, one may derive a reasonable estimate of a stable age distribution. In this study, the raw data were obtained from the bounty kill information of Fourchu and Charlotte County combined respectively from 1968 to 1971, and from the bounty kill of the three maritime provinces of eastern Canada combined from 1966 to 1971, thus providing two groups of data for individual localities and one group of data for the overall Maritimes. The young of the year are greatly overrepresented in the sample. This problem is eliminated by assuming that the age distributions are those of the population just at the onset of the pupping season. This assumption is reasonable as most hunters operate from the beginning of the pupping season until 3-4 months after, with few seals being shot in late fall and almost none during winter.

A theoretical number of pups born is calculated from the known pup production of harbour seals on Sable Island, where field counts indicate that a population of 100 seals at the onset of pupping will produce 25.7 pups (Boulva, 1973). By adding the total number of seals aged one year or more in the sample and multiplying by 0.257, the theoretical pup production is calculated and serves as the initial size of the cohort.

The Fourchu and Charlotte County samples are small and the relation of the $\log_{10}$ of the number present in each age to the corresponding age gave an irregular line which was smoothed by linear regression. In the overall sample from the Maritimes, due to a larger sample, the line becomes irregular only after age 11, and linear regression was then used to obtain a smooth age distribution for older seals. This corrects the situation for example where there would be 60 animals of age 5 and 65 of age 6, an impossible situation if the age distribution is assumed to be equivalent to the survivorship of a cohort.

It was mentioned earlier that the bounty kill is a shot sample and is assumed to represent the structure of the population alive at the time of sampling. This differs from a sample of animals having died of natural causes, and constitutes a survivorship series (l_x) while the latter is a death series (d_x), the two being treated differently in the analysis. This point is confused by Quick (1963) and others using his suggested format but is clarified by Caughley (1966).

Because the seals were shot by hunters receiving a bounty independent of age or size for animals over 1 year of age, it is assumed that the age distributions to be described were obtained from samples randomly collected. As mentioned earlier, there might be a bias towards the younger age classes but it should be fairly small in animals aged one year old or more. The fertility rates calculated in the section on reproduction are from samples collected mainly in Fourchu and on Sable Island where the populations have been little hunted prior to 1968. Therefore, these fertility rates may not apply to other areas of eastern Canada where bounty hunting has been intensive for many years, such as Charlotte County.

Sex ratio

The data from the bounty kill do not include the sex of the animals. However, the sex has been noted in the 246 seals aged one year old or more collected for the biological study and it was found that this sample consisted of 52% females. This compares to the 53% females found by Bigg (1969a) for harbour seals of same ages in British Columbia. The females are more numerous in older ages and no males older than 25 years were found in eastern Canada while one female aged 29 years and another aged 30 years were collected. The decreasing proportion of males with age is illustrated in Fig. 28; the eye-fitted line was used to obtain age-specific sex ratios which were applied to the bounty kill data and thus supplied different male and female age structures. It is important to take into account this changing sex ratio with age as it will give a number of pups born to the population different from the number calculated if the sex ratio is assumed to be unity throughout the age distribution. Bigg (1969a) obtained similar results with the oldest male reaching only 20 years of age and the females living as old as 29 years. It seems unlikely that the differential mortality of males and females noted here and in Bigg (1969a) might be the result of sampling error unless old males of this species have a behaviour keeping them away from the hunting areas, an improbable supposition.

Population structure

<u>Fourchu</u> - Data for population parameters, kl_x, kL_x, m_x, e_x and q_x are best presented in the form of a life table as described by Deevey (1947). The data for the Fourchu population are given in Table 11. The observed number of animals in each age class l_x are smoothed as explained

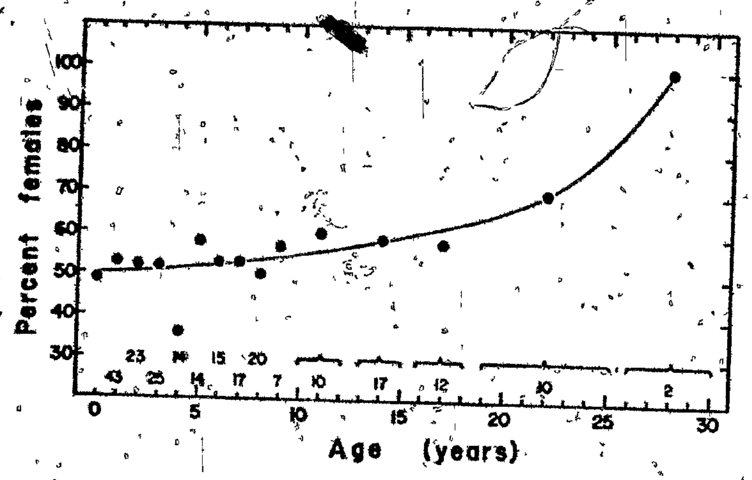


Fig. 28. Eye-fitted line indicating the changes in sex ratio with age of harbour seals in eastern Canada. The numbers along the abscissa indicate the sample size for each age or group of ages.

Table 11. Life table for the population of harbour seals in Fourchu, Cape Breton.

	Males and females				Females only					
Age	l_x	Adjusted l_x	kl_x	Proportion of females	kl_x	kL_x	m_x	$kL_x m_x$	e_x	q_x
0		22.00	1000	.50	1000	757			4.67	.487
1	13	11.29	513	.50	513	481			7.7	.127
2	14	9.87	448	.50	448	424			7.7	.107
3	11	8.62	392	.51	400	375			7.5	.127
4	10	7.53	342	.51	349	330	.167	55	7.6	.109
5	6	6.58	299	.52	311	292	.297	87	7.4	.125
6	5	5.75	261	.52	272	257	.407	105	7.4	.110
7	4	5.02	228	.53	242	229	.500	115	7.3	.107
8	4	4.39	200	.54	216	204	.500	102	7.0	.115
9	2	3.83	174	.55	191	182	.460	84	6.9	.100
10	2	3.45	157	.55	172	161	.460	74	6.6	.134
11	2	2.92	133	.56	149	141	.460	65	6.6	.114
12	3	2.55	116	.57	132	125	.460	58	6.4	.106
13	2	2.23	101	.58	118	111	.460	51	6.1	.119
14	2	1.95	88	.59	104	98	.460	45	5.8	.115
15	1	1.70	77	.60	92	88	.460	40	5.5	.098
16	1	1.49	68	.61	83	78	.460	36	5.0	.120
17	1	1.30	59	.62	73	69	.460	32	4.6	.110
18	0	1.14	52	.63	65	62	.460	29	4.2	.108
19	0	.99	45	.64	58	55	.460	25	3.6	.103
20	2	.87	39	.66	52	50	.460	23	3.0	.096
21	0	.76	34	.68	47	45	.460	21	2.2	.106
22	0	.66	30	.70	42	40	.460	18	1.4	.095
23	1	.58	26	.73	30	19	.460	9	0.5	1.000
Totals:		107.18						1074		

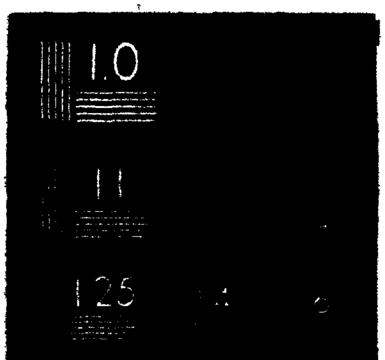
above, to obtain the "adjusted l_x" column. The total number of seals for ages 1 to 23 is calculated (total of 85.2) and multiplied by 0.257 to give an estimate of the numbers of pups born (22). The number of pups is then set equal to 1,000 and the other age frequencies are adjusted proportionaly to the age class 0, giving the kl_x column. The age specific sex ratios (Fig. 28) are then used to calculate the age structure of the female segment of the population which is given in a kl_x series. The kL_x series provides the number of seals in the age group alive halfway through the age period while m_x is the age specific fecundity rate for the production of female pups only. This value multiplied by the corresponding kL_x value will therefore provide the number of female pups born (kL_xm_x) while e_x and q_x are respectively the expectation of further life for an animal reaching age x and the proportion of animals dying during the age interval x to x + 1. As can be seen from the table, summing column kL_xm_x will give the total female pup production for one year, or 1,074. This value is obtained from fertility rates deduced from the ovaries of seals originating mainly from Fourchu and Sable Island. This value of 1,074 is very close to the 1,000 pups in age class 0 which was calculated from the known pup production in the stable Sable Island population. Therefore these two partly independent values (they both depend in part on the assumed age determination) are in good agreement and this suggests that the Fourchu population is also in a stable state.

Charlotte County - If this age frequency distribution (l_x) is treated as above, the pup production, 755, is found to be well below the 1,000 pups expected from the Sable Island pup production data (Table 12). There are three possible explanations for this low pup production.

Table 12. Life table for the population of harbour seals in Charlotte County, New Brunswick.

	Males and females				Females only					
Age	l_x	Adjusted l_x	kl_x	Proportion of females	kl_x	Kl_x	m_x	$Kl_x m_x$	e_x	q_x
0		53.78	1000	.50	1000	882			4.56	.236
1	60	41.07	764	.50	764	689			4.8	.196
2	43	33.06	614	.50	614	560			4.9	.178
3	37	26.62	494	.51	505	456			4.8	.196
4	24	21.43	398	.51	406	370	.167	62	4.9	.177
5	23	17.25	320	.52	334	302	.297	90	4.8	.195
6	10	13.89	258	.52	269	245	.407	100	4.9	.182
7	13	11.18	208	.53	220	200	.500	100	4.8	.182
8	6	9.00	167	.54	180	164	.500	82	4.8	.178
9	4	7.25	135	.55	148	134	.460	62	4.7	.189
10	5	5.84	109	.55	120	109	.460	50	4.7	.183
11	3	4.70	87	.56	98	89	.460	41	4.6	.184
12	5	3.78	70	.57	80	73	.460	34	4.6	.175
13	2	3.05	57	.58	66	60	.460	28	4.4	.197
14	2	2.45	46	.59	53	49	.460	23	4.4	.170
15	1	1.97	37	.60	44	40	.460	18	4.2	.182
16	2	1.59	30	.61	36	33	.460	15	4.0	.167
17	0	1.28	24	.62	30	27	.460	12	3.7	.200
18	1	1.03	19	.63	24	22	.460	10	3.5	.168
19	0	.83	15	.64	20	18	.460	8	3.1	.200
20	0	.67	12	.66	16	15	.460	7	2.8	.125
21	0	.54	10	.68	14	13	.460	6	2.1	.143
22	0	.43	8	.70	12	11	.460	5	1.3	.250
23	1	.35	6	.73	9	5	.460	2	0.6	1.000
Totals:		263.04						755		

2 OF/DE 2



AHC-374

First, it is possible that the value of 25.7 pups produced for 100 older seals present at the onset of whelping does not apply and that the Charlotte County value would be below 25.7 pups, a result of the change in age structure due to hunting; however, Bigg's (1969a) study of a hunted population of harbour seals in British Columbia also provided a value of 25.7 which tends to refute the above argument. Overhunting might constitute a second explanation if the fecundity rates are assumed to be the same as in Fourchu. It can be seen from Fig. 29 that survival is better in the younger age classes in Charlotte County (C), but mortality higher in older age classes than in Fourchu (F); this results in a shortage of reproducing females in Charlotte County. The third and most likely explanation is that fecundity rates from Fourchu do not apply to Charlotte County if we consider the possibility of females becoming sexually mature at a younger age in that county, as the population there has been hunted fairly heavily for many decades. Sergeant (1966) has indicated a lowering of the mean age at which sexual maturity takes place in the female harp seal, Pagophilus groenlandicus, following a decrease in population size because of hunting. The same has been observed in the elephant seal, Mirounga leonina (Carrick, Csordas and Ingham, 1962). In British Columbia, the hunted female harbour seals mature one year earlier than those in Fourchu. If the fecundity rates given by Bigg (1969a) for the British Columbia females are applied to Charlotte County female harbour seals, the female pup production becomes 1,011 animals. Hence, this suggests that if the fertility rates of the Charlotte County population have shifted, as a consequence of hunting, from the Fourchu type of rates to the British Columbia rates, a balanced population could be maintained, as a sufficient number

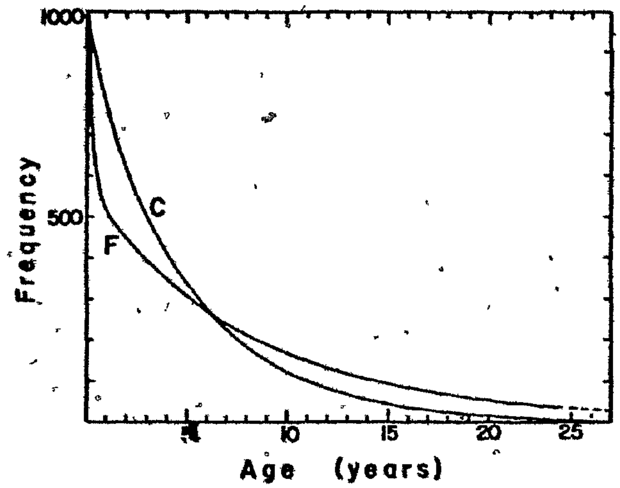


Fig. 29. Smoothed age frequency distribution (kl_x) of harbour seals in an area of low hunting intensity, Fourchu, Cape Breton (F) and in an area of high hunting intensity, Charlotte County, New Brunswick (C).

of pups would be born.

The possibility that the pup production is lower in Charlotte County than on Sable Island as explained above, should be retained. A sample of females from the county would indicate the age at sexual maturity and give fecundity rates for that area and would allow a better comparison with the Fourchu and Sable Island data. If this possibility were verified, it would be a sign that the population is greatly overhunted.

Maritimes - Having looked at age structures in two different situations, it is of interest to know what type of age structure the overall Maritime population exhibits compared with the two well defined cases just examined. Table 13 is a life table for female harbour seals in Nova Scotia, New Brunswick and Prince Edward Island. In this case, the pup production is slightly below 1,000, suggesting that for these three provinces, the age structure of the population might not be very different from that of the Fourchu population. However, there is still a deficit in the number of pups born from such a population, which can be explained as with the Charlotte County population by either overhunting or different fecundity rates. The Fourchu population differs from this more general model in having a higher mortality during the first year of life.

The age structure of males is given in Table 14. The expectation of life at birth, 4.14 in males, is less than the 4.7 years for females. This is a consequence of the higher mortality rates of males as illustrated in Fig. 30. The combined male and female age frequency curve (Fig. 31) which has not been smoothed by linear regression before age 11 shows that mortality decreases from age 3 to 7, suddently increases at age 7 and 8

Table 13. Life table of female harbour seals from data cumulated for the period 1966-1971 and obtained from the bounty kill in the Maritimes.

	Males and females				Females only					
Age	l_x	Adjusted l_x	kl_x	Proportion of females	kl_x	kl_x	m_x	$kl_x m_x$	e_x	q_x
0		171	1000	.50	1000	860			4.66	.28
1	175	123	719	.50	719	633			5.3	.24
2	109	93	546	.50	546	485			5.8	.23
3	71	71	415	.51	423	391			6.3	.15
4	60	60	351	.51	358	347	.167	58	6.4	.06
5	55	55	322	.52	335	320	.297	95	5.8	.09
6	50	50	292	.52	304	301	.407	123	5.3	.02
7	48	48	281	.53	298	243	.500	122	4.4	.37
8	28	29.5	173	.54	187	164	.500	82	5.7	.25
9	19	21.9	128	.55	141	126	.460	58	6.5	.21
10	21	17.3	101	.55	111	101	.460	46	7.1	.18
11	13	13.9	81	.56	91	86	.460	40	7.5	.12
12	14	12.0	70	.57	80	75	.460	35	7.5	.13
13	12	10.2	60	.58	70	66	.460	30	7.5	.13
14	9	8.9	52	.59	61	57	.460	26	7.5	.13
15	6	7.6	44	.60	53	51	.460	23	7.5	.09
16	6	6.6	39	.61	48	45	.460	21	7.3	.14
17	6	5.6	33	.62	41	38	.460	18	7.4	.10
18	5	4.8	28	.63	35	34	.460	16	7.6	.09
19	4	4.2	25	.64	32	30	.460	14	7.3	.13
20	5	3.6	21	.66	28	26	.460	12	7.2	.14
21	2	3.1	18	.68	24	23	.460	11	7.3	.08
22	1	2.7	16	.70	22	21	.460	10	6.9	.09
23	3	2.3	14	.73	20	19	.460	9	6.6	.10
24	2	2.0	12	.77	18	17	.460	8	6.3	.11
25	1	1.7	10	.81	16	16	.460	7	6.0	.06
26	1	1.5	8.8	.87	15	15	.460	7	5.3	.07
27	1	1.3	7.6	.93	14	14	.460	6	4.6	.14
28	1	1.1	6.4	1.00	12	12	.460	5	4.3	.08
29	1	1.0	5.6	1.00	11	11	.460	5	3.5	.09
30	0	.8	4.8	1.00	10	10	.460	5	2.8	.20
31	0	.7	4.2	1.00	8	8	.460	4	2.3	.13
32	0	.6	3.6	1.00	7	7	.460	3	1.4	.14
33	1	.5	3.0	1.00	6	3	.460	1	0.5	1.00
Totals:		834.8						900		

Table 14. Life table of male harbour seals from data cumulated for the period 1966-1971 and obtained from the bounty kill in the Maritimes.

Age	Males only: Proportion of males	kl_x	kL_x	e_x	q_x
0	.50	1000	860	4.14	.281
1	.50	719	633	4.6	.241
2	.50	546	475	4.9	.255
3	.49	407	376	5.4	.155
4	.49	344	327	5.2	.102
5	.48	309	295	4.8	.094
6	.48	280	272	4.2	.057
7	.47	264	212	3.4	.398
8	.46	159	137	4.4	.277
9	.45	115	103	4.8	.209
10	.45	91	81	5.0	.220
11	.44	71	66	5.2	.155
12	.43	60	55	5.1	.167
13	.42	50	47	5.0	.140
14	.41	43	39	4.7	.186
15	.40	35	33	4.7	.143
16	.39	30	28	4.3	.167
17	.38	25	23	4.1	.160
18	.37	21	20	3.8	.143
19	.36	18	16	3.3	.222
20	.34	14	13	3.1	.143
21	.32	12	11	2.5	.167
22	.30	10	9	1.9	.200
23	.27	8	7	1.3	.250
24	.23	6	3	0.5	1.000

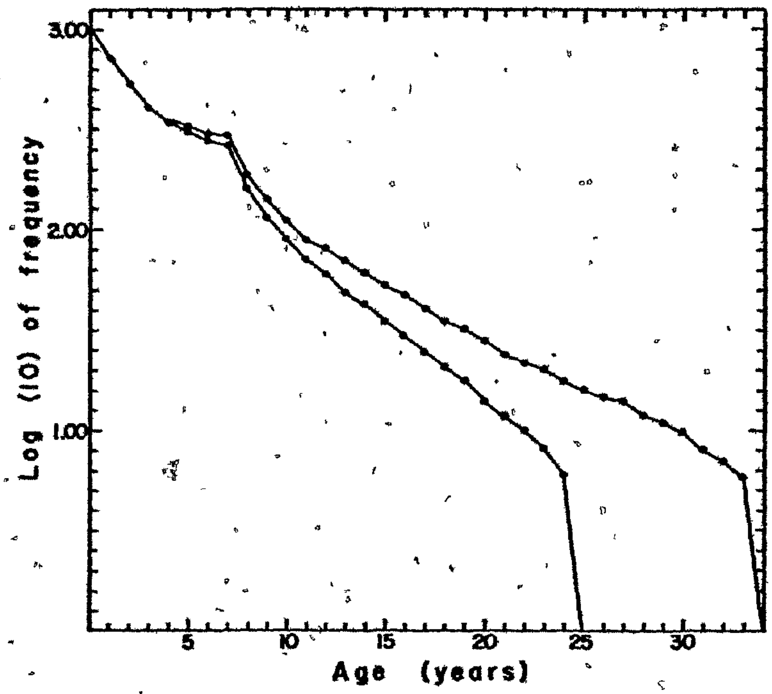


Fig. 30. Age-$\log_{10}$ frequency distribution showing survival of males (closed symbols) and females (open symbols). Data from Table 13 and 14.

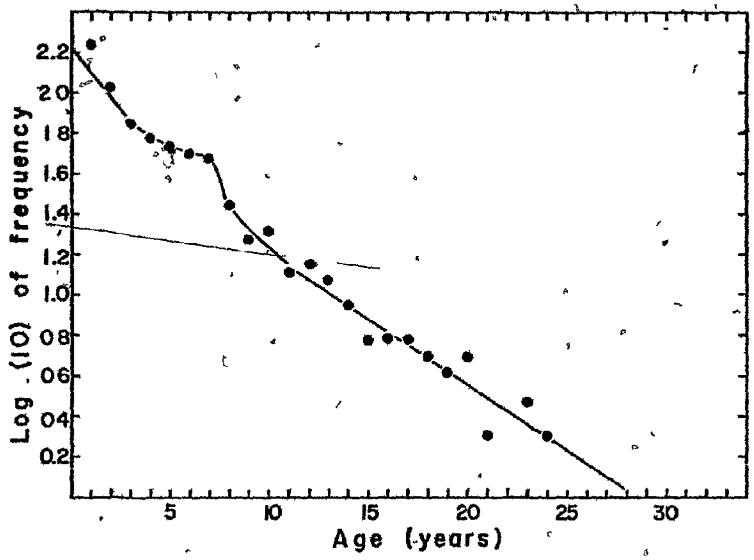


Fig. 31. Age-$\log_{10}$ frequency distribution of the total bounty kill from 1966 to 1971 in New Brunswick, Nova Scotia and Prince Edward Island. Data are from Table 13.

to become afterwards somewhat constant. If the unadjusted age frequencies (l_x) of Fourchu and Charlotte County are examined, similar increases in mortality are found respectively at age 4 and 7. These are the ages around which most males and females mature. The increased mortality then might indicate that transition into adulthood is marked by a noticeable death toll for the population. Bigg's (1969a) data show that only males are affected by a higher mortality at age of sexual maturity, possibly the result of fighting during the breeding season. This explanation could well apply to most of the Maritimes and to Charlotte County but not to Fourchu where the increased mortality takes place at age four (l_x column, Table 11), when most females bear a pup for the first time. Other evidence also suggest however that males might have a higher mortality at age 7: the age specific lengths given on Fig. 11 show that males reach a maximum length at 7 years of age and become smaller on the average from age 8 to 12 even though the differences from year to year do not differ significantly. If Bigg's data for age specific lengths of males are examined (1969a, p. 22), a peak is noted at age 5 which is also the age before male mortality starts increasing in British Columbia harbour seals. The decrease in length after age 7 and 5 respectively in eastern and western Canada is explained if the increase in mortality noted to occur at these two ages affects mainly the large newly matured males, perhaps the first to attempt aggressive encounters with fully adult males.

Population changes in the Maritimes

<u>The bounty</u> - Having examined how hunting affects the structure of harbour seal populations, it is of interest to examine more closely

what the consequences of the bounty have been on the overall population of harbour seals in the Maritimes. The bounty was implemented around 1927 to reduce the number of "seals" harassing fishermen. However, in the three maritime provinces, even though the bounty was aimed at harbour seals, an unknown proportion of grey seals, Halichoerus grypus, was killed each year until 1949 and included in the catch. Before 1949, only the snouts were required to justify the claim and numerous fishermen became very clever at manufacturing seal snouts out of the skin. The catch of seals before 1949 is therefore considered useless for the purpose of analysing the changes in the population of harbour seals in the Maritimes.

In 1949, the lower jaws became the required proof of seal destruction for bounty and this change made it possible to verify the species' identity and also to eventually age the catch. Since that year, the exact number of harbour seal adults and pups reported killed annually for bounty has been recorded and this provides the basis for examining possible changes in the total population of harbour seals in New Brunswick, Prince Edward Island and Nova Scotia excluding Sable Island.

The number of adults reported killed each year needs to be corrected as most seal hunters stated that they always lose a few seals because of sinking. Twelve of them gave an indication of the number of seals they lose and which are assumed to die (Table 15). An average of 65% of the seals one-year-old or more shot were retrieved. The number of seals one-year-old or older reported killed was thus multiplied by 1.54 (or 100/65) to correct for sinking. All hunters stated that few or no pups are lost as they are killed ashore or float well because of their thick blubber layer. The corrected annual bounty kill of harbour seals in the

Table 15. Calculation of a correction factor to account for adult seals likely killed for bounty but not retrieved, mainly due to sinking. All hunters agreed that most pups were retrieved as they float well after being killed. Thus no correction factor was calculated for pups. Corrected number of adults killed = number of adults reported killed X 1.54; 1.54 = 1/0.65.

Hunter	Locality	Adults shot (X)	Adults retrieved (Y)	Y/X
1	Fourchu, N.S.	10	5	.50
2	Canso, N.S.	10	5	.50
3	Ecum Secum, N.S.	25	24	.96
4	Sheet Harbour, N.S.	10	2	.20
5	Port Mouton, N.S.	32	27	.84
6	Jordan Bay, N.S.	10	5	.50
7	Port Clyde, N.S.	10	10	1.00
8	Penfield, N.B.	30	25	.84
9	Beaver Harbour, N.B.	10	7	.70
10	Campobello Island, N.B.	50	38	.76
11	Grand Manan Island, N.B.	10	5	.50
12	Grand Manan Island, N.B.	10	5	.50
	12 localities		AVERAGE:	.65

three maritime provinces is given in Table 16 for the period 1950 to 1971.

Population estimates - Estimates of the number of harbour seals in the three provinces are available for 1949 and for 1971. Fisher ~~(MS 1949)~~ assessed the population to number between 10,000 and 15,000 harbour seals. My own estimate for 1971 is 5,500 in the corresponding areas (data from Fig. 3), and it may be considered as an average value for that year. However, in a stable population of seals, the number of animals present fluctuates annually between a high value just after the pupping season and a low value just before that season. Comparison of population estimates for different years should be from the same month of the year; the number of seals present just before pupping will provide a comparison of the lowest numbers of seals present in the population during the year. If an average value is available, then the size of the prewhelping population is needed. Bigg (1969a) and Boulva (1973) gave evidence that 100 harbour seals just before whelping will yield about 26 pups. If the population is near stable, about 26 animals will die during the year. Then the average number of seals in this population is (126 + 100)/2 = 113, and multiplying the average of 5,500 seals for 1971-72 by 0.885 (or 100/113), will give the estimated size of the prewhelping population for 1972 or 4,850. Assuming that Fisher's highest estimate of 15,000 seals was that of the postwhelping population, the prewhelping population size in 1950 would have been 15,000 X (100/126) = about 12,000 harbour seals. Assuming the above two population estimates to be relatively correct, the numbers of harbour seals in New Brunswick, Nova Scotia and Prince Edward Island during early May would have dropped from about 12,000 in 1950 to about 5,000 in 1972.

Table 16 . Number of harbour seals killed for bounty in the Maritimes between 1950 and 1971, corrected for adults (1-year-old or more) by taking the product of the number claimed killed, and of 1.54 (Table 15).

Year	Number of Adults	Number of Pups	Year	Number of Adults	Number of Pups
1950	[illegible]	1120	1961	273	430
1951	500	[illegible]	1962	230	550
1952	631	[illegible]	1963	275	408
1953	477	[illegible]	1964	100	291
1954	[illegible]	[illegible]	1965	155	349
1955	[illegible]	760	1966	126	370
1956	233	[illegible]	1967	74	199
1957	401	[illegible]	1968	[illegible]	323
1958	461	[illegible]	1969	261	414
1959	330	[illegible]	1970	315	375
1960	243	[illegible]	1971	251	276

Natural mortality - If the reproductive rate of 25.7 pups per 100 seals present just before whelping (Bigg, 1969a; Boulva, 1973) is applied to harbour seals in the Maritimes for the last 22 years, and if the hunting mortality accounts for all the deaths during the year, the the population should increase. Obviously, there is an additional natural mortality with animals dying of old age or being attacked by predators. For simplicity, this natural mortality is assumed to be constant during these 22 years. Furthermore, it is assumed that most pups that died along the shore before weaning were found by fishermen or hunters and reported in the bounty kill; this is suggested by some weathered jaw bones of pups included in the bounty returns.

The pup production, hunting and natural mortalities can be related to the prewhelping population size to obtain the prewhelping population size of the following year. An estimate of the natural mortality can be derived from the estimated population size in 1950 and 1972, the known hunting mortality during these 22 years and the known pup production rate of 0.257. The following equation gives the number of seals present at the beginning of the next pupping season (N_{t+1}), using the number present at the begining of the pupping season on year t (N_o) and the total number of seals killed for bounty n that year (M_t):

$$N_{t+1} = [N_o(1 + 0.257) - M_t] \quad C_1$$

By starting with a N_o value of 12,000 for 1950, and using the annual bounty kills in Table 17, the equation was run by computer first for a value of the natural survivorship C_1 equal to 1.0000 and then decreasing at each iteration by 0.0001 until a prewhelping population in May 1972 having between 4,800 and 4,900 seals was obtained. A prewhelping population of 4,872 was produced on the 1636th iteration with a corresponding annual survivorship to natural mortality of 0.8365; the annual natural mortality is therefore 1 - 0.8365 = 0.1635. This is an estimate of natural mortality and is only as accurate as the 1950 and 1972 population estimates and is dependent on several implicit assumptions about unchanging age structure and lack of seasonality and density dependence of survivorship rates. The annual numerical changes in the population from 1950 to 1972 based on this estimate of natural mortality are given in Table 17. When the future annual bounty mortalities become available from year to year, it will be possible to revise the population size in the three provinces.

Rate of increase - It is possible to forecast approximately the numerical changes which will take place if the mortality due to bounty can be averaged. The annual hunting mortality, defined as the ratio of the total numbers of seals killed in a year to the estimated postwhelping population on that year, has declined since 1950 (Fig. 32). This drop in hunting effort is probably a result of a lower return for the hunting effort because of the diminishing population size. Therefore if average hunting mortalities specific to adults and to pups are calculated, it is preferable to use the average of 1961 to 1971 rather than the 22-year mean to obtain a better approximation of the current hunting effort. The ten-year average survivorship from hunting mortality for adults (C_2) and for pups (C_3) can be obtained from the formulas:

$$C_2 = 1 - \left(\sum_{1961}^{1971} \text{adults killed} / \sum_{1961}^{1971} N_0\right) = 0.965$$

$$C_3 = 1 - \left(\sum_{1961}^{1971} \text{pups killed} / \sum_{1961}^{1971} 0.257\ N_0\right) = 0.760$$

The constants C_2 and C_3 can be related to the annual survivorship from natural mortality, C_1, and to the prewhelping population size (N_0) to calculate the prewhelping population size of the following year (N_{t+1}):

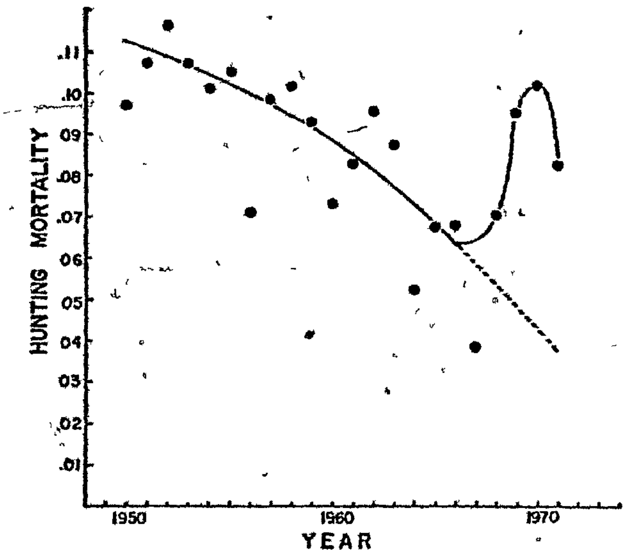


Fig. 32. Hunting mortality of harbour seals in the three maritime provinces for the period 1950-1971, calculated from the number of seals reported killed for bounty each year and corrected for sinking loss and from the estimated numbers of seals in the postwhelping population in the corresponding year. Sustainable yield would be obtained with a hunting mortality of 0.049. The marked increase in hunting during the period 1969-1971 is attributed to a greater reward per seal to obtain scientific specimens. The eye-fitted line indicates the main trend.

Table 17. Calculated changes in numbers of harbour seals in the Maritimes between 1950 and 1971, starting with an estimated prewhelping population of 12,000 in 1950. The value of 0.8365 for the annual survivorship was obtained by computer iterations. The number of pups born was calculated by multiplying the number of seals in the prewhelping population each year by 0.257.

Year	Prewhelping population	Pups born	[Postwhelping population	− Total kill]	× [0.8365 or annual survivorship to natural mortality]
1950	12,000	3,084	15,084	1,458	11,398
1951	11,398	2,929	14,327	1,530	10,705
1952	10,705	2,751	13,456	1,566	9,946
1953	9,946	2,556	12,502	1,347	9,332
1954	9,332	2,398	11,730	1,183	8,822
1955	8,822	2,267	11,089	1,160	8,306
1956	8,306	2,134	10,441	741	8,114
1957	8,114	2,085	10,199	1,003	7,693
1958	7,693	1,977	9,670	982	7,267
1959	7,267	1,867	9,135	848	6,932
1960	6,932	1,781	8,714	637	6,756
1961	6,756	1,736	8,492	703	6,516
1962	6,516	1,674	8,191	780	6,191
1963	6,199	1,593	7,792	683	5,946
1964	5,946	1,528	7,474	371	5,926
1965	5,926	1,523	7,449	504	5,809
1966	5,809	1,493	7,302	496	5,693
1967	5,693	1,463	7,156	273	5,757
1968	5,757	1,480	7,237	508	5,629
1969	5,629	1,447	7,076	675	5,354
1970	5,354	1,376	6,730	690	5,053
1971	5,053	1,299	6,352	527	4,872

$$N_{t+1} = C_1 (C_2 N_0 + 0.257\ C_3 N_0).$$

From this equation, a more general one is found, allowing calculation of the number of seals present in the population after t years (N_t) when the size of the prewhelping population on year 0 (N_0) is known:

$$N_t = N_0 C_1^{\ t} (C_2 + 0.257\ C_3)^t$$

or

$$N_t = N_0\ e^{\ln [C_1(C_2 + 0.257\ C_3)]\ t};$$

this equation is identical to the equation of population growth, $N_t = N_0\ e^{rt}$, where r is the realized intrinsic rate of increase, also called instantaneous rate of increase, as defined in Wilson and Bossert (1971) and therefore:

$$r = \ln\ C_1(C_2 + 0.257\ C_3) = -0.030$$

for the current values of C_1, C_2 and C_3. It is now possible to examine how the population of harbour seals in the three provinces will increase or decrease if hunting conditions change and assuming that natural mortality is constant and equal for adults and weaned pups.

Prediction

Case 1: bounty maintained - If the bounty is maintained, then the average survivorships to hunting mortality, C_2 and C_3, can be used to predict in approximately how many years the following numbers of seals will occur:

Number	Years after 1972
4,000	7
3,000	16
2,000	30

1,000 53

However, it is possible that at low population density, a female in oestrus will not find a potent male; this would decrease the reproductive rates and would accelerate the extinction of the species in an area. The minimal permissible population density required to maintain the present reproductive rate is unknown but it is felt that if the population in the three provinces drops below the level of 2,000 scattered seals, it will face a serious danger of extinction.

Case 2: bounty discontinued - If hunting is stopped entirely, the intrinsic rate of increase may reach its maximal value for this species in nature:

$$r = \ln \left[C_1(1 + 0.257)\right] = 0.050.$$

This assumes that pups before weaning suffer the same natural mortality as the adults because the population of harbour seals in the Maritimes is considered to be at present well below its maximum size. However, as the population increases, the pup mortality before weaning would also probably increase as reported for grey seals, *Halichoerus grypus*, in England (Bonner and Hickling, 1971). On Sable Island, where the harbour seal population is remaining at a fairly constant level, which is assumed to be the maximum level, the mortality of pups during the first month of life is 17.2% (Boulva, 1973); if the survivorship to this early mortality, 1 - 0.172 = 0.828, is included in the equation to replace the survivorship of pups to the hunting mortality, we find that:

$$r = \ln C_1(1 + (0.257 \times 0.828)) = 0.014,$$

which suggests a very slow growth of the population.

However, in the absence of information on the increase of preweaning pup mortality with the density of the population, the maximum rate of increase, $r = 0.050$, can be used to estimate the number of years required before the population reaches its 1950 size of 12,000 seals. By transforming the equation $N_t = N_o e^{rt}$ to find t, 18 years would be needed for the population to number 12,000 seals. This differs by 4 years from the 22 years needed for the population to drop from about 12,000 to about 5,000 seals. The difference is explained by a rate of increase after the suspension of the bounty higher than the rate of decrease (natural mortality plus hunting) while the bounty was in effect.

<u>Case 3: sustainable yield</u> - The hunting mortality required to maintain the population at its present level can be calculated from one of the above formulas:

$$N_{t+1} = C_1 N_o (C_2 + 0.257\ C_3).$$

If no distinction is made between adults and pups, the survivorship to hunting (C_4) will be, when $N_{t+1} = N_o$:

$$C_4 = 1/(1.257\ C_1) = 0.951,$$

which corresponds to an annual hunting mortality of 0.049. To illustrate, 300 seals would have to be taken from the 1972 postwhelping population of $4{,}872 + (4{,}872 \times 0.257) = 6{,}124$ seals, for the population to remain at its present level. Given constant natural mortality and birth rates, the sustainable yield would be about 5% of any postwhelping population size. These seals could be pups, adults or a combination of both. If only pups are taken, then 24% of the pups born in one year would constitute the sustainable yield.

Discussion

Even though based on the overall population of harbour seals found in New Brunswick, Nova Scotia and Prince Edward Island, the prediction of the three cases examined here are dependent on the accuracy of the numerous assumptions discussed above. Furthermore, when it is remembered that the seals in these three provinces are grouped in small discrete populations, the danger is then greater of having one small colony exterminated rather than seals in all areas destroyed at once, as the hunting pressure seems to be higher in some localities depending on the enthusiasm of the local seal hunter. However, examination of the overall catch of harbour seals, as done in this chapter, supplies a useful knowledge of the general trends of the population as a whole; for the present time, this trend appears to be a decreasing one with a realized rate of increase of $r = -0.030$.

Should the bounty be discontinued, the age structure of numerous populations presently hunted would change considerably. In those populations, the age when sexual maturity occurs in the female would probably increase but the overall pup production rate can be expected to remain around 26 pups per 100 seals present at the onset of pupping; it was mentioned that this rate is found in both a regularly hunted population in British Columbia (Bigg, 1969a) and in an unhunted population on Sable Island (Boulva, 1973). The mechanism which maintains this rate of pup production in a heavily hunted population appears to consist in a decrease in the age when sexual maturity in females is reached possibly because of a more rapid growth of individuals; this earlier maturity would counterbalance the diminution in numbers of older females.

If the pup production rate is assumed constant and independent of the age structure in a large population of harbour seals, then the increasing population possibly limits itself through a higher preweaning mortality of pups at high population density. Such a density-dependent mortality of pups has been described in the grey seal, Halichoerus grypus (Bonner and Hickling, 1971). In the harbour seal, the availability of sand bars or islets for females to haul-out undisturbed with their pup could control the growth of the population. Even though pups can swim at birth, they generally have to come on land to be nursed. In large nursing herds as found on Sable Island, there is a higher probability of a female losing her pup after a period of disturbance because of the great number of pups present and, as often seen, not accepting to nurse another abandoned pup. At high population density, enough pups could become deserted and die before weaning to stop the growth of the population as seems to be the case on Sable Island.

FEEDING AND PRODUCTION

Sufficient qualitative and quantitative data on the feeding of wild mammals are necessary for the realisation of adequate studies of mammal production. In seals, most past feeding studies have emphasized qualitative descriptions of stomach contents and on the frequency of occurrence of the various foods without attempting a careful examination of the quantity of food being eaten per meal by seals of known size in nature. This aspect is stressed in the present study, using approximations to obtain an estimate of the feeding rates of harbour seals under natural conditions. The results thus obtained allow quantitative estimations of energy flow through a theoretical population of harbour seals.

Consumption in nature

Foods consumed - Harbour seals in eastern Canada rely mainly on fish for their diet, and to a lesser extent, on invertebrates. Data on 189 stomachs examined by Fisher (MS 1950 and MS 1951), on 61 stomachs examined by the Arctic Biological Station (Mansfield, personal communication) were added to my own data from 352 stomachs, giving a total of 602 harbour seal stomachs examined from eastern Canada. Of these, 299 (49.7%) were empty, 24 contained milk and the remaining 279 (46.4%) contained food in various stages of digestion.

The food species are listed in their order of importance in Table 18 and probably give a good indication of the food preferences of this seal in eastern Canada, even though there are doubtless some geographic

Table 18. Percentage of different food items found in 279 harbour seals.

Species	% of occurrence	Species	% of occurrence
Fish	74.8	Skate egg case, Hypotremata	0.8
Herring, Clupea harengus	24.2	Ocean pout, Macrozoarces americanus	0.7
Flounder, Pleuronectidae	14.1	Sea raven, Prionotus sp.	0.6
Alewife, Alosa pseudoharengus	6.8	Wolffish, Anarhicas sp.	0.6
Hake, Merluccius sp. and Urophycis sp.	6.0	Bass, Roccus sp.	0.4
Smelt, Osmerus mordax	3.7		
Mackerel, Scomber scombrus	3.6	Invertebrates	24.1
Sand lance, Ammodytes sp.	2.9	Squid, Illex illecebrosus	20.6
Capelin, Mallotus villosus	2.9	Srimp, Crustacea	2.2
Cod, Gadus sp	2.1	Crab, Crustacea	1.0
Redfish, Sebastes marinus	1.9	Limpet, scallop and clam	0.3
Haddock, Melanogrammus aeglefinus	1.8	Algae	1.1
Pollock, Pollachius virens	1.1		
Cunner, Tautogolabrus adspersus	0.9		
Shad, Alosa sapidissima	0.8		

and possibly temporal variations in abundance of a given food item. For example, Fisher's samples which came predominently from the lower Bay of Fundy, contained a much higher proportion of squid (15%) than my sample which originates mainly from Sable Island and south-eastern Cape Breton (7%). Flounders were reported by Fisher to be a common food item (28%) in all areas while my data give them as representing only 2% of the diet. As there has been 20 years between Fisher's work and this study, a change in abundance of this group of fish during that period of time could explain the change in frequency.

Herring is the most common species in the seal's diet (24%). It is followed by squid (21%), the 6 specimens examined being identified as _Illex illecebrosus_, then flounders (14%), mainly _Pseudopleuronectes americanus_, alewife (7%) and hake (6%). These five types of fish constitute the main part of the diet of the harbour seal in eastern Canada. Other fishes have a percentage of occurrence below 4%. The last items on Table 18, limpet, scallop and clams, probably originate because of their small size, from the stomach of the fish ingested by the seal. On the average, the diet of the harbour seal in eastern Canada consists chiefly of 73% fish, 26% invertebrates and 1% alga

The food of this species has been relatively well studied elsewhere. In the eastern Atlantic, seals in Holland have been found to feed mainly on flatfish, _Pleuronectes flesus_ (30%), cod (17%) and herring (15%) (Havinga, 1933). In eastern Scotland, 41% of the stomachs contained Gadoids, mainly _Gadus virens_ and _G. merlangus_, 17% contained flatfishes and 13% Clupeids (Rae, 1968). In the Wash, England, Sergeant (1951) found the seals feeding largely on the whelk, _Buccinum undatum_

(94% of diet).

In the eastern Pacific, harbour seals of the Washington State have been reported to eat mainly flounder, Pacific herring and tomcod, listed here in decreasing order (Scheffer and Slipp, 1944). British Columbia seals feed chiefly on salmon (23%), octopus (20%), squid (10%) and rockfish (12%) (Spalding, 1964). In southeastern Alaska, food consisted mainly of gadids (22%), herring (16%), flounders (11%) and shrimps (.5%) (Imler and Saber, 1947), while in the Aleutian area, Atka mackerel and octopus are the main part of the diet (Kenyon, 1964 and Wilke, 1957). Thus, with the exception of the population in the Wash, specialised on whelk, the most common food items found in harbour seal stomachs are herring, flatfish, and either cod or cephalopods.

Changes in feeding with age - After weaning, the young harbour seal first nibbles on small amphipods (one specimen from Sable Island aged five weeks), then turns to the larger shrimps for its subsistence. One pup from Fourchu, Cape Breton, aged approximately five weeks had in its stomach 95% Decapods (73% Lebbeus groenlandicus and 22% Pandalus sp.) and 5% unidentified amphipods. Interestingly, this seal was already host of five codworms, Porrocaecum decipiens, ranging in length from 0.8 to 1.5 cm and their mouth was lipped, a characteristic of worms having reached the final host stage; therefore, they must have been in the seal's stomach already for some time (G. McLellan, personal communication). From Crustacea, the young seal eventually changes to a fish and cephalopod diet which it retains into adult life.

How fish is eaten - From the examination of the food remains in stomachs, it was noted that fish can be eaten in all possible ways: swallowed whole, bitten in mouthfuls, swallowed without tail and head.

The heads are probably seldom eaten as very few otoliths were found in the stomachs. Small fish are swallowed under water but larger ones can be taken to the surface and bitten in pieces while held with the fore flippers as I have seen it done on a few occasions. The largest intact fish found in stomachs were herrings, up to 30 cm in length.

Seasonal changes in condition - The deposition of blubber in seals is probably related to the intake of food. Changes in blubber thickness can be monitored with the condition index which is calculated with the formula: girth X 100 / nose-tail length. In this study, this index (Fig. 33) is high in winter and early spring, variable and decreasing in late spring and low from early summer until late autumn. The percentage of empty stomachs (Table 19) remains relatively constant, from May to September, increasing slightly during the period October to January. No data are available for the period February to late April, but the difference in blubber thickness in summer and winter appears not to be caused by a reduction in the frequency of feeding.

Sergeant (1973) published a similar curve for harp seals in the north-west Atlantic and the trends are almost parallel to those of the harbour seal except that the rapid decrease phase following weaning and mating occurs in late April. During this decrease phase in the harp seal, there is a corresponding increase in feeding rates as indicated by the occurrence of empty stomachs, which gradually drops from 73% in March to 4% in May.

A possible explanation for this variation of the condition index might be the change in condition of the fishes following winter and spawning. An examination of the seven species of fish which represent 61% of the normal diet of the harbour seal (Table 20) indicates that

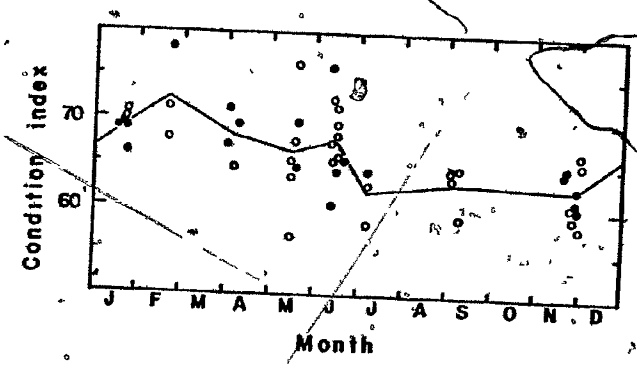


Fig. 33. Monthly changes in the condition index (maximum girth x 100)/nose-tail length, of harbour seals in eastern Canada. Solid circles are males, open are females.

Table 19 . Seasonal variations in feeding intensity of harbour seals in eastern Canada.

Month	No. in sample	% stomachs empty
May	25	60
June	58	59
July	55	60
August	53	57
September	56	41
October	31	71
November	20	65
December-January	12	66

Table 20. Spawning time of the fish species regularly eaten by the harbour seal in eastern Canada. Spawning data from Leim and Scott (1966).

Species	Spawning period	% of seal's diet
Herring (inshore)	May - June	24.2
Winter flounder	April - May	14.1
Silver hake	June - September	6.0
Alewife	April - May	6.8
Smelt	Late April - June	3.7
Mackerel	May - early July	3.6
Capelin	June - July	2.9
	Total	61.3

these fish spawn from April to September with the mean spawning occurring in late May. Following spawning, fish are generally in a very lean condition and probably build up their fat reserves during the summer and fall months.

An example of this is given by MacKinnon (1972) who has shown that the energy content of the american plaice, Hippoglossoides platessoides reaches a maximum in November and December, then decreases slowly until late April, representing at that time 79% of the maximum late fall value. After this time, the energy content increases rapidly for one month until early June when, following spawning, it drops suddenly to a minimum (74% of maximum). The condition of the fish improves afterwards until the maximum is reached. The curve for seasonal energy content of the plaice thus greatly resembles the curve describing the seasonal changes of the condition index of harbour seals.

Animals relying on fish for their diet and keeping their consumption constant during spring and summer with respect to stomach capacity, would therefore be affected by a sharp drop around May and June in the food's calorific value. The probable corrective mechanism for the seal would be to borrow on its accumulated blubber reserves and this would yield lower values of the condition index. Another explanation would be a decrease in the average size of a meal, which is very difficult to measure because of the scarcity of data.

Quantity of food ingested per meal - This measurement is essential in the study of energy flow in seals. During the examination of stomachs, the weight of the content was noted when it was estimated to be 30% or less digested, along with an estimate in percent of the amount of food already digested. An estimate of the weight of the food consumed was calculated: (weight of food as found in stomach / % not digested) X 100, and this weight was plotted against the seal's weight (Fig. 34). In the absence of the latter information, the seal's weight was approximated by means of the equation describing the length-weight relationship (Fig. 13). A linear regression was fitted to the $\log_{10}$ transformed data and an exponential equation was derived to predict the amount of food eaten in one meal by a harbour seal of a given weight:

$$\text{Weight of food (g)} = 228.26 \text{ Weight of seal (kg)}^{0.4944}$$

From this equation, it is seen that the average meal of a 20 kg seal represents 5% of its body weight, while for a 100 kg seal, it represents about 2.2% of its body weight.

Consumption in captivity

Replies to questionnaires distributed in February 1973 to institutions keeping marine mammals supplied information on the feeding rates of harbour seals in captivity. The answers received indicate two attitudes among seal keepers. Some give just enough food to satisfy the energy requirements of the moderately active seal. This type of controlled diet is more common in research institutions where seals fed the proper maintenance ration perform better than when overfed. On the other hand, numerous public aquaria and zoological gardens are obviously overfeeding their seals. The information from these latter institutions is therefore left out of this analysis, as the aim here is to determine the minimum ration required daily for a moderately active seal.

Table 21 lists the information received from those institutions giving a controlled diet to their seals. The seals are generally fed

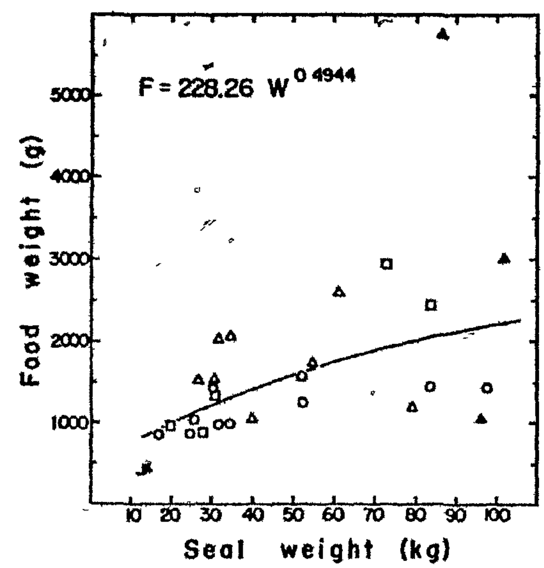


Fig. 34. Relationship between the estimated stomach content's weight before digestion (F) in nature and the weight of the corresponding harbour seal (W). Solid symbols are from Havinga (1933). Open symbols are from this study: triangles indicate food estimated to have been 5% digested at the time of examination; circles, 30% digested; squares, no data on state of digestion.

Table 21.- Feeding rates of harbour seals in captivity. The last two columns before the references give meal weight calculated from the equation on Fig. 34, and the meal weight expressed as % of body weight. Asterisks in the first column indicate captive animals surviving on daily rations close to those calculated for wild animals.

Sample no.	Seal weight	No. of seals	Age	Captivity		From equation (fig. 34)		References
				Food/day	Food/day / body wt.	Food/day (in nature)	Food/day / body wt.	
	kg			kg	%	kg	%	
1	40	1	9 m.	1.634	4.09	1.444	3.5	K. Ronald, pers. comm.
2	40	1	9 m.	1.961	4.90	1.444	3.5	"
3	38	1	9 m.	2.009	5.29	1.379	3.6	"
4	35.3	5	1 yr	1.514	5.14	1.329	3.8	J. J. Wright, pers. comm.
5 *	77.1	1	5 yr	2.041	2.64	1.956	2.5	T. C. Poulter, pers. comm.
6 *	31.8	1	9 m.	1.555	4.69	1.262	4.0	"
7 *	50	1	-	1.600	3.20	1.579	3.15	Altman and Dittmer (1968)
8	37.3	2	2 m.	2.000	5.36	1.366	3.7	C. L. Wheeler, pers. comm.
9	33.1	2	1 yr	1.810	5.47	1.287	3.9	L. F. Bryniarski, pers. comm.

thawed fish, mainly herring or mackerel. The data of those sample numbers in Table 21 marked with an asterisk indicate that captive harbour seals can survive and be active on a daily diet consisting of 4.9% of the body weight for a 32 kg seal, of 3.2% of the body weight for a 50 kg seal and of 2.6% of the body weight in the case of a 77 kg seal.

From the measurement of the weight of the stomach content described above for wild seals, it seems possible that harbour seals in nature eat on the average one meal per day and that the quantity eaten is a function of the seal's weight as described by the equation in Fig. 34. This equation gives for the above three captive harbour seals, a theoretical meal weight which is close to, but slightly smaller than their actual daily food consumption (Table 21).

Production

Having obtained data on the age distribution of the population of harbour seals in eastern Canada, on the growth in weight and an estimate of the daily consumption rates for given seal weights, it is possible to attempt a detailed calculation of the flow of energy through a seal population and simultaneously of the production from such a population.

Population model - A model is built of a population of 1000 harbour seals, which is stable, has an assumed stable age distribution and which is isolated with no emigration or immigration. Data on age distribution and growth in weight are takenrespectively from Table 13 and Fig. 12; numbers and weights of males and females are averaged for each age and only one model, independent of sex differences, is prepared. This model is estimated to be typical of an average population of harbour seals in eastern Canada.

With the population being assumed stable and having a stable age distribution, the biomass of that population at a given time each year, for example, halfway between two birth dates, should be a constant value from year to year. The only energy intake is the food consumed while the energy output is threefold, consisting of rejecta (faeces plus excreta), respiration (heat lost and energy dissipated through activity) and production (P) which in this case consists of the animals dying because of old age, illness or accident, and consumed by decomposers, or because of predators. This approach to estimation of production is described by Mann (1969).

Description of terms used - The following symbols and concepts related to biological production are taken from Ricker (1968):

N Population size, in this case taken halfway between one birth period and the next.

C Consumption, in this case the total intake of food during one year.

F Faeces.

U Excreta, including urine and epidermal secretions.

UF Rejecta (= U + F)

A Assimilation (= C - F - U = P + R) the food absorbed less rejecta.

R Respiration (= C - F - U - P) that part of assimilation which is converted to heat or mechanical energy and is used in life processes.

In this model, C, F, U, A and R will be expressed in Cal. or kCal., or metric tons (m.t.). One Cal. equals 1,000 cal., one kCal. equals 1,000 Cal. and one m.t. equals 1,000 kg. Other concepts are also required:

L_x Age specific number of seals in the population at a time halfway between two birth periods. The L_x series used here is calculated for a population of 1,000 animals, from the "adjusted l_x" series in Table 13.

ΣL_x Population size, here 1,000 seals (= N).

W_x Age specific mean weight of the seals in a given age group, obtained from the growth curve for weight (Fig. 12).

B_x Biomass of the age group.

ΣB_x Population biomass.

F_x Age specific daily feeding rates, expressed as proportion of body weight: $F_x = 0.22826\ W_x^{0.4944} / W_x$. The equation is the one used to calculate the weight of food (kg) consumed in nature, from the weight of the seal (Fig. 34).

C_x Consumption by age group during one year (= $365\ L_x W_x F_x$).

ΣC_x Population consumption during one year (= C).

Mb Basal metabolism, or minimal energy required to maintain in life a resting animal in a neutral temperature environment and in a post absortive state.

Mb_x Age specific basal metabolism, in Calories per day, for one seal without blubber ($0.64\ W_x$), the blubber constituting 36% of the seal's weight (Dorofeev and Freimann, 1935; Slijper, 1958). The equation for basal metabolism is taken from Brody (1945): Cal. = $70.5\ kg^{0.734}$.

SMb_x Basal metabolism of age group in kCal. per year (= $365\ L_x Mb_x$).

ΣSMb_x Population basal metabolism in kCal. per year.

D_x Seals dying in each age group per year.

Bd_x Biomass of seals dying in each age group per year.

ΣBd_x Total biomass of seals dying per year (in this case, = P)

Energy flow table - Having now defined the variables, we can prepare an energy flow table which is presented in a format similar to the more common life table. The energy flow table (Table 22) consists of: Age, L_x, W_x, B_x, F_x, C_x, Mb_x, SMb_x, D_x and Bd_x; at the bottom of the table are found ΣB_x, C (= ΣC_x), ΣSMb_x and P (= ΣBd_x).

To prepare the diagram of energy flow, we need to know also the calorific value of the food consumed by the population and the calorific value of the dying seals. Approximations for these values are given by Altman and Dittmer (1968). Table 23 gives the water content and the calorific value of eleven species of fish eaten by the harbour seal in eastern Canada. The calorific values are for the raw edible portion of the fish and it is assumed that these values do not differ greatly from those of the whole fish. A mean value is calculated for water and calorie content and the value of 120.7 Cal. / 100 g (wet weight) of fish is used to convert the food consumption from metric tons to calories. Squid is included in the table and has a calorific content comparable to those of fish.

The calorific value of seals which have 36% of their weight in blubber, can be approximated by the mean calorific value of three types of meat consisting of 63% lean and 37% fat (Table 24); this value is 396 Cal./ 100 g (raw, wet weight).

Also required for the diagram, is the assimilation efficiency of the seals. As was the case for the calorific value of a seal, this information is not available for seals to my knowledge, and has to be approximated with values from other mammals. Data are available

Table 22. Energy flow table for a population of 1000 harbour seals in eastern Canada. See text for details.

Age	L_x	W_x (kg)	B_x (m.t.)	F_x	C_x (m.t.)	Mb_x (Cal/day)	SMb_x (kCal/yr)	D_x	Bd_x (m.t.)
0	194	27.6	5.354	.0426	83.25	573.6	70811	50	1.380
1	144	37.9	5.458	.0363	72.31	733.2	52560	35	1.327
2	109	42.6	4.643	.0342	57.96	796.4	39786	22	0.937
3	87	50.9	4.428	.0313	50.59	909.6	31756	10	0.509
4	77	60.9	4.689	.0286	48.95	1057.1	22230	7	0.426
5	70	65.0	4.550	.0277	46.00	1087.9	25551	5	0.325
6	65	74.6	4.849	.0258	45.66	1202.9	23726	13	0.970
7	52	74.9	3.895	.0257	36.53	1206.6	18931	18	1.348
8	34	75.0	2.555	.0257	23.97	1208.4	12411	8	0.600
9	26	68.7	1.786	.0269	17.53	1133.7	10758	5	0.344
10	21	76.5	1.606	.0254	14.89	1226.9	9404	4	0.306
11	17	"	1.301	"	12.06	"	7613	2	0.153
12	15	"	1.148	"	10.64	"	6717	2	0.153
13	13	"	0.995	"	9.22	"	5822	2	0.153
14	11	"	0.841	"	7.80	"	4926	1	0.076
15	10	"	0.765	"	7.09	"	4478	1.8	0.138
16	8.2	"	0.627	"	5.81	"	3672	1.2	0.091
17	7.0	"	0.536	"	4.97	"	3135	0.9	0.069
18	6.1	"	0.467	"	4.33	"	2731	0.9	0.069
19	5.2	"	0.393	"	3.69	"	2329	0.7	0.054
20	4.5	"	0.344	"	3.19	"	2015	0.6	0.045
21	3.9	"	0.298	"	2.76	"	1746	0.5	0.038
22	3.4	"	0.260	"	2.41	"	1523	0.5	0.038
23	2.9	"	0.222	"	2.06	"	1299	0.4	0.031
24	2.5	"	0.191	"	1.77	"	1120	0.2	0.153
25	2.3	"	0.175	"	1.62	"	1030	0.4	0.031
26	1.9	"	0.143	"	1.33	"	850	0.3	0.023
27	1.6	"	0.122	"	1.13	"	717	0.2	0.153
28	1.4	"	0.107	"	0.99	"	627	0.2	0.153
29	1.2	"	0.091	"	0.84	"	537	0.2	0.153
30	1.0	"	0.076	"	0.70	"	447	0.1	0.076
31	0.9	"	0.068	"	0.63	"	403	0.2	0.153
32	0.7	"	0.054	"	0.50	"	313	0.4	0.031
33	0.3	"	0.029	"	0.27	"	134	0.3	0.023
	N = 1000		ΣB_x = 53.071		C = 583.45		ΣSMb_x = 372158		P = 10.529

Table 23. Water content and calorific values of the edible portion of various fishes eaten by the harbour seal (from Altman and Dittmer, 1968).

Species	Water %	Food energy of raw sample Cal / 100 g wet weight
Haddock	80.5	79
Halibut	76.5	100
Herring, Atlantic	69.0	176
Pacific	72.4	98
Cod	81.2	78
Squid	80.2	84
Mackerel, Atlantic	67.2*	191
Pacific	69.8	159
Shad	70.4	170
Smelt	79.0	98
Pollock	77.4	95
Mean	75.5	120.7

Table 24. Calorific value of three types of raw meat (from Altman and Dittmer, 1963)

Beef steak	% lean	% fat	% water	Cal/100 g wet
Porter House	63	37	48.3	390
T Bone	62	38	47.5	397
Rib	64	36	47.2	401
Mean	63	37	47.7	396

for three carnivores, the dog, the weasel and the bobcat and for one herbivore specialised on lipid-rich food (Table 25). The assimilation efficiency is defined for Table 25 as follows: (C - F - U)/ C, and the mean efficiency for the four species is 84.6%.

Energy flow diagram - The above information can be summarised in an energy flow diagram for the population of 1,000 harbour seals (Fig. 35). The value for rejecta is: C (1 - assimilation efficiency), while respiration is (C - rejecta - production). The metabolic ratio: metabolism under active condition / basal metabolism, equivalent here to $(R + P)/ \Sigma SMb_x$, can be a useful figure, for example to compare the the energy requirements of various species in their respective environment or to establish the food ration for captive animals of known weight. In this case, the metabolic ratio is 1.6. This compares to a ratio of 1.56 for a moderately active man, for example operating a desk calculator (data from Aron and Grassé, 1966).

The information contained in the energy flow diagram also allows the calculation of the ecological efficiency defined as production / consumption (Petrusewicz and MacFadyen, 1970). Harbour seals thus have an ecological efficiency of 41,695 kCal./ 704,224 kCal. = 5.9%. This is half the usual 10% value given for lower trophic levels.

Discussion

The values given in the preceeding sections might be modified slightly in the future, as more refined data become available on the seasonal changes of the calorific values of the food species taken by seals, on the seasonal variations in feeding, mainly from January to May, and on the assimilation efficiency and energy content of seals.

Table 25 . Assimilation efficiency (AE) in four mammals. AE = (energy consumed - energy of faeces - energy of urine)/energy consumed.

Species	AE % of energy consumed	Reference
Dog	82.5	Robinson *et al.* (1953)
Bobcat	83	Golley et al. (1965)
Weasel	89.9	Golley (1960)
Squirrel	83	Smith and Follner (1972)
Mean	84.6	

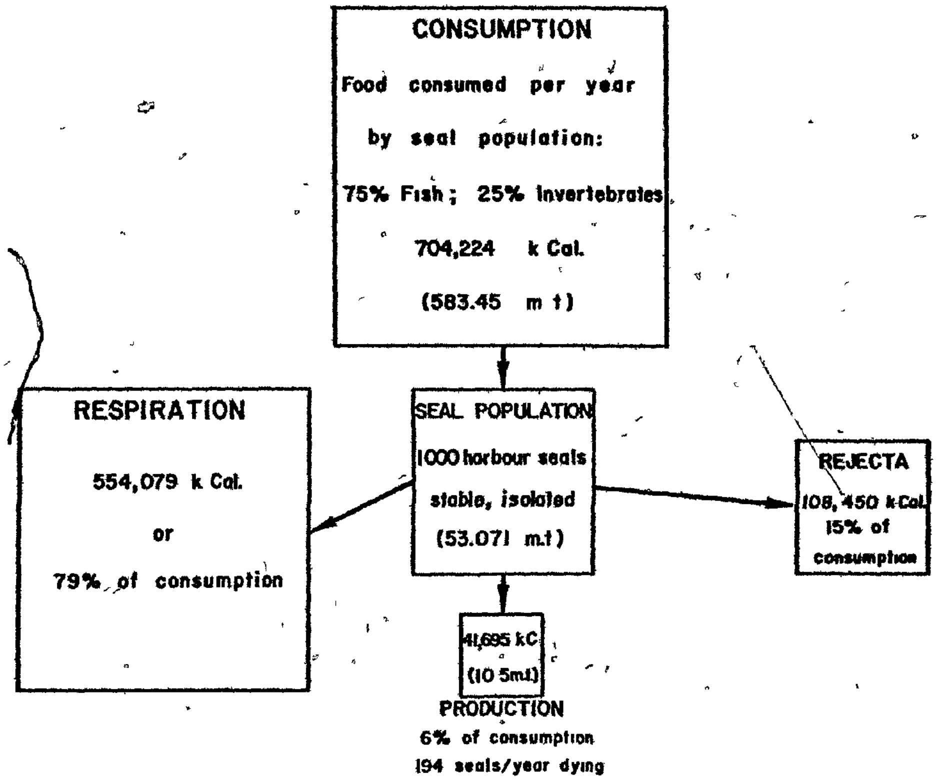


Fig. 35. Diagram of energy flow in a population of 1,000 harbour seals in eastern Canada. See text for details.

In the absence of this information, it is felt that the above calculations give a fairly accurate description of the flow of energy through a seal population.

It does appear that seals are normally efficient food converters. The metabolic ratio of 1.6 indicates that they are as efficient as man in utilising the consumed energy. This can be expected of an animal which is well insulated against heat loss, which, because of its aquatic life, is subjected to a reduced gravity force and therefore reduced muscular work, and which is specialised on one type of food, fish, in the same way a land carnivore is.

The statement by Sergeant (1973) that harp seals, *Pagophilus groenlandicus*, are inefficient converters of fish flesh may be inexact. The calculations are based on the assumption that wild harp seal pups eat 10% and, 100 kg adults 5% of their body weight per day. The basis for this assumption was information received from two institutions feeding captive harp seals ad libitum rations and two highest weights of stomach contents from wild seals compared to their estimated body weight. From the evidence presented in this study, it is possible that the feeding rates suggested for harp seals are twice the rates of animals in nature, if wild seals eat on the average only one meal per day. This is an important difference when attempting to assess the quantity of commercial fish eaten by seals. Should wild seals feed on the average twice daily, annual consumption would be doubled while production would remain the same; thus ecological efficiency for harbour seals would become 3% instead of 6%.

Having established the food consumption of 1,000 harbour seals, it is possible to extrapolate the amount of commercial fish eaten by harbour seals in the area covered by this study. It is assumed that Newfoundland harbour seals, for which little information is available, have a food preference similar to that of the seals from the areas which supplied the stomach samples.

As an example, the amount of herring taken by the estimated 12,400 harbour seals in the area covered by this study is calculated as follows:

(0.242 herring X 583.45 m.t./yr. X 12,400 seals)/ 1,000 seals

= 1,750 m.t. of herring per year.

This quantity is doubled if harbour seals feed on the average twice daily. For comparison, 100,000 tons of herring were taken by commercial fisheries in 1968 in the Gulf of St. Lawrence (Anon., 1970).

ACKNOWLEDGEMENTS

I wish to express my gratitude to Dr. I. A. McLaren, Department of Biology, Dalhousie University, for accepting to supervise this work and for his constant interest and useful suggestions during all phases of this study. I am most indebted to numerous persons for their assistance, mainly to: Mr. D. A. Welsh, Department of Biology, Dalhousie University, for his very close association with the field work on Sable Island and for his comments during the preparation of the text; Mr. B. Beck and G. Sleno of the Arctic Biological Station of the Fisheries Research Board of Canada, for their help with the field work and for the preparation of the samples sent by the seal hunters; Mr. K. Ross, Department of Biology, Dalhousie University for his assistance with the identification of the stomach contents; Dr. M. C. Mercer, St. John's Biological Station, Fisheries Research Board of Canada, who identified the cephalopod remains. This research would not have been completed without the collaboration of the seal hunters who supplied a good part of the samples used in this work, and of Dr. W. Stobo and the personnel of the weather station of Sable Island who helped at some stage of this work.

I would like to thank also the Fisheries Officers who kindly answered to the questionnaire on the distribution and abundance of seals, and the following persons or institutions who replied to a request for information on the feeding rates of captive harbour seals: Dr. W. N. Bonner, Seals Research Division, U.K.; Mr. L. F. Bryniarsky, Aquarium of Niagara Falls; Dr. R. A. Dieterich, Institute of Arctic Biology, University of Alaska; Mr. J. P. Gardner, Cleveland Aquarium; Mr. L.

Garibaldi, New England Aquarium; Mr. I. Kang, Sea Life Park; Dr. P. Montreuil, Montreal Aquarium; Dr. G. Morin, Aquarium de Québec; The Norfolk Wildlife Park; Mr. J. M. Olguin, Cabrillo Beach Marine Museum; Dr. T. C. Poulter, Biological Sonar Laboratory; Mr. J. H. Prescott, New England Aquarium; Dr. K. Ronald, College of Biological Science, University of Guelph; Dr. J. Sweeney, Sea World Inc.; the Vancouver Aquarium; Mr. J. F. Watkins, Lincolnshire, England; Mr. W. R. Welch and C. L. Wheeler, U. S. National Marine Fisheries; Mr. J. J. Wright, Scripps Institute of Oceanography.

The following persons offered useful criticism of the manuscript: Dr. B. K. Hall, Dr. K. H. Mann and Dr. D. E. Sergeant.

This research was supported by the Fisheries Research Board of Canada and by the National Research Council through a grant to Dr. I. A. McLaren, and used the facilities of the Department of Biology of Dalhousie University. The author was supported by a National Research Council of Canada post-graduate scholarship.

REFERENCES

Allen, J. A. 1880. History of north american Pinnipeds. Washington, U.S. Geol. and Geogr. Surv. Terr., Misc. Publ. 12. xvi + 785 p.

Altman, P. L. and D. S. Dittmer. 1968. Metabolism. Committee on biological handbooks, Federation of American Societies for Experimental Biology, Bethesda, Maryland. 737 p.

Anon. 1970. International commission for the Northwest Atlantic Fisheries. Statistical Bulletin 18 for the year 1968. Dartmouth, N.S. 141 p.

Aron, M. et P. Grassé. 1966. Précis de biologie animale. Masson, Paris. 1421 p.

Bigg, M. A. 1969a. The harbour seal in British Columbia. Fish. Res. Board Can. Bull. 172. 33 p.

1969b. Clines in the pupping season of the harbour seal *Phoca vitulina*. J. Fish. Res. Board Can. 26 : 449-455.

Bishop, M. W. H. and A. Walton. 1962. Spermatogenesis and the structure of mammalian spermatozoa, p. 1-101. *In* A. S. Parkes (ed.) Marshall's physiology of reproduction. Vol. 1. Pt. 2. Longmans. 877 p.

Bishop, R. H. MS, 1968. Reproduction, age determination, and behavior of the harbor seal, *Phoca vitulina* L., in the Gulf of Alaska. MSc. Thesis. Univ. Alaska, College, Alaska. 121 p.

Bonner, W. N. and G. Hickling. 1971. The grey seals of the Farne Island. Transactions of the Natural History Society of Northumberland 17 : 140-162.

Boulva, J. 1971. Observations on a colony of whelping harbour seals, *Phoca vitulina concolor*, on Sable Island, Nova Scotia. J. Fish Res. Board

Can. 28 : 755-759.

Boulva, J. 1973. Temporal variations in birth period and characteristics of newborn harbour seals. In Proc. Symp. Biol. of the Seal, Rapports et Procès Verbaux, International Council for the Exploration of the Sea. In press.

Brody, S. 1945. Bioenergetics and growth. Reinhold, New York. 1023 p.

Caldwell, D. K. and M. C. Caldwell. 1969. The harbor seal Phoca vitulina concolor in Florida. J. Mammal. 50 : 379-380.

Carrick, R, S.E. Csordas and S. E. Ingham. 1962. Studies on the southern elephant seal, Mirounga leonina (L.) IV - Breeding and development. C.S.I.R.O. Wildlife Research 7 : 161-197.

Caughley, G. 1966. Mortality patterns in mammals. Ecol. 47 : 906-918.

Comeau, N. A. 1945. La vie et le sport sur la côte nord du bas Saint-Laurent et du Golfe, Garneau, Québec. 372 p.

Deevey, E. S. 1947. Life tables for natural populations of animals. Quart. Rev. Biol. 22 : 283-314.

Dorofeev, S. V. and S. J. Freimann. 1935. The marine mammalia of U.S.S.R. far east. Trans. U.S.S.R. Inst. Fish. Ocean. (V.N.I.R.O.), 3.

Doutt, J. K. 1942. A review of the genus Phoca. Ann. Carnegie Mus. 29 : 61-125.

Fisher, H. D. MS, 1949. Harbour seals. Annu. Rep. 1949, Atlantic Biol. Sta., Fish. Res. Board Can. p. 104-106.

MS, 1950. Stomach contents of harbour seals. Annu. Rep. 1950, Atlantic Biol. Sta., Fish. Res. Board Can. p. 111-113.

MS, 1951. Food habits of harbour seals. Annu. Rep. 1951, Atlantic Biol. Sta., Fish. Res. Board Can. p. 114.

1952. The status of the harbour seal in British Columbia, with particular reference to the Skeena River. Fish. Res. Board Can. Bull. 172. 33 p.

1954. Delayed implantation in the harbour seal, Phoca vitulina. Nature (London) 173 : 979-880.

Fisher, H. D. and B. A. Mackenzie. 1955. Food habits of seals in the Maritimes. Fish. Res. Board Can. Progr. Rep. Atl. Coast Sta. 61 : 5-9.

Gilpin, J. B. 1874. On the seals of Nova Scotia. Proc. and Trans. Nova Scotia Inst. Sci. 3 : 377-384.

Golley, F. B. 1960. Energy dynamics of a food chain of an old field community. Ecol. Monogr. 30 : 187-206.

Golley, F. B. et al. 1965. Food intake and assimilation by bobcats under laboratory conditions. J. Wildl. Manage. 29 : 442-447.

Harrison, R. J. 1960. Reproduction and reproductive organs in common seals (Phoca vitulina), in the Wash, East Anglia. Mammalia 24 : 372-385.

Harrison, R. J. 1963. A comparison of factors involved in delayed implantation in badgers and/seals in Great Britain, p. 99-114. In A. C. Enders (ed.) Delayed implantation. Univ. Chicago Press, Chicago, Ill. 318 p.

Havinga, B. 1933. Der Seehund (Phoca vitulina L.) in den Hollandischen Gewassern. Tijdschr. Ned. Dierkundige Ver. (Leiden) 3 : 79-111.

Hewer, H. R. and K. M. Backhouse. 1968. Embryology and foetal growth of the grey seal, Halichoerus grypus. J. Zool. London 155 : 507-533.

Huggett, A. St G. and W. F. Widdas. 1951. The relationship between mammalian foetal weight and conception age. J. Physiol. 114 : 306-317.

Imler, R. H. and H. R. Sarber. 1947. Harbor seals and sea lions in Alaska. U. S. Dept. Inter., Fish and Wildl. Serv., Spec. Sci. Rept. 28. 22 p.

Kenyon, K. W. 1965. Food of harbor seals at Amchitka Island, Alaska. J. Mammal. 46 : 103-104.

Leim, A. H. and W. B. Scott. 1966. Fishes of the Atlantic coast of Canada. Fish. Res. Board Can. Bull. 155. 485 p.

MacKinnon, J. C. 1972. Summer storage of energy and its use for winter metabolism and gonad maturation in American Plaice (Hippoglossoides platessoides). J. Fish. Res. Board Can. 29 : 1749-1759.

Mann, K. H. 1969. The dynamics of aquatic ecosystems. Advances in Ecol. Res. 6 : 1-81.

Mansfield, A. W. 1967a. Distribution of the harbour seal, Phoca vitulina Linnaeus, in Canadian arctic waters. J. Mammal. 48 : 249-257.

1967b. The mammals of Sable Island. Canad. Field-Nat. 81 : 40-49.

1967c. Seals of arctic and eastern Canada. Fish. Res. Board Can. Bull. 137. 35 p.

MS, 1968. Seals as vectors of Porrocaecum in the Maritime Provinces. Annu. Rep. 1967-68, Arctic Biol. Sta., Fish. Res. Board Can. p. 31-33.

Mansfield, A. W. and H. D. Fisher. 1960. Age determination in the harbour seal, Phoca vitulina. Nature (London) 186 : 192-193.

MS, 1962. Grey and harbour seals at Sable Island. Annu. Rep. 1961-62, Arctic Biol. Sta., Fish. Res. Board Can. p. 29-36.

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.

1973. A speculative overview of phocid evolution. In Proc. Symp. Biol. of the Seal, Rapports ét Procès Verbaux, International Council for the Exploration of the Sea. In press.

Naito, Y. and M. Nishiwaki. 1972. The growth of two species of the harbour seals in the waters around Hokkaido. Sci. Rep. Whales Res. Inst. 24 : 127-144.

Newby, T. C. 1966. Viability of premature fetal harbor seal. Murrelet 47 : 46.

Newby, T. C., F. M. Hart and R. A. Arnold. 1970. Weight and blindness of harbor seals. J. Mammal. 51 : 152.

Perry, J. S. 1971. The ovarian cycle of mammals. Oliver and Boyd, Univ. Review in Biol. 13. 219 p.

Petrusewicz, K. and A. Macfadyen. 1970. Productivity of terrestrial animals. IBP Handbook 13, Blackwell, Oxford, England. 190 p.

Pilson, M. E. Q. and A. L. Kelly. 1962. Composition of the milk from Zalophus californianus, the California sea lion. Science 135 : 104-105.

Poulter, T. C. MS, 1965. Derivation of a simple equation for determination of the weight of a seal or sea lion from measurements of its length and girth. Stanford Res. Inst., Prog. Rep., Chapt. 1.

Quick, H. F. 1963. Animal population analysis, p. 190-228. In H. S. Mosby (ed.), Wildlife investigational techniques. The Wildlife Society, Washington, D. C.

Rae, B. B. 1968. The food of seals in Scottish waters. Dept. Agric. Fish. Scottland, Mar. Res. 2. 23 p.

Ricker, W. E. 1968. Methods for assessment of fish production in fresh waters. IBP Handbook 3, Blackwell, Oxford, England. 313 p.

Robinson, H. E. et al. 1953. Nutrients requirements for domestic animals. No. 5. Nutrients requirements for dogs. Agricultural Board, National Research Council Publication 300, Washington, D. C. 30 p.

Scheffer, V. B. and J. W. Slipp. 1944. The harbor seal in Washington State. Amer. Midl. Natur. 32 : 373-416.

Scott, D. M. 1953. Experiments with the harbour seal, Phoca vitulina, a definite host of a marine Nematode, Porrocaecum decipiens. J. Fish. Res. Board Can. 10 : 539-547.

Scott, D. M. and H. D. Fisher. 1958. Incidence of the Ascarid Porrocaecum decipiens in the stomach of three species of seals along the southern Canadian Atlantic mainland. J. Fish. Res. Board Can. 15 : 495-516.

Sergeant, D. E. 1951. The status of the common seal (Phoca vitulina) on the east Anglian coast. J. Marine Biol. Assoc. U. K. 29 : 701-717.

MS, 1961. Whales and dolphins of the Canadian east coast. Arctic Unit, Fish. Res. Board Can. Circ. 7. 17 p.

1966. Reproductive rates of harp seals, Pagophilus groenlandicus (Erxleben). J. Fish. Res. Board Can. 23 : 757-766.

1973. Feeding, growth and productivity of northwest Atlantic harp seals (Pagophilus groenlandicus). J. Fish. Res. Board Can. 30 : 17-29.

Slijper, E. J. 1958. Organ weights and symmetry problems in porpoises and seals. Arch. Néer. Zool. 13, suppl. 1 : 97-113.

Smith, C. and D. Follner. 1972. Food preferences of squirrels. Ecol. 53 : 82-91.

Smith, T. G. MS, 1970. Population dynamics of the ringed seal in the Canadian eastern Arctic. Ph. D. Thesis, Mc Gill Univ., Montreal. 168 p.

(4)

Spalding, D. J. 1964. Comparative feeding habits of the fur seal, sea lion and harbour seal on the British Columbia coast. Fish. Res. Board Can. Bull. 146. 52 p.

Templeman, W. 1966. Répartition des requins dans l'Atlantique canadien et plus particulièrement dans les eaux de Terre-Neuve. Fish. Res. Board Can. Bull. 140. 83 p.

Templeman, W., H. J. Squires and A. M. Fleming. 1957. Nematodes in the fillets of cod and other fishes in the Newfoundland and neibourghing areas. J. Fish. Res. Board Can. 14 : 831-897.

Tikhomirov, E. A. 1966. O razmnozhenii tyulenei semeistva Phocidae severnoi chasti tikhogo okeana. (Reproduction of seals of the family Phocidae in the north Pacific). Zool. Zh. 45 : 275-281. (Transl. from Russian by Fish. Res. Board Can. Transl. Ser. No. 1889, 1971).

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.

Venables U. M. and L. S. V. Venables. 1955. Observations on a breeding colony of the seal Phoca vitulina in Shetland. Proc. Zool. Soc. London 125 : 521-532.

1957. Mating behaviour of the seal Phoca vitulina in Shetland. Proc. Zool. Soc. London 128 : 387-396.

1959. Vernal coition of the seal, Phoca vitulina in Shetland. Proc. Zool. Soc. London 132 : 665-669.

Wilke, F. 1957. Food of sea otters and harbor seal at Amchitka Island. J. Wildl. Manage. 21 : 241-242.

Wilson, E. O. and W. H. Bossert. 1971. A primer of population biology.

Wilson, E. O. and W. H. Bossert. 1971. A primer of population biology. Sinauer, Stamford, Conn. 192 p.

PREVIOUS COPYRIGHTED MATERIAL
IN APPENDIX A NOT MICROFILMED:

Leaf 135 - 139

APPENDIX B

TEMPORAL VARIATIONS IN BIRTH PERIOD AND CHARACTERISTICS OF NEWBORN HARBOUR SEALS

by

Jean Boulva

Department of Biology,

Dalhousie University

Halifax, N.S.

ABSTRACT

From 1970 to 1972, the Sable Island harbour seal population showed variation in the period of whelping. Heavier and longer pups, a less frequent occurrence of whitecoat pups and a better survival between birth and weaning were associated with a later mean birth date. Colder environmental temperatures or possibly human disturbances could have caused the delay in whelping in 1972.

Paper presented at the Symposium on the Biology of the Seal held at Guelph, Ontario, Canada, 14 to 17 August 1972. This paper is now in press, and will be published in 1973.

Few quantitative data have been published on annual variations in numbers, birth period and characteristics of newborn harbour seals, *Phoca vitulina*, mainly because of the difficulty of finding a discrete population of this species which can be studied easily and accurately counted at all times of the year, and where the absence of immigration or emigration can be assumed during the period of study. Boulva (1971) gave an account of such a population on Sable Island, located about 165 km south of the nearest Nova Scotia mainland, and which he studied from May 14 to June 19, 1970. The island is a vegetated sand bar, 37 km long, and seals on its continuous beach are easily surveyed from a vehicle. Following this first study, I revisited the island mainly from April 12 to July 12, 1971 and from May 8 to June 13, 1972.

METHODS

Ground censuses were made regularly during the whelping period and during shorter visits to the island at other times in the year. Counting techniques were similar to that described earlier (Boulva, 1971). During the whelping period, a constant daily effort was made to catch as many pups as possible around the island. Captured pups were tagged with numbered cattle ear tags placed through the web between the hind flipper and the tail. Sex, nose-tail length, weight, condition of the umbilicus, condition of pelage, and status of the pup wheter attended, deserted or weaned, were recorded. The measurements were also taken on recaptured pups.

The umbilicus was classed in one of five categories : 0 = newborn; 1 = fresh, red umbilical cord with bloody tip = 1-day-old; 2 = fresh, red umbilical cord, but extremety whitish and dried out = 3-day-old;

3 = dried out umbilical cord = 5-day-old; 4 = healed umbilicus = no age estimate. These ages corresponding to the condition of the umbilicus are averages determined during the 1971 field season from recaptured tagged pups.

Each pup captured for the first time with an umbilicus of category three or less was assigned a birth date. Using this information, it was possible to calculate the daily numbers of births for tagged pups. Assuming that the birth rate recorded from tagging is proportional to the overall birth rate on a given year, the tagging data can be used to calculate the mean birth date, when 50% of the pups are born. In 1971 and 1972, more than 70% of the total pup production was tagged.

The total number of pups born in one season was estimated from the tagging data, numbers of tagged and untagged animals captured after the end of whelping, and from field counts. Notes were kept on pups found dead. Post-canine teeth were counted on dead seals. Other samples of lower jaws from harbour seals shot in the Maritimes, in Labrador and in Eastern Arctic Canada were supplied by the Arctic Biological Station of the Fisheries Research Board of Canada.

The daily growth rate in weight and length was found to be relatively constant during the first 20 days of life in nursed pups (Boulva, unpublished data). Therefore, linear regressions of weight and length on age for captured and recaptured pups aged from 0 to 20 days were made to obtain the mean birth weight and length, which respectively is the value where the line crosses the Y axis. All regression coefficients were highly significant ($P < 0.001$). The positions and slopes of the lines were compared statisticaly as described by Mather (1964), to detect any differences between sex and between years of sampling.

RESULTS

Population Size

The Sable Island harbour seals appear to form a discrete population, with no evidence of emigration or immigration having been obtained. Over 550 pups have been tagged and 50 branded in 1971 and 1972, and none of these have been reported from elsewhere in the maritime provinces where a bounty on this species is in effect. Animals branded in June 1971 have been seen on the island regularly during visits in January, April, May and June 1972. The population has remained relatively constant during the last three years, oscillating around 1200 animals before whelping (Figure 1). This likely geographic isolation is supported also by a charcteristic of the Sable Island harbour seals which is rarely noted elsewhere : there is a high proportion of animals having only four post-canine teeth on at least one of the two mandibles instead of the normal complement of five. I have obtained values from the Maritimes, Labrador and Eastern Arctic Canada which are compared to those of Sable Island:

Origin of Sample	No. examined	% of seals with only 4 post-canine teeth on at least one of the two mandibles
Sable Island	34	38%
Maritimes	15	13%
Labrador	42	2%
Eastern Arctic	11	0%

The two individuals from the Maritimes having only four post-canine teeth came from St. Mary's Bay, Newfoundland, about 530 km to the north-east of Sable Island. The finding by McLaren (this meeting) of a significantly higher percentage of harbour seal skulls from Sable Island with teeth set straight, compared with samples from elsewhere in maritime and eastern Arctic Canada also suggests isolation of this population.

For the three years of study, the prewhelping populations and the estimated numbers of pups born were respectively 1223 and 262 in 1970, 1329 and 331 in 1971, and 1147 and 359 in 1972. The average of these three years gives a proportion of 20.47% pups in the total postwhelping population. This compares to the value of 20.45% obtained from Bigg's (1969) theoretical population of 308 westcoast harbour seals at the close of whelping, including 63 pups. The percentage of pups with respect to the prewhelping population would be from my data and Bigg's data 25.7%. The value of 32% given by Bishop (1967) for harbour seals in the Gulf of Alaska seems high.

Mean Birth Dates

The mean birth date (50% born) occurred on May 24 in 1970, on May 21 in 1971 and on May 26 in 1972. In 1970, the birth period was spread from approximately May 8 to June 8, or 32 days. In the following two years, the spread was respectively from May 11 to June 7 or 28 days, and from May 7 to June 10 or 35 days. The averages for the three years are May 24 for the mean birth date and 31 days for the duration of the birth period.

Neonatal Pelage

The difference in mean birth dates during the three years of study was reflected by different frequencies of occurrence of lanugo in newborn pups. Figure 2a suggests an inverse relation between the percentage of pups born with lanugo and the corresponding mean birth date. In 1971, when there was the highest occurrence of whitecoat pups, 50% of those born with the lanugo, retained it for more than nine days, one individual shedding it only after 15 days. The length of the longest lanugo hair in a sample obtained from these pups was 21 mm.

Neonatal Weight and Length

The mean birth weight and mean birth length in 1970, 1971 and 1972 both seem to be related to the corresponding mean birth dates as illustrated in Figure 2b and 2c. Although the differences are not significant, the males were consistently heavier at birth (1971: 9.53 kg; 1972: 10.59 kg) than the females (1971: 9.49 kg; 1972: 10.40 kg), and longer at birth (1971: 75.94 cm; 1972: 78.16 cm) than female pups (1971: 75.76 cm; 1972: 77.27 cm). However, the mean birth weight and length for 1971 differ significantly at the 0.001 level from the corresponding values in 1972.

Mortality

The effect of annual variations of mean birth dates on pup mortality prior to weaning was assessed in 1971 and 1972. The 12% mortality figure for 1970 (Boulva, 1971) is considered low due to a less complete coverage of the island on that year. A better survival of the pups which were born later in 1972 is evident from Figure 2d. The average mortality before weaning for these two years is 17.2% of the total number of pups born. Possibly due to the pups' larger mean birth size in 1972, stillbirths accounted on that year for 29% of the total preweaning mortality, as compared to only 10% in 1971.

DISCUSSION

The graphic relations presented in these results would benefit from further data, but are given here because they may provide some orientation in future studies of these and other seals.

The data seem to imply that in the three years of study, variations in time of implantation of the blastocyst were not reponsible for the observed variations in the time of birth. Had this been so, we could have expected similar mean birth length and weight as well as a similar occurrence of whitecoat pups, irrespective of the mean birth dates in the three years of study. Instead, the later-born pups were larger at birth and there were more whitecoats in 1971. It appears, rather, that the length of active gestation was longer in 1972. This of course assumes that the average fetal growth rate does not change from year to year.

This longer gestation time in 1972 is further supported by the difference of 1.85 cm in mean birth length between the 1971 and 1972 pups. Using Bigg's (1969) graph for fetal growth of harbour seal, I calculated an approximate prenatal growth rate of 0.404 cm per day. At this rate, the shorter 1971 pups should have spent an average of 4.6 additional days in utero to average as large at birth as the 1972 pups. In view of the observed difference of five days between the 1971 and 1972 mean birth dates, there is here also a strong suggestion of identical mean implantation dates during these two years.

What mechanism controls the time of implantation with an apparently high precision has yet to be determined. Air or sea water temperatures are unlikely controls as they fluctuate from year to year at the time of implantation. Inconclusive experiments on the effect of external temperatures on implantation in the european badger (<u>Meles meles</u>) have been reported by Notini (1948) and by Canivenc and Bonnin-Laffargue (1963). However, normal dates of implantation in the marten have been modified by appropriate photo-period manipulation (Pearson and Enders, 1944). A high regularity in time of implantation could be insured in a species like the harbour seal by a photoperiodic control mechanism. Such a regulatory mechanism at time of implantation seems essential in this seal to reset the synchrony of the annual cycle, in view of its long mating season which appears to spread from prior whelping to after the weaning of the pups (Venables and Venables, 1957 and 1959; Harrison, 1963; Boulva, personal observations), or over almost four months.

Two possible explanations are suggested for the later mean birth date in 1972. For three consecutive years, the Sable Island harbour seals have been, somewhat by beach traffic, disturbed during parturition. The seals could have responded by delaying the onset of parturition, as observed in hunted populations of this species, where a delay of seven days was noted in two localities in Shetland, U.K., between 1962 and 1967 (Tickell, 1970); this compares to the five day delay observed on Sable Island between 1971 and 1972. Such a delay has also been reported in an exploited population of elephant seals at South Georgia (Laws, 1956). However, the disturbance of the Sable Island seals started in 1970, and in 1971, the mean birth date was earlier than on the previous year; it would have been later if the above explanation were correct.

The other explanation is a possible dependance of time of birth on environmental conditions, in this case air or sea water temperature. The latter data are not available, but mean monthly air temperatures for Sable

Island have been obtained for May 1970, 1971 and 1972 from the Maritime Weather Central of the Department of Environment of Canada and they are compared to the corresponding mean birth dates on Figure 3. There seems to be a relation between these two variables, but again additional data would be needed to verify its significance. It should be remembered that on a small island, air temperatures closely follow the surrounding sea water temperatures.

Finally, in view of its temporal variation, the high percentage of occurrence of whitecoat pups among the Sable Island harbour seals should not be used as a taxonomic criterion, for example to link the Sable Island seal to Phoca v. largha. The data presented here suggest that these whitecoats could disappear completely, should the mean birth date be delayed increasingly in the future. Furthermore, the lanugo of these whitecoat pups is the same length as the prenatal lanugo of Phoca v. richardi which in turn is much shorter than the 30 mm long lanugo of P. v. largha (Stutz, 1966).

AKNOWLEDGMENTS

While in the field, I received considerable help from Mr. D. A. Welsh, of the Department of Biology at Dalhousie University. Dr. I. A. McLaren offered useful criticism of the manuscript. The field-work was supported by the Arctic Biological Station of the Fisheries Research Board of Canada.

REFERENCES

Bigg, M. A. 1969. The harbour seal in British Columbia. Fish. Res. Board Can. Bull. 172: 33 p.

Bishop, R. H. MS 1967. Reproduction, age determination and behaviour of the harbour seal, Phoca vitulina L., in the Gulf of Alaska. M. Sc. Thesis. Univ. of Alaska, College, Alaska. 121 p.

Boulva, J. 1971. Observations on a colony of whelping harbour seals, Phoca vitulina concolor, on Sable Island, Nova Scotia. J. Fish. Res. Bd. Canada 28: 755-759.

Canivenc, R. and M. Bonnin-Laffargue. 1963. Inventory of problems raised by the delayed ova implantation in the european badger (Meles meles L.). In Allen C. Enders (Editor), Delayed implantation. The University of Chicago Press. x + 318 p.

Harrison, R. J. 1963. A comparison of factors involved in delayed implantation in badgers and seals in Great Britain. In Allen C. Enders (Editor), Delayed implantation. The University of Chicago Press. x + 318 p.

Laws, R. M. 1956. The elephant seal (Mirounga leonina Linn.). II. General, social and reproductive behaviour. Scient. Rep. Falkland Isl. Depend. Surv., 13, London.

Mather, K. 1964. Statistical analysis in biology. 2nd ed. Methuen, London. 267 p.

Notini, G. 1948. Biologiska Undersokningar over Gravlingen. Uppsala.

Pearson, O. P. and R. K. Enders. 1944. Duration of pregnancy in certain mustelids. J. Exp. Zool. 95: 21-35.

Stutz, S. S. 1966. Foetal and postpartum whitecoat pelage in Phoca vitulina. J. Fish. Res. Bd. Canada 23: 607-609.

Tickell, W. L. N. 1970. The exploitation and status of the common seal (Phoca vitulina) in Shetland. Biological Conservation 2: 170-184.

Venables, U. M. and L. S. Venables. 1957. Mating behaviour of the seal Phoca vitulina in Shetland. Proc. Zool. Soc. London 128: 387-396.

1959. Vernal coition of the seal Phoca vitulina in Shetland. Proc. Zool. Soc. London 132: 665-669.

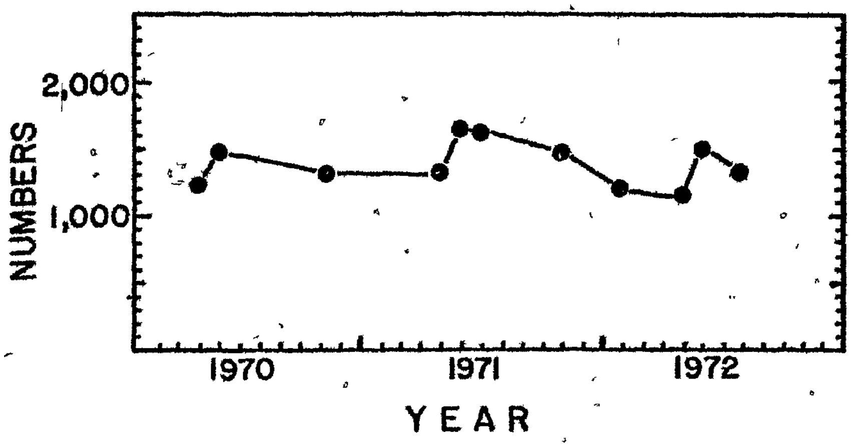


Fig. 1. Number of harbour seals counted on Sable Island, Nova Scotia.

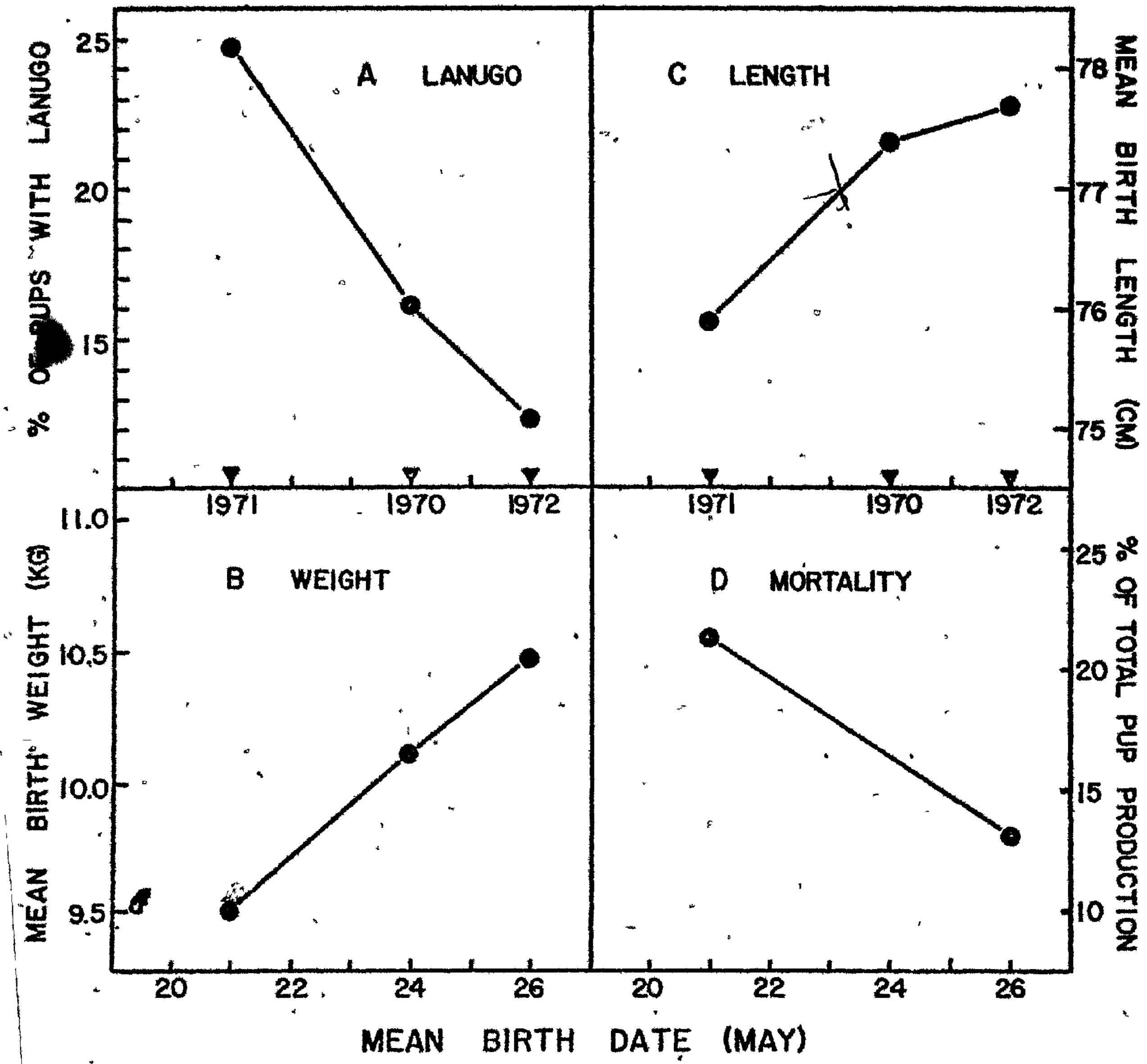


Fig. 2. Annual variations in the percentage of occurrence of harbour seal pups born with lanugo (A), in mean birth weight (B), in mean birth length (C), and in preweaning mortality of pups (D), with respect to mean birth date.

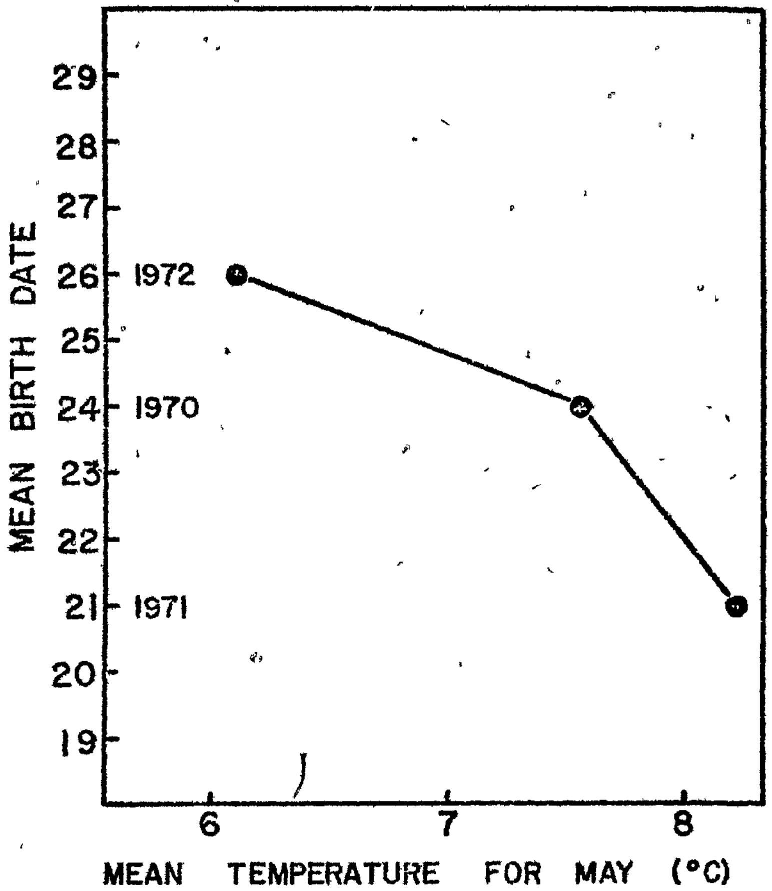


Fig. 3. Relation between mean birth date of harbour seal pups and mean monthly temperature for May 1970 to 1972, Sable Island, Nova Scotia.