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The Biology of the Ringed Seal (*Phoca hispida* Schreber) in the Eastern Canadian Arctic

By

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ABSTRACT

The ringed seal (*Phoca hispida* Schreber) was studied in the eastern Canadian arctic, particularly in southwest Baffin Island and northern Foxe Basin.

Canine teeth, which deposit incompletely calcified dentine in the spring season of low nutrition, are shown to be reliable indicators of age. The claws are useful for the first ten years. The seal grows from 65 cm. (2.1 feet) to a final adult length of about 135 cm. (4.4 feet). At least 72 food species were identified. *Mysis oculata*, decapods, and *Boreogadus saida* were most commonly taken in inshore waters, while most offshore seals feed on plankton, particularly *Themisto libellula* in southwest Baffin Island. Food does not limit the range or abundance of this seal. The basking and fasting season, in June and early July, results in much blubber loss, which is regained by summer feeding. Late departure of ice, giving longer opportunity for basking, may increase blubber loss. The moult occurs mainly in June. The sex ratio is about 53.5 males to 46.5 females. The male matures at about seven years, and the first ovulation of the female, which may be outside the breeding season and not result in pregnancy, usually occurs in the seventh year. The males are in rut from March to mid-May and the female ovulates during lactation, shortly after parturition. The blastocyst implants after about 3½ months delay, in early August, and the corpus luteum changes its structure and increases in size at this time. The pup is produced in one of two basic types of birth-lair on the fast ice, generally in early April, and may be attended until the ice breaks up. Coastal configuration and latitude govern the amount of fast ice, its stability, and its snow cover, all of which determine the suitability of an area for pupping. More starvelings and small pups are produced on simple coasts, and the adult population of complex coasts is older and the seals are larger in size. Seals of higher latitudes are also larger. There is an annual, small-scale migration, and a dispersal of young seals from productive complex coasts to simple coasts. Ice conditions govern the distribution and abundance of this seal throughout the eastern Canadian arctic.

INTRODUCTION

The ringed seal, *Phoca hispida* Schreber, is a widely ranging hair seal inhabiting arctic and subarctic waters (as defined by Dunbar, 1951) of the entire northern hemisphere. In North American waters it is found from the Gulf of St. Lawrence (rarely, Fisher, 1950) across the Canadian arctic to the Bering Sea. No overall biological study has been made of this seal in North America. Much of our knowledge comes from Eskimo observations and much that is presumed from these sources has not been checked by careful observation and collection. Allen, in his monograph on the Pinnipedia (1880), offers the best early summary of the biology of this animal. Dunbar (1949) brings in more recent material and reviews the knowledge of the species to that date. Chapsky (1940) apparently gives a thorough review of the species in the Siberian arctic, but this paper has not been available to the author. Particular studies have included those of Sleptsov (1943) on reproduction, Dunbar (1941) and Pikharev (1947) on feeding in the Canadian and Siberian arctic respectively, and Anderson (1942) on the taxonomy of the Canadian arctic groups. Manning (1944) describes well the methods and implements used by the Eskimos in hunting this animal. Other published material consists largely of incidental observations made on several expeditions to Greenland and the Canadian arctic.

The ringed seal is exploited by most of the Eskimo groups inhabiting the Canadian arctic. In some areas it contributes much of the food, clothing and fuel to the Eskimo welfare and is, in fact, the backbone of the native economy. In recent years some concern has been felt over the utilization of arctic sea mammal stocks. The problem, in the case of the ringed seal, has two main aspects:

1. Primitively, the Eskimo filled many of his needs with this animal; today, his needs have increased through the development of a trapping economy. Also, the seal itself has become an item of trade (for example, 2,506 skins were turned in to the Hudson's Bay Company at Cape Dorset, Baffin Island, in 1953-1954). It is not known whether the hunting pressure in such areas constitutes a danger to the maintenance of the seal stocks.

2. In some areas, local and seasonal scarcities result in depression of the native economy.

This paper deals with some basic features of the biology of the ringed seal in the eastern Canadian arctic. Economic problems are not treated directly here, but it is hoped that some of the biological findings, particularly the factors of distribution, will be of assistance in the management of the species as a valuable resource in the Canadian north. The development of an accurate ageing technique has stimulated research on seals in recent years. This technique has not hitherto been applied to the ringed seal and has been of great value in this study. The application of the ageing method to the study of reproduction and patterns of distribution constitutes the core of the work. Two phases of the study, parasitology and taxonomy, are not included in this paper and will be published at a future date.

METHODS AND MATERIALS

The study of the ringed seal was initiated with the analysis of stomach contents of seals from Ungava Bay, collected from 1947 to 1950. In the summer of 1953, the Fisheries Research Board ketch, M/V *Calanus*, worked near Cape Dorset, southwest Baffin Island, where collections from 44 ringed seals were made; these served as the basis for an overall biological study. The success of the 1953 operations suggested that southwest Baffin Island would be a suitable area for the study of the ringed seal in 1954. The author arrived at Cape Dorset, by chartered aircraft, on March 2 and departed, by ship, on October 2, 1954. It soon became apparent that many features of ringed seal biology revolve around local and seasonal distributions and movements, and that populations differ in their make-up throughout southwest Baffin Island. Thus, extensive travelling was required in the area between Cape Dorset and Markham Bay, about 135 miles to the east. The author was completely dependent on the Eskimos for transportation and securing seals and about two-thirds of the season was spent travelling and living with these people, the remainder of the time being spent in working out of the trading post at Cape Dorset. The bulk of the material in this paper is the result of collections made during that seven-month stay on southwest Baffin Island. Substantial collections were also made by the author between mid-September and mid-November from the *Calanus* in northwest Foxe Basin, in 1955. Very limited material was collected between 1951 and 1955, from Frobisher Bay, Cumberland Sound, and Churchill, Manitoba. Valuable collections have been made available through the efforts of other individuals in the pursuit of other arctic field-problems. Seals from Southampton Island, northern Baffin Island and northern Foxe Basin were obtained in some numbers, and smaller collections were offered from Ellesmere and Prince Patrick Islands, southwest Baffin Island, and Nettilling Lake on Baffin Island.

The lower jaws of all seals examined were collected for the purpose of ageing and preserved dry or rotted; whole skulls were taken when possible. The extracted canine teeth were placed in glycerine and water, with thymol as a preservative, and were sectioned and ground according to the techniques described by Fisher and Mackenzie (1954). The teeth sections were examined, in reflected and transmitted light, under a binocular microscope. In many cases an optical micrometer was used to measure tooth thickness, size of pulp cavity and thickness of dentinal bands in section. One or two claws were removed from many individuals and generally preserved rotten.

Stomach contents were examined in the field or collected for laboratory analysis. Those collected were identified to species, where possible. Organisms were counted, except where the stomach contents consisted of large numbers of small crustacea; in such cases the numbers were estimated by volumetric subsampling. The dominant food (in bulk) was estimated by eye, or, in doubtful cases, by displacement methods.

The reproductive organs of males and females were examined or collected; those of immature seals were not always examined. Measurements were generally taken of the fresh tracts and glands in the field. Portions of testes and epididymides, chiefly those of adults, were preserved in Bouin's fixative or 10% formalin, sectioned, and stained with haematoxylin and eosin or Mallory's stain. Ovaries were sectioned by hand, with a razor blade, into slices one to three millimetres in thickness. These sections were examined for corpora lutea, corpora albicantia and extent of follicular development, and the diameters of these were measured. Selected corpora lutea were sectioned, and stained with haematoxylin and eosin, or azocarmine, phloxine and fast-green. Embryos were preserved when found. Attempts were made, without success, to find unimplanted blastocysts in the uteri. Bacula, or penis bones, were collected from the males and preserved dry or rotted. After a superficial cleaning, these were boiled in a dilute solution of ammonium hydroxide, then weighed and measured. The cleaning was not rigidly standard, but it is felt that the small variation in residual fat content has little effect on the weights of bacula.

Notes were kept on the moult and other individual characteristics of the specimens.

Field numbers were given to all specimens. In this paper, reference to various years and localities is as follows: "S-" was used in southwest Baffin Island in 1953; "SD-" was used in the same area in 1954; "S-55-" applies to specimens from northwest Foxe Basin in 1955; "S-56-" designates northern Foxe Basin seals in 1956; "A-" is for Southampton Island seals.

AGE DETERMINATION

AGEING BY DENTINAL ANNULI

The technique of ageing by dentinal annuli has been thoroughly discussed by one of the discoverers of the method (Laws, 1953a) and by Fisher (1954a). The work of Fisher, on the harp seal (*Phoca groenlandica*), is more applicable to studies of the ringed seal, since the construction and nature of the dentinal rings is similar in these two species. The validity of the method, the physiological basis of dentine deposition, and much background information has been given by both authors. In this section it is proposed to deal chiefly with the evidence for the annual nature of annulus formation. The nutritional basis for differential dentine deposition will be discussed on page 11.

GENERAL APPEARANCE. A thin cross-section of a ringed seal canine tooth usually shows alternating bands of dense and thin dentine. Dense dentine is more opaque under transmitted light and is solidly constructed. Thin dentine may have one of two basic forms; it may be clear and continuous, transmitting more light than does the dense dentine, or it may be reflective, vacuolar and reticulated in structure. A typical series of bands, especially in the earlier-formed, outermost annuli, consists of dense dentine followed by thin, followed by reticulated, followed again by dense dentine; sometimes the thin or the reticulated dentine is absent. The density of the dense band varies considerably in comparison with its associated thin band. The relative widths of the bands within different series may be variable, as small, misplaced thin bands occasionally break the continuity of a dense band. In spite of all this variation, the pattern is distinct; denser and more fully calcified dentine alternates with thinner and less well-formed dentine. The deposition rate of the dentine appears to be regular within one year, but decreases as the number of annuli increases. In very old teeth, the annuli are very narrow. In the most typically annulated teeth the widths of adjacent annuli are similar. The adventitious nature of occasional variations and anomalies can be shown up by the use of an optical micrometer on the binocular microscope.

Both Laws (1953a) and Fisher (1954a) have offered convincing evidence that the deposition of the two major types of dentine occurs at different times of the year in the harp seal and the elephant seal (*Mirounga leonina*), and that this justifies the use of dentinal annuli in determining the age of these seals. The same reasoning applies to the ringed seal.

EVIDENCE FOR THE ANNUAL FORMATION OF DENTINAL ANNULI. Teeth from over 750 ringed seals have been sectioned for the study of ageing. From some of these teeth a histogram (Fig. 1) has been constructed showing, in two-week periods, the deposition of dense dentine at the pulp cavity. Many teeth obtained from the Eskimos were not dated, and not all the dated teeth could be entered into this histogram. Where the innermost annuli were smaller and crowded the detection of a dentine change would be difficult until some time after its occurrence. Thus, the histogram represents only those seals with fewer than four complete annuli. Probably there is a lag in the detection of dentinal change in all teeth, but this can be kept at a minimum by excluding older teeth. All suitable teeth collected from southwest Baffin Island in 1953 and 1954, as well as those collected from Foxe Basin in September and October, 1955, and February to April, 1956, are included in the histogram.

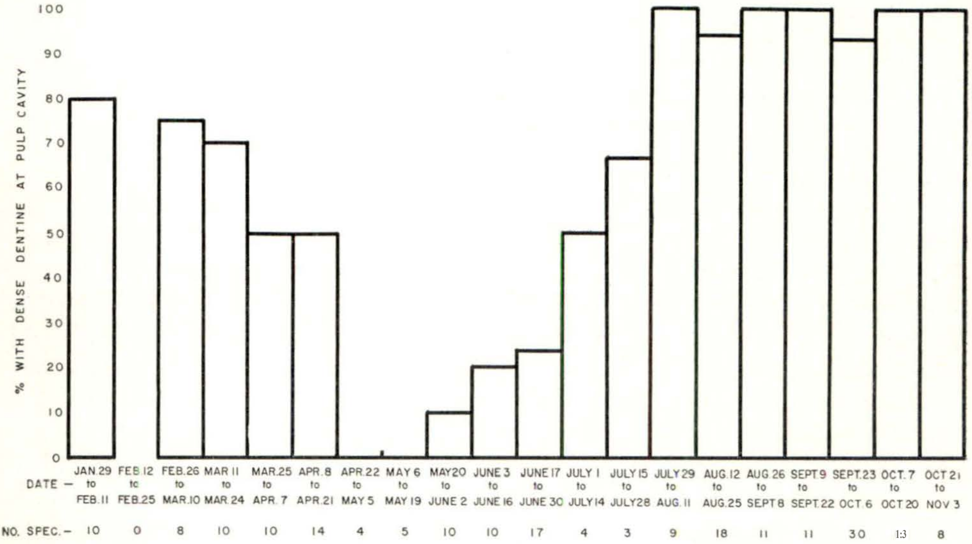

FIGURE 1. Seasonal changes in the deposition of dense dentine at the pulp cavity of the canine tooth of *Phoca hispida*, in 205 specimens.

Reference to Figure 1 shows that of ten teeth taken between January 29 and February 11, eight showed no interruption of the most recently formed dense dentine. One had a very narrow, thin band and another showed thin dentine in a fairly broad band next to the pulp cavity. The first tooth with reticulated, as opposed to merely thin, dentine was taken on March 11. Dense or thin dentine bordering the pulp cavity was found in seals taken up to April 19. Only thin or reticulated dentine was found in the next members of the series, killed on April 29, and in all seals taken after this date until late May. At this time one seal, which may have been anomalous, showed a broad, dense band bordering the pulp cavity with no evidence of recent thinning. The first teeth to show an obvious change from thin to denser dentine were two taken shortly before mid-June. The last reticulated dentine was being formed on July 3, and thereafter the proportion of teeth depositing dense dentine next to the pulp cavity increased. Only 3 out of 100 teeth taken between August 6 and October 30 had thin bordering dentine. Two seals taken in November were depositing dense dentine, although another with 8 dense bands on December 17 showed what appeared to be slight thinning of the dentine at this date. The majority, however, must continue to deposit dense dentine through the winter, judging from the suggestion of the first few histogram units of Figure 1. In those seals which showed the broadest bands of thin dentine in the spring, there was a tendency for the most recently formed dentine to be even thinner, or reticulated. The evidence for the deposition of the "poorest" dentine in the spring, from about mid-March to the beginning of July, is thus based on a series of teeth which covers this entire period. The annual nature of annulus formation may be taken as established and the structure of the dentine may be used with confidence to deduce the age of the seal. Thus, a seal taken in late summer with no annular pattern will be in its first year. Occasionally, however, a tenuous line of thin dentine, which may represent a line of birth or weaning, may be present. A seal taken in May with a single annulus of thinner or vacuolar dentine next to the pulp cavity, will have been born in March or April of the previous year. Figure 2 illustrates a variety of tooth sections, showing the seasonal changes as elaborated above. Some seals could not be aged accurately by this method after the tenth year and few could be aged after 20 years of age. This is due to the decrease in

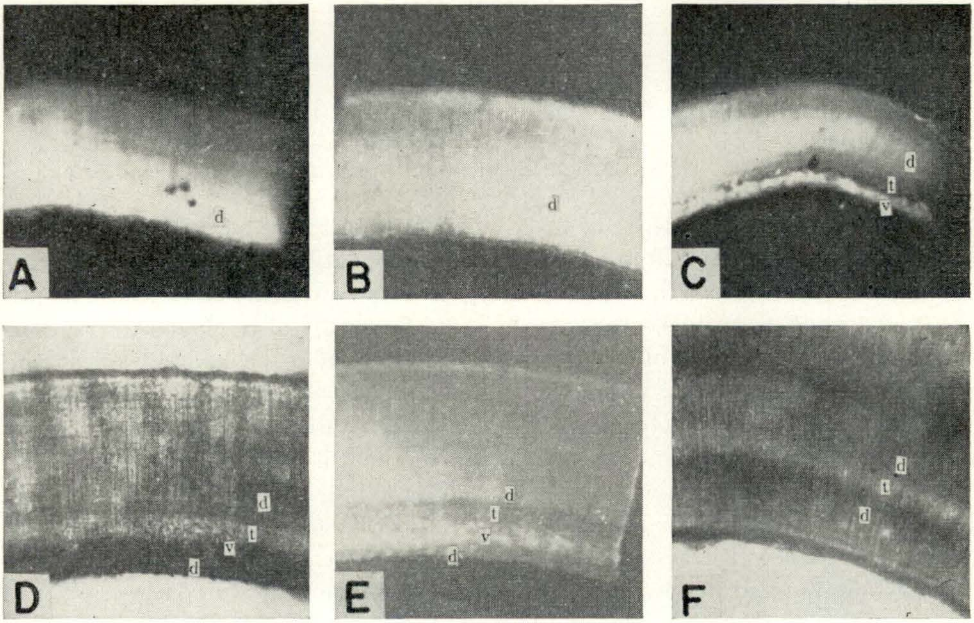

FIGURE 2. Tooth sections of young seals in various seasons. On the sections: d = dense dentine, t = thin dentine, and v = vacuolar or reticulated dentine.

A. S-50, August 31, 1953. Reflected light. This tooth, dense to the pulp cavity, is taken from a seal of the year.

B. S-56-12, February 11, 1956. Reflected light. A seal of the previous year. No thinning of the dentine is apparent. The narrow dark border is the face of the pulp cavity.

C. SD-177, July 3, 1954. Reflected light. A moulting seal, born in the previous year. Note that the vacuolar dentine, on the inner border, is highly reflective.

D. S-55-57, October 16, 1955. Transmitted light. One thin band, deposited in the previous spring, indicates that this animal is in its second year. The dentine bordering the pulp cavity is dense.

E. S-55-57, October 16, 1955. Reflected light. The same section as in D. Note that the vacuolar dentine, which is not visible in the transmitted light of D, is here revealed as a reflective band (as in C.)

F. S-56-15, February 12, 1956. Transmitted light. Dense dentine is being deposited at the pulp cavity, although it is not as dense as the dentine of the previous summer, which had been laid down immediately following the spring thin band. Second year.

dentine deposition rate, which results in crowding of annuli after many years of age. In very old seals the annular structure of the cementum served as an added check. Dense cementum bands show a one-to-one correlation with dense dentine bands in younger seals and do not decrease in size with age. By this technique one male, the oldest seal obtained, was found to be about 43 or more years in age.

OTHER METHODS OF AGEING

The Eskimos of southwest Baffin Island are able to distinguish what they suppose to be the younger age-classes of the ringed seal. The ringed seal (*netserk* s.l.) is divided into seven age-groups with the following Eskimo names (spelling based on Thibert, 1954);

Netsiak	the white-coat
Netsiavinerk	a seal of the year, before the first moult
Pivinerk	a seal of the second year, before the second moult
Saggalak	a seal of the third year, before the third moult
Togrotinerk	a seal of the fourth year, before the fourth moult
Netsilak	a seal of the fifth year, not always distinguishable

All other seals are considered to be adult (*netserk* s.s.); the adult female is often called *nunerk* and the adult male *tiggak*. Thus the natives consider that maturity is reached after the fourth or fifth year. The names actually refer to the length of the hair and its state of growing; the same names are also applied to stages of the moult and formation of the new coat. Thus a seal of the second year may be called *pivinerk* on the basis of age, but if taken shortly after the moult, it may also be referred to as *saggalak* (translated approximately as "new-grown hair"). Naturally, the determination of age by this method, if it is valid, is most simple after the hair is fully grown and before the moulting season. The author was unable on this basis to distinguish any of the young age-classes except the seal of the year, which, in softness and length of hair, is quite distinct. All twelve seals which were entered in the field-notes as young of the year were correctly aged. Three out of four *pivinerk* were in the second year and one was in the third year, but had not yet moulted. Four third-year seals, *saggalak*, were correctly aged by the natives; another seal, actually in its first moult, was put into this class by the Eskimos. The class *torgrotinerk* was less reliable. Four out of seven of this class were correctly aged; however, two in their fifth year should have been called *netsilak* and one, in the seventh year, was actually a *netserk* in the strict sense.

The Eskimos also make use of the claws in determining the age of the seal. They consider that a large number of alternating light and dark claw annuli in some way indicates an old seal. Plekhanov (1933) noted annular bands on the claws of the harp seal. He presumed that these represented annual increments of growth. Doutt (1942) found the same pattern on ringed seal claws.

The claws of 105 ringed seals were collected between April 28 and October 27, in order to assess their value in age determination. Dried or rotted claws are easily removed from the phalanges, but those preserved in formalin cannot easily be removed from the attached bone and flesh. The claws show alternating dark and light bands. The light bands are variable in width, but are usually marked in the middle by a narrow, encircling ridge. Claws showing few bands are capped at the tip by a section of more or less translucent structure. This translucent tip, when not worn off, is usually separated from the rest of the claw by a narrow constriction which may represent the limit of prenatal growth. The band at the growing base is very narrow and light in the early spring, broadening through the summer, and darkening before the autumn. The slight ridges in the light band appear to be laid down in the spring. These features are shown in a typical claw on Figure 3. The hypothetical age of a seal may be determined by assuming that the dark bands are the result of autumn and winter growth and that the light bands are formed in the spring and summer. The ages derived in this manner are checked against ages determined from dentinal annuli in Table I. The claws, which generally have a regular and clear pattern, are very useful in checking tooth-determined ages and for preliminary ageing in the field. Wear at the tip obliterates first the 'constriction of birth' and then the first year's growth. Ageing by claws is invalid beyond about the tenth year, judging from comparisons of age-estimations of seals of 9 to 17 years in the Table.

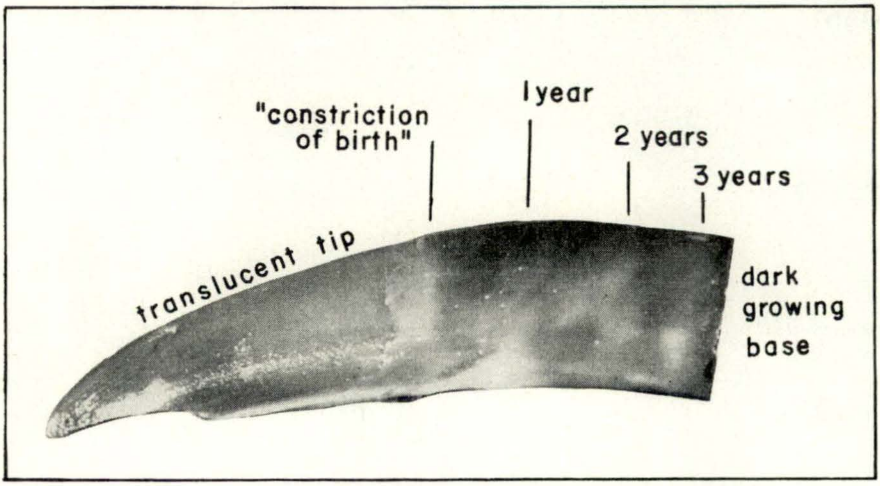

FIGURE 3. A typical claw, of a fourth-year seal killed on October 4, 1955.

TABLE I. Comparison of ages of *Phoca hispida* deduced from teeth and claws. A query following an age indicates that this age is the less accurate of the two, due to anomalies or obscurities. A plus sign indicates that wearing of the claw has eliminated the first year's growth.

Deduced age	Number of specimens	Tooth age	Claw age
First year	4	1	1
Second year	11	2	2
	2	2	3?
Third year	7	3	3
	1	2?	3
	1	3	2?
Fourth year	8	4	4
	1	5?	4
	1	4	5?
Fifth year	3	5	5
	2	4?	5
Sixth year	9	6	6
Seventh year	2	7	7
	1	6?	7
Eighth year	3	8	8
	1	7?	8
Ninth year	2	9	9
	1	9	7+
Tenth year	1	10	10
	1	10	8+
Eleventh year	1	11	10+
	1	11	8+
Twelfth year	1	12	10+
Thirteenth year	1	13	10+
	1	13	11+
Fourteenth year	1	14	10+
	1	14	12+
Seventeenth year	1	17	10+

FACTORS AFFECTING THE FORMATION OF DENTINAL ANNULI AND CLAW BANDS

The general appearance, variability and times of deposition of the dentinal annuli have been discussed. Essentially, incompletely calcified dentine is laid down in the spring season, and solid, well-formed dentine is deposited in the summer and generally through the winter. The springtime is featured by a relaxation of feeding, followed by more intensive fasting as the season progresses. Fewer than 60% of seals were feeding in each of the two-week periods between April 22 and June 30, which corresponds to the period in Figure 1 when fewer than 25% of the seals were depositing dense dentine at the pulp cavity. Thus, there is a distinct correlation between seal feeding or fasting, and the deposition of dentine. Dense dentine is deposited from early summer until the following spring when feeding intensity is greater. Mellanby (1928) found that a diet deficient in cod-liver oil, but complete in other respects, would result in poor dentine formation in puppies, and other workers have found that the necessary factor is Vitamin D. Fisher (1954a) and Laws (1953a) discuss this effect of Vitamin D in greater detail. Certain individual seals show thinning of the dentine before the season of more intensive fast and some of these, as suggested above, may have been depositing such dentine through much of the winter. It is possible that a sufficient Vitamin D intake is assured only by voracious feeding, for even though a seal may be eating enough to maintain its condition of fatness, as seems to be usual in the winter, it may not be ingesting sufficient Vitamin D to ensure the formation of the densest form of dentine. Moreover, adults experience the metabolic strain of the breeding season during the spring and this may well effect the formation of dentine. The moult normally occurs from mid-May until mid-July, with a peak in the month of June, but the physiological cause of the process may well extend back to an earlier period and effect the balance of dentine deposition. Several animals were taken in August and September which were in very late or prolonged moult. In these abnormal cases the seals were all feeding and dense dentine was being deposited at the pulp cavities of their teeth. Seals of the year, whose moult is not associated with a prolonged fast, do not deposit poorly formed dentine until the following spring. Thus the moulting process, possibly through further drain on the resources of Vitamin D, may be a supporting factor in thin dentine formation, but it cannot be the sole cause. Some teeth may show narrow bands of adventitious thin dentine within the dense dentine and it is probable that this a reflection of individual variations in feeding. Teeth from seals taken at Herschel Island, in the western arctic, are often difficult to interpret for this reason, and these anomalies may be due to abnormal feeding circumstances imposed by the geography and productivity of the area.

The pattern of annular deposition in the ringed seal is in accord with the findings of Fisher (1954a) on the harp seal, although Laws (1953a) has reached different conclusions from his work on the elephant seal. He considers that dense, fully formed dentine is laid down while the animal is fasting and points out that Vitamin D may be formed in optimum amounts by irradiation, when the animal is lying in the sun; the same factor may be available in sub-optimum amounts when the animal is feeding in the water. Fisher (1954a) discusses the opposition of the two views, but the present author can add nothing more in explanation of the two different conclusions.

The claws are less subject to individual variation than the teeth and their growth is probably more closely dependent on the moulting cycle, which is a more precisely annual phenomenon than the fasting season.

GROWTH AND MORPHOMETRY

The ringed seal is probably the smallest of the hair seals (Phocidae). The largest specimen taken for this study was a male, 156 cm. (5.1 feet) from nose to tip of tail and 222 lb. in weight; the longest female measured 152.5 cm. (5.0 feet). Soper (1928) recorded a male of slightly greater length, 162.5 cm. (5.3 feet), and Stefansson (1944) weighted one of 225 lbs. or more, including estimated blood loss. Five and one-half feet (168 cm.) and 250 lb. are probably close to the limits for the male of this species. There is great individual variation in adult size, which appears to be independent of age; the factors governing this variation will be discussed in a later section.

The relationship between standard length and age of the ringed seal is outlined in Figure 4. The symbols represent the mean of size and age of seals

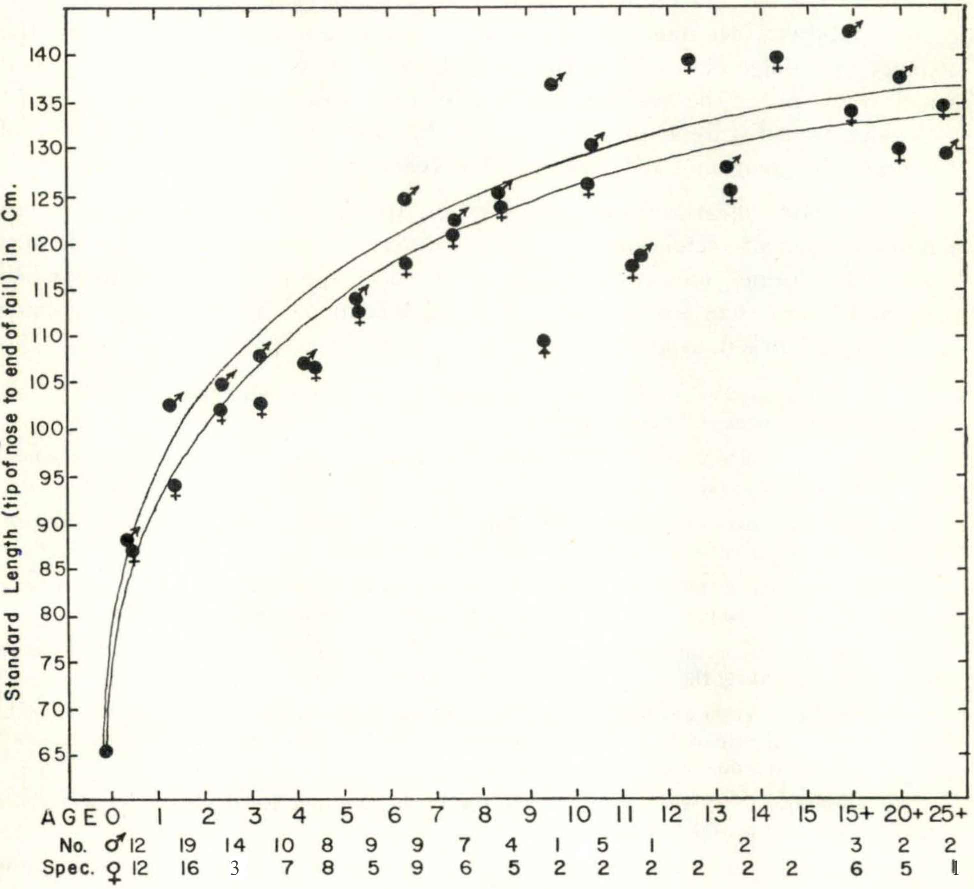

FIGURE 4. Growth of *Phoca hispida*. Each symbol represents the average, in length and age, of each age-group. The curves are fitted by eye with the aid of several straight lines of least squares.

from each age-group. The size at birth (65 cm. or 25.5 inches, derived from three full-term foetuses and two new-born pups and averaged for April 1) is not fixed with accuracy, but the first-year size-mean, derived from 24 specimens, is more firmly based. The high degree of individual variation and the different geographical origins of the specimens make it difficult to fit exact growth curves. The curves on Figure 4 must be considered to be approximate only, although they were fitted with the aid of several successive straight lines of least squares. During its life, the ringed seal appears to grow from approximately 65 cm. at birth to a final adult size of about 135 cm. (4.4 feet), the males averaging about 3 cm. longer than the females after maturity. The shape of the growth curve is similar in both sexes. The slight negative deviation of the third, fourth and fifth year size-means is considered to be a result of sampling error, and not related to the double sigmoid growth-curve found in the males of polygynous species (Laws, 1953b; Scheffer and Wilke, 1953).

Laws (1956a) has related growth rates of Pinnipedia and Cetacea to their ages at puberty. He found that about 86% of the final length is attained by the females at the age of sexual maturity. This rule holds well for the ringed seal which ovulates for the first time, on the average, when about 6 years old. At this time, from Figure 4, the female would measure about 117 cm., or 87.6% of the final adult length of 133.5 cm. at 25+ years.

Other body measurements are given in Appendix Tables I and II. Since field-measurement techniques and criteria differ, the measurements are defined here. The "same" measurements often produced quite different results when applied by more than one person to the same specimen. These Tables are made up of the author's data alone.

1. *Standard length* was measured in a straight line from tip of nose to the end of the tail, with the head and neck in a natural position.

2. *Axillary girth* was taken with the aid of a piece of string around the body, under the fore-flippers, at the level of the axillae.

3. *Maximum girth* was taken around the largest circumference of the chest or abdomen; this did not always exceed the axillary girth in very thin seals.

4. *Navel to anus* distance was measured from the centre of the umbilical scar to the anterior notch of the anus of the male and the vestibule of the female, along the body contour.

5. *Penis to anus* distance was measured from the centre of the penis orifice to the anterior notch of the anus, along the body contour.

6. *Foreflipper length* was measured in a straight line along the radial border of the forelimb, from the axilla to the tip of the longest digit (not claw). The forelimb was held flat and extended posteriorly along the side of the body.

7. *Foreflipper width* was taken from the tips of the first and last digits (not claws) of the stretched flipper, in a straight line.

8. *Hindflipper length* was measured from the base of the tail, along the inner edge of the extended flipper, to the level of the longest digit.

9. *Hindflipper width* was taken from the tips of the first and last digits with the flipper stretched to its fullest extent.

10. A probe was inserted into a small incision over the sternum. The *blubber thickness* was then marked on the probe from the bared bone of the sternum to the inner surface of the hide.

11. *Weight* was taken by a spring balance of 200 lb. capacity. No estimate was made for loss of blood.

A few data on tail length and distance between mammae are not included in the Table. The tail length appears to increase from about 6.5 cm. in 80 cm. seals, to about 9 cm. in 150 cm. seals(from line of regression of tail length to standard length of 29 specimens). The distance between mammae (from 22 specimens) appears to range from about 5 cm. in seals of 85 cm. in length, to about 9 cm. in seals about 140 cm. long.

For comparative purposes, some of the measurements have been reduced to percentages of the standard length and each such percentage plotted against its standard length. Straight lines of least squares have been fitted to the measurements expressed in this fashion, with the sexes separated. Appendix Table II gives the results of this analysis. The percentage of standard length of each measurement is given for seals of 60 cm. and 160 cm. in standard length and serves to fix the line of regression, and one standard error of the estimate is given to express the variation around this line. The seasonally variable girths, weight, and blubber thickness are excluded. Heterogonic growth is suggested in several of these comparisons. The limbs seem to grow proportionately less rapidly than the animal as a whole. The hind end of the body appears to grow only slightly more rapidly than the anterior end, as demonstrated by the comparison of the distance from navel to anus with standard length; thus there is little evidence for an antero-posterior growth gradient in this species.

A large series of skulls was collected from southwest Baffin Island. Morphometric studies of these have led to the consideration of taxonomy, and in particular to the status of the two subspecies described by Anderson (1942). Taxonomic matters will be left for a later paper and the morphometry of the skulls will be discussed then.

FEEDING

FOOD PREFERENCES

Of the 216 seal stomachs examined in the field by the author, 36 were empty and 104 were sampled, in whole or in part, for laboratory analysis. The stomach contents of 48 seals, collected by other groups and individuals, were also available. At least 72 species were detected in these stomachs. Appendix Tables III to IX list the food species, along with data on their incidence, according to localities.

The ringed seal makes use of a wide variety of planktonic, nektonic, and benthonic food species. It is apparently widely adaptable in its feeding habits, but does not seem to eat many of the slow-moving, sedentary or burrowing animals (molluscs, echinoderms, tubeworms, large prawns, etc.) which are the chief components of the diet of the bearded seal (*Erignathus barbatus*). The few molluscs taken were small, with the shells present, and were probably more or less accidentally ingested. Among the decapod food species, only one crab (*Hyas coarctatus*) and none of the heavily armoured *Sclerocrangon boreas*[2] were detected. The smaller individuals of the natantic decapods were common and such food may be selected just off the bottom, not benthonically. The most abundant food elements were *Themisto libellula*, *Mysis oculata*, and the polar cod, *Boreogadus saida*.

The ringed seal probably feeds by individual selection of each food organism. It is known to feed only on the larger *Themisto* of a population having a bimodal size distribution (Dunbar, 1941). The possibility of a sifting or filtering method of feeding cannot be excluded, however. For example, two seals from Foxe Basin were feeding almost exclusively on the small (10–12 mm.) amphipod *Apherusa glacialis*, of which there were about 1,100 individuals in each stomach. These amphipods were noted in thick surface swarms at the time and almost certainly, due to their small size, could not have been taken individually. Small terrestial leaves and bird feathers were occasionally found in plankton-filled stomachs, especially in seals feeding inshore on mysids, indicating that selection was not too critical. Bearded seal stomachs which have been examined by the writer often contained stones, sand and mud. Such evidence of indiscriminate feeding was rarely found in the ringed seals which were feeding benthonically. Pebbles were found in the otherwise empty stomachs of three seals taken during the fasting season. These may have been swallowed purposely, perhaps to get rid of the nematode worms with which the stomachs were infested (see also Hahn, 1884).

Little evidence is avilable on the depth at which ringed seals may feed, for hydrographic charts of the areas studied are not generally available, or are not complete. One ringed seal taken near Churchill, Manitoba, in February, 1954,

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[2] Squires (1957) lists 39 *Sclerocrangon boreas* in ringed seal stomachs from Ungava Bay, and other differences are found between the decapod food species in Appendix Table III of the present paper and those listed by Squires from the same collection of seal stomachs. Mr. Squires has kindly informed the author that these discrepancies are due almost entirely to the mistaken inclusion in his list of the findings from a single bearded seal stomach.

was feeding on benthonic decapods in 14 to 15 fathoms (26–28 m.) of water and decapods were also eaten by seals in 15 to 20 fathoms (28–37 m.) of water in Foxe Basin in the autumn of 1955. Several seals killed in over 20 fathoms of water in the winter of 1956 were feeding benthonically and at least one of these, judging from the few soundings in this northern area of Foxe Basin, might have been in around 50 fathoms (90 m.) of water. The fur seal (*Callorhinus ursinus*) is known to dive to at least 40 fathoms (70 m.) (Scheffer, 1946) and the walrus (*Odobaenus rosmarus*) to 44 fathoms (80 m.) (Vibe, 1950). One undisturbed seal, observed in a fairly shallow bay of southwest Baffin Island, stayed down for an average period of 3 minutes and 13 seconds, and surfaced for an average of 1 minute and 29 seconds, during four successive dives.

No differences were apparent in the choice of food species through the season and no differences could be detected in feeding with respect to seal age. It is evident that the choice of food depends on its availability, and that feeding falls into a pattern which is partly determined by depth of water and distance from the coast.

PATTERNS OF FEEDING

In southwest Baffin Island (Fig. 5) all seals which had been feeding in deep offshore waters were subsisting mainly on *Themisto libellula*, a planktonic amphipod. Seals taken in bays or in shoal water were feeding predominantly on the

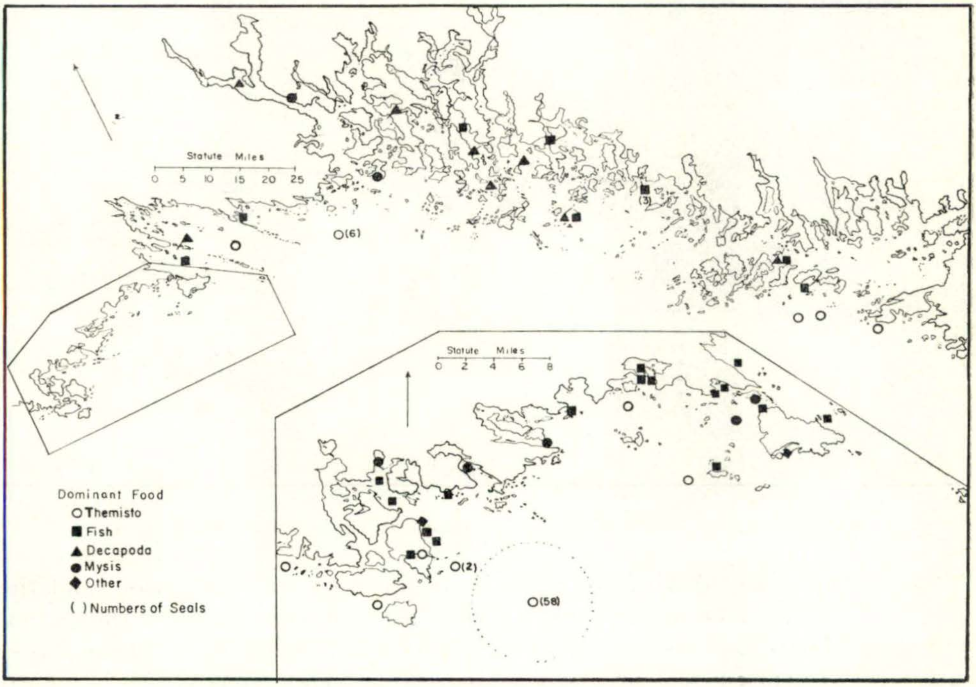

FIGURE 5. The pattern of feeding of *Phoca hispida* in southwest Baffin Island

polar cod (*Boreogadus saida*), *Mysis oculata*, and on various decapods; *Themisto* was dominant in the stomach of only one inshore seal. This stomach contained fresher decapod material, including a single crab (*Hyas coarctatus*), and the seal had probably come in recently from the offshore waters. Two seals taken near land fronted by the open sea had been feeding largely on the amphipods *Haploops setosa* and *Gammarus setosus*. Other seals killed near the open coast were feeding on polar cod, or *Themisto*, or both.

In northern Foxe Basin (Fig. 6) the delimitation between inshore and offshore feeding is not so apparent. Foxe Basin is generally shallow and almost all the seals were taken well within the 25-fathom limit (see Campbell and Collin, 1956). Also, *Themisto* does not appear to be as abundant here as in Hudson Strait. The polar cod appears to be the most common food choice in shoal water and *Mysis oculata* also figures largely at such depths. The insert in Figure 6 suggests that *Mysis* is not taken in the shallowest water and this is in keeping with the known habits of this crustacean. Large numbers of polar cod were taken in nine out of eleven seals feeding over the shallow bar of Turton Bay (Figure 6).

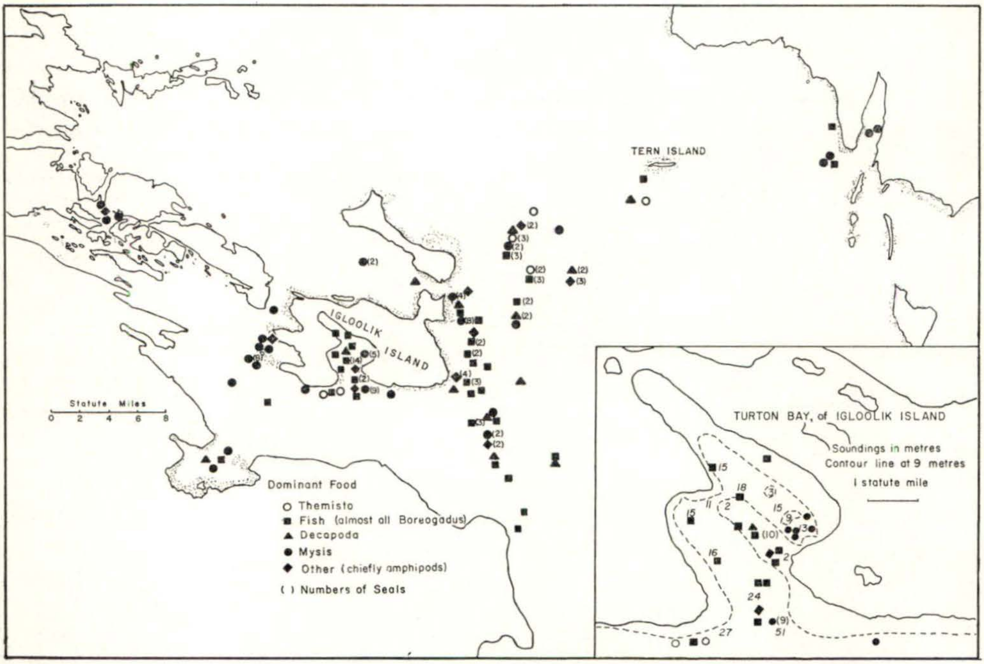

FIGURE 6. The pattern of feeding of *Phoca hispida* in northern Foxe Basin.

This bar was covered with grounded ice during much of the season, and the Eskimos reported having seen great schools of this fish there earlier in the season. All the seal stomachs shown in Figure 6 which are distributed to the southeast and east of Igloolik Island, and between Igloolik and Tern Islands, were examined in the field during the winter of 1956 (*Calanus* field notes, 1956). *Themisto* was dominant in four stomachs from the waters between the northern tip of Igloolik Island and Tern Island, where the depths range around 50 fathoms. It is perhaps of interest that the two other stomachs in which *Themisto* was dominant were taken from the southwest corner of Turton Bay (Fig. 6) which is probably the deepest water from which seals were taken, excluding the area to the southwest of Tern Island. Thus, in spite of the obscurity of the pattern in Foxe Basin, a similar correlation between choice of food and depth is suggested.

Many of the stomachs in Ungava Bay were collected by Eskimos and were not accompanied by precise data on origin. Nevertheless, most were probably taken in inshore waters, for the dominant food species, *Mysis* spp., *Thysanoessa* spp., and the fish are all inshore forms; *Themisto* was a minor food element there. Seals from bays and fiords of Frobisher Bay were feeding largely on *Mysis* and fish. *Mysis*, pelagic amphipods such as *Gammarus* spp. and *Apherusa*, and the benthonic genera *Atylus*, *Socarnes* and *Anonyx*, and fish were found in inshore stomachs from Ellesmere and Prince Patrick Islands. The geographical pattern of feeding is not clear in Southampton Island, where *Themisto*, *Mysis* and *Thysanoessa* were the most commonly found food species. A seal off the mouth of the Churchill River, in 14–15 fathoms (26–27 m.) of water, was feeding largely on Decapoda.

The literature suggests that a similar feeding pattern may apply in other parts of the arctic. Johansen (1910) states that seals shot in the pack ice off East Greenland were feeding on pelagic amphipods, but the polar cod was the principal food for fiord-dwelling seals in May to August. The old fiord-seals of East Greenland feed on the larger species of Crustacea (Decapoda?) according to Pedersen (1930). Offshore and inshore seals of the same region may feed on polar cod (*idem*, 1942). The adult seals of Cumberland Sound feed largely on unspecified Crustacea (Kumlien, 1879); in the winter they live inshore, under the fast ice, and subsist to a considerable extent upon fish. Vibe (1950) considers that the polar cod is the principal food when the seals are foraging at great depths and that amphipods and decapods are the chief food elements near the coast of northwest Greenland. This is just the reverse of the feeding pattern displayed in southwest Baffin Island and other localities in the eastern Canadian arctic. Vibe found polar cod almost exclusively in stomachs from Neqe, which, judging from his map of the area, is actually an inshore region. At Lake Harbour, on southern Baffin Island, Dunbar (1941) found *Themisto* dominant in seals taken during August; the stomachs were taken in offshore waters (M.J. Dunbar, personal communication). Other references in the literature, lacking in geographical specificity, do not illustrate the pattern of feeding and depth, but do suggest that the ringed seal has some latitude in choice of food.

Thus, in shallow, inshore waters the ringed seal may feed benthonically or near the bottom, chiefly on fish, *Mysis*, and decapods. It can turn quite easily to strictly planktonic feeding, particularly on Amphipoda, and in the offshore waters of southwest Baffin Island its chief food is *Themisto libellula*. The ringed seal has the ability to utilize organisms at several points of the food chain (as outlined in Dunbar, 1953) and although there may be individual, seasonal and geographical differences in their nutritional histories, food is not likely a limiting factor in the local distribution and numbers of the seal. Important food species, such as *Mysis* and *Boreogadus*, are available in areas where seals are scarce (for example, parts of Hudson Bay) and food availability is evidently not a critical factor in determining the abundance of ringed seals over various parts of their wide range.

THE FASTING SEASON

Figure 7 shows, in histogram form, the season of fasting. The degree of fullness of stomachs is not incorporated into this histogram, which is made up of seals sampled from southwest Baffin Island, Southampton Island and northern Foxe Basin. Although there is some suggestion of relaxation of feeding in late winter and early spring, the period of more intensive fasting would appear to extend from April to late June. The fast seems to be strongly associated with the habit of hauling out onto the fast ice, for Freuchen (1935), Pedersen (1930,) and Kumlien (1879) mention the relative emptiness of stomachs from seals which have been basking on the ice. In southwest Baffin Island in 1954, seals began to appear on the fast ice as early as late March, but the numbers were very small until May. On May 14, a day of low cloud-cover, only 3 seals were seen in about 21 miles of travel on the fast ice. On May 16, a day of bright sunshine, eleven seals were seen during 30 miles of travel. The numbers were still relatively small in late May, for this period was generally cold and windy. During the hot days of mid-June to early July, large numbers of seals were seen on the ice of Andrew Gordon Bay (see Fig. 21). On June 18, 16 seals were observed lying

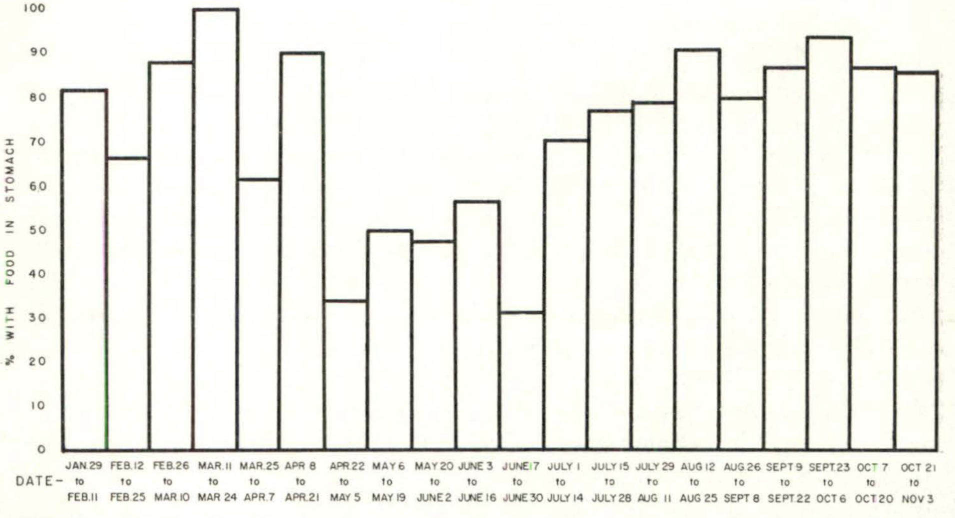

FIGURE 7. The annual cycle of feeding intensity of *Phoca hispida*, from 381 specimens.

alongside a tide-crack in the fast ice, about 150 yards (140 m.) in length. On July 13, 27 animals were sunning on a sheet of ice, about ¾ square mile in area. After mid-June large numbers of immature animals, which had spent the winter in the open water, moved into the fast ice of southwest Baffin Island. Seals were very common on the fast ice of Southampton Island before mid-June of 1955, when the season was hot and sunny (A. W. Mansfield, personal communication). In northwest Foxe Basin in 1956, on the other hand, the sunny weather occurred much later in the season and seals were not very common on the ice before late June and early July. Table II lists the proportions of food-containing and empty stomachs in relation to the fast ice, for the crucial period of late April to mid-July. During this period, 29% of seals killed in the open water outside the fast ice had empty stomachs, whereas 79% of those taken on the fast ice were not feeding. It appears, then, that there is a general relaxation of feeding in the early spring, perhaps more pronounced in seals living under the fast ice, most of which are adults concerned with reproduction in late March until mid-May. The season of most intensive fasting coincides with the periods when most seals are sunning on the fast ice, and it may be that the timing and intensity of this pronounced fast is dependent on the conditions for hauling out in the sun.

TABLE II. Seal feeding in relation to fast ice.

Origin of stomach	Contents	Date						Totals
		April 22 to May 5	May 6 to May 19	May 20 to June 2	June 3 to June 16	June 17 to June 30	July 1 to July 14	
Outside fast ice	Empty	1	1	4	5	2	1	14
	With food	1	1	8	14	6	4	34
Inside fast ice (cracks and tide-rips)	Empty	...	4	...	...	...	...	4
	With food	...	7	...	...	...	...	7
On fast ice	Empty	1	4	6	8	13	2	34
	With food	...	1	1	3	1	3	9

Feeding and Seal Condition

Some of the routine measurements taken in the field are useful in determining the condition or degree of fatness of the seals. From these measurements, the following indices of seal condition may be derived:

Index 1. Blubber thickness may be compared directly with standard length. The thickness of the blubber of the ringed seal is small and this comparison is subject to error of measurement.

Index 2. The cube root of the weight may be compared with the standard length. This index shows a very wide range of values and the seasonal trends are not too clear. Since loss of blood cannot be controlled, the wide range of values is not unexpected.

Index 3. This index of condition has been applied by Sivertsen (1941) to the harp seal and by Laws (1953b) to the elephant seal. The circumference of the seal, which reflects blubber thickness by a ratio of change of about 6 to 1 ($2\pi r$), is compared with the length of the seal. The size of the seal enters into both numerator and denominator of the formula:

$$\text{Seal condition} = \frac{\text{Maximum girth}}{\text{Standard length}} \times 100$$

This formula was applied to 326 seals, excluding seals of the year, since these have not fasted in the spring, and illustrates the seasonal trends of condition (Fig. 8). The different geographical origins of the seals and the wide range of variation in condition suggest that some data on individual seals and circumstances are required to clarify the picture of seasonal changes.

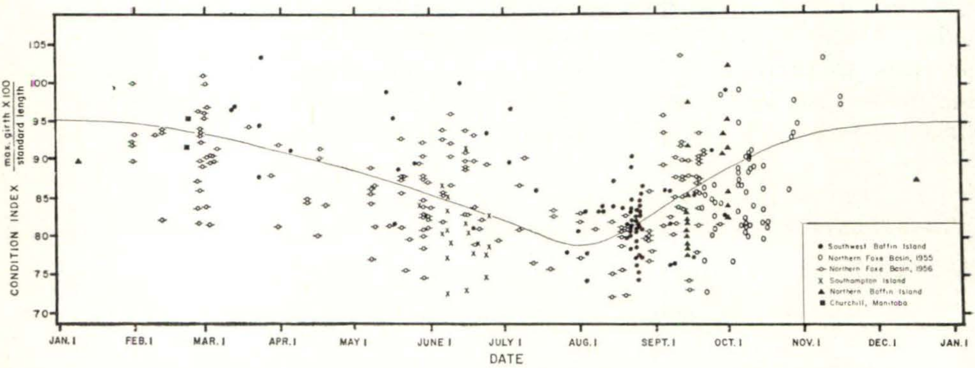

FIGURE 8. Seasonal changes in seal condition. The curve has been fitted by eye, with the aid of semi-monthly means, and has been raised at the left and lowered at the right, in the belief that seal condition does not change much during the winter months.

The average condition index of 6 seals taken in southwest Baffin Island between March 11 and April 4 was 94.9. The average for 5 seals killed on the fast ice during May was 90.9. One of the May seals had been badly wounded a few days previously and its poor condition (index 81.7) may have resulted from this abnormal stress. Thus, there appears to have been little loss of blubber in May and this is in accord with the relative scarcity of seals basking on the ice at this time. At Southampton Island in May, numbers of seals were basking on the fast ice, and in June, all the seals from this locality were killed on the ice; their condition is correspondingly poor, giving an average index of 80.0. The average condition index of the Foxe Basin specimens changed from 90.8 in the period of February to March, to 86.0 in the period of mid-May to mid-June. Both these values are lower than those for the equivalent periods in southwest Baffin Island, but the decrease in condition is about the same in each region. The figures may represent actual differences in seal condition between southwest Baffin Island and Foxe Basin, though they may result from different measuring techniques, since the measurements of the Foxe Basin seals were not made by the author. In southwest Baffin Island on June 12 and 23 two offshore animals were feeding heavily and were in winter condition (indices 100.0 and 93.6); in living outside the fast ice, presumably neither had experienced much fasting. Seals taken on the fast ice of this area showed a wide range of condition. It is believed that those seals taken near the outer edge of the fast ice in June and early July had come in recently from the open water. Those taken well inside the fast ice were probably winter residents, which had had a longer opportunity for basking and associated fasting. Six seals taken at the head of Andrew Gordon Bay (see Fig. 21) were all quite thin in mid-June. On the other hand, seals taken near the edge of the fast ice in this area were either fat or thin. Two measured from this area in early July exceeded in condition index all but one of the 43 August specimens from southwest Baffin Island and were expected to lose much more blubber before the summer season. In northern Foxe Basin the seals were not common on the ice until late June and early July and, with the late departure of the ice in that area, were common on the ice throughout July. The condition index of the population continued to drop during this period, being 82.1 in the first half of July and 78.8 in the first half of August. The southwest Baffin Island seals, which had probably resumed feeding somewhat earlier, were slightly fatter than the Foxe Basin seals in mid-August. The curve of Figure 8 shows that blubber thickness increases throughout the summer and fall and probably reaches winter condition around the time for freezeup. The northern Foxe Basin specimens best show this trend in late August and early September.

Thus Figure 8 does not adequately express the blubber changes of an individual seal. In brief, a seal probably maintains a high condition index through the winter, undergoes a gradual decline in blubber thickness through the early spring, and loses condition more rapidly during the intensive basking and fasting period of late spring. The blubber increases with resumed feeding in the early summer until a maximum thickness may be reached in the late fall.

The specific gravity of a seal is lowest when the blubber is thickest, and the percentage of sinking seals is greatest immediately after the fast, when the seals are thin. Table III gives the percentages of sinking seals, in two week intervals, for the period of July to the end of September in southwest Baffin Island. Many seals, hunted from rowboat, whaleboat or schooner are retrieved at the last possible moment; the table cannot account for these potential sinkers, nor for variations in the harpooners' abilities. The hunters are much more diligent when the seals are most likely to sink and these factors have an effect on the proportions retrieved.

There may be differences in the feeding activity of inshore and offshore seals of southwest Baffin Island. Thus, 9 out of 40 seals killed in inshore waters after July 15 had empty stomachs whilst all but one of 57 killed during the same period in the offshore waters southeast of Cape Dorset (Fig. 5, insert) had been feeding. Inshore stomachs were also inclined to be less full, whereas those from the offshore area were almost always crammed with *Themisto*. This does not necessarily imply that inshore animals were experiencing sub-optimal feeding conditions. *Themisto* probably offers less food, weight for weight, than do fish and perhaps decapods, for the intestinal contents of offshore seals often contain much indigestable exoskeletal material; the faeces of fish-eating seals are considerably more liquid and further digested. It is possible that the intensity of feeding is dependent on the nature of the food, and seals eating *Themisto*, or other plankton, must apply themselves more diligently to feeding.

TABLE III. Seasonal sinking percentages of offshore *Phoca hispida* in southwest Baffin Island in 1953 and 1954.

	July 1-15	July 15-31	Aug. 1-15	Aug. 15-31	Sept. 1-15	Sept. 15-30
Killed	15	1	24	34	23	32
Sank	9	1	4	5	1	1
Percentage sinking	60	....	16.6	14.7	4.4	3.1

There is no evidence of poorer condition of inshore seals in the Cape Dorset area in August, and seals taken from the fast ice in the period of March to late May were certainly not more undernourished than those taken offshore during the same period. Nevertheless, seals living deep within the archipelago to the east of Cape Dorset in September may have been in poorer condition than those living in offshore waters at the same time. From September 6 to 9, 1954, the author accompanied some Eskimos on trips within this region, some 20 to 30 miles from the open sea. Fifteen seals were killed here, but only five were retrieved. This loss is much larger than that found near Cape Dorset in August and early September (66.7% as opposed to 12.4%; the standard error of the difference in percentage is 11.4% and the chance that these were random samples from the same population is less than 0.006 in 100). The flotation of a seal is delicately balanced and it is clear that the fresher superficial water layer, resulting from the pouring of rivers into the coastal bays and lagoons, would not support the seals as well as the more saline and denser offshore waters. However, this is probably not the whole answer. The condition indices of 43 seals from near Cape Dorset in August ranged from 74.1 to 90.3, with a mean index of 81.8. Four seals from within the archipelago in early September ranged from 76.2 to 85.9 and had a mean condition index of 80.1. These means are not significantly different, but since the seal with the lowest index from the deep-inshore waters was actually recovered from the bottom, the ten which were not recovered may have been as thin as or thinner than this seal. This may indicate that the seals inhabiting deeply indented coasts are thinner than offshore seals at the same time. It has been pointed out in the last paragraph that it cannot be presumed that there is a shortage of available food in the inshore waters. However, it is possible that the long duration of ice in these deeply indented coasts results in a more prolonged period of spring and early summer fasting among the resident seals, and this will be reflected in a greater lag in the return to floating condition after feeding has been resumed.

In 1955, according to A. H. Macpherson (personal communication), seals in the Cape Dorset area were sinking in unusually large numbers throughout the early summer. The spring season was unusually hot and the ice departed rather later than in 1954. It seems likely that the high sinking rate was caused by better conditions for spring basking, which resulted in a lower average index of condition in the summer seals.

THE MOULT

The moult in Pinnipedia is annual and always coincides with a period when the seals are able to haul out on the land or ice. Table IV summarizes the moulting season from observations made in southwest and northern Baffin Island and Southampton Island. The moulting season may extend from mid-May to mid-July, though the phenomenon is most marked in June. At this time the seals are able to take advantage of the basking season and the animals are observed to scratch and rub the moulting skin while lying in the hot sun. The Eskimos of southwest Baffin Island believe that hauling-out behaviour, in enabling the seal to free itself of the old hair and epidermis, is necessary for the completion of the moult, and their reasoning is as follows: they suppose that those seals in which the moulting process is prolonged throughout the summer months to the fall were unable to crawl out onto the ice during the basking season, perhaps because they were caught too far offshore in areas lacking suitable ice; but the evidence for their not having been able to come out onto the ice is in the protracted moult, and the argument is thus circular.

TABLE IV. Number, by weekly periods, of moulting *Phoca hispida* of southwest and northern Baffin Island and Southampton Island in 1954, 1955 and 1956.

Dates (inclusive)	Moulting	Not moulting	Percentage moulting
	No.	No.	%
May 1–7	....	3	0
May 8–14	....	2	0
May 15–21	1	9	10
May 22–28	....	3	0
May 29–June 4	8	5	62
June 5–11	8	12	40
June 12–18	6	4	60
June 19–25	6	2	75
June 26–July 2	3	5	38
July 3–9	1	....	....
July 10–16	1	4	20
July 17–23	....	5	0
July 24–30	....	3	0

When moulting seals are taken much later in the season, the condition is considered to be abnormal. Individuals in this state were taken on August 6 (southwest Baffin Island), September 1 (Southampton Island) and on October 8 and 28 (Foxe Basin). The September 1 and October 28 specimens were second year females, and were extremely small and delicate for seals of this age (81 and 79 cm. in length respectively, the average length of females in this age-group being about 93 cm.). The September 1 specimen, with an almost bare skin, is illustrated in Figure 9. Another abnormal animal, which was completely devoid of hair, was reported to have been killed in early September, 1954, in southwest Baffin Island, and Kumlien (1879) reports similar hairless seals in Cumberland Sound.

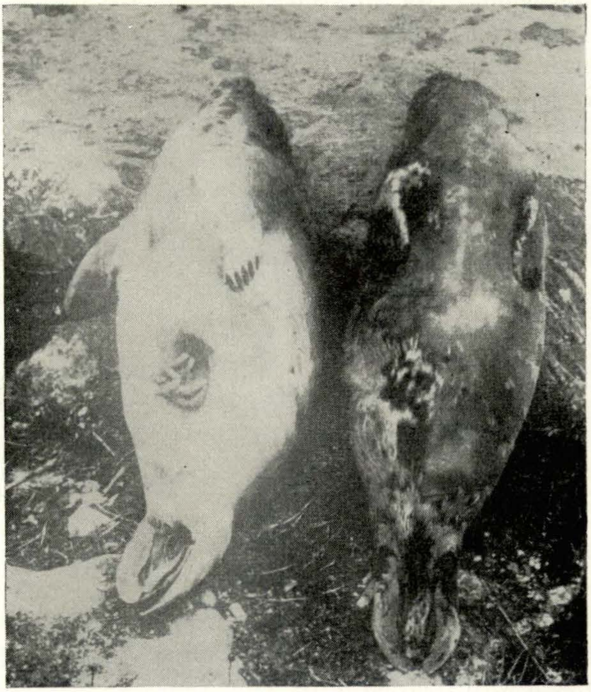

FIGURE 9. An abnormally late and complete moult on September 1. This unusual specimen, on the right, is compared with a non-moulting first-year seal. Note that very little hair remains, chiefly on the right flank, and that the new hair is very short.

REPRODUCTION

AGES AT SEXUAL MATURITY

Until the development of an accurate ageing technique, the question of age at sexual maturity for various pinnipeds could not be answered satisfactorily. Data on age at sexual maturity of the ringed seal are scarce and are based on general considerations, rather than on absolute ageing methods. Sleptsov (1943) assumes that maturity is reached after two years. Pedersen (1926) and Freuchen (1935) suggest that the ringed seal is not fully developed until the fifth year, although neither gives any direct evidence for this assumption. It is interesting to note that the latter two authors, both of whom lived with the Eskimos, give estimates which coincide with Eskimo conclusions on southwest Baffin Island and Foxe Basin (see page 8).

THE MALE. The advent of sexual maturity in the male may be considered to coincide with the appearance of spermia in the ejaculatory ducts for the first time. A large sample of seals taken during the breeding season would be required to fix the peak and range of age at sexual maturity, by this definition. Due to the difficulties of hunting at this season (March to mid-May), no such large sample could be obtained.

Two males of 5 years of age and all younger males lacked spermia in the ducts during the breeding season. Another 5-year-old seal on June 5 showed no evidence of having contained spermia (degenerate remains) in the past breeding season, and the epididymis of a 6-year-old on May 3 was aspermous. The youngest male taken with spermia in the epididymis was 7 years in age (SD-27, April 7, 1954).

Other criteria are useful in establishing age of sexual maturity in the male. As with all other mammals, adult seals have a larger testis than immature animals, even outside the breeding season (see Scheffer, 1950). Figure 10 indicates that an increase in testis size occurs during the seventh year and there is a corresponding increase in the diameters of the tubules in the testis and also the epididymis (Table V). Apparently there is an increase of sexual activity during the breeding season in immature males as well as in adults and this results in the wide range of histological appearance and tubule size, as demonstrated in the Table. Spermatids were detected in the one fifth-year seal shortly after the breeding season. All sixth and seventh-year testes bore spermatids, and small numbers of spermia were found in the testis, but not in the epididymis, of a sixth-year seal in early June.

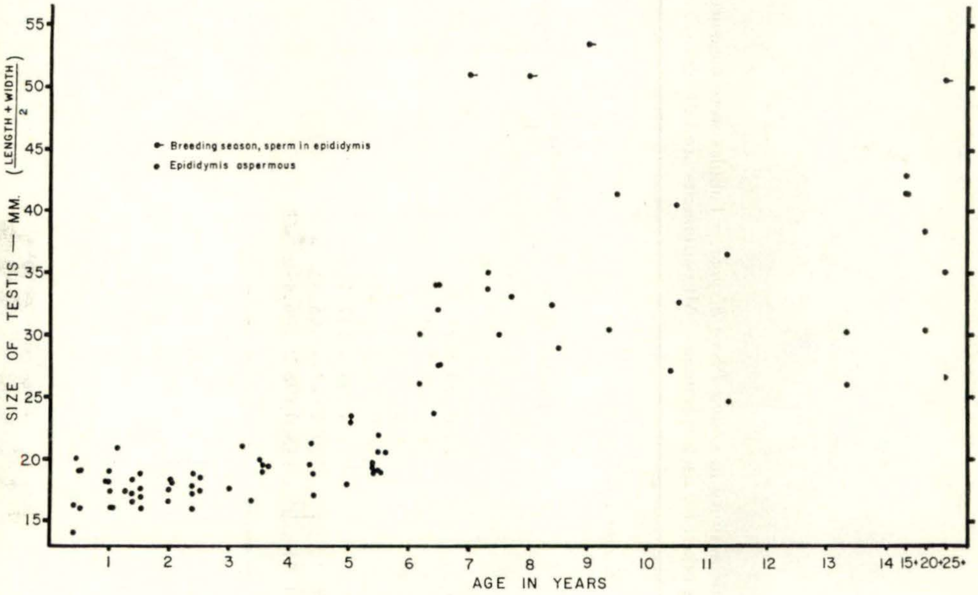

FIGURE 10. Growth of the testis of *Phoca hispida*.

TABLE V. Tubule diameter and spermatogenetic activity in young *Phoca hispida*. Tubules were measured from the basement membranes across the narrowest diameter; the mean of 25 tubules was taken for each specimen. Measurements are in microns and the ranges are bracketed after the means.

Age group	Number of specimens	Diameter of tubules		Spermatogenetic stages			
		Testis	Epididymis	Spermatogonia only	Spermatocytes	Spermatids	Spermia
0–1	5	52.8 (45.1–66.2)	72.0 (59.5–87.4)	1	4	....	....
1–2	2	49.8 (45.8–53.8)	58.5 (55.7–61.2)	1	1	....	....
2–3	2	48.2 (43.6–52.8)	51.9 (51.2–52.5)	1	1	....	....
3–4	4	55.4 (47.0–63.0)	74.9 (58.2–91.5)	....	4	....	....
4–5	4	69.1 (68.2–70.1)	101.4 (66.6–157.1)	....	4	1	....
5–6	6	76.8 (58.9–126.1)	100.2 (65.3–165.4)	....	6	2	1
6–7	4	109.1 (98.9–121.6)	145.0 (98.2–206.4)	....	4	4	....

Both baculum length and baculum weight (Fig. 11, 12) show a steep rise in the seventh year, though the increase may begin before the seal is 6 years old. Growth appears to level off during the eighth year. The baculum continues to grow throughout the life of the seal, but most of the weight increase appears to result from increase of thickness, and perhaps density, of the bone.

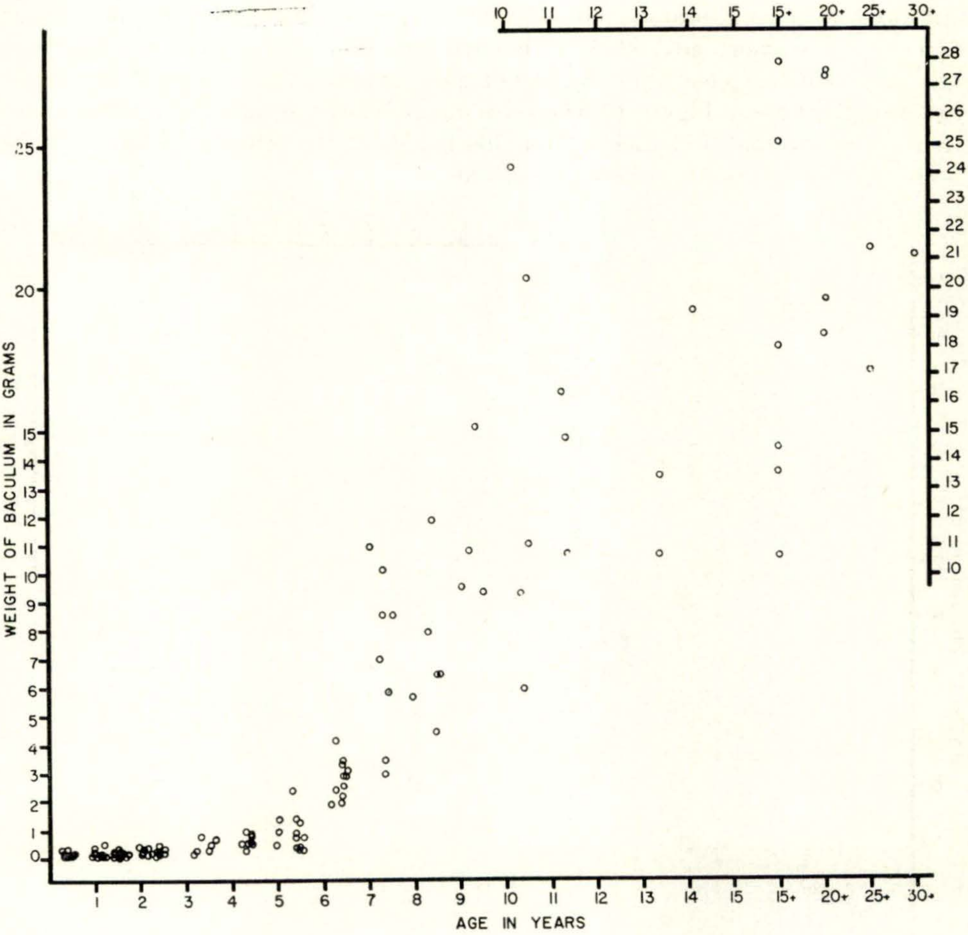

FIGURE 11. Increase in weight of the baculum with age in *Phoca hispida*.

During the breeding season, the adult male is peculiarly malodorous. Such seals are referred to as *tiggak* by the Eskimos, and the youngest seal recorded in this class proved to be 7 years old. It is also of interest to note that two seals of the early sixth year were the oldest taken outside the limit of fast ice of southwest Baffin Island in the winter and early spring. Residence in the fast ice is a response to breeding urges (see page 38), and this is probably analogous to the incomplete representation of the immature harp seals in the southward breeding migration (see Fisher, 1954a).

All these features suggest that, on the average, the male ringed seal is capable of breeding for the first time when about 7 years of age, though some seals may mature a year earlier. Thus, of 2 seals (SD-106 and 107), both 6 years and about 2 months in age, one had larger testes and these were associated with a baculum of almost twice the weight of the other. The epididymis of the smaller testis was empty except for cellular detritus, whilst the other epididymis contained what appeared to be small numbers of degenerate spermia, together with the cellular detritus. The more advanced of the two individuals may thus have been in breeding condition when about 6 years of age. It is also probable that some seals, for example those in Figure 12 whose bacula are closer to the 7th-year size-mean than to the size-mean of their companion bacula of the 8th year, may not have been capable of breeding when 7 years old.

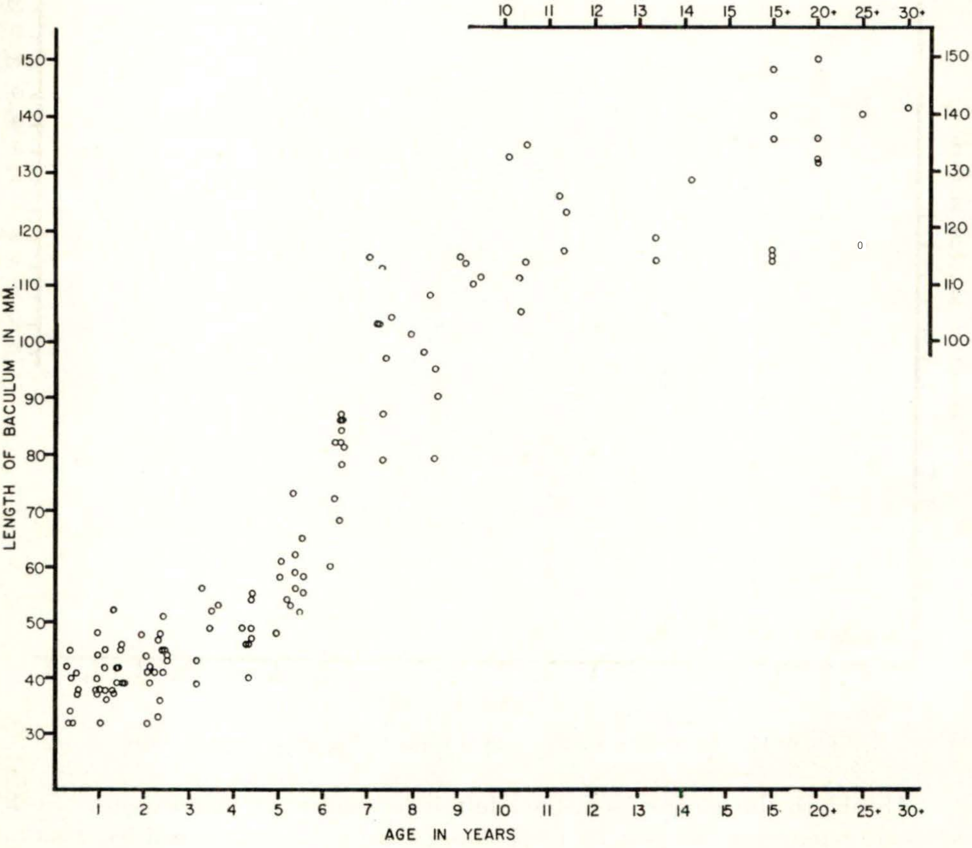

FIGURE 12. Increase in length of the baculum with age of *Phoca hispida*.

Fisher (1954a) found an average maturation at 8 years in the harp seal male. However, spermia were found in the testes, although not in the ejaculatory ducts, of harp seals as young as 4 years old, and on this basis Fisher considered seals of 4 to 7 years old to represent a class of adolescents. In the ringed seal, a very few spermia were found in only one of the 6 breeding-season testes from the age-group 4 to 6+ years (A-15, 5 years and 2 months old); thus, the adolescent class is not well defined.

THE FEMALE. The age at maturity of the female may be defined as the age when ovulation first occurs. Productive maturity, the age when the female is first capable of conceiving, may or may not coincide with the age of first ovulation. Ovulation may be detected, after its occurrence, by the development of the corpus luteum at the site of ovulation. In many mammals, especially in pinnipeds, the corpus luteum regresses to a fibrous scar, the corpus albicans, which may persist for some time after parturition. If these scars were retained throughout the life of the seal, they would be of great value, in conjunction with the known age of the seal, in determining the ages of first ovulation. Bertram (1940), assuming them to be permanent, attempted to use corpora albicantia for age determination of the Weddell seal (*Leptonychotes weddelli*), but the assumption has been found to be unsound for this species (Mansfield, in press). Laws (1953b) suggests that corpora lutea of missed pregnancies in the elephant seal do not result in persistant corpora albicantia as do those of completed pregnancies. Thus there are limits to the value of the corpora albicantia in determining ovulation history.

Macroscopically visible follicles were first noted in one of the 8 fourth-year seals examined. All but 2 of the 10 fifth-year animals showed follicles. Five of the 7 sixth-year ovary pairs and all ovaries from older seals were folliculating.

The youngest seal with a corpus luteum was a fifth-year animal taken in northern Baffin Island between September 9 and 14. The corpus luteum was very small and showed definite signs of regression; at this late date an embryo should have been apparent. Another small corpus luteum was observed in a nulliparous 5-year-old taken on March 25, in southwest Baffin Island. The gland showed some vascular intrusion and was not of recent ovulation. This seal was large and measurements of its reproductive tract indicated that it was considerably advanced sexually beyond 7 other seals of its age-class. It may be concluded that these fifth-year seals were pseudopregnant[2], the corpora lutea reflecting neither pregnancy in the former animal, nor recent parturition in the latter.

Two out of 7 sixth-year females had ovulated. One, killed on August 24 in southwest Baffin Island, had a less well-developed reproductive tract than the 5-year-old described above. The left ovary contained a small corpus luteum, in which connective tissue was found to be replacing the luteal elements, and the seal was undoubtedly pseudopregnant. The other specimen, a nulliparous female with a well-developed tract, was killed on July 26. The corpus luteum was large, and appeared quite functional. This seal might well have been pregnant, but an unimplanted blastocyst would have been difficult to detect at this time.

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[2] This term is used here and later to describe several possible types of ovulation without fertilization. Although the corpus luteum in the ringed seal is retained for some time, there are not the associated changes in the reproductive tract which are found in pseudopregnancy of some mammals.

Nine of the seventh-year seals had ovulated and showed corpora lutea. Five of these seals were pregnant and the other 4 were taken at a time when the embryos might not have been apparent. One seal had a normal corpus luteum, measuring 9 by 10 mm. in section on June 18, and another killed on August 9 had a substantial corpus luteum of 10 by 13 mm. and probably contained an unimplanted blastocyst. The other 2 seals, killed on August 6 and 21, had corpora lutea of 8.5 by 8.5 mm. and 8.5 by 9 mm. respectively. The average size of 6 other pre-implantation corpora lutea in August was 10.7 by 12.3 mm., the smallest being 9 by 12 mm. in section. It is probable that the smaller corpora lutea were not supporting blastocysts, though these would be very difficult to detect in the preserved material. Two seventh-year females had not ovulated.

All 7 seals in the eighth-year group had ovulated and 2 contained foetuses. One seal taken on August 6 had a quite large (10 × 12.5 mm.) corpus luteum and was probably pregnant. An attempt was made to locate a blastocyst in the cornu of a female taken on August 25 (corpus luteum 11 × 11.5 mm., and probably pregnant) with no result, but this does not invalidate the assumption that the normal-appearing corpus luteum reflected pregnancy. Three other eighth-year females were taken in September and early October, long after the normal time of implantation of the blastocyst. Their corpora lutea were small (7 × 7 to 9 × 9 mm.); two resembled those of pre-implantation seals and the other was regressing, with development of connective tissue and vascular intrusion. These three seals would not be expected to produce young in the following pupping season.

The development of the corpus luteum will be dealt with in a later section. The above discussion is necessary for a consideration of the ages of sexual maturity, here defined as age of first ovulation, in the female.

Table VI summarizes the ages of first ovulation in the female, based on counts of corpora lutea and corpora albicantia. It is assumed, for example, that a female in the tenth year with one corpus luteum and four albicantia will have ovulated for the first time in age-group 5–6; a female in her ninth year, with one luteum and one albicans, will have ovulated for the first time in age-group 7–8. The ovaries of 35 seals younger than three years old were examined in the field or laboratory, but since none of these had ovulated, they are not included in the Table. Laws (1953b) suggests that corpora lutea are absorbed within a year in most elephant seals, while Fisher (1954a) found that a balance between addition and loss of corpora albicantia develops after ten years of life in the average female harp seal. Figure 13 suggests that the latter phenomenon holds true in the ringed seal and Table VI is thus limited to the fourth to tenth-year age-groups. A discrepancy is found between the percentage of mature seals within each age-group (second column from the right of Table VI) and the percentage ovulating for the first time in each age-group (lower line of Table). The latter percentages, based on the assumption that corpora albicantia of the first ovulation are retained up to the tenth year, are derived from greater population samples. But, since no evidence of first ovulation in the age-group 4–5 is found in the higher age-

TABLE VI. Summary of deductions on ages of first ovulation in *Phoca hispida* from counts of corpora lutea and corpora albicantia. Explanation in the text.

Age-group	Number of specimens	Number ovulating for the first time in age-group							Percentage mature	Percentage mature (adjusted)
		3–4	4–5	5–6	6–7	7–8	8–9	9–10		
									%	%
Fourth year	8	....	....	....	....	....	....	....	0	0
Fifth year	10	....	2	....	....	....	....	....	20	12
Sixth year	7	....	....	2	....	....	....	....	28	22
Seventh year	11	....	..	2	7	....	....	....	81	78
Eighth year	7	....	....	....	5	2	....	....	100	100
Ninth year	5	....	....	1	1	3	....	....	100	100
Tenth year	3	....	....	1	2	....	....	....	100	100
Totals	51	....	2	6	15	5	....	....		
Numbers of specimens in age-groups 3–10, 4–10, 5–10, etc.		51	43	33	26	15	8	3		
Percentage ovulating for first time in age-groups 3–4, 4–5, etc.		0.0	4.7	17.9	57.7	33.3	0.0	0.0		

groups, the assumption that *all* albicantia are retained until the tenth year may well be invalid. It is quite possible that the smaller corpora lutea of pseudopregnancy, described above, are not retained for long, and this is supported by Laws (1953b), who suggests that those of missed pregnancies are not retained at all in the elephant seal. It is felt that a closer approximation of the true picture may be gained by assuming that a given ovulation is apparent until at least the end of the following year (one year after parturition, if this occurs), but that it may or may not be apparent after this time. Thus, limiting the ovulation history of each age-group to the end of the following year, the adjusted percentages of the last column of Table VI are derived. For example, of 7 seals in the sixth year, 2 had ovulated; of 11 seals in the seventh year, 2 showed a single corpus albicans each, and had thus ovulated in the previous year, in age-group 5–6. Thus of 18 seals in the sixth *and* seventh year age-groups, 4 or 22.2%,were mature in the sixth year.

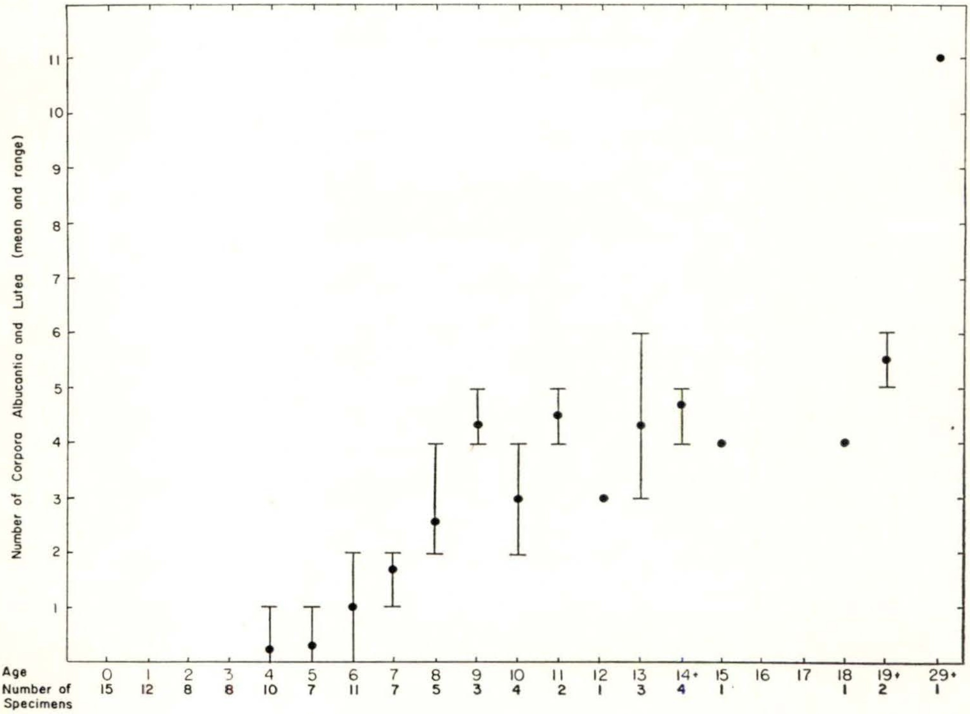


FIGURE 13. The relationship between number of corpora lutea and corpora albicantia, and the age of the female of *Phoca hispida*.

It appears that the left ovary is generally the first to ovulate, for of 13 first corpora lutea, 9 were produced in the left ovary, and if the evidence from corpora albicantia of seals younger than 10 years old is included, then 18 out of 26 first ovulations were in the left ovary. H. D. Fisher (personal communication) found that early collections of harp seal ovaries revealed the same tendency for first ovulation in the left ovary; however, this pattern was not found in later and larger samples. It may be that the phenomenon is due to small samples, but Laws (1956b) found very good evidence that one ovary, in this case the right, tends to ovulate first in the elephant seal.

Fisher (1954a) found fertilization to be 80% successful in mature female harp seals. In the ringed seal, it appears that corpora lutea are not as likely to indicate pregnancy in young seals as in older seals. The virgin uterine cornu is distinctive in its lack of folding and rugosity and is not vascularized as much as are cornua which have been pregnant. Table VII shows the percentages of virgin females in the younger year-classes. Virgin cornua were identified by the criteria mentioned above. Presence of embryos, or of corpora lutea which appeared normal for the pre-implantation period, were taken to indicate contemporary pregnancy. Absence of corpora lutea, or presence of regressing or abnormally small corpora lutea, were taken to reflect absence of an embryo. In order to increase the samples determining the percentages of virgin females, it may be assumed that seals of one age-group show the history of the previous age-groups, at least up to the level of one previous pregnancy. Thus, 7 out of the 11 seals in age-group 6–7 were pregnant, and 2 out of the 7 seals in the age-group 7–8 exhibited one previous pregnancy and were therefore pregnant in the age-group 6–7. This means that 9 out of 18, or 50%, of seals in these age-groups were virgin in the age-group 6–7. The results of this adjustment are shown on the lower line of Table VII and are probably as close to the real picture as the size of the sample will permit.

TABLE VII. Virginity in young and newly matured *Phoca hispida*. Explanation in the text.

	Age Group				
	4–5	5–6	6–7	7–8	8–9
Number of specimens	10	6	11	7	5
Virgin	10	6	4	3	
Contemporary pregnancy only	....	....	5	2	
One previous pregnancy	....	....	2	2	1
One or more previous pregnancies	....	....	....	....	4
Percentage virgin in each age-group	100	100	36	43	0
Adjusted percentage virgin	100	92	50	25	0

The approach toward maturity in the fifth to eighth year in the female is accompanied by an increase in the size of the genitalia, which is demonstrated in Table VIII. Only tracts from nulliparous females are included, since the cornua are considerably distorted after pregnancy. A series of measurements from 31 older seals show that adult ovary size is reached by the seventh or eighth year; these ovaries averaged 26.1 mm. in length (range, 17–39) and 13.3 mm. in width (range, 10–19).

TABLE VIII. Growth of the virgin female reproductive tract of *Phoca hispida*. Lengths of cornua are measured externally from the junction of cornua to the beginning of the fallopian tube. Average widths are derived from the mean of maximum and minimum widths. Measurements are in millimetres and the ranges are bracketed after the means.

Age-group	Ovaries			Cornua		
	Number of specimens	Length	Average width	Number of specimens	Length	Average width
		mm.	*mm.*		*mm.*	*mm.*
First year.........	7	16.7 (14–18)	7.4 (5–10.5)	6	38.3 (27–57)	3.3 (3–4)
Second year.......	6	18.7 (15.5–25)	7.5 (6–8.5)	5	47.4 (35–53)	3.6 (3–4)
Third year........	4	18.1 (12.5–25)	7.8 (6–10.5)	3	53.3 (36–71)	3.6 (3.25–4)
Fourth year.......	6	17.0 (15–19)	6.9 (5.5–8)	4	58.8 (44–72)	3.8 (3.5–4)
Fifth year.........	8	19.9 (16–27)	8.2 (6–13)	4	67.0 (60–73)	5.8 (5–8)
Sixth year.........	6	19.9 (17–25.5)	8.8 (6.5–11)	5	71.4 (58–81)	5.3 (4–7)
Seventh year......	6	23.8 (18–28)	11.9 (8.5–15)	5	75.1 (70–87)	10.3 (9.5–12)
Eighth year.......	5	24.2 (17–28)	12.7 (10–19)	4	76.9 (63–88)	8.8 (6–10.5)

There was one senile female aged 35 or more years. No folliculation was detected and each ovary was a mass of scar tissue. At least 11 corpora albicantia stood out distinctly (Fig. 13).

THE BREEDING SEASON AND THE ANNUAL SEXUAL CYCLE

THE MATING SEASON. The literature dealing with the ringed seal has little to offer on the subject of the timing of the pairing season. Freuchen (1935) considered that mating occurred shortly after the break-up of the winter ice. Pedersen (1930) suggests that younger females are impregnated first and that copulation takes place from the beginning of May until the end of June. Neither author mentions actual observations of the mating act and neither offers any anatomical evidence for his conclusions. Sleptsov (1943) was probably the first to approach the problem from an anatomical point of view. He concludes that pairing of the Okhotsk Sea *Phoca hispida* occurs in late July through August. The validity of Sleptsov's results will be discussed later in this section.

The only sound methods of establishing the breeding seasons of animals whose mating activities are difficult to observe are histological examination of the testes and sperm ducts and determination of the time of ovulation in the female. Several assumptions on the timing of seal breeding seasons, even when supported by accounts of apparent mating activity, have been proved false by critical anatomical studies (see Fisher, 1954b, on the harbour seal).

A high level of spermatogenesis and, more specifically, presence of spermia in the epididymis, are the sure indications of sexual activity in the male. Eleven adult males fulfilling both these conditions were taken during the period of March 23 to May 15.

The epididymides of 12 adult males taken between May 19 and June 30 were all aspermous, though one on May 22 contained a very few scattered spermia in some tubules. Most contained varying concentrations of cellular detritus, sloughed spermatogenetic cells, consisting mostly of spermatids, and what appeared to be degenerate spermia. Most summer and fall epididymides contained such detritus and sloughed cells.

Spermatogenetic activity declined after mid-May. Spermia were found in only 9 out of 100 testis tubules of a specimen killed on May 24. No spermia were noted in the testes of males taken on May 27 and May 28 and of 2 killed on June 7, although 3 testes taken on May 19, May 22 and June 7 were still quite active, with spermia present in most tubules. No spermatogenetic stages beyond spermatids were detected in the testes of 5 adults killed between June 16 and June 30. Spermatids were present in varying numbers in all testes from later dates.

Although the majority of males are sexually quiescent during the summer and fall seasons, 2 specimens from Foxe Basin disturb the pattern somewhat. Spermia were present in many of the testis tubules of one killed on August 28, 1956, although the epididymis was aspermous. Both testis and epididymis of another killed on October 10, 1955, contained spermia. Sixteen tubules out of 200 in the section of epididymis contained spermia and 5 of these, which were grouped and possibly represented a single convoluted tubule, were packed full. Both seals were very large, one being the largest and the other the fourth largest in size of males taken during the entire study. Their testes were also among the largest secured in this season. The significance of these active males is not known. They may be quite abnormal and cannot be considered to represent the general fertility of the male population in the summer and fall seasons. An adult from northern Baffin Island on December 19, 1954, was sexually inactive and stages only up to spermatids were represented. Two adult males from Foxe Basin in late February, 1956, less than one month before the date when an active male was taken in southwest Baffin Island, showed considerable activity in the testes, but spermia were not present in the epididymis.

Table IX summarizes the spermatogenetic activity of all adults, 7 or more years in age, as observed from histological sections. Photomicrographs of a selected series of these sections are displayed in Figure 15.

The size of a testis is governed by its internal activity. Breeding season testes are swollen and compact, while those of males taken outside this season are smaller and more flaccid. These differences are due in most part, or entirely, to the increase and decrease of the diameters of the testis tubules, as shown in Table IX. The average tubule diameter in the August 14 to October 10 specimens is 70.5% of the average diameter in the March 23 to May 15 group. This difference is highly significant ($P<0.01$) and this has also been demonstrated in changes in the epididymis tubules. Mean external measurements of the testis show that the average size in the period of August to October is only 67% of the size from March to May. These measurements reflect the size of the enclosed tubules within a few per cent, though regression of the interstitial elements between the tubules may contribute slightly to a decrease in testis size. Harrison *et al.* (1952) and Laws (1956b) found a similar cycle of tubule size in antarctic seals.

TABLE IX. Seasonal spermatogenetic activity and tubule diameters of adult testes and epididymides of *Phoca hispida*. Tubules were measured from the basement membranes across the narrowest diameter; the mean of 25 tubules was taken for each specimen. Measurements are given in microns and ranges are bracketed after the means.

Dates (inclusive)	Number of specimens	Spermia in testis	Spermia in epididymis	Diameter testis tubules	Diameter epididymis tubules
	No.	*No.*	*No.*	*microns*	*microns*
March 23-April 30......	7	7	7	154.6 (126.1–178.3)	224 (180.8–272.0)
May 8-28..............	9[a]	7	4	146.9 (130.6–168.3)	216.6 (178.9–256.6)
June 7-30..............	8	1	0	119.4 (102.7–147.5)	186.9 (128.3–249.6)
August 14-24...........	7	1	0	113.9 (90.9–153.3)	146.6 (121.6–185.6)
September 8-29.........	2	0	0	102.7 (99.5–105.9)	139.2 (137.9–140.5)
October 2-10...........	5	1	1	104.6 (79.4–144.0)	125.4 (113.9–139.5)
December 19...........	1	0	0	91.8	123.2
February 27-28.........	2	2	0	142.4 (113.3–171.5)	194.0 (143.7–244.3)

[a] Measurements taken on only 6 of these, due to poor preservation.

Figure 14 shows the annual cycle of testis size in scatter-diagram form. The eye-fitted curve gives an indication of the period of testis activity, the peak occurring shortly after mid-April. As will be pointed out below, pups are probably produced in greatest numbers near the beginning of April; thus impregnation might be expected to occur, on the average, about two weeks after parturition.

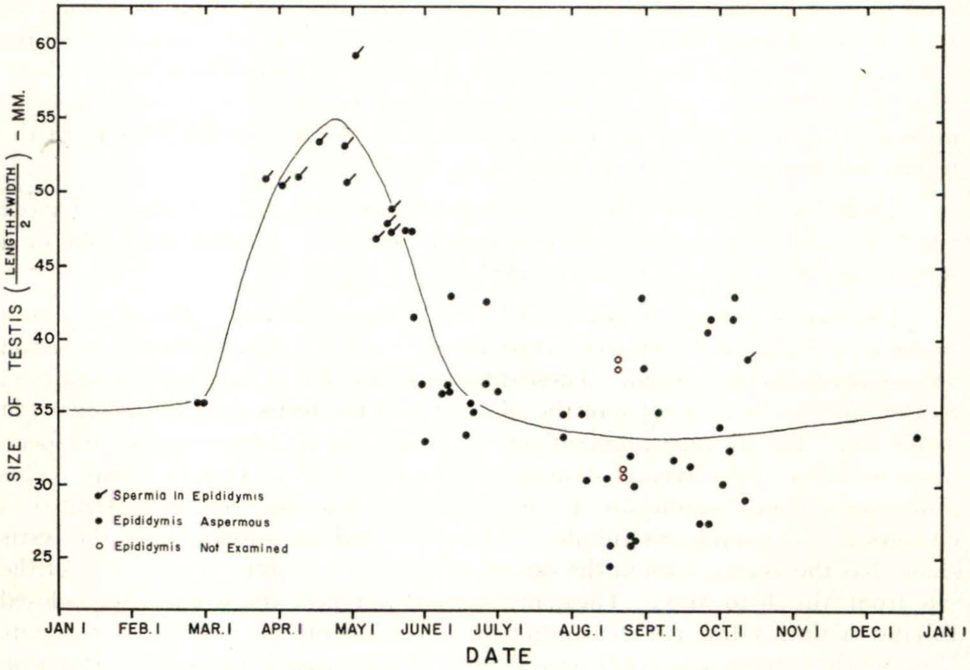


FIGURE 14. The seasonal variation in testis size in *Phoca hispida*.

Adult males taken in this early spring season have a peculiar musky odour. This is probably of sexual significance and is further field-evidence for the occurrence of the breeding season at this time.

In the central and western Canadian arctic, the ringed seal is commonly taken at its breathing holes. This technique is less often practiced in the eastern arctic, where hunting at the limit of fast ice, or at tide-rips, proves more profitable. The adult female is rarely taken by the native hunter after the beginning of March, until the season of basking on the spring ice. A few females are taken in the fast ice by lowering a firmly secured white-coat seal through the exit of its birth-cave, where it acts as a bait to lure the mother within striking distance of the harpoon. In the hope of determining the state of folliculation and ovulation before the females had weaned their pups, the author entrusted a native with materials for preserving the reproductive tract of a female with pup. Such a tract, well preserved and accompanied by the jaws of the female and pup, was brought to the author in August. It had been taken in mid-April. The right ovary contained the corpus luteum of the previous pregnancy, which, in fact, consisted largely of connective tissue with a few islands of luteal tissue. The opposite ovary contained a new, completely formed corpus luteum, though somewhat smaller than maximum size; it was probably more than one week old, by the criteria used in Fisher's harp seal study (1954a). Three lactating females taken on May 15, May 17 and May 20 all contained fully regressed corpora lutea of previous pregnancy (i.e., corpora albicantia) and new corpora lutea of pregnancy. Thus, the evidence indicates that the male is in full breeding condition before the peak of the pupping season and that the post-parturient female ovulates before the termination of lactation. It is suggested that the peak of mating comes shortly after the peak of pupping, perhaps in mid-April. Among other Phocidae, the harp seal and the harbour seal (Fisher, 1954a, 1954b), and the Weddell seal (Mansfield, in press) probably ovulate shortly after weaning; the elephant seal comes into oestrus during lactation (Laws, 1956b). Of the Otaridae, the Cape fur seal (*Arctocephalus pusillus*) ovulates about six days after parturition, during lactation (Rand, 1954). Post-partum female harp seals do not establish much contact with the male population until the abandonment of the young, and timing of ovulation is linked with this fact. In the case of the ringed seal, the adult males, which become increasingly potent as the season progresses, and the pregnant adult females live together under the fast ice throughout the winter. Here again, the timing of ovulation with respect to parturition seems to insure a high reproductive success. Pedersen's (1930) suggestion, that young females are impregnated first, may have some basis in fact, when it is considered that nonpregnant females would be the first available to the sexually active males.

Sleptsov (1943) gives a quite different picture of the breeding season in the Okhotsk Sea *Phoca hispida*. His material was collected by a pelagic sealing expedition, between May 11 and October 20, 1939. He states that the onset of ovulation occurs in late June and early July. The probability that the adult seals would not be found outside the fast ice before break-up suggests that this conclusion may be the result of sampling error, due to the absence of adult females in the catch before late June. His conclusions on spermatogenesis in the male are apparently based on field observations of exudate in the spermatic ducts, and not on histological examination. The former approach may be very misleading, for a milky exudate of cellular detritus and degenerate spermia may be present after the breeding season. Sleptsov's whole thesis is a refusal to acknowledge delayed implantation of the blastocyst, which had been suggested by several workers to occur in seals of other Russian waters. In the author's opinion, further work on the Okhotsk Sea pinnipeds will reveal inadequacies in Sleptsov's results.

THE FOLLICULAR CYCLE AND OVULATION. Hamilton (1939), Bertram (1940) and Fisher (1954a) have all commented on the primary importance of the male pinnipeds in determining the timing of the breeding season. In the several species which have been studied, the peak of testicular activity has been seasonally very precise.

One effect of the developing corpus luteum is in the suppression and control of folliculation in some species of seals. Harrison *et al.* (1952) suggest that there are two periods of follicular stimulation in the seals which they studied. The first, in the ovary with the corpus luteum, extends from probably a week after implantation of the blastocyst until the embryo is about 50 mm. in length, and the second occurs in late pregnancy, in the ovary without the corpus luteum, and continues throughout the remainder of gestation, during parturition and until ovulation. Laws (1956b), in his more representative study of the elephant seal, found a more complicated picture of follicular activity. In this species there is a stimulation of folliculation in the ovary destined to release an ovum just before parturition, and there is a period after ovulation in which follicles of both ovaries increase in size and number. After this latter period, a progressive decline is demonstrated in number and size of follicles until implantation occurs, after which there is again an increase in follicular activity, corresponding to the increase found by Harrison at this time. Folliculation is suppressed after the embryo reaches 3–4 cm. in length and this suppression is probably maintained throughout the remainder of gestation. A number of ringed seals are available from the period of pre-implantation and early pregnancy, and examination of the ovaries shows no evidence of very strong follicular stimulation in this period. Table X does suggest that folliculation is suppressed in the ovary containing the corpus luteum from some time in late pregnancy until after parturition, for no follicles of over 3 mm. were detected in the ovary of the post-parturient cornu of a female taken in mid-April. However the opposite ovary, containing the new corpus luteum of pregnancy, was very active and included one 10 mm. follicle. Other ovaries collected on May 15, 17, and 20 did not show marked suppression in the ovaries without corpora lutea. There is a slight increase during early pregnancy in the average number of follicles of ovaries without corpora lutea, and a slight decrease in ovaries with corpora lutea, but the range of variation implies that the changes are not invariable.

TABLE X. Summary of seasonal follicular and corpus luteum development in adult female *Phoca hispida*. (Ranges are bracketed below mean values.)

Time of year and status of pregnancy	Number of specimens	Ovary with Corpus Luteum				Ovary without Corpus Luteum				Diameters of corpus luteum in section
		Numbers of follicles			Largest follicle	Numbers of follicles			Largest follicle	
		3 mm.	3–5 mm.	5 mm.		3 mm.	3–5 mm.	5 mm.		
	No.	*No.*	*No.*	*No.*	*mm.*	*No.*	*No.*	*No.*	*mm.*	*mm.*
Mid-April: attending young	1	4	1	5	10	6	0	0	2.5	10.0 × 8.5
May 15-20: one or more months after breeding season	3	7.7	7.4	3.7	5.7	8.4	8.4	0.7	5.2	11.0 × 8.8
		(2–17)	(5–9)	(3–4)	(5.5–6)	(1–14)	(5–12)	(0–2)	(4.5–6)	(9–13 × 7.5–11)
June 8-15: about two months after breeding season.	4	12.8	5.5	2.0	4.9	5.8	1.8	0.8	4.3	11.0 × 9.6
		(8–17)	(0–8)	(0–5)	(2–7.5)	(3–8)	(0–3)	(0–1)	(1–6)	(10–12 × 9–10)
June 18-26: two or more months after breeding season	6	5.5	6.5	3.7	6.8	4.8	3.0	0.7	4.4	11.2 × 8.8
		(3–7)	(2–16)	(1–11)	(5.5–8)	(3–7)	(0–5)	(0–1)	(1–7)	(10–13 × 7–11)
July 20-31: three plus months after breeding season	3	8.0	5.0	1.0	5.5	5.9	2.7	0.3	4.2	10.8 × 8.8
		(7–9)	(3–6)	(0–3)	(3.5–8)	(3–7)	(1–5)	(0–1)	(3.5–5)	(10.5–11 × 8–10.5)
Aug. 6-25: no embryo found, but probably pre-implantation	6	4.4	2.5	1.8	6.5	6.5	5.2	2.0	5.6	12.3 × 10.7
		(3–5)	(0–5)	(0–6)	(0–6)	(5–9)	(3–8)	(0–5)	(3.5–7)	(11–14 × 9–13)
Aug. 16-24: embryo less than 25 mm. long	8	5.0	2.4	0.9	5.8	6.4	5.5	1.6	6.1	11.5 × 9.3
		(1–14)	(1–8)	(0–3)	(4–8)	(2–17)	(1–14)	(1–3)	(4–8)	(10–14.5 × 8–10)
Aug. 24-Sep. 27: embryo 28-42 mm. long	9	6.7	4.2	1.3	5.3	10.5	2.8	1.0	5.1	12.2 × 10.9
		(2–15)	(0–9)	(0–4)	(3.5–7)	(5–48)	(0–7)	(0–4)	(3–9)	(11–14 × 10–12)
Sep. 9-Oct. 7: embryo 63-110 mm. long	11	9.0	5.7	1.9	5.8	6.8	7.3	2.6	6.4	12.7 × 10.8
		(2–24)	(1–10)	(0–6)	(5–7)	(4–15)	(2–11)	(0–7)	(5–8)	(10–14 × 9–13.5)
Aug. 6-Oct. 9. virgins with small corpora lutea in various stages and probably pseudopregnant	7	8.3	2.3	0.4	3.6	10.0	1.4	1.1	3.4	7.8 × 7.4
		(3–16)	(0–9)	(0–2)	(1–6)	(2–22)	(0–6)	(0–6)	(1–7)	(5–9 × 4–9)
Sep. 9-14: missed pregnancy, corpus luteum regressing	1	14	2	0	3.5	26	0	0	2.5	12.0 × 10.0
Oct. 4: no corpus luteum, but with large follicle, probably about to ovulate	1	4	0	1	8.5	0	0	0	....	....
March 25: virgin with regressing corpus luteum	1	4	5	2	7.5	12	4	2	9.0	8.5 × 5.0

The control of folliculation around the time of ovulation tends to impart an alternation of pregnancy between right and left uterine cornua. The unbalance of corpora albicantia in some ovary pairs (e.g.: S-4, 3 to 1; S-27, 4 to 1; SD-528, 4 to 1) suggests that alternation does not always occur. It may be that presence of an embryo most effectively suppresses ovulation in the ovary of the pregnant cornu. Thus the female SD-58, taken on May 17, 1954, contained a new corpus luteum in the left ovary. This ovary also held what was probably the regressed corpus luteum of the previous pregnancy. The *right* cornu was flabbier and more heavily vascularized, and was probably the site of the previous pregnancy; here the ovum, or the blastocyst, probably passed from the site of its origin to the opposite horn. A definite case of this was found in a pregnant August specimen. It would seem, from the May example, that the influence of this transmigration has permitted ovulation to occur in the ovary which contained the corpus luteum. This may be one of the factors which upsets any regular alternation of ovulation in the ringed seal.

THE DEVELOPMENT OF THE CORPUS LUTEUM. The corpus luteum develops rapidly after ovulation in seals, staying relatively small until implantation of the blastocyst and then increasing to its full size. It then maintains this size, or regresses slowly, according to the species concerned (Harrison, 1948). The first part of this cycle, up to the early development of the embryo, is outlined in Table X. The Table reveals an increase in the diameters of the corpus luteum in August, both in pregnant seals and in seals in which implantation was not yet evident. The means of the average diameters of the two groups of corpora lutea, from mid-April to July 31 and from August 6 to October 7, differ by 1.354 mm. with a standard error of 0.31 mm.; thus there is a highly significant increase in size of the corpus luteum around the time of implantation in August.

Structural changes occur during the life of the corpus luteum; these are shown macroscopically in Figure 16 and microscopically in Figure 17. The new corpus luteum (SD-443, mid-April) is pale yellow in appearance, with little vascularization apparent macroscopically. Histologically, the gland is rather loosely packed with large, occasionally vacuolated cells and there is little connective tissue present, except along the trabeculae which project from the old follicle wall into the cell mass. The condition of corpora lutea in May and June is more or less similar; the luteal elements are more packed, but there is little development of connective tissue between the cells. Near the time of implantation, in late July and early August, the appearance of the gland is considerably changed. There is much vascular intrusion, particularly along the trabeculae, which become readily visible macroscopically. Nodules of connective tissue develop and almost all the luteal cells are separated by collagenous fibres, which stain very well with fast-green. Corpora lutea of later pregnancy, corresponding to foetuses up to 110 mm. in length, do not differ materially from this condition. No late pregnancy ovaries were secured in this study, but some of the regressing corpora lutea of pseudopregnancy exhibited increased connective tissue and vascular intrusion as well as the heavier rusty colour described by Fisher

(1954a) in late pregnancy harp seals. The corpus luteum of the previous pregnancy in the mid-April female was considerably changed. Luteal tissue remained isolated in small islands cut off by radiating masses of connective tissue, and individual luteal cells were shrunken and surrounded by collagenous fibres.

These changes in size and structure of the corpus luteum have been described by Harrison *et al.* (1952) and Laws (1956b). They found that the sudden increase in size and change of structure is associated with the implantation of the embryo in the several species studied, as it is in the ringed seal. In the ringed seal, the gland retrogresses rapidly after parturition and ovulation occurs during lactation, as Laws found in the elephant seal. The corpus luteum of the Weddell seal also degenerates rapidly after parturition, but this animal does not ovulate until the completion of the lactation period of about two months (Mansfield, in press). In the harp seal, on the other hand, the gland appears to maintain its size and activity until the short, two-week lactation period is complete (Fisher, 1954a). The harp seal does not ovulate until after lactation and the abandonment of the young, and Fisher suggests that the maintenance of the glandular activity of the corpus luteum in this species is linked with the timing of the breeding season. If the corpus luteum thus has a direct effect in suppressing oestrus, it is not known how the Weddell seal (Mansfield, in press) prevents ovulation from occurring until the end of lactation, long after the regression of the corpus luteum of the last pregnancy. It would seem that the whole question of timing of ovulation and development of the corpus luteum cannot be subjected to too much generalization, and that specific patterns are adapted to environmental and behavioural circumstances.

POLYOESTRUS IN THE YOUNG FEMALES. It is by no means an established fact that all female seals are monoestrus, ovulating only once annually, within the breeding season. Fisher (1954a) offers good evidence for a period of follicular stimulation during the breeding season, even in immature harp seals. On the other hand, the unimpregnated southern sea lion (*Otaria byronia*) can folliculate outside the normal breeding season (Hamilton, 1939). The newly matured cape fur seal may experience its first ovulation three months before the normal season of the older adults. Such premature oestrus may result in pregnancy in this species, as the male may be in rut at this time (Rand, 1954). The material from the ringed seal suggests that it too may be polyoestrus. On March 25, 1954, a five-year-old female was found to have a regressing corpus luteum in the left ovary. The animal was nulliparous, judging from the condition of her reproductive tract. Three other nulliparous females with small, relatively regressed corpora lutea were killed in August and September and small corpora lutea, with less vascularization and connective tissue, were found in four specimens taken during the period of August to October. The differences in macroscopic and histological appearance are shown in Figures 16 (J, K & E) and 17 (E & F), and their smaller sizes and associated follicular patterns are outlined on Table X. Unless there is an inexplicably great difference in the rates of regression of corpora lutea of pseudopregnancy, for several of these seals were taken long after the embryo should have been apparent, it is difficult to believe that all these corpora lutea resulted from breeding season ovulations. A ninth-year seal, which had borne young in the past, was found not pregnant in early September. The corpus luteum, which had presumably resulted from a breeding season ovulation, was regressing. This may have been an example of missed impregnation. It is suggested, in the belief that corpora lutea of pseudopregnancy are likely to regress after a relatively short time, perhaps after the normal lapse in time of pre-implantation, that the March specimen represents an ovulation which occurred in the winter season. The regressing corpus luteum taken in August may have resulted from ovulation shortly before the breeding season. The corpora lutea of pseudopregnancy taken from September 30 and October 9 seals are younger in appearance and may have resulted from ovulations after the normal breeding season. More direct evidence for such unseasonable ovulation is shown in a fifth-year female secured on October 4. The left ovary of this specimen contained a large follicle, which appeared all but mature (Table X, Fig. 16A). It will be noted that the phenomenon of pseudopregnancy seems almost confined to the younger, nulliparous seals (see also the section on virginity in the young females, page 37); only one seal of the nine in which pseudopregnancy was known or suspected had borne young previously. It may be that the follicular cycle is fixed by the advent of full maturity, or by the first pregnancy, or by both.

Implantation and Development of the Embryo

It has been shown that the female is impregnated shortly following the birth of the young. The first pregnant specimen was taken on August 6, 1954, but unfortunately the thickened uterine tract was eaten by dogs. Twenty-eight embryos, in various stages of development, were removed from females in August to early October. Another 7 embryos from later dates were available in the collections of the National Museum of Canada. Measurements of a foetus killed on January 9, 1954, in northern Baffin Island, complete the series available for study. The smallest embryos were removed shortly after mid-August, in southwest Baffin Island; their average size at this time suggested that implantation had occurred one to two weeks earlier. If we consider that impregnation occurs in mid-April, a delay in the development of the foetus of about 3½ months is implied. This is somewhat longer than the delays found in most other pinnipeds.

Attempts were made, without success, to locate unimplanted blastocysts in fresh and preserved material. Since the centers of the uterine swellings of three tracts in August were 28 mm., 35 mm., and 24 mm. from the junctures of the uterine cornua, this gives some indication of the length of tract which would have to be sectioned with a view to discovering pre-implantation embryos in serial section. Also, anomalies do occur, such as the trans-uterine migration of the blastocyst, described above. Thus it was felt that the size and state of the corpus luteum gave sufficient evidence of hidden pregnancy.

Figure 18 illustrates the size of these embryos and their dates of removal. A straight line of least squares fitted to these points (not shown on the Figure) indicated an average date of implantation on August 27 and a birth size of 657 mm. on March 1. A spread of implantation times from August 3 to September 17 (45 days) was derived from lines parallel to the line of least squares running through the two extreme deviations on either side of this line. Actual birth size approximates 65 cm. (from three full-term foetuses and two newly born whitecoats in northern and southwestern Baffin Island and Foxe Basin). If the

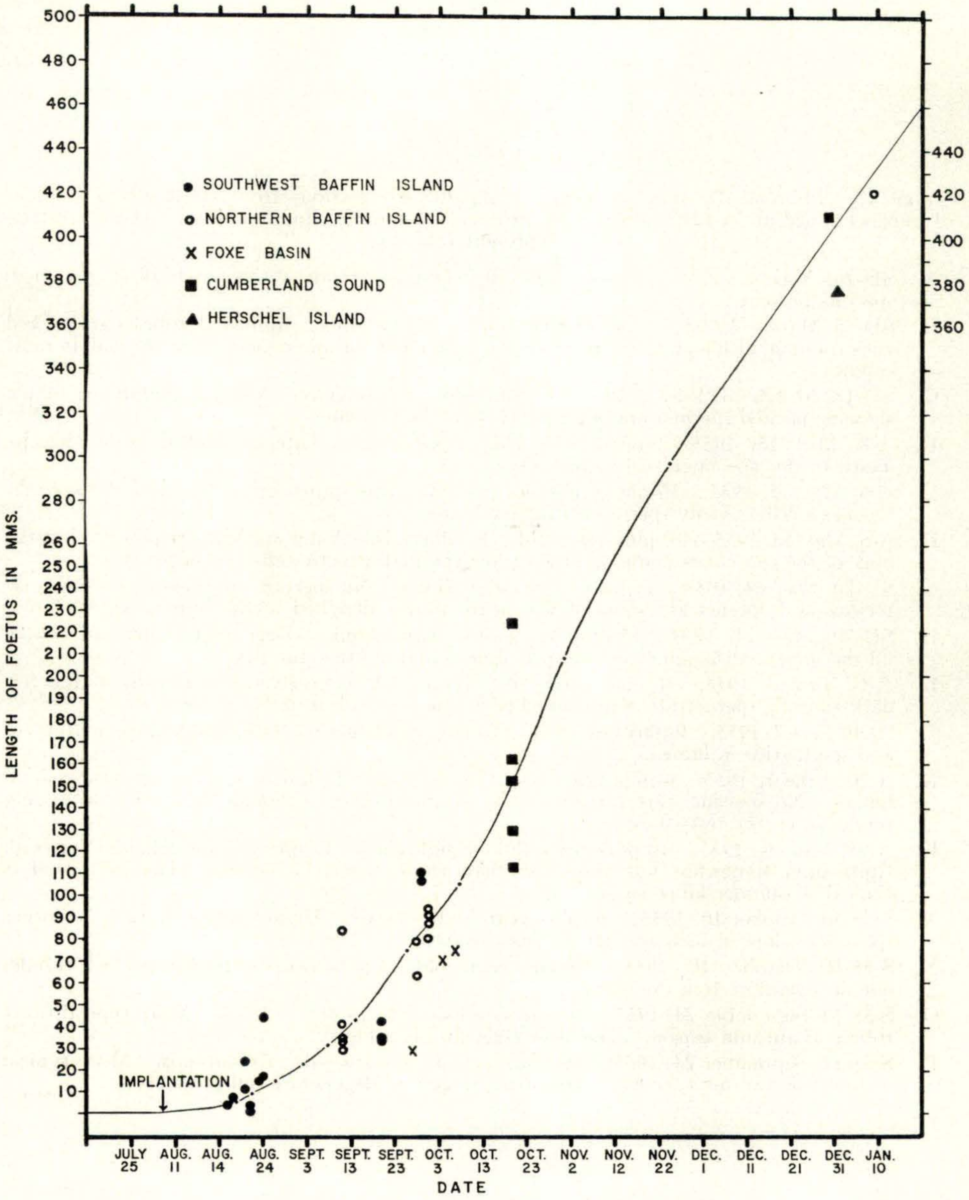


FIGURE 18. Early growth of the ringed seal foetus. The curve is derived from human embryonic growth data, as described in the text.

FIGURE 15. Photomicrographs of testis and epididymis sections from adult *Phoca hispida.* All were sectioned at 7μ and stained with Delafield's haematoxylin, and eosin. The black bars represent 75μ.

A. SD-20, April 1, 1954. 25-plus years old. Testis. Highly active, with all stages up to spermia present.

B. SD-18, March 23, 1954. Almost 8 years old. Epididymis. Almost all tubules are packed with spermia, although the mass of cells is somewhat shrunken away from the wall in most tubules.

C. SD-18, March 23, 1954. Almost 8 years old. Epididymis. A single epididymis tubule showing packed spermia and high, active lining epithelium.

D. A-8, May 15, 1955. 9-plus years old. Epididymis. Tubules packed with spermia. Testis of this specimen still highly active.

E. A-6, May 15, 1955. 10-plus years old. Testis. Still quite active, but note the spermatogenetic cells (chiefly spermatids) in the lumen.

F. A-6, May 15, 1955. 10-plus years old. Epididymis. A few spermia are present, but the bulk of the content is made up of sloughed spermatogenetic cells and detritus.

G. SD-70, May 24, 1954. 15-plus years old. Testis. No spermia are present, but spermatocytes and spermatids, some of which are shown sloughed in the lumen, are common.

H. SD-70, May 24, 1954. 15-plus years old. Epididymis. Degenerate cells and colloid fill the lumen, although a few spermia were found in other tubules.

I. A-16, June 7, 1955. 10-plus years old. Testis. A relatively inactive testis with a few dark-staining spermatids, some detached in the lumen, but with no spermia.

J. A-20, June 7, 1955. 9-plus years old. Testis. Quite active, with sloughed spermatocytes and spermatids in lumen.

K. A-20, June 7, 1955. 9-plus years old. Epididymis. Detail of spermatogenetic cells in lumen. No spermia were present in any of the tubules, although these were still being produced by the testis (see J).

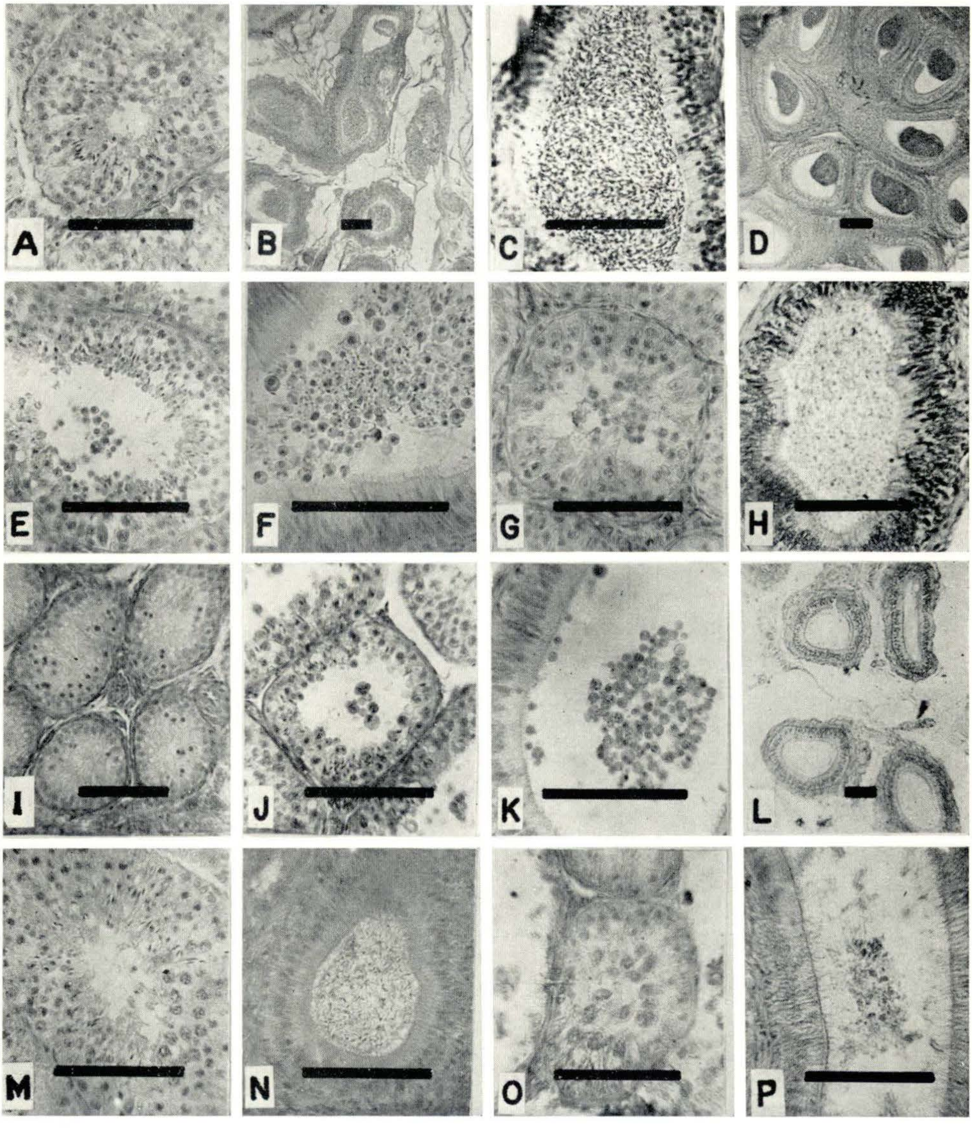
L. A-35, June 24, 1955. 10-plus years old. Epididymis. Empty but for colloidal material. Epithelium somewhat less columnar than those earlier in season. This condition is typical of summer-killed seals.

M. S-55-50, October 10, 1955. 20-plus years old. Testis. Highly active testis. No other specimens showed such activity at this season.

N. S-55-50, October 10, 1955. 20-plus years old. Epididymis. Spermia-packed tubule, one of several such in the section.

O. S-55-13, September 24, 1955. 10 years and six months old. Testis. More typical testis tubule of autumn season. The large cells are probably spermatocytes.

P. S-55-12, September 24, 1955. 16 years and six months old. Epididymis. More typical contents of autumn specimens, consisting largely of degenerate cell products.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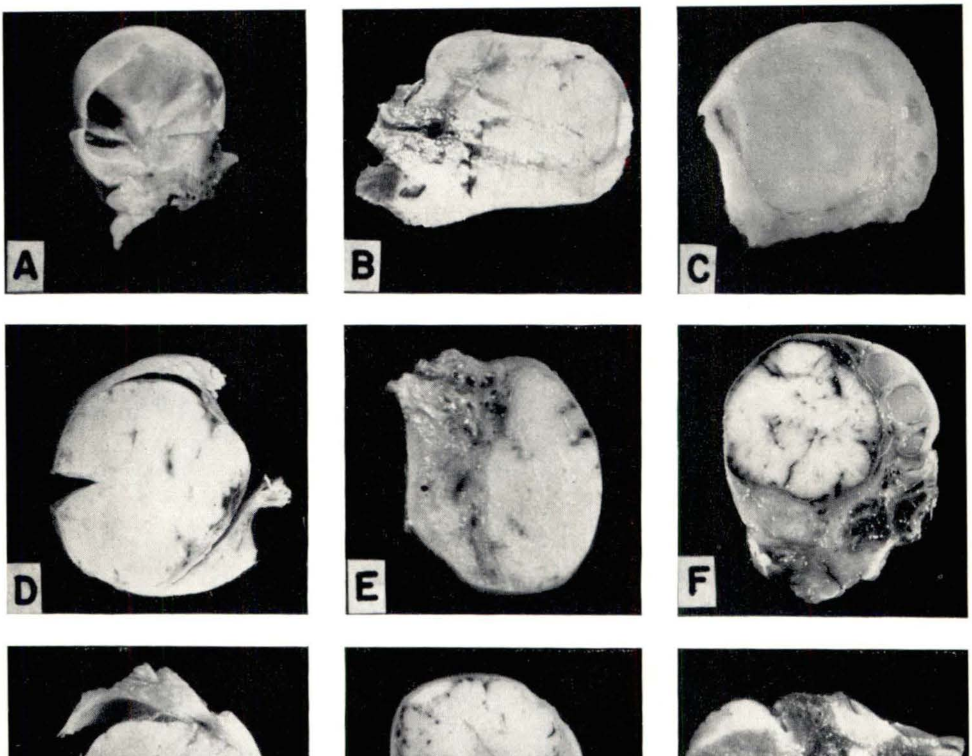
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FIGURE 16. Macroscopic appearance of ovaries in section.

A. S-55-28. Enlarged follicle of fifth-year ovary in section. Follicle 8.5 mm. in maximum diameter and probably close to ovulation size.

B. SD-443. New corpus luteum of eighth-year post-partum female in mid-April. Very little vascularization or connective tissue in gland, which is somewhat crumbled due to loose packing of cells. The gland is 8.5 mm. by 11 mm. in section.

C. A-33. A fairly recent corpus luteum from a female of nine-plus years taken on June 23. Lack of vascularization typical of corpora lutea at this stage of pre-implantation of the embryo. The gland is 13 mm. by 11 mm. in section.

D. # 50. Corpus luteum of a fourteenth-year female killed on August 11. Tract was very slightly swollen, but field examination revealed no embryo. The gland is large (14 mm. by 13 mm.) and some vascularization (dark areas) is evident.

E. SD-461. Corpus luteum of fourteenth-year female on August 20, supporting an 11 mm. embryo. The gland is 14.5 mm. by 8 mm. and slight vascularization is evident.

F. S-36. Corpus luteum of eighth-year female on August 24, with a 44 mm. embryo. The gland is not very large (11 mm. by 11 mm.) but much vascularization is shown.

G. S-55-39. Corpus luteum of a female in her tenth year on October 7, with a 74 mm. embryo. Very little change from F, although the vascularization is less dark due to differences in preservation. The gland is 12 mm. by 11 mm. in section.

H. SD-527. Corpus luteum of a ninth-year female on September 29. The seal was carrying a 110 mm. foetus and the gland, which was 11 mm. by 11 mm. in section, shows little change from G and F in amount of vascularization.

I. SD-58. The corpus albicans of a female fifteen or more years in age on May 17. The scar was probably more than one year old: the scar of the more recent corpus luteum, not shown in this section, was more conspicuous in this same ovary.

J. SD-15. The corpus luteum of a nulliparous female, about five years old, on March 25. The ovaries were frozen and poorly preserved for histological study, but the gland is small (8.5 mm. by 8 mm.) and shows vascularization too extensive for recent formation.

K. SD-291. A rather young corpus luteum from a nulliparous seventh-year female on August 6. The gland was only 8.5 mm. by 8.5 mm. in section, pale yellow and unvascularized, and was probably not supporting an unimplanted blastocyst.

L. SD-533. The corpus luteum of an eighth-year female which was not pregnant on September 30, long after the normal implantation time. The gland is small (9 mm. by 9 mm.) and quite heavily vascularized.

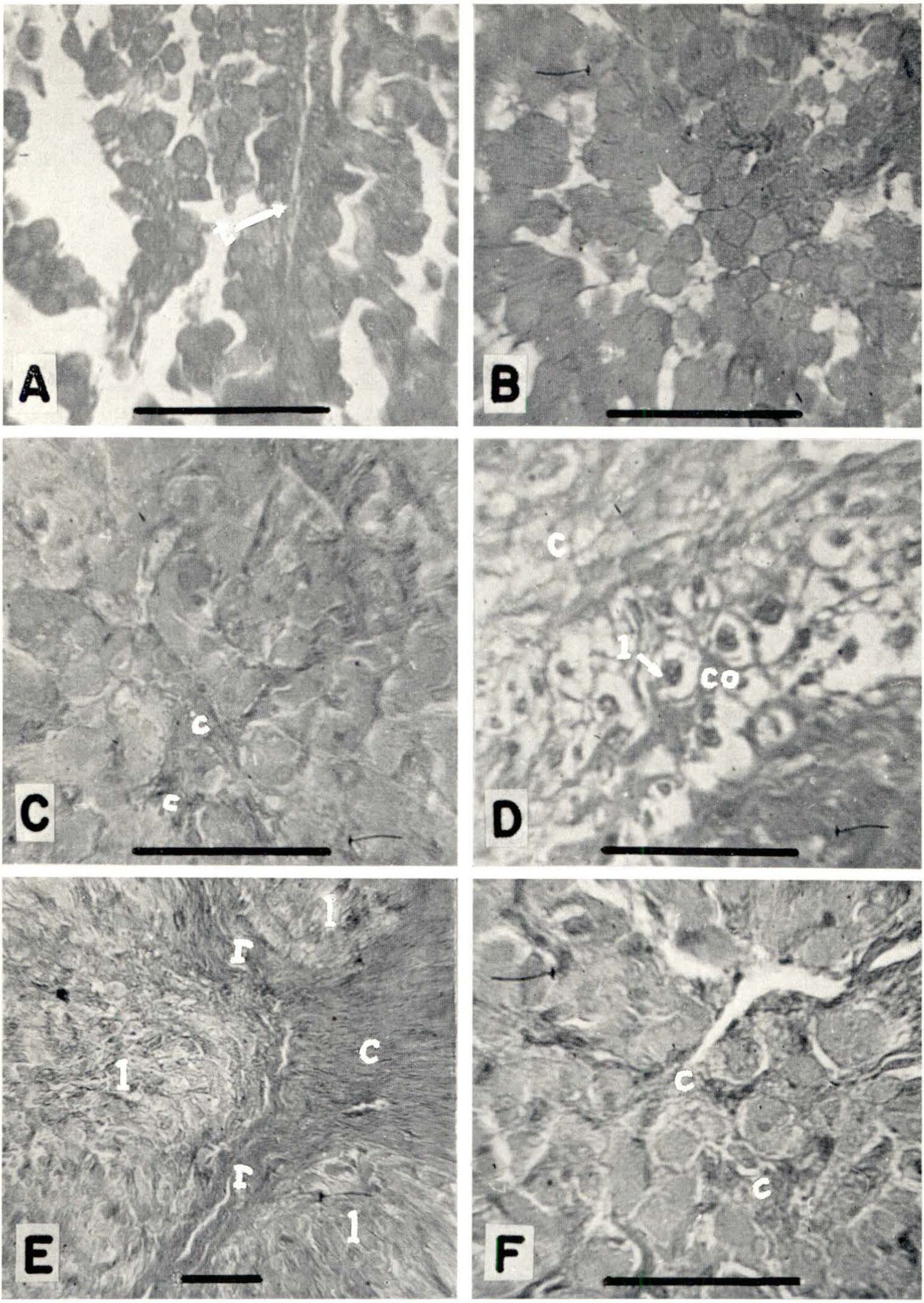
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FIGURE 17. Photomicrographs of sections of corpora lutea from *Phoca hispida*. All were sectioned at 10μ and stained with azocarmine, phloxine, and fast-green. The lines represent 100μ.

A. SD-443. New corpus luteum of mid-April. Note the loose-packed cells, denser along the trabeculum.
t = trabeculum.

B. SD-59. Corpus luteum on May 20, probably about one month old. The luteal cells are loose-packed and there is little connective tissue between them.

C. SD-528. Corpus luteum of September 29, supporting a 106 mm. foetus. Note the development of connective tissue between the more closely packed luteal cells.
c = connective tissue.

D. SD-443. Old, post-partum corpus luteum in mid-April. Note the large connective tissue masses and the network of collagenous fibres constricting the luteal elements.
c = connective tissue mass.
co = collagenous network.
l = luteal cell.

E. S-39. Regressing corpus luteum of nulliparous sixth-year female on August 24. Bodies of luteal tissue are being cut off by connective tissue instrusions.
c = large connective tissue mass.
r = radiating arm of this mass.
l = luteal tissue.

F. SD-533. Corpus luteum of a nulliparous eighth-year animal on September 30. No embryo was present, but the structure of the gland is similar to that of pregnant seals (as in C, above).
c = connective tissue.

spread of implantation dates is related to the length of the breeding season, this should be about 45 days (equivalent to April 1 to May 15). Thus the line of least squares for these data gives a birth size and implantation spread in keeping with the expected figures. But the line does not fit well the sizes of the earliest embryos, taken from August 16 to August 24 in southwest Baffin Island; these are larger than the line would imply. Arey (1954) gives figures of human embryonic growth. Table XI converts these data into the hypothetical growth curve of the ringed seal embryo. No measurement exactly comparable with the crown-rump length of the human could be applied to the ringed seal foetuses, which were measured from tip of nose to tip of tail, along curvatures and flexures, but the proportionate growth is considered to be of the same form. The growth period is here considered to be 240 days (for the sake of a round figure, from August 1 to March 29), and the birth size to be 650 mm. The growth curve derived from these assumptions fits the points of Figure 18 somewhat better, particularly the earlier growth stages.

TABLE XI. Conversion of rate of human embryonic growth data into ringed seal embryonic growth.

HUMAN		RINGED SEAL	
Age	Crown-rump length	Age	Nose-tail length
days	*mm.*	*days*	*mm.*
7	0.1	6	0.2
14	0.2	12	0.4
17.5	1.5	15	2.8
21	2.0	18	3.7
24.5	2.5	21	4.6
28	5.0	24	9.3
35	8.0	30	14.9
42	12.0	36	22.3
49	17.0	42	31.6
56	23.0	48	42.7
70	40.0	60	74.4
84	56.0	72	104.0
112	112.0	96	208.0
140	160.0	120	297.0
280	350.0	240	650.0

Figure 18 reveals a quite large spread in implantation time. This is perhaps confirmed by the occurrence of one embryo of 24 mm. on August 20 and another of 28 mm. on September 27, suggesting that the range of implantation time is, at least, just over one month. The straight line growth curve, when applied to the extremes of the range, suggests an implantation period from August 3 to September 17 (45 days). The hypothetical curve gives an implantation period from July 9 to August 22 (46 days) and is more in keeping with the sizes of early-August embryos. Since the period of rut of the male and post-pregnancy availability of the female is also about 45 days (early April to mid-May), the spread in implantation dates may reflect the period of impregnation time.

It has been suggested (page 37) that nulliparous females might be impregnated earlier in the breeding season. No statistical difference could be shown in the comparison of deviations from the hypothetical line of nulliparous and parous females; nor could differences be demonstrated in the means of implantation times of embryos from the four localities, southwest Baffin Island, northern Baffin Island, Foxe Basin and Cumberland Sound, although the pupping season may be somewhat later at higher latitudes. The sample is small for statistical treatment and it may be that any effect of impregnation date on implantation time is masked by inherent variations of implantation times among females.

BIRTH AND CARE OF THE YOUNG

THE BIRTH-LAIR. The young seal is always, as far as is known, born on land-fast ice. From March 25 to April 15, 1954, no pregnant or post-parturient female was taken in many days of hunting at the tide-rips within the fast ice of southwest Baffin Island. Kumlien (1879) suggests that the relative scarcity of females in the tide-rips of Cumberland Sound, as early as the beginning of March, indicates that the females have chosen localities for producing pups by this time.

The young seal is born on the ice, generally in an excavation hollowed out by the female in the overlying snow (Fig. 19, 20A). The cavity is usually elongate, 10 or more feet long, with the entrance from the water situated at one end. The height of the roof above the ice depends on the depth of snow. The

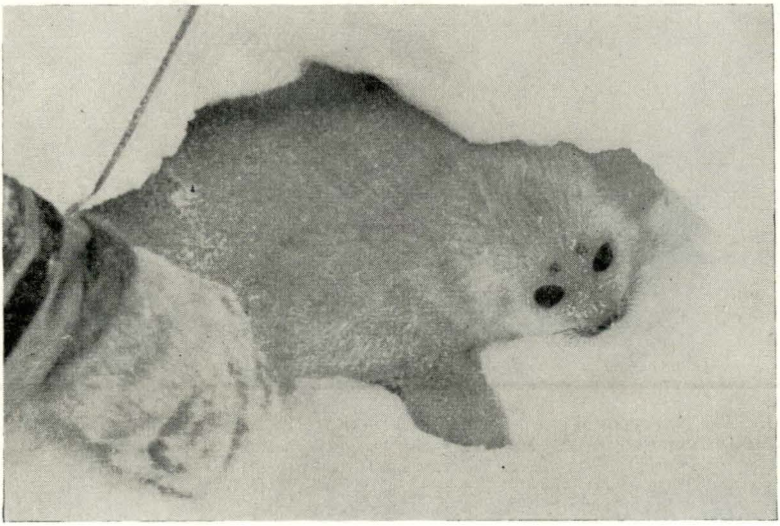

FIGURE 19. Ringed seal pup, April 8, 1954.

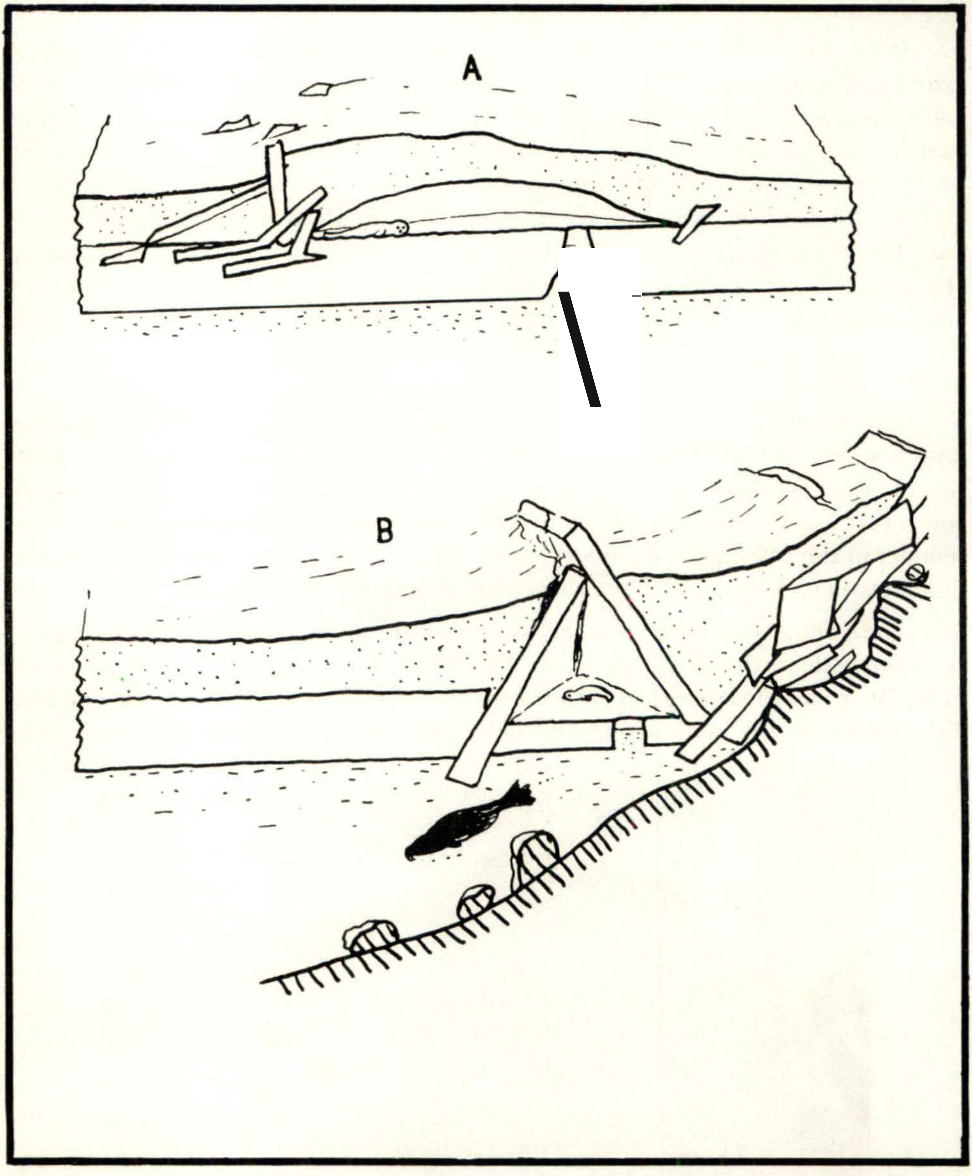

FIGURE 20. The two types of pupping-lair. (A) is the form hollowed out by the female in drifted snow. Note the exposed broken ice, causing drift. (B) shows a pup in a natural pressure-ridge lair.

extremities of the lair may be very low, suggesting that it is constructed by scraping and ploughing with the extended foreflippers. Radiation and breathing of the seal increase the stability of the lair, through icing of the inner surface. Many of those lairs observed in the spring of 1954 could be broken into only by vigorous and repeated jumping on the roof.

A sufficient depth of snow is required for the construction of the birth-lair. It is interesting to note that most of the lairs observed in 1954 were built in the drifted snow which tends to develop in areas of rough ice, but it is not known if suitable snow depth is chosen directly. Within the areas where fast ice forms in the autumn, the seals may tend to congregate in patches of open water, some of which result from the break-up of newly formed ice. This would enable the seals, for a short time before refreezing occurred, to maintain a simpler existence, without the necessity for breathing holes. Indirectly, a sufficient final snow cover would result on the rough ice formed at the temporary break-up. The following observations, extracted from the author's field-notes, may indicate an active choice, or 'prediction', of suitable snow depth.

> On April 2, 1954, 16 breathing holes, 100 or more feet apart, and four pupping-lairs, from one of which a white-coat was removed, were discovered by the dogs in a long, narrow band of heavily drifted broken ice. By its general appearance, this band was thought to have represented a boundary between ice and open water, at some time during the season of freezing. Floating ice, trapped and frozen at this boundary, or the grinding action of newly formed ice sheets against the older sheet of ice, could have resulted in the rough ice pattern as found in April. Several traverses of smooth, poorly covered ice in the area failed to reveal any birth lairs, although breathing holes, including those of several malodorous males, were found in such ice.

This distribution suggests that the females moved to the edge of the older sheet of ice before further freezing took place, or that they moved into the rough ice at the boundary through recently congealed surroundings. Such areas of broken ice may be encompassed by stable, early-formed ice, so that ice stability and snow cover, both desirable for pupping success (see page 60) need not in this case be antagonistic. Observations in northern Baffin Island (Ellis, 1957) show that seals may often appear in surprisingly large numbers at newly formed tide-cracks in the fast ice in mid-winter. The seals may be taking advantage of easier conditions for keeping open the fresh breathing holes in the new ice which forms in these cracks. Drifted snow may also form along such cracks, thus making them more suitable for birth-lairs. Most seals give birth in deep bays and close to shore, where the basic snow cover and ice stability are optimal. Figure 20A depicts a lair of the broken-ice type.

Some seals produce pups in the pressure ridges which often form just outside the ice which lies on the shore at low tide (Fig. 20B). The chief advantage of this sort of lair is that its canopy of solid ice makes it less assailable by foxes and humans, but its instability probably more than outweighs this. Ice movement may take a heavy toll of pups born in these pressure-ridge lairs.

THE YOUNG SEAL. By all accounts, the great majority of white-coats are born from mid-March until mid-April, though a few may be produced outside these dates. Freuchen (1935) states that in the Canadian eastern arctic and north of Hudson Bay, "in the years of the [Fifth Thule] Expedition . . . most of the seals had their young in the beginning of April". The Eskimos of southwest Baffin Island were of the opinion that a similar average birth date applies in that area. Ellis (1957) considers that the pupping period in northern Baffin Island extends from about April 9 to at least April 16 and it seems likely that the season is delayed somewhat in higher latitudes as Freuchen also suggests.

In southwest Baffin Island, a full-term foetus, taken by the natives near the beginning of March, weighted 9.5 lb. (4.3 kg.); and a recently-born female of 10.5 lb. (4.8 kg.), with a raw umbilical cord, was tagged on April 2. Another fully developed foetus and a new-born white-coat in northern Baffin Island weighed 10 and 11.5 lb. respectively (4.5 and 5.2 kg.). Kumlien (1879) gives a range of weight of 4 to 6.5 lb (1.8–2.9 kg.) for new-born pups in Cumberland Sound, weights considerably smaller than those found in the above localities. An older male white-coat tagged on April 8, weighed 24 lb. (10.9 kg.), indicating a rapid gain in weight. As stated earlier, the length at birth appears to be about 65 cm. (25½ inches).

The young begin to shed the foetal coat after two weeks (Pedersen, 1930) or at least before 20 or 30 days (Kumlien, 1879). A white-coat on Southampton Island exhibited slight darkening on the face and flippers on May 2 (A. W. Mansfield, field-notes, 1955), but another pup examined by the present author on southwest Baffin Island had only small amounts of foetal hair clinging to the mid-dorsal area on May 14. On the other hand, a young of the year in Foxe Basin was still almost all white on June 10 (*Calanus* field-notes, 1956) and patches of white hair were still present on another killed on June 18 in northern Baffin Island (D. V. Ellis, personal communication). The latter two localities are more northerly and the later retention of the foetal coat may be the result of later birth dates.

The stomach of the pup taken on May 14 contained nothing but curdled milk. In late May several young were observed sunning themselves in the depressions formed after the birth-lairs had caved in. A large seal, probably the mother, was observed lying beside one of these young on May 26. Milk was found in the incised mammae of three females killed on May 17, 19, and 20. No other post-parturient female was taken before June 26, when a single non-virgin female showed no signs of lactation. According to native information, some females lactate until at least late June and the stomachs of young seals in mid-June may contain milk, a mixture of milk and sea-food, or sea-food alone. The statement of Freuchen (1935) that "milk is to be found in the stomachs as late as in September or October" seems erroneous; no first-year animal taken by the author in summer or fall was milk-fed.

This long period of parental care, potentially from April until the break-up of winter ice, is of great significance in the determination of movements and distributions of this species and will be enlarged upon in the last section.

THE SEX RATIO

Too few new-born pups were taken for an estimate of the sex ratio at birth. During the study, 259 males and 229 females were taken, these figures excluding all samples on which sexual selection might have been practised by Eskimos or the author. There is, however, some sexual segregation of the adults in certain seasons. During the pupping season, only adult males and immature seals of both sexes were killed in the open water of tide-rips within the fast ice; the adult females presumably were occupied with their pups at this time. The adults are about equally represented on the fast ice, following the breeding season. Four adult females and 11 adult males were taken in Foxe Basin, some distance from the favoured breeding areas, in the autumn of 1955. Most of the adult females would be pregnant at this time, and they may have been attracted to the more suitable areas in anticipation of the requirements for pupping in the following spring. The immature seals are probably unaffected by the sexual urges and requirements which cause segregation of the adults. Of seals younger than 6 years old, 190 males and 165 females were killed, a ratio of 53.5 males to 46.5 females. Sleptsov (1943) found a sex ratio in this species of 40 males to 60 females, but concluded that the preponderance of females was due to sampling error and that the true ratio is close to 50:50.

LOCAL MOVEMENTS, DISTRIBUTIONS, AND FACTORS OF ABUNDANCE

REPRODUCTIVE ECOLOGY

The formation of the birth-cave has been described on page 55. As far as is known, this lair is never found outside the fast ice. The Eskimos believe that if a section of this ice is broken off around the time for pupping, any pregnant seals will desert the area for another patch of fast ice.

The young may not be completely independent until they are more than two months old, this long period of parental care probably being a reflection of the habit of pupping in the fast ice. Bearded seals and harp seals, both of which bear their young in moving and unstable pack ice, wean the young after a much shorter period of parental care. Obviously, on fast ice, the mechanics of attending the young are simplified and the dangers of separation of mother and young are lessened. These circumstances probably enable the female to feed normally in the vicinity of the young seal until the June season of intensive fasting (page 21). The female harp seal, on the other hand, loses much weight through lactation and starvation, during the shorter, more intense suckling period.

Of course, any effect of pupping habits will apply equally to the distributions and movements of adult males and females. The proximity of pupping and impregnation times indicates that the adult males must, in general, follow the patterns set by the adult females.

THE AMOUNT OF FAST ICE. Due to the habit of pupping in the fast ice, the total ringed seal production in a region is likely to be in some way proportional to the amount of fast ice available for the birth-lairs. In southwest Baffin Island, as in most areas of the eastern Canadian arctic, the extent of fast ice in winter is more or less fixed by the nature of the coastline and is much the same from year to year. Figure 21 shows the outer limit of fast ice. Obviously different sections of this coast differ markedly in the amount of fast ice which forms. Areas of fast ice, in ten-mile strips extending inshore from the ice edge, have been determined from the topographic map of the region. During the pupping season, coastal sections A, B, C, D, and E (Fig. 21) have approximately 43, 48 165, 193, and 181 square miles of stationary ice respectively. Thus a strip from the ice edge in the relatively complex areas of C, D, and E delimits about four times the amount of fast ice of an equivalent strip in the areas A and B.

ICE STABILITY AND SNOW COVER. The total amount of fast ice is only one of the factors determining the suitability of an area for pup production. In regard to the formation of fast ice, several generalizations may be made. Ice forms from the shore outwards. The deepest inlets and most sheltered, island-filled regions are frozen earliest and most securely. Islands act as anchor-points in the formation of stable ice in offshore waters. The most recently formed ice, usually nearest the ice edge, is the least stable, and is more subject to the destructive effects of winds and tides. These factors indicate the greater suitability of areas of coastal complexity for stable ice formation. If the distribution of pups is considered to be randon throughout the fast ice, and if a strip of ice, one mile in width, is broken off at the ice edge from A to E (Fig. 21) carrying all its pups to death through separation and starvation, the resulting losses in the year's pup production would be about 22% in areas A and B and only about 5.5% in areas C, D, and E. This example, involving pup production as a function of ice stability, is considerably oversimplified. Nevertheless, there are several facts which suggest that ice instability has its effect on the structure of seal populations.

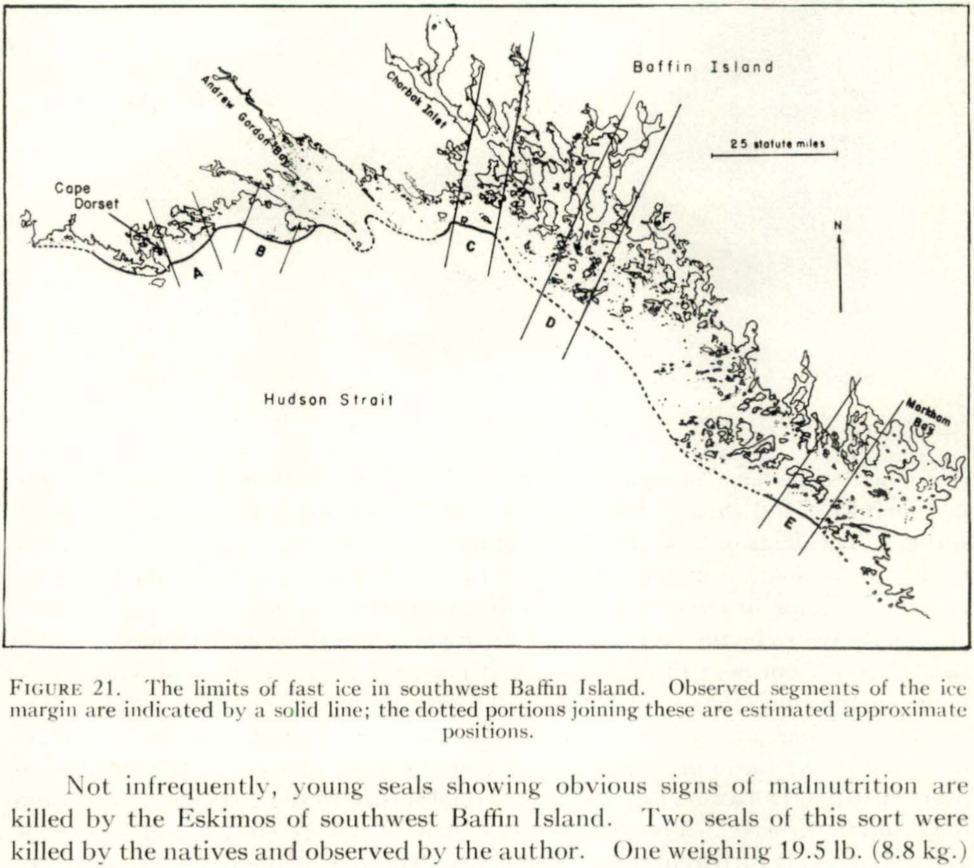

FIGURE 21. The limits of fast ice in southwest Baffin Island. Observed segments of the ice margin are indicated by a solid line; the dotted portions joining these are estimated approximate positions.

Not infrequently, young seals showing obvious signs of malnutrition are killed by the Eskimos of southwest Baffin Island. Two seals of this sort were killed by the natives and observed by the author. One weighing 19.5 lb. (8.8 kg.) was killed at the ice edge on July 1, 1954 (Fig. 22). The other, which weighed 20 lb. (9.1 kg.), was killed well offshore on August 6. Five other seals of the year killed during the summer season in southwest Baffin Island ranged from 28.5 to 38 lb., mean 33.2 lb. The Eskimos call these small seals *sierkolik*, the term referring to the prominence of the knee joint, and presume them to be starvelings which had been abandoned by the mothers before being properly weaned. The

Eskimos have found the *sierkolik* on large floating ice pans off the ice edge in the spring. Whether the young seal has been born, perhaps abortively, on moving ice, or whether the ice has been separated from the fast ice-sheet after the birth of the young, is not known. The latter possibility seems to be more likely. The majority of starvelings are taken by natives of southern Andrew Gordon Bay and from camps to the west of Cape Dorset (Fig. 21). In June, when the bearded seal is hunted from boats launched at the ice edge, the *sierkolik* is taken in the open water. In this same season, young ringed seals of the year, in the peak of condition, are being taken by Eskimos hunting on the fast ice.

FIGURE 22. A starveling, July 1, 1954, on southwest Baffin Island.

There is evidence of an average size difference between seals produced in the peripheral ice and those taken in areas where the ice is stable until late in the spring. The skins of first-year seals, which are known as "silver jars" in the fur trade, are of some commercial value. In this respect, the skins taken by the natives of camps situated deep within the archipelago to the east of Cape Dorset are considered to be the best. Figure 23 shows one of these larger, more valuable skins, taken from near the camp marked F on Figure 21, compared with a skin taken in the same season (early August) near Cape Dorset. The smaller skin was the intermediate in size of 3 skins from the Cape Dorset area, and the larger was close to the mean in size of 7 skins from its area. The largest of the 3 skins from the Cape Dorset region was about equal in size to the 2 smallest skins from the camp to the east. A possible cause of such a size difference of pups lies in the different periods of parental care which are expected in these two regions. In northwest Foxe Basin, the same differences of white-coat and "silver jar" size were suggested by a few specimens and confirmed by statements from the natives. In the areas around Igloolik Island, close to the winter ice edge, the young are small. Around Fury and Hecla Strait, Richards Bay and Murray Maxwell Bay, all areas of stable winter ice and far from the ice edge, the young are larger (H. N. Andersen & E. H. Grainger, personal communications).

Premature separation of mother and young is not the only danger in areas of unstable ice. Occasionally the natives find pups in pressure-ridge lairs (page 57) apparently crushed to death by shifting ice. High winds and tides, and the resulting ice pressure and movement, would have their greatest effect at the periphery of the fast ice.

A sufficient depth of snow is required for the construction of the birth-lair. Some mechanisms whereby the female may "predict" the snow depth of a localized area have been discussed on page 57. A good depth of snow is probably required for its insulatory effect, for pups born too early in the spring season run the risk of death by freezing. A small (59 cm. 23.2 in.) white-coat was found dead in its lair by E. H. Grainger (*Calanus* field-notes, 1956) on March 14, and the natives of Foxe Basin informed him that this was a common fate of young born in March. The amount of snow is directly related to the time of formation of the fast ice; it is also governed by the amount of shelter and windbreak. It is easily seen that snow depth is a function of the same forces that control ice stability.

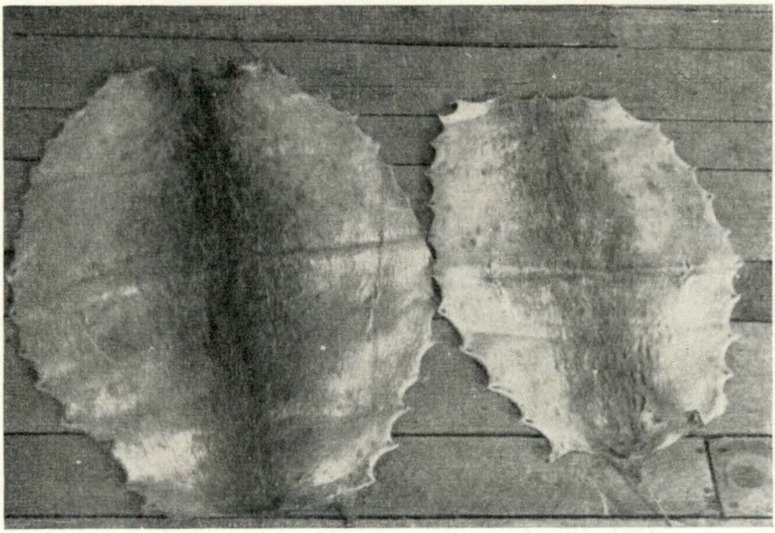

FIGURE 23. Comparison of a large first-year skin of *Phoca hispida* from the complex coast, and a small first-year skin from the simple coast of southwest Baffin Island.

In Greenland, many young lose their lives in bad weather, according to Hansen (no date), and bad weather may also sometimes cause the mother to abandon her young. Clearly a pup born on an unmoving substrate, under a thick blanket of snow, is little affected by the vagaries of wind and weather.

These features of fast ice—stability and snow cover—result in a much higher production potential in the coastal complex between Chorkbak Inlet and Markham Bay than on the relatively simple coasts of the region near Cape Dorset. Thus, the ratio 4:1 between amounts of fast ice in areas C and A (Fig. 21) will be much smaller than the ratio in seal production in these two regions.

ICE CONDITIONS AND THE AGES AND SIZES OF SEALS. As a general rule, the more suitable the ice of an area for pupping purposes, the greater the average age of adult seals making use of this ice. Young adult and newly matured seals are found in the regions of coastal simplicity and in the peripheral ice of more complex coastlines. Older seals are proportionately more common in the innermost bays and lagoons of ramified coastlines. This pattern suggests that penetration of the most suitable breeding areas is a function of experience with age. Kumlien (1879) observed six instances of "young" females pupping on the ice with no snow cover whatsoever. "The young exposed in this manner almost always fall prey to foxes and ravens before they are old enough to take care of themselves." Another factor which may affect this age-cline is population pressure, where the age of the seal might determine the success of competition for the most suitable areas.

Residents of the Canadian arctic, both white and Eskimo, are quite familiar with these differences in seal populations. The names "bay-ice seal" and "sea-ice seal" are used to differentiate the larger and smaller types of seal. Several authors, of whom Freuchen (1935) is the most specific, have commented on these matters. Freuchen found great differences in the size of adult seals "in the Upernavik district, where on the outer coast, for instance at the colony of Upernavik itself, or at the trading post of Taiussaq, one finds full-grown seals that are no longer than about one metre, whereas in near the glaciers, or up in Melville Bay, there are seals of two metres or more." In this he makes "due allowances for the fact that the seal . . . requires about five years to become fully developed"; but since he did not have available an accurate method for age determination, it is probable that these size differences may be, in fact, largely based on age.

In southwest Baffin Island the Eskimos are convinced, through observation, that "bay-ice seals" average larger regardless of age. The largest seal measured by the author in this area was a male, 25 or more years old, 140 cm. (55 inches) long, and 192 lb. (87 kg.) in weight. The innermost bays and lagoons at the north end of the area D of Figure 21 are said to harbour many such large seals. Unfortunately, time did not permit a trip to this area in the breeding season of 1954. In early September many very big seals were seen there, but these were too wary and none was killed. It was felt that if the seals of the innermost bays were larger, the same phenomenon might be reflected in differences between seals of simple and complex coastlines. Unfortunately, measurements of seals from the complex coast, the area between Markham Bay and Chorkbak Inlet, are too few to demonstrate possible differences. However, Figure 24 does suggest that the average sizes within the same age-class do differ in the two regions.

Perhaps the most satisfactory explanation of this situation revolves around the ice ecology and care of the young, which have been elaborated above. Summer starvelings are more common on open coasts, and there may be an average size difference in summer yearlings of simple and complex coasts. The ringed seal is not truly migratory and it is probable that a given section of coastline is replenished to a large extent by its own residents. If small young are the rule, the entire population may bear this stamp. Actually, as will be pointed out in a later section, dispersal is probably directed from complex to simple coasts. Thus, if the size at weaning is of significance, a wider range of seal size might be expected on simple coasts. There is a suggestion of this wider range in Figure 24.

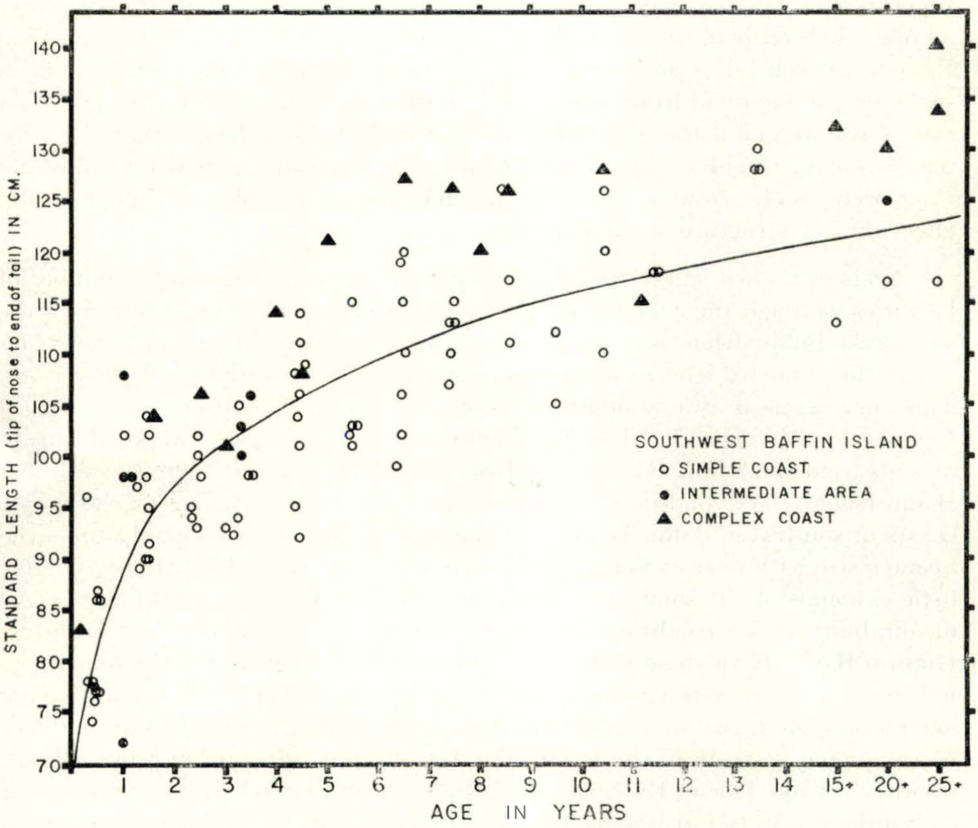

FIGURE 24. Size and age of *Phoca hispida* of southwest Baffin Island. The curve is drawn only through the simple coast specimens, with the aid of several straight lines of least squares.

Other factors may enter in: first, if there is competition for the best breeding sites, the success of the competitor may depend more on size than on age; secondly, it is not known if the age and size of the mother have an effect on the size of the young at birth. As regards the latter possibility, Pedersen (1930) suggests that old female ringed seals give birth about two weeks later than younger females, on the average. Direct correlation between the age-structure of a population and the size of the young produced would be valid only where all the young sampled were still under parental care. Many "silver jar" skins taken in these circumstances were shipped out of Cape Dorset before the problem presented itself. After weaning, nutritional factors, which may have an individual effect, are not likely to act at the population level, especially as the young, fast-growing seals from both the simple and complex coasts of southwest Baffin Island are almost all feeding in the same offshore waters, on the planktonic *Themisto* (see page 17).

Over its wider range, in the Canadian eastern arctic, the ringed seal shows the same variations in size. Latitude, as it governs the formation of fast ice, is superimposed on the effect of coastal complexity. Thus, the common belief among inhabitants of the north that seals in the high arctic areas are larger than those of the south has some basis in fact. Soper (1944) considers that a cline of seal size is to be found from southwest to northeast Baffin Island. An examination of his original field-notes (*idem*, 1924-25 & 1928-29) indicates that this cline may be partly a result of sampling variability; the coastlines on which his observations were made show a corresponding increase of complexity, which would effect the age structure of the populations.

Seals of known length and determined age are available from a number of localities, through the courtesy of several field workers, for comparison with the southwest Baffin Island material. The growth curve of Figure 24 is fitted by eye to the standard lengths of the simple-coast seals of southwest Baffin Island. This curve is used as a standard for comparison with seals from other areas in Figures 25, 26, and 27. The Southampton Island sample, composed chiefly of seals from the South Bay area, is from about the same latitude as southwest Baffin Island. Ice conditions here are comparable with conditions on the simple coasts of southwest Baffin Island and the seals exhibit approximately the same average size with respect to age. The two seals from Churchill, Manitoba, give little evidence of the smaller size of seals which would be expected, due to the unsuitability of ice conditions along the smooth, open coastlines of southwest Hudson Bay. Both these seals were adult females, which were not pregnant in February, another indication of poor conditions for breeding. Ice conditions in northwest Foxe Basin are excellent for care of the young, and the fast ice may not be completely gone from the harbour at Igloolik until the end of July or later, whereas at Cape Dorset Harbour on southwest Baffin Island, and Coral Harbour on Southampton Island, the ice has gone by early July. The seals from northwestern Foxe Basin are correspondingly larger. In northern Baffin Island and Ellesmere Island, where the complex fiord-coasts and lower mean temperatures result in conditions of stable, long-lasting ice, the seals are considerably larger. Only 3 of the 29 seals from these regions are smaller than the mean sizes determined for the simple-coast seals of southwest Baffin Island.

It cannot, of course, be stated definitely that the size differences between northern and southern populations as shown in Figures 24 to 27 are entirely environmentally imposed. However, the facts suggest that the control of size through the mechanism of ice conditions is the overriding cause. Genetic differences can hardly be postulated to explain the size differences in the continuously distributed population inhabiting the 135 mile coastline of southwest Baffin Island, and it is reasonable to suppose that genetic differences need not be invoked to explain a similar north to south cline in seal size. The well-known

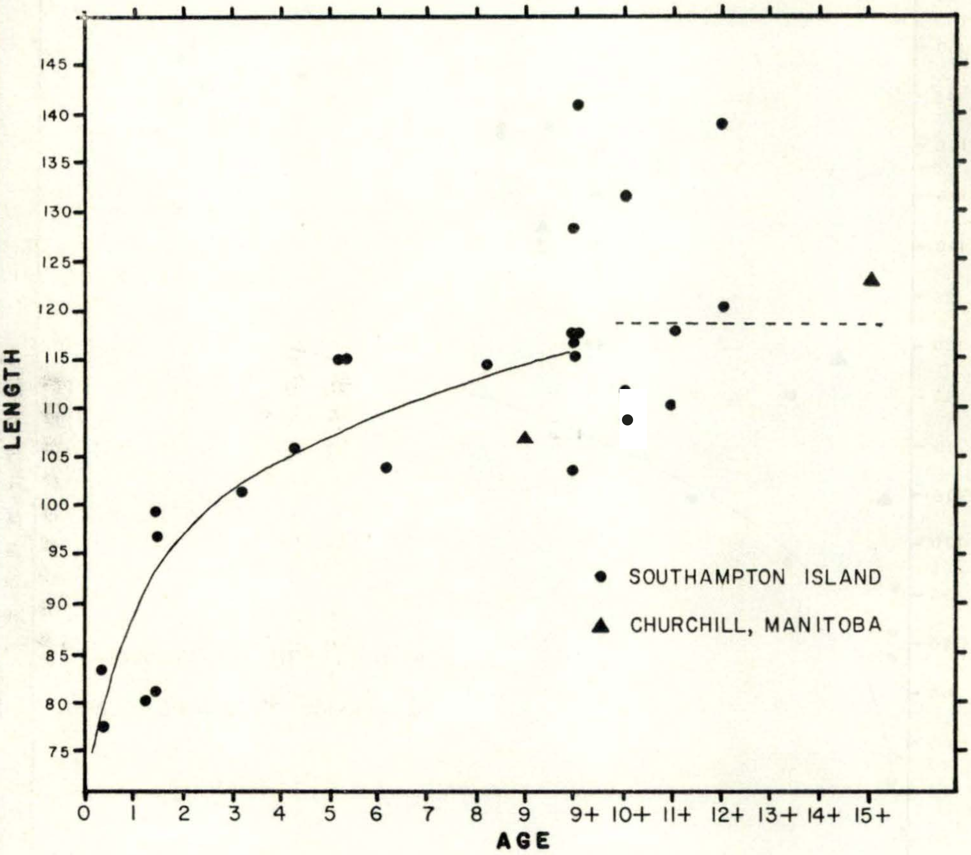

FIGURE 25. Size and age of *Phoca hispida* of Hudson Bay. The curve is for southwest Baffin Island specimens, as in Figure 24. As the older seals from Southampton Island are all claw-aged, the curve is not extended beyond 10 years; the dotted line is drawn through the mean size of 10 to 25+ years seals from Figure 24.

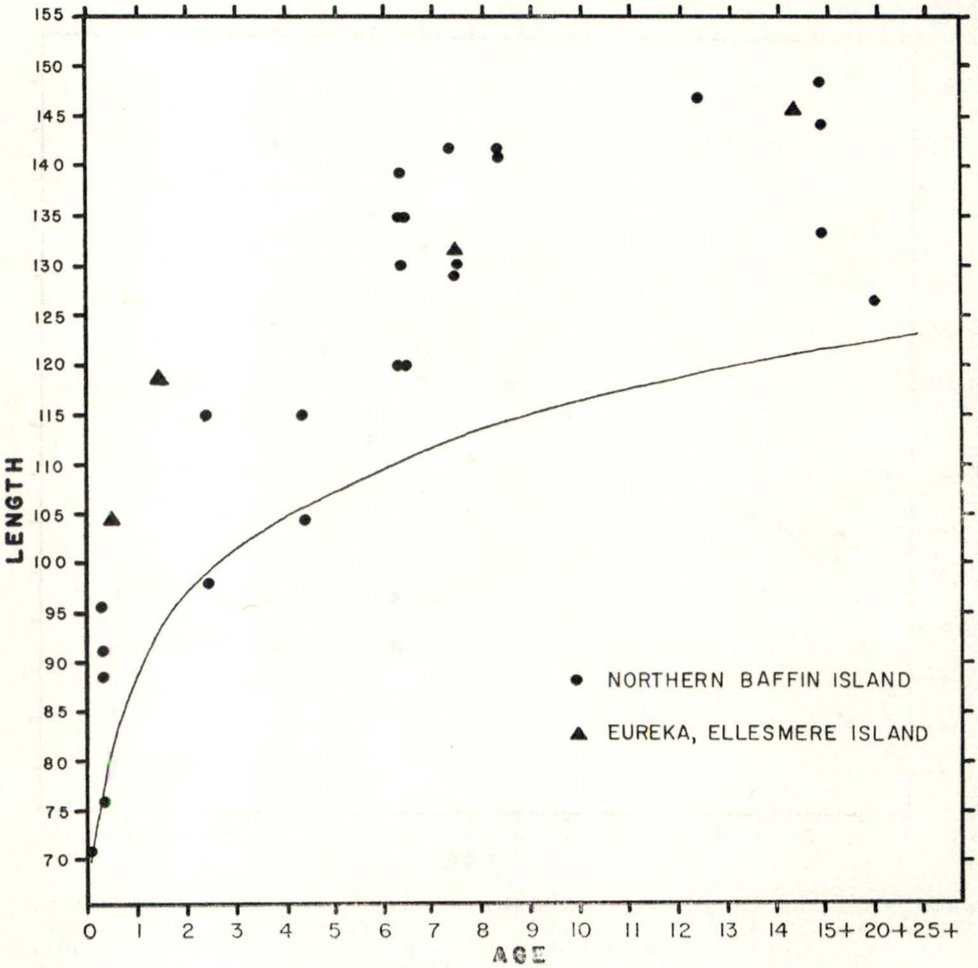

FIGURE 26. Size and age of *Phoca hispida* of two high arctic localities. The curve is for southwest Baffin Island specimens, as in Figure 24.

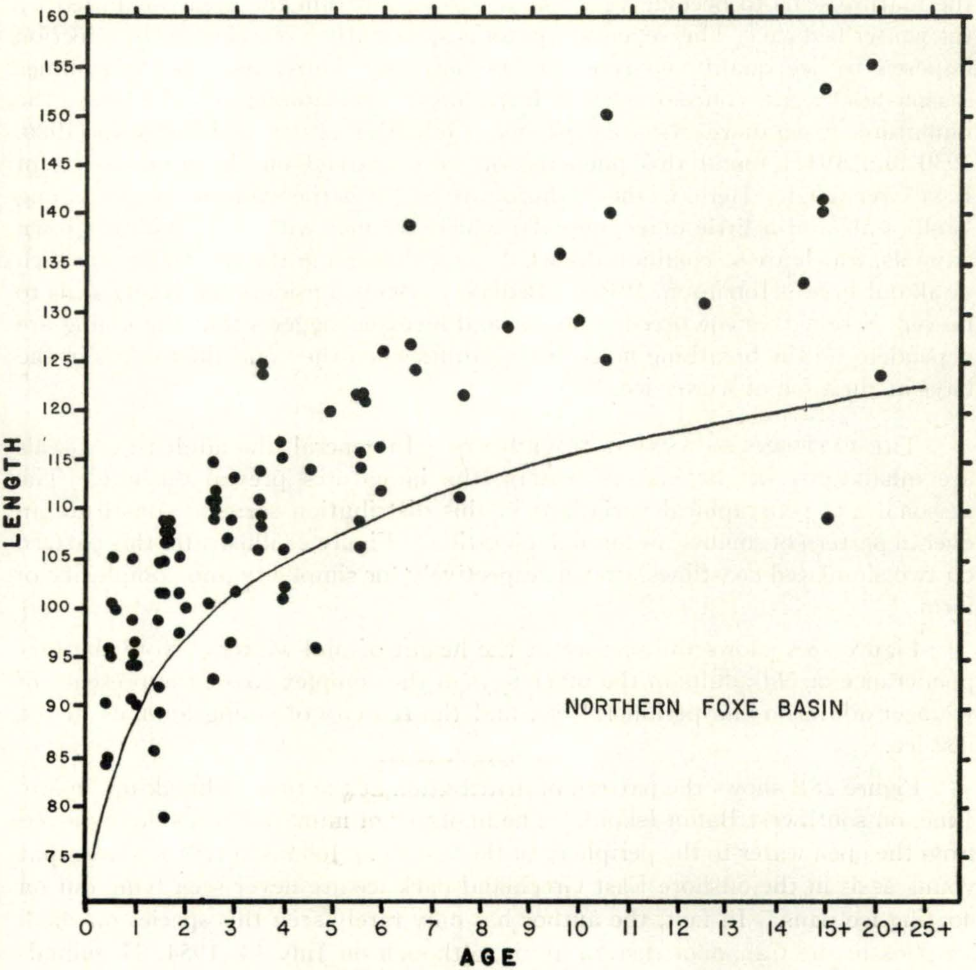

FIGURE 27. Size and age of *Phoca hispida* of northern Foxe Basin. The curve is for southwest Baffin Island specimens, as in Figure 24.

advantage of larger body size in homeothermic animals living in cold latitudes (Bergmann's rule) would not be very effective among ringed seals which live in relatively uniform temperatures throughout their range.

MOVEMENTS

THE SEDENTARY HABITS OF THE ADULTS. There is a general tendency for the mature seals to become year-round residents within the areas delimited by the winter fast ice. This sedentary habit is apparently a reaction to the selection imposed by ice quality on reproductive success. Thus, even in the summer season adults are concentrated in bays, fiords and among islands, while the immatures live a more offshore existence. Johansen (1910) and Pedersen (1926, 1930 and 1942) found this phenomenon very marked on the fiord coasts of East Greenland. Here, in the offshore waters, "it is the small seals (the young 'troll' seals and a little older animals) which are met with . . .; the full-grown animals, which are so common the whole year through in the fjords, are not seen at all out here" (Johansen, 1910). Pedersen (1930) considers the young seals to be very rare within the breeding areas, and he even suggests that the young are dependent on the breathing holes of the adults when they find themselves in the bays at the time of winter ice.

THE PATTERNS OF ANNUAL MOVEMENTS. In general, the adult ringed seals are inhabitants of the inshore waters; the immatures prevail offshore. The seasonal and geographical variations in this distribution seem to constitute an overall pattern of small-scale annual migration. Figure 28 illustrates this pattern on two simulated coastlines, drawn respectively for simplicity and complexity of form.

Figure 28A shows the picture at the height of mid-winter. Note the preponderance of old adults in the inner bays of the complex coast, the presence of younger adults in the peripheral ice, and the scarcity of young animals in the fast ice.

Figure 28B shows the pattern of distribution at the time of break-up, in late June, on southwest Baffin Island. The majority of immature seals have moved from the open water to the periphery of the fast ice. Johansen (1910) states that young seals in the offshore East Greenland pack ice are never seen lying out on floating ice pans. In fact, the author has only rarely seen this species on small ice pans in the Canadian eastern arctic, although on July 14, 1954, 27 animals were counted on a very large ice pan, measuring about one mile by three-quarters of a mile, which had been recently torn from the ice edge. It would appear that the ringed seal prefers to haul out on fast ice. The movement of young seals into this ice was most marked in southern Andrew Gordon Bay (see Fig. 21) after mid-June of 1954. On June 12, and for several days afterwards in this area, the weather was chilly and occasionally sunny; the ice remained relatively solid. A few seals were seen on the ice at this time, and a number, chiefly young adults, were taken. From June 17 to 20, days of warm sunshine and warm rain, the

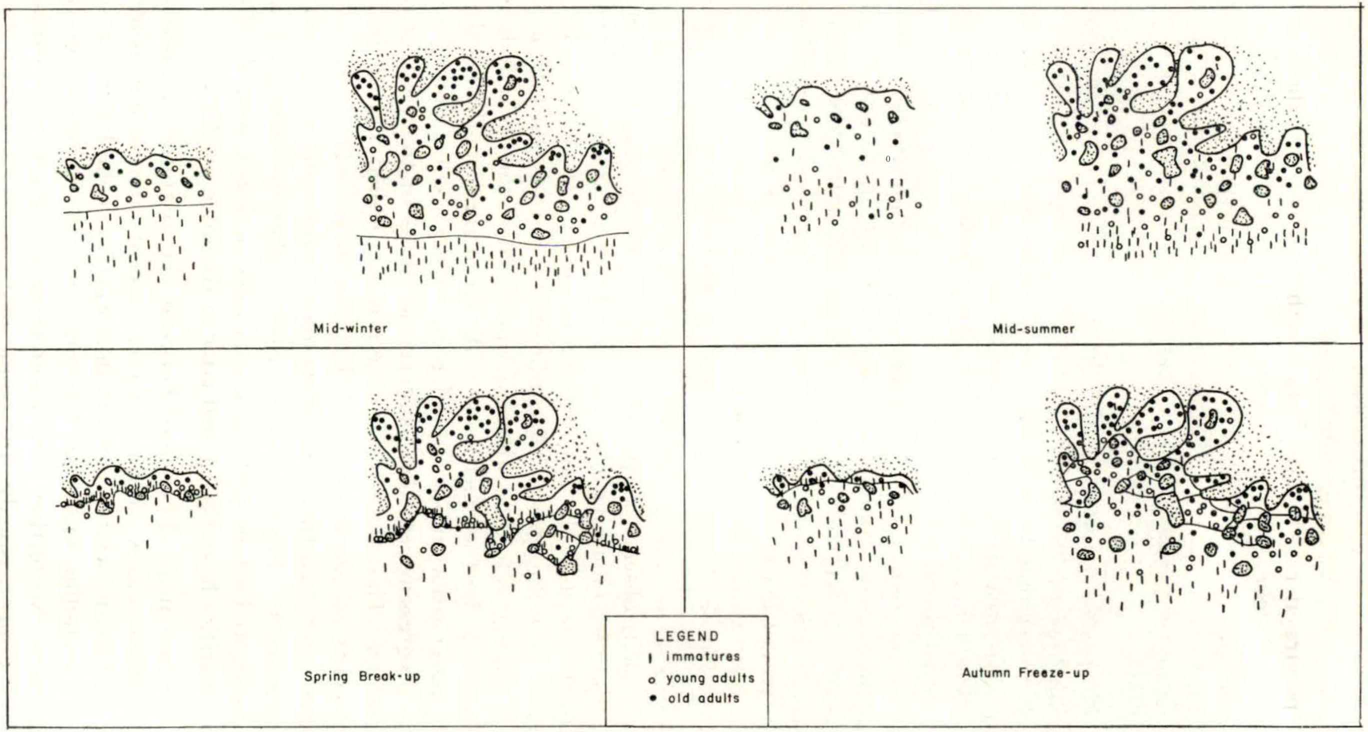

FIGURE 28. The patterns of annual movement of *Phoca hispida*. Explanation in the text.

ice underwent considerable change. The extensive and deep pools of melt-water dispersed, and the ice became rotten with sink-holes and fissures. At this time large numbers of young seals began to haul out. Most were close to the ice edge, though some had penetrated considerable distances through leads in the ice. Several offshore whaleboat trips in late June and early July produced very few ringed seals, and few of the species were seen. This movement of the immature seals into the fast ice in spring was also observed in Foxe Basin in the spring of 1955 (E. H. Grainger, personal communication) and in northern Baffin Island in 1954 (Ellis, 1957).

Figure 28C shows a return to the "normal" distribution in mid-summer. The young seals have moved offshore, apparently following the natural tendency which had been overcome by a desire to haul out on the fast ice in the spring. In the simple coast area of Cape Dorset, seals of all ages were rather scarce in the inshore waters in summer; the most profitable hunting was carried out in the waters a few miles to the southeast of the Cape. This was not so in the more complex coast to the east. In early September large numbers of seals of all sizes were seen in the waters around the camp marked F in Figure 21. Two seal counts in this area on September 7 and 9 resulted in 57 seals being seen in approximately 28 square miles of water. These figures are minimal, since great care was taken not to recount individual seals. Several immature seals and young adults were killed in these waters, but none of the warier older seals was taken. No very large seal was seen on the return trip to Cape Dorset, outside the archipelago.

Figure 28D shows the population status at the time of freeze-up. The author was unable to observe the pattern at this season in southwest Baffin Island and the figure is based on native information. There is a movement of young and old seals into the coast in the fall, but the movement of young seals is not as pronounced as it is in the spring. According to the natives, the fall movement of young seals is analogous to the spring movement, where the desire to haul out on the fast ice seems to be the chief cause. As the nights lengthen and the days become cold, fewer seals are seen sunning on the ice. Most young seals move out with the progressing ice edge, leaving the adults in their winter residence under the fast ice. Thus the winter pattern is established and the distribution remains relatively static until spring. It has been suggested by the natives living in the complex coast area that some seals may return from year to year to the same winter residence. Pupping-lairs may be found at the same point each year in this area, along well-established dog-team routes, and seals wounded by bullets of known peculiarities have been killed later in the same locality.

There are two main differences between the patterns of movement on simple and complex coasts. First, a higher concentration of immature seals is found, both summer and winter, in the inshore waters of complex coasts; secondly, seals of all ages, including adults, are less common in the inshore waters of simple coasts in summer. No further basic assumptions are required to explain these differences. It seems reasonable to assume that coastal complexity itself has a modifying, damping effect on seal movement and dispersal. Thus, for example, the coastal area where large numbers of immature seals were seen (near F, Fig. 21) was actually a maze of bays, lagoons and islands; in fact, every entrance to this area is probably cut off by bars and overfalls at low tide. It is thus probable that many young seals find themselves trapped in such circumstances, even when the instinct to escape to the open sea is strong. The fast ice in such complex areas forms rapidly and extensively, cutting off large expanses of open water in its progression. Little chance of avoiding this ice would be offered to young seals living in the area at freeze-up. Immature seals living in the inshore waters of simple coasts in autumn would find it easier to avoid the fast ice as it crept more slowly outward. The same reasoning may apply to the summertime abandonment of inshore waters by adult seals of simple coasts, keeping in mind the fact that adults are inclined to be sedentary. Random movements of dispersal, even on a small scale, would disrupt any tendency for the adults to be confined to bays in the summer. In effect, once a seal has left a bay in the Cape Dorset area, it is all but offshore; when a seal has left its particular breeding-bay in the complex coast, it may be still perhaps 30 miles from the open sea. Another possibility is that the suitability of an area for pupping and the age and experience of the adult seal have effects on the tendency of a given seal to remain sedentary in the immediate area of its past choice, and it has been shown that the adult population of the simple coasts is younger in make-up.

In East Greenland the lack of mixing between adult and immature populations is very pronounced (Pedersen, 1942; Johansen, 1910). The coastal complex of southwest Baffin Island is not a fiord coast; fiord coasts are deeply indented and may harbour a great deal of stable fast ice, but they do not approach southwest Baffin Island in complexity of configuration. Normal seal movements and dispersal may not be damped to the same extent on true fiord coasts. For example, if the young seal, in avoiding inshore waters, were sensitive to directional tidal-flow, this mechanism would be of less value in the coastal maze of southwest Baffin Island. Dunbar (1941) describes a summertime departure from the coasts of the Lake Harbour area. This area is, in distance from the more complex coast and in degree of complexity, similar to the Cape Dorset area, where the same seal movements are found. In northwest Foxe Basin the patterns of distribution and movements are in accord with those found in southwest Baffin Island, according to observations made by E. H. Grainger and H. N. Andersen in 1955 and 1956 (personal communications). In fact, the general pattern of movements seems the same throughout the eastern Canadian arctic, with modifications imposed by the local geography.

DISPERSAL. The ringed seal is not truly migratory, and its movements, other than the small-scale patterns described above, seem to represent dispersal from productive centers, the extent and nature of which varies with the area concerned. Dispersal may be directed offshore or along coasts; both types are discussed here.

The largest summer concentration of seals in the Cape Dorset area is to be found between about 3 and 10 miles offshore. Hunting becomes rapidly less productive when the outer limit is exceeded. Farther out in Hudson Strait ringed seals are decidedly scarce, although harp seals may be seen in large numbers at certain seasons. Seal hunting is very poor 50 miles across the strait on the northern Quebec coast. Johansen (1910) found no ringed seals farther than about 80 miles from land; they occur "only rarely in the outer parts of the drift ice, but in the middle and inner parts of this [ice] . . . everywhere on the coasts of East Greenland". Thus the ringed seal is essentially a coastal species.

There is evidence that the populations of areas of poor breeding potential may be maintained, to a large extent, by areas of high seal production along the same coast. It is believed that the highly successful hunting at Cape Dorset and at Lake Harbour to the east is mainly due to the large reservoir of breeding seals in the complex area between these two trading posts. Seals rapidly become less common around the west coast of Foxe Peninsula. This may indicate the limits of dispersal from the east. If many of the seals found around Cape Dorset are actually produced in the production center to the east, then we might expect that the take of seals of the year will show an increase in the Dorset area throughout the period following the pupping season and after the departure of the fast ice. This seems to be the case. Table XII shows the change in the catch near Cape Dorset, west of Andrew Gordon Bay (Fig. 21), through the period of July to the end of September. The September increase is believed to be real, although a χ^2 analysis of the material in Table XII (contingency table, with Yate's correction for continuity) reveals a 9% probability of such difference occurring by chance. September and October always produce more of the valued "silver jars" in the Cape Dorset area, according to Eskimo information. After mid-July, 17 first-year and 22 second-year animals were taken from the offshore waters near Cape Dorset. Assuming that all the young age-classes are well represented offshore in summer, first-year seals should have outnumbered the second-year animals in this sample, if all the second-year animals were born in the area. The figures therefore suggest that local pup production is supplemented from the more suitable breeding areas to the east. In northwest Foxe Basin, samples from around Igloolik and Skeoch Bay, some distance from the main productive centers around the entrance to Fury and Hecla Straits, produced 15 second-year animals and 9 first-year animals in September and October. The same factors are probably responsible for this unbalanced proportion.

TABLE XII. Change in the proportion of first-year seals in the catch near Cape Dorset, southwest Baffin Island.

	July	August	September
First-year seals	1[a]	8	11
Older seals	6	73	38
Percentage first-year seals	14	10	22.4

[a] This seal was the starveling shown on Figure 22.

POPULATION SAMPLES

Large collections of teeth for ageing from known localities were taken in southwest Baffin Island in 1953 and 1954. In developing the ecological patterns of the ringed seal populations of this area, little reference has been made to these collections; if the reasoning is sound, the teeth should reflect differences in the age-structure of populations inhabiting various localities at different times of the year.

Six populations have been distinguished, chronologically or geographically, and their make-up is depicted in Figures 29 to 31. The few seals taken before April 1 (the birthday of seals for the purpose of these figures) are put into the age-class of the following seal-year. Only seals for which there is definite evidence of source and date of collection are included in the histograms. In the discussion which follows, all seals of the seventh year or older are considered to be adult.

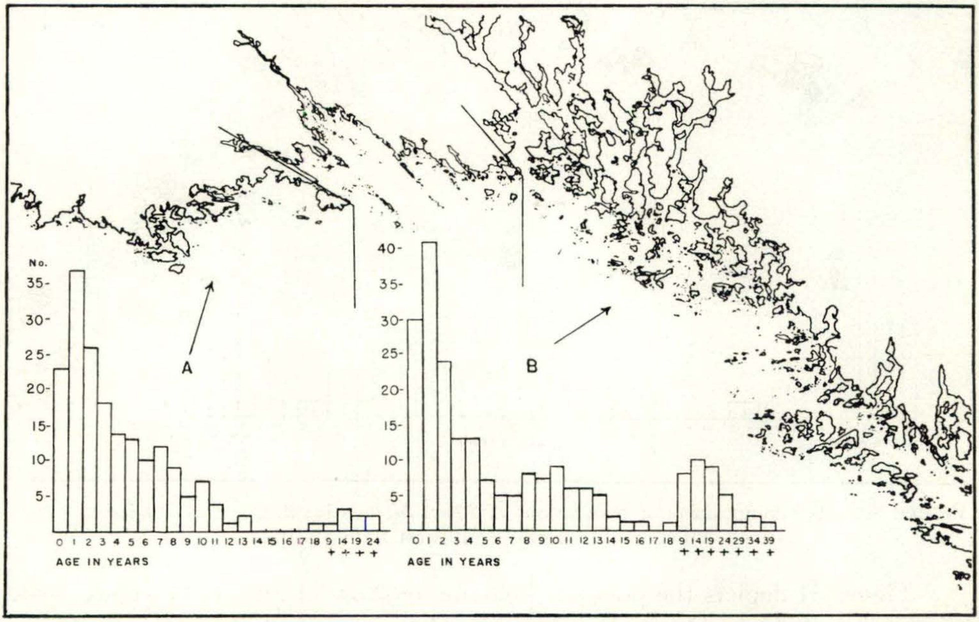

FIGURE 29. Age composition of the total samples of *Phoca hispida* from southwest Baffin Island.

Figure 29 shows the total samples for 1953 and 1954 from the simple coast near Cape Dorset (A) and from the more complex coast to the east (B). The difference between the adult populations of these coasts is quite apparent. (A) probably gives a fair picture of the structure of population of this coast, as it represents seals taken in all seasons, under all conditions. (B) does not represent a random sample of the immature seals of this coast, as large numbers of the teeth for ageing were taken in the late winter, when most immatures would be excluded from the catch. This, however, does not affect the difference between the adult sections of the histogram; the complex coast sample is considerably older in make-up.

Figure 30 compares populations living in the fast ice. The adult population dwelling in the less suitable ice of simple coasts and near the outer periphery of the ice of more deeply indented coastlines is younger in age-structure. The complex coast sample was taken before mid-June, before the large numbers of young seals had invaded the area during and following spring break-up. Thus it is believed that all, or almost all, the young seals shown on this histogram were winter residents. Most of the immature seals shown on the simple coast sample were taken during late June, when these had entered the fast ice from the offshore waters.

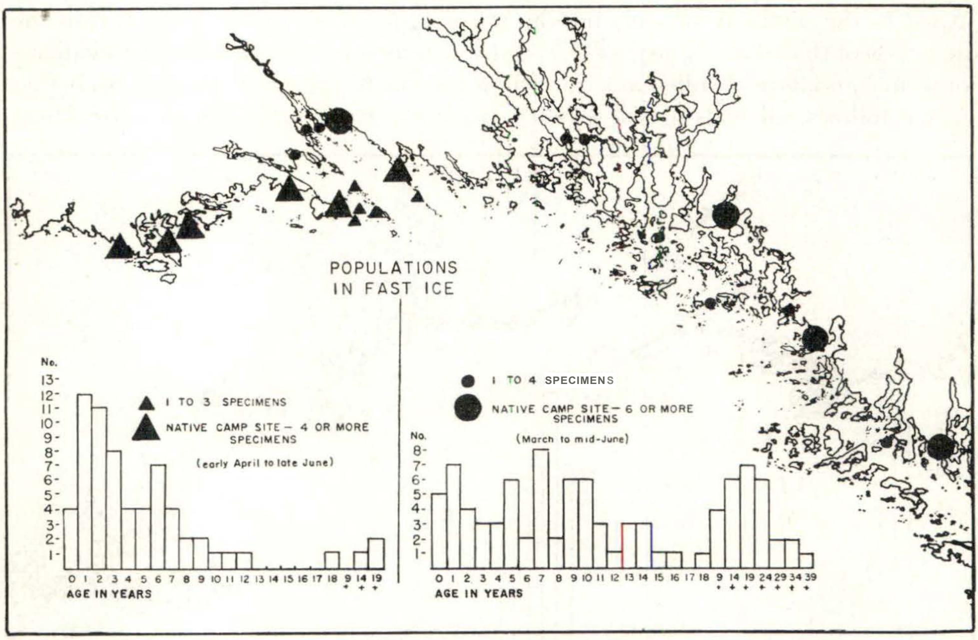

FIGURE 30. Age composition of populations of *Phoca hispida* inhabiting the fast ice of simple and complex coasts of southwest Baffin Island.

Figure 31 depicts the populations living offshore at all fast-ice edges in the winter and off Cape Dorset in summer. The winter sample is exclusively immature. The rapid falling off of adult seals in the older age-classes and the scarcity of first-year animals are both apparent in the summer offshore samples. A sample of open water seals from Foxe Basin in the period of January 31 to April 18 was similarly young in make-up. There were 10 one-year-olds, 9 two-year-olds, 7 three-year-olds, 5 four-year-olds, 2 five-year-olds, and 3 six-year-olds. The only older animal from the fast-ice edge was a sexually active male, 15 or more years old, taken on February 27. Residence in the fast ice, away from the open water, is a response to breeding needs. Neither of two adult females, of 9 and more than 15 years, taken in the open water off Churchill, Manitoba, on February 22, 1954, was pregnant. This unusual condition probably accounts for their presence there. An adult male jaw secured several miles off shore in the pack ice off Cape Dorset (SD-36, 1954) was in a badly diseased condition. The canines, which were very worn, were decayed through to the pulp cavity. Rings in the cementum, which were not affected by the decay, suggested an age of about 10 years. The presence of this animal outside the fast ice was probably related to this abnormality.

It can be seen from the diversity of these seasonal and geographical samples that it is difficult to obtain a true picture of the total population inhabiting any stretch of coast. For this reason, such features as mortality rates and effect of hunting pressure may be impossible to determine accurately, regardless of the size of the population samples.

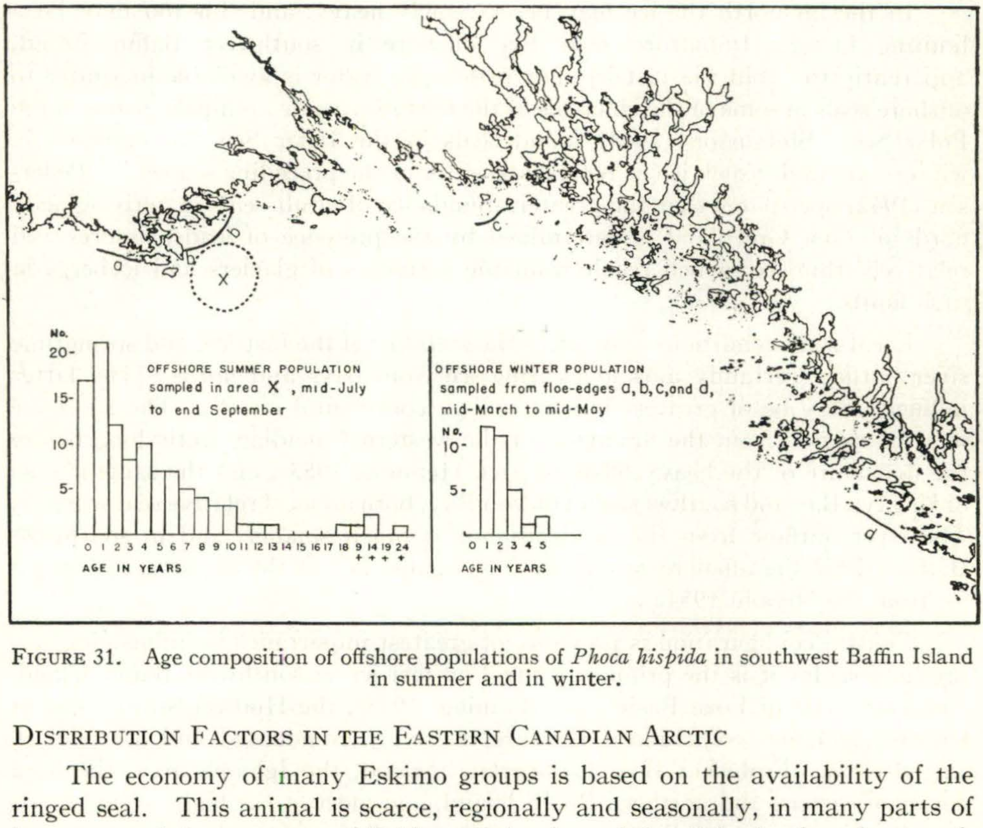

FIGURE 31. Age composition of offshore populations of *Phoca hispida* in southwest Baffin Island in summer and in winter.

DISTRIBUTION FACTORS IN THE EASTERN CANADIAN ARCTIC

The economy of many Eskimo groups is based on the availability of the ringed seal. This animal is scarce, regionally and seasonally, in many parts of its range and the economy of Eskimos living in such localities is often depressed. The previous few sections have dealt with the importance of quantity and quality of fast ice in determining local seal production, particularly in southwest Baffin Island. Ice conditions may well be the key to ringed seal distribution throughout its range.

Temperature, as this affects the formation of fast ice, certainly delimits the southern range of this species. This is undoubtedly the limiting factor in southwest Greenland, where little ice forms south of latitude 67° N and the ringed seal is correspondingly scarce. In Canada, the animal becomes progressively scarcer south along the Labrador coast, although a few may pup as far south as northern Newfoundland (Fisher, 1950). Even in northern Labrador conditions may not be optimal. Late freezing and light snow cover is found in the fiords of this area and seals are scarce on the bay ice until the late spring thaw, although they may be more common on the ice outside the fiords earlier in the spring (Wheeler, 1953). At Hopedale, at about 55°N on the Labrador coast, an Eskimo who was familiar with conditions on southwest Baffin Island informed the author that few seals give birth on the bay ice of this area. More seals pup on the fast ice of the outer skerries, which, due to the influence of the ice-laden Labrador Current, is formed early and develops a sufficient snow cover.

In the far north the ice may be extremely heavy, and this too may be a limiting factor. Immature seals live offshore in southwest Baffin Island, apparently to avoid the fast ice, but little open water is available in winter to offshore seals in some of the channels of the northern arctic archipelago and in the Polar Sea. Stefansson (1944) found seals in the Polar Sea "in numbers in winter only under such ice as represents water of the preceding season." Pedersen (1942) speculates that the greater abundance of adult seals in active-glacier fiords of East Greenland is determined by the presence of leads, fissures and relatively thin ice, which result from the activities of glaciers and icebergs in such fiords.

Local wind conditions may affect the stability of the fast-ice, and springtime river outflow certainly aids in clearing ice from bays and fiords. The latter influence may be of greatest importance on continental coasts. The shore ice may be cleared from the mainland of the western Canadian arctic long before the departure of the heavy offshore pack (Jenness, 1953), and the same is true of Ungava Bay and southwestern Hudson Bay, both areas of relative seal scarcity. The river outflow from the arctic islands is much smaller, and in southwest Baffin Island the offshore waters were navigable before the departure of much ice from the bays in 1954.

Coastal configuration is probably of greatest importance in influencing seal production, for it is the primary control on fast ice in southwest Baffin Island. The east coast of Foxe Basin (see Manning, 1943), the Hudson Strait coast of Quebec, and most of Hudson Bay are relatively unindented and are poor in ringed seals. Frobisher Bay, Cumberland Sound, the Igloolik area, the fiord coasts of eastern and northern Baffin Island, and most of the high arctic islands are all complex in coastline and plentifully supplied with seals. The coasts of Ungava Bay and northwestern Hudson Bay, intermediate in complexity, are intermediate in hunting productivity. Although no exact correlation may be drawn between seal abundance and coastal topography, nevertheless, a connection seems to be established on the basis of known seal distribution.

It appears, then, that population make-up, seal productivity, and abundance are related chiefly to natural geographical circumstances, as these affect the formation of stable fast ice for the purposes of reproduction.

SUMMARY

1. The material consists of large collections of stomach contents, jaws and claws for ageing, reproductive organs, and body measurements from *Phoca hispida* of southwest Baffin Island and northern Foxe Basin, with smaller collections from other areas of the eastern Canadian arctic.

2. Over 750 seals were aged by the dentinal annuli of the canine teeth. Incompletely calcified dentine, which may be thin and transparent or vacuolar and reflective, is laid down in the spring, generally during the fasting season. It may be that Vitamin D, which has been found to be an active agent in dentine deposition, is required in large quantities for the formation of the densest dentine, although seal fatness may be maintained by smaller amounts of food. The Eskimo method of ageing by pelage is of limited reliability. The claws are marked by alternating light and dark bands, the light band being formed in the spring and early summer; these are useful for ageing seals up to about the tenth year, beyond which wearing makes them unreliable.

3. The nose-tail length increases from about 65 cm. at birth to about 135 cm. in adults, the females being slightly smaller. An extreme adult size of about 5.5 feet (168 cm.) and 250 pounds (113 kg.) is suggested. There is little antero-posterior growth gradient, but the flippers grow less rapidly than the animal as a whole.

4. At least 72 food organisms were detected in stomachs from seven localities. The crustaceans *Themisto libellula* and *Mysis oculata*, and the polar cod (*Boreogadus saida*) were the most common food elements. The seal may dive to about 50 fathoms or 100 metres, but generally turns from inshore feeing on *Mysis*, decapods, or fish to strictly planktonic feeding when in deeper offshore waters, and in southwest Baffin Island its offshore food is almost exclusively *Themisto*. The patterns of feeding suggest that food is not a limiting factor in the distribution and abundance of the ringed seal.

5. There is a general relaxation of feeding in the early spring, but intense fasting does not take place until June and early July, when most seals are basking on the fast ice. Feeding is resumed and blubber is restored after departure of the ice. Not much blubber loss occurs before the basking season, and immediately after the departure of the fast ice, seals killed in the open water are more inclined to sink. There is some evidence that seals living inshore in deeply indented coastlines, where the late departure of the ice may facilitate a more prolonged basking and fasting season, show a greater lag in the return to floating condition in the summer. Annual variations in the departure time of the ice may also affect the proportion of seals which sinks in the summer.

6. The moulting season extends from mid-May to mid-July, with a peak in June. Some abnormal individuals may moult much later.

7. Studies of the testes and bacula reveal that the male does not mature, on the average, until 7 years old. Most females ovulate for the first time, usually in the left ovary, when about 6 years old; 12% were mature in the fifth year, 22% in the sixth year, and 79% in the seventh year. Early ovulations are not as likely to result in pregnancy.

8. The males are in rut from sometime in March until mid-May at the latest, and the females normally ovulate shortly after parturition, while still lactating; the peak of mating activity probably occurs in mid-April.

9. The control of folliculation by the corpus luteum imparts an alternation of ovulation between right and left ovaries. Transmigration of the ovum or blastocyst to the uterine cornu opposite its side of origin may be one of the factors upsetting this alternation.

10. The corpus luteum increases in size and develops more connective tissue and vascularization at the time of implantation of the blastocyst. It regresses rapidly after parturition, freeing the opposite ovary for ovulation.

11. First ovulations do not always result in pregnancy, and it appears that the newly matured female may ovulate outside the normal breeding season.

12. The blastocyst implants, on the average, in early August, after about 3½ months, delay in development. Embryos may implant over a period of about 45 days, corresponding to the length of the breeding season. The curve of human embryonic growth fits the data on ringed seal embryonic growth very well, when adjusted for birth-size and gestation period.

13. The young seal is born on the fast ice in a lair hollowed out by the female in the overlying snow or in a natural hollow in a pressure ridge near shore. Seals may move into areas of broken ice in autumn or appear at tide-cracks in winter; in both situations drifting results in suitable depths of snow for construction of pupping-lairs.

14. The peak of pup production occurs near the beginning of April, or perhaps somewhat later at higher latitudes. The new-born seal weighs about 10 pounds (4.5 kg.) and measures about 25½ inches (65 cm.) in standard length. The foetal hair is completely shed in May or June. The females may attend the young seals until the break-up of winter ice, although weaning may occur sooner in most cases.

15. The sex ratio of immatures is about 53.5 males to 46.5 females.

16. The habit of pupping on the fast ice makes ice quantity and quality of primary importance in the reproductive ecology of this species. Coastal configuration governs the amount of fast ice and also the depth of snow cover which is available for construction of the pupping-lair. Ice stability is affected too, and this is important, for pups born on the unstable ice of simple coasts are in danger of premature separation from the females. Starvelings are most common in such areas, and there may be a difference in the average size of first-year seals from complex and from simple coasts. The most suitable ice for pupping

purposes is inhabited by the older adults, and younger adults are proportionately more common in less stable ice. This may result from experience with age, or from competition for more suitable areas. There is a size difference, without respect to age, between seals of simple and complex coasts. This probably results from the larger average size of pups produced on the stable-ice complex coasts. Seals of higher latitudes are considerably larger, probably through the same effect of better ice conditions in more northerly localities.

17. The adults tend to be sedentary in the areas delimited by the fast ice of winter, while the immatures are generally offshore residents. There is a movement of immature seals into the fast ice at break-up, and a less pronounced movement in the same direction at freeze-up. Coastal complexity may exert a damping effect on seal movements, and this may be the factor behind the greater abundance of immature seals inshore on complex coastlines and the smaller numbers of inshore summering adults on simple coastlines. Ringed seals do not disperse very far offshore, and dispersal in southwest Baffin Island seems to be directed from the more productive complex coasts to the simple coasts of lesser production potential.

18. The factors affecting ice formation appear to determine the distribution and abundance of the ringed seal, throughout its wide range in the eastern Canadian arctic.

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APPENDIX

Tables giving body measurements of ringed seals, and details of the food found in their stomachs.

TABLE I. Detailed body measurements of 102 *Phoca hispida* from southwest Baffin Island and northwest Foxe Basin. The measurements are defined in the text.

Age in years	Field number	Sex	Standard length	Maximum girth	Axillary girth	Navel to anus	Penis to anus	Foreflipper length	Foreflipper width	Hindflipper length	Hindflipper width	Blubber thickness	Weight
			cm.	*cm.*	*cm.*	*cm.*	*cm.*	*cm.*	*cm.*	*cm.*	*cm.*	*mm.*	*lb.*
Full-term foetus......	SD–33	M	61	..	40	16	9	12	7.5	15	18	10	9.8
0.3	SD–267	F	78	72	72	22	n.a.	15	10.5	21	27	18	32
0.3	SD–282	F	74	54	55	21	n.a.	14	9	19	24	17	20
0.4	S–8	M	76	68	65	24	..	..	11	..	27	25	..
0.4	S–10	F	87	68	66	24	n.a.	..	11.5	..	28	25	..
0.4	S–26	M	86	64	64	23	11.5	..	11	..	30	25	33
0.4	S–49	F	77	65	64	21	n.a.	..	9	..	24	28	29
0.4	S–50	F	77	65	65	19.5	n.a.	..	11	..	27.5	25	29
0.4	S–51	F	86	72	70	24	n.a.	..	11	..	27	32	38
0.5	S–55–6	M	101	86.5	86.5	28.5	15	15	11.5	23.5	29	29	61
0.5	S–55–16	F	85	77	75.5	26	n.a.	14.5	11.5	23	27.5	27	45
0.5	S–55–17	M	95	82.5	81.5	28	16	16	12	22	29	32	59
0.5	S–55–32	M	90.5	83	79	29.5	15	14	11	21	27.5	28	..
1.0	SD–3	M	102	98	88	31	16	..	..	..	..	43	83
1.4	S–7	F	95	79	76	25.5	n.a.	..	11.5	..	29	32	..
1.4	S–9	F	81	70	68	24	n.a.	..	11.5	..	28	25	..
1.4	S–12	M	104	83	83	29	14	..	14	..	35	25	63
1.4	S–29	M	98	77	71	27	13	..	11.5	..	29	22	48
1.4	S–31	F	92	73	70	25.5	n.a.	..	11.5	..	28.5	28	45
1.4	S–47	M	102	79	77	29	14.5	..	13	..	32	25	57
1.4	S–48	F	90	77	75	26	n.a.	..	11.5	..	30	25	48
1.5	S–55–29	M	99	94	88.5	29.5	17	18	12	19.5	27	37	88
1.5	S–55–33	M	102	83	83.5	30	15.5	16	12.5	23	30	31	..
1.5	S–55–51	F	109	97	93	32	n.a.	16.5	14	24	34	43	..
1.5	S–55–54	F	105	91	89.5	31	n.a.	15	13	23	32.5	31	81
1.5	S–55–57	M	109	88.5	87	31.5	16	17.5	12.5	25	32	27	..
1.5	S–55–66	F	79	75	72.5	24	n.a.	13	10	19	26	32	..
2.4	S–11	M	102	85	83	30	15	..	14	..	35	32	..
2.4	S–22	M	93	84	81	28	14	..	11	..	28.5	..	..
2.4	SD–482	M	106	91	90	29	15	16.5	14	26	33	26	82
2.5	S–55–11	F	111	94	91	30.5	n.a.	15	11.5	21.5	31.5	30	..
2.5	S–55–53	M	93.5	74.5	72	23	13.5	13.5	11	20	24	30	49
2.5	S–55–55	M	115	96	92	34.5	18	16.5	13	24	31	38	92
3.0	SD–22	M	101	92	90	27	13	..	..	..	..	40	76
3.2	SD–119	F	105	85	83	29	n.a.	19	14	29	32	30	75
3.4	S–32	F	98	80	79	26	n.a.	..	12	..	30.5	28	57.5
3.4	SD–479	M	106	91	91	31	16.5	18	15	27	34	29	81
3.5	S–55–3	M	114	96.5	94	33.5	18	18	14.5	28	35.5	42	84
4.4	SD–215	M	95	..	..	29	14	16	13.5	24	33	33	63
4.4	SD–266	F	104	80	81	29	n.a.	17	13	26	34.5	32	67
4.4	SD–275	M	108	80	78	31	16	15	13.5	24	33	18	66
4.4	S–14	F	111	99	95	28	n.a.	..	14	..	37	38	90

TABLE I. Continued

Age in years	Field Number	Sex	Standard length	Maximum girth	Axillary girth	Navel to anus	Penis to anus	Foreflipper length	Foreflipper width	Hindflipper length	Hindflipper width	Blubber thickness	Weight
			cm.	*cm.*	*cm.*	*cm.*	*cm.*	*cm.*	*cm.*	*cm.*	*cm.*	*mm.*	*lb.*
4.4	S–16	M	101	83	76	29	15	..	11.5	..	32	..	..
4.4	S–19	M	106	86	81	30.5	16.5	..	13	..	32	..	..
4.4	S–33	M	114	88	88	33	18	..	14	..	36	32	..
4.5	SD–496	F	109	84	83	36	n.a.	21	14	26	33	33	..
4.5	S–55–28	F	114	113	105	35	n.a.	20	13	23.5	31	49	122
5.4	S–17	M	102	80	..	..	16	..	11.5	..	32	..	..
5.4	S–18	M	101	84	82	30.5	16.5	..	13	..	33	..	..
5.4	S–34	M	103	83	81	28	15	..	12	..	33	32	..
5.4	S–39	F	101	76	75	30	n.a.	..	11.5	..	30	28	54.5
5.4	S–45	M	115	93	89	33	18	..	13.5	..	36	35	92
5.5	SD–516	M	103	94	91	33	17.5	18	14	25	32	36	..
5.5	S–55–1	F	122	102	99	33.5	n.a.	16	13.5	29	33.5	48	117
5.5	S–55–2	M	106.5	81.5	81.5	31.5	17	16	12.5	25.5	33	28	64
5.5	S–55–4	M	116	99	97.5	33	19	18.5	15	28.5	37	44	95
5.5	S–55–15	F	114.5	96.5	94	30	n.a.	16.5	13.5	23	..	48	94
5.5	S–55–19	M	122	103	102	35	18.5	18	14	28	37	40	119
5.5	S–55–52	F	109	98	96	31	n.a.	17.5	15	22.5	..	49	97
5.5	S–55–56	M	121	99	99	36	20	16	12.5	27.5	32.5	44	..
6.4	SD–296	F	119	99	95	37	n.a.	19	14	28	38	42	..
6.4	S–3	F	102	..	86	32	n.a.	..	12.5	..	33	45	..
6.4	S–15	F	115	92	91	30	n.a.	..	14	..	36	32	84
6.4	S–21	F	106	90	85	30.5	n.a.	..	13	..	33	..	..
6.4	S–41	M	120	89	86	33	19	..	12	..	34	27	81.5
6.4	SD–485	M	127	97	95	39	18	19.5	14.5	27	38	38	114
6.5	SD–493	M	110	94	91	33	15.5	15	12.5	22	29	44	..
6.5	S–55–9	M	139.5	107.5	103.5	41.5	22	20.5	15.5	29	43	31	135
6.5	S–55–14	M	127	110	108.5	39.5	19	18	14.5	30.5	..	55	142
7.3	SD–274	M	113	94	93	32	16.5	16	14	22	34	31	90
7.3	SD–276	M	107	83	81	29.5	16	17	12.5	22.5	30	24	..
7.4	S–36	F	115	95	94	36	n.a.	..	13.5	..	34	42	91
7.4	S–46	F	113	98	95	34	n.a.	..	13.5	..	33	44	97.5
7.5	S–55–49	F	112	91	91	31	n.a.	15.5	12	26.5	33.5	33	..
8.4	S–28	M	126	105	103	33	19	..	14	..	37	44	..
8.4	SD–480	M	126	96	92	37	20	18	15	27	36	26	104
8.5	SD–523	M	117	97	92	32	17	17	13	23	36	49	106
8.5	SD–527	F	111	110	103	31	n.a.	17	14	25	32	52	118
8.5	S–55–47	M	129	117.5	113	36	21	17	15	28	..	52	..
9.4	S–20	F	105	84	85	28	n.a.	..	11	..	30.5	..	..
9.4	S–38	F	112	94	88	34	n.a.	..	13.5	..	32	32	81
9.5	S–55–26	M	136.5	119	114.5	40	21.5	..	..	..	..	56	..
10.3	SD–273	F	128	103	102	37	n.a.	20	15.5	29	37	34	121
10.3	SD–279	M	110	98	93	32	18	17	14	27	34	33	97
10.4	SD–464	M	126	102	102	35	19	19	15	27	39	29	..
10.4	S–25	M	120	100	98	33	17	..	14	..	33	37	100
10.5	S–55–13	M	140.5	116	116	40.5	21.5	19	14.5	30.5	38.5	54	169
10.5	S–55–20	M	150.5	114.5	111	42.5	24	23	16	31.5	39.5	30	150
10.5	S–55–39	F	123	111	110	37.5	n.a.	17.5	14.5	27	38	41	..
11.4	SD–301	M	118	99	95	36	20	17	13	26	35	31	..
11.4	S–4	F	118	..	104	36	n.a.	..	14	..	38	44	..
13.4	SD–461	F	130	106	104	38	n.a.	18	15	26	39	33	..
13.4	S–30	M	127	105	105	38	20	..	14	..	36	38	123
13.4	S–40	M	127	106	102	38	20	..	13.5	..	38	33	121.5
13.5	S–55–18	F	120	118.5	113.5	33.5	n.a	18.5	14.5	28	35.5	52	153
15+	S–27	F	113	86	84	33	n.a.	..	13	..	33	25	73

TABLE I. Concluded

Age in years	Field Number	Sex	Standard length	Maximum girth	Axillary girth	Navel to anus	Penis to anus	Foreflipper length	Foreflipper width	Hindflipper length	Hindflipper width	Blubber thickness	Weight
			cm.	*cm.*	*cm.*	*cm.*	*cm.*	*cm.*	*cm.*	*cm.*	*cm.*	*mm.*	*lb.*
16.5	S–55–12	M	153.5	129	127	48.5	25.5	26	16	33	..	63	214
ca. 20	S–55–31	M	141	122	119.5	45.5	23.5	23	18	30	43	47	..
20+	SD–302	M	117	102	97	35	16.5	18	13	28	34	29	..
20+	S–55–50	M	156	131	131	49	24	20.5	16	30	41	52	222
25+	S–37	M	117	95	94	38	20	..	13	..	34	35	94

TABLE II. Certain measurements of *Phoca hispida*, expressed as percentages of standard lengths. These are derived from regression lines for which standard errors of the estimates are given.

	Navel to anus	Penis to anus	Fore-flipper length	Fore-flipper width	Hind-flipper length	Hind-flipper width
FEMALE:						
Percentage of standard length of 60 cm....	28.46	....	19.41	13.04	26.65	34.86
Percentage of standard length of 160 cm...	29.07	....	12.00	10.46	18.85	26.00
Standard error of estimate...............	1.79	....	1.44	0.74	1.68	1.45
MALE:						
Percentage of standard length of 60 cm....	27.97	14.57	18.26	13.79	24.83	33.08
Percentage of standard length of 160 cm...	30.07	17.05	13.70	10.17	19.42	27.43
Standard error of estimate...............	1.57	0.97	1.23	0.78	1.59	2.00

TABLE III. Food specimens taken from *Phoca hispida* of Ungava Bay and northern Labrador in 1947 to 1950.

Origins of stomachs:

A. Near Inuksilik, approximately 58° 47′ N. by 68° 23′ W. (1 stomach).
B. Mouth of Koksoak River, approximately 58° 32′ N. by 68° 10′ W. (11 stomachs).
C. Mouth of Leaf Bay, approximately 59° 00′ N. by 68° 40′ W. (5 stomachs).
D. Tunnusaksuk Fiord, approximately 60° 15′ N. by 64° 30′ W. (7 stomachs).
E. Keglo Bay, approximately 59° 10′ N. by 65° 45′ W. (1 stomach).
F. Port Burwell and Forbes Sound, approximately 60° 22′ N. by 64° 50′ W. (3 stomachs).
G. Button Islands, approximately 60° 25′ N. by 64° 50′ W. (1 stomach).
H. Adlorlik Fiord, approximately 59° 30′ N. by 65° 25′ W. (1 stomach).
I. Near Imilik, approximately 60° 45′ N. by 69° 27′ W. (1 stomach).
J. West of Cape Hope's Advance, approximately 61° 05′ N. by 69° 37′ W. (2 stomachs).

Food species	Number of specimens	Number of times in stomachs	Number of times dominant	Areas of occurrence
Turritellidae (unidentified)	1	1	...	G
Limacina helicina (Phipps)	2	1	...	G
Cephalpoda (unidentified squid beaks)	6	5	...	J, H, F
Calanus hyperboreas Krøyer	1	1	...	B
Pareuchaeta norvegica (Boeck)	1	1	...	F
Mysis oculata (Fabricius)	8535	6	5	D, F, G, L
Mysis mixta Lilljeborg	2346	21	4	A, B, C, D, F, H
Gammaridea (unidentified)	5	5	...	B, C, F, H
Orchomenella pinguis (Boeck)	1	1	...	F
Ampelisca eschricti Krøyer	1	1	...	J
Haploops setosa Boeck	2	1	...	F
Ampeliscidae (unidentified)	1	1	...	F
Amphithopsis longicaudata Boeck	1	1	...	F
Atylus carinatus (J. C. Fabricius)	1	1	...	G
Rachotropis aculeata (Lepechin)	1	1	...	H
Pontogeneia inermis (Krøyer)	1	1	...	B
Weyprechtia pinguis (Krøyer)	1	1	...	F
Gammarellus homari (J. C. Fabricius)	1	1	...	H
Gammarus oceanicus Segerstråle	7	4	...	A, B, I
Gammarus wilkitskii Birula	11	5	...	A, B, C, D
Ischyrocerus anguipes Krøyer	1	1	...	F
Themisto libellula (Mandt)	36	10	...	A, B, C, D, F, H
Euphausiacea (unidentified)	1	1	...	J
Thysanoessa inermis (Krøyer)	270	5	2	A, C, D
Thysanoessa raschi (M. Sars)	800	9	4	A, B, C, E, F
Decapod larvae (unidentified)	3	1	...	C
Natantia (unidentified)	9	2	1[a]	F, I

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[a] Dominance as a group; specimens identified to species where possible.

TABLE III. Concluded.

Food species	Number of specimens	Number of times in stomachs	Number of times dominant	Areas of occurrence
Sergestes arcticus (Krøyer)	1	1	...	D
Pandalus montagui Leach	29	2	1	J, F
Hippolytidae (unidentified)	31	6	1[a]	B, E, F, I, J
Lebbeus groenlandicus (J. C. Fabricius)	1	1	...	B
Lebbeus polaris (Sabine)	5	1	...	F
Eualus fabricii (Krøyer)	20	4	...	C, F
Eualus gaimardi (Milne-Edwards)	23	3	...	E, F
Eualus macilentus (Krøyer)	3	3	...	F, J
Spirontocaris spinus (Sowerby)	1	1	...	F
Argis dentata Rathbun	3	1	...	C
Fish (unidentified)	39	19	5[a]	A, B, C, D, F
Boreogadus saida (Lepechin)	2	2	1	B
Reinhardtius hippoglossoides (Walbaum)	15	3	1	J, F
Ammodytes sp.	55	1	1	B
Small sculpins (unidentified)	7	4	...	B, J
Triglops pingeli Reinhardt	9	1	...	B
Triglops sp.	4	1	...	C
Lumpenus fabricii Reinhardt	2	1	...	B
Lumpenus sp.	2	2	...	B, C

[a] Dominance as a group; specimens identified to species where possible.

TABLE IV. Food specimens taken from *Phoca hispida* of southwest Baffin Island in 1953 and 1954. The contents of 153 stomachs, of which 30 were empty, are listed here. The geographical distribution of the dominant food forms is outlined on Figure 5. A plus sign following the number of specimens indicates that, due to examination of stomachs in the field or to subsampling for laboratory analysis, a full count cannot be given.

Food species	Number of specimens	Number of times in stomachs	Number of times dominant
Maldanidae (unidentified tubes)	2	1	....
Pelecypoda (unidentified)	1	1	....
Astarte elliptica Brown	1	1	....
Astarte sp.	2	1	....
Cephalopoda (unidentified squid beaks and fragments)	8	3	....
Balanus sp. (shell fragments)	1	1	....
Mysis oculata (Fabricius)	6,365+	14	9
Mysis mixta Lilljeborg	7	6	....
Mysis sp.	350	1	....
Gammaridea (unidentified)	1	1	....
Pseudalibrotus littoralis (Krøyer)	1	1	....
Pseudalibrotus sp.	4	2	....
Ampeliscidae (unidentified)	300	1	1
Haploops setosa Boeck	106	5	....
Pardalisca cuspidata Krøyer	1	1	....
Calliopius laeviusculus (Krøyer)	3	1	....
Gammarellus homari (Fabricius)	2	2	....
Gammarus setosus Dementieva	269	4	1
Gammarus oceanicus Segerstråle	1	1	....
Gammarus wilkitskii Birula	2	1	....
Hyperia galba (Montague)	55	2	....
Themisto libellula (Mandt)	18,645+	93	75
Euphausiacea (unidentified)	24+	5	....
Meganyctiphanes norvegica (M. Sars)	34	10	....
Thysanoessa inermis (Krøyer)	29	5	....
Thysanoessa raschi (M. Sars)	328	25	....
Thysanoessa sp.	64	8	....
Natantia (unidentified)	76+	2	1[a]
Hippolytidae (unidentified)	13	7	1[a]
Lebbeus polaris (Sabine)	50	8	3
Lebbeus groenlandicus (Fabricius)	15+	7	3
Spirontocaris phippsi (Sowerby)	5	3	....
Spirontocaris spinus (Krøyer)	1	1	....
Eualus gaimardi (Milne-Edwards)	6	3	....
Eualus fabricii (Krøyer)	11	4	....
Argis dentata Rathbun	81	3	1

[a] Dominance as a group; specimens identified to species where possible.

TABLE IV. Concluded.

Food species	Number of specimens	Number of times in stomachs	Number of times dominant
Sabinea septemcarinata (Sabine)	2	2	....
Hyas coarctatus Leach	1	1	....
Fish (unidentified)	56+	11	7
Boreogadus saida (Lepechin)	94+	22	19
Lycodes sp.?	1	1	1
Small sculpins (unidentified)	35+	5	....

TABLE V. Food specimens taken from *Phoca hispida* of northern Foxe Basin in September and October, 1955. The contents of 51 stomachs, of which 6 were empty, are listed here. The geographical distributions of the dominant food forms are outlined on Figure 6. A plus sign following the number of specimens indicates that, due to examination of stomachs in the field or to subsampling for laboratory analysis, a full count cannot be given.

Food species	Number of specimens	Number of times in stomach	Number of times dominant
Polychaeta (unidentified setae)	?	1	....
Maldanidae (unidentified tubes)	6	1	....
Pelecypoda (unidentified)	1	1	....
Nucula tenuis (Montague)	3	2	....
Portlandia arctica (L.)	2	1	....
Gastropoda (unidentified operculum)	1	1	....
Margarita helicina (Phipps)	6	1	....
Fusus sp.	1	1	....
Buccinum sp.	2	1	....
Cephalopoda (unidentified squid beak)	1	1	....
Balanus sp. (unidentified shell fragment)	1	1	....
Calanoidea (unidentified)	1	1	....
Calanus hyperboreas Krøyer	1	1	....
Mysis oculata (Fabricius)	8,933+	26	20
Gammaridea (unidentified)	1	1	....
Pseudalibrotus glacialis G. O. Sars	147	9	....
Pseudalibrotus nanseni G. O. Sars	70	6	....
Stegocephalus inflatus Krøyer	9	2	....
Acanthostephia malmgreni (Gøes)	2	2	....
Apherusa glacialis (Hansen)	2,252	3	2
Atylus carinatus (Fabricius)	5	2	....
Pontogeneia inermis (Krøyer)	12	1	....
Gammarus wilkitzkii Birula	489+	15	3
Gammaracanthus loricatus (Sabine)	28+	10	....
Themisto libellula (Mandt)	1,746	16	2
Hippolytidae (unidentified)	6	3	....
Lebbeus polaris (Fabricius)	6	3	1
Spirontocaris spinus (Sowerby)	2	1	....
Spirontocaris phippsi (Krøyer)	1	1	....
Eualus gaimardi (Milne-Edwards)	12	4	....
Eualus fabricii (Krøyer)	4	3	....
Argis dentata Rathbun	2	2	....
Chaetonymphon hirtripes (Bell)	1	1	....
Fish (unidentified)	40+	14	5
Boreogadus saida (Lepechin)	66+	14	11
Cottidae (unidentified)	5	1	1

TABLE VI. Food specimens taken from five *Phoca hispida* of Frobisher Bay in 1948, 1951 and 1952.

Origins of seals:

A. Estuary of Sylvia Grinnell River, approximately 63° 45′ N. by 68° 36′ W. July 22, 1948.
B. Ney Harbour, approximately 62° 51′ N. by 67° 21′ W. August 28, 1951.
C. Head of Frobisher Bay. September 2, 1951.
D. Same position as A. July 10, 1952.
E. Jackman Sound, approximately 62° 15′ N. by 66° 18′ W. August 19, 1952.

Food species	Number of specimens	Number of times in stomachs	Number of times dominant	Areas of occurrence
Margarita helicina (Phipps)	19	1	...	C
Limacina helicina (Phipps)	1	1	...	D
Calanus finmarchicus (Gunnerus)	1	1	...	E
Mysis oculata (Fabricius)	701	4	2	A, B, D, E
Pseudalibrotus littoralis (Krøyer)	1	1	...	D
Gammarus sp.	1	1	...	C
Themisto libellula (Mandt)	105	4	...	A, B, D, E
Thysanoessa inermis (Krøyer)	3	1	...	D
Thysanoessa raschi (M. Sars)	12	3	...	B, D, E
Thysanoessa sp.	4	1	...	D
Lebbeus microceros (Krøyer)	1	1	...	A
Fish (unidentified)	11	3	2	B, C, D
Boreogadus saida (Lepechin)	1	1	...	D
Small sculpins (unidentified)	310	2	1	D, E
Icelus sp.	1	1	...	D

TABLE VII. Food specimens taken from *Phoca hispida* of three high arctic localities in 1951, 1952 and 1955.

Origins of stomachs:

A. Parr Inlet, approximately 82° 30′ N. by 67° 30′ W. August, 1951. (3 stomachs).

B. Slidre Fiord, approximately 79° 50′ N. by 86° 10′ W. August and September, 1955. (3 stomachs).

C. Mould Bay, approximately 76° 20′ N. by 119° 30′ W. August 23, 1952. (1 stomach).

Food species	Number of specimens	Number of times in stomach	Number of times dominant	Areas of occurrence
Pelecypoda (unidentified shell frag.)	2	2	...	A
Cephalopoda (unidentified beaks)	2	2	...	A, B
Polychaeta (unidentified)	1	1	...	B
Polynoidae (unidentified)	1	1	...	A
Mysis oculata (Fabricius)	11,511	6	4	A, B, C
Pseudalibrotus glacialis G. O. Sars	5	2	...	B
Pseudalibrotus nanseni G. O. Sars	28	2	...	A, B
Anonyx nugax (Phipps)	480	1	1	A
Socarnes bidenticulatus (Bate)	127	1	...	A
Apherusa glacialis (H. J. Hansen)	100	1	...	A
Atylus carinatus (J. C. Fabricius)	49	2	...	A
Gammarus setosus Dementieva	50	1	1	A
Gammarus wilkitzkii Birula	21	2	...	A, B
Gammaracanthus loricatus (Sabine)	5	1	...	A
Themisto libellula (Mandt)	25	2	...	A, B
Natantia (unidentified)	1	1	...	B
Lebbeus polaris (Sabine)	1	1	...	B
Spirontocaris phippsi (Krøyer)	1	1	...	A
Sabinea septemcarinata (Sabine)	13	4	...	A, B, C
Small fish (unidentified fragments)	2	2	...	B
Boreogadus sp. (and larger Gadidae?)	5	1	1	A
Cottidae (unidentified)	1	1	...	A

TABLE VIII. Food specimens taken from *Phoca hispida* of Southampton Island in 1955.

Origins of stomachs:

A. Off Native Point, 63° 41′ N. by 82° 38′ W. May 5. (1 stomach).
B. Near Seahorse Point, approximately 63° 47′ N. by 80° 10′ W. August 31. (2 stomachs).
C. South Bay, 64° 04′ N. by 82° 24′ W. September 1. (2 stomachs).

Food species	Number of specimens	Number of times in stomach	Number of times dominant	Areas of occurrence
Mysis oculata (Fabricius)	6603	3	1	B, C,
Halirages nilssoni Ohlin	1	1	...	B
Themisto libellula (Mandt)	980	3	2	B, C
Thysanoessa raschi (M. Sars)	122	3	1	A, B, C
Thysanoessa inermis (Krøyer)	1	1	...	C
Lebbeus polaris (Sabine)	4	1	1	A
Spirontocaris spinus (Krøyer)	3	1	...	A
Fish (unidentified)	4	2	...	C

TABLE IX. Food specimens taken from two *Phoca hispida* near the mouth of the Churchill River, Manitoba, at 58° 54′ N. by 94° 10′ W. February 22, 1954.

Food species	Stomach 1	Stomach 2
Lysianassidae (unidentified)	1	
Hippolytidae (unidentified)	4	
Lebbeus polaris (Sabine)	3	1
Lebbeus groenlandicus (Fabricius)	47	
Eualus gaimardi (Milne-Edwards)	11	
Eualus fabricii (Krøyer)	12	
Small fish (unidentified)	2	2
Cottidae (unidentified)	....	1

Some Aspects of Growth and Reproduction of the Bearded Seal, *Erignathus barbatus* (Erxleben)[1]

"CALANUS" SERIES NO. 13

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ABSTRACT

This preliminary study is based on material from 113 specimens from the eastern Canadian Arctic. Animals may be aged from the claws up to 9 to 16 years. The male matures at 7 and the female at 6 years. The pup is produced around May 1 and the males are probably in full rut in mid-May. Females which have produced a pup forego ovulation until after the male rut, thus establishing a two-year cycle of pup production. The embryo implants during a 1½-month period around early August, after 2½ months of delay in development. The animal grows from 120 cm. in nose–tail length at birth to about 235 cm. The female increases her length by about 33% in the first year and reaches about 91% of her final length at puberty, at 6 years; these figures are somewhat larger than expected from the growth patterns of other Pinnipedia.

INTRODUCTION

THE BEARDED SEAL, *Erignathus barbatus* (Erxleben), is rather sparsely distributed in the eastern Canadian Arctic. It is utilized as food by seal-hunting Eskimos, and its thick skin is particularly valuable for use in dog-team traces, harpoon lines, footgear, and other native products which require strong, durable hide. Material from 113 specimens has been collected from 1947 to 1956 by the M.V. *Calanus* and associated parties, in Ungava Bay, southwest and northern Baffin Island, northern Foxe Basin, and northern Hudson Bay.

Application of the tooth-aging technique has elucidated the patterns of growth and reproduction in several species of Pinnipedia. A number of workers, utilizing the recent findings, are engaged in comparative studies of this group. For example, some of the relationships between growth and sexuality of Pinnipedia have been published by Laws (1956a). The bearded seal has been the subject of two important papers by Russian workers (Chapsky, 1938; Sleptsov, 1943), but the animal has not been studied in detail in the American Arctic. The present study, though preliminary, may be of value, since it is the first to utilize an accurate aging method.

The method of aging seals from sections of their canine teeth (Laws, 1953; Fisher and Mackenzie, 1954; McLaren, in press) was found to be not applicable to the bearded seal, whose teeth are degenerate and often missing. Aging harp seals, *Phoca groenlandica*, from their claws was first practised by Plekhanov (1933) and has been fully described for the ringed seal, *Phoca hispida*, by McLaren (in press). The same method offers a valid indication of age of the

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bearded seal. A study of 62 claws, collected since 1954, indicates that a light band is laid down in the spring and summer, and that generally a ridge is formed during the period of moult in the spring. Wearing at the tip eliminates the first year's growth after 9 to 16 years of life.

GROWTH AND AGE

The size at birth of the bearded seal has not been well established. The pup is rarely taken, and most lengths of young bearded seals in the literature are from animals which have achieved independence of their parent. Sleptsov (1943), working with a large number of specimens, considered the birth size to be about 120 cm., from extrapolation of known summer lengths. A new-born pup observed east of Belle Isle on April 19, 1952, was 47 inches (119.5 cm.) from tip of nose to end of tail (D. E. Sergeant, personal communication). A full-term foetus was taken in Cumberland Sound on April 28 by Kumlien (1879) and was 4 feet 7 inches in extreme length. The hindflippers were 12 inches (30 cm.) long, and the tail of an animal of this length would be about 3 inches or 7.6 cm. (from regression line of 13 older animals); this suggests a nose–tail length of about 3 feet 10 inches (117 cm.). Another advanced foetus from Greenland measured 112 cm. from nose to end of tail on March 17 (Vibe, 1950). The youngest animals taken in the present study, from June 17 to July 4, ranged from 117 cm. to 147.5 cm. in length.

Figure 1 outlines the sizes of seals of known ages. Seals from all areas are

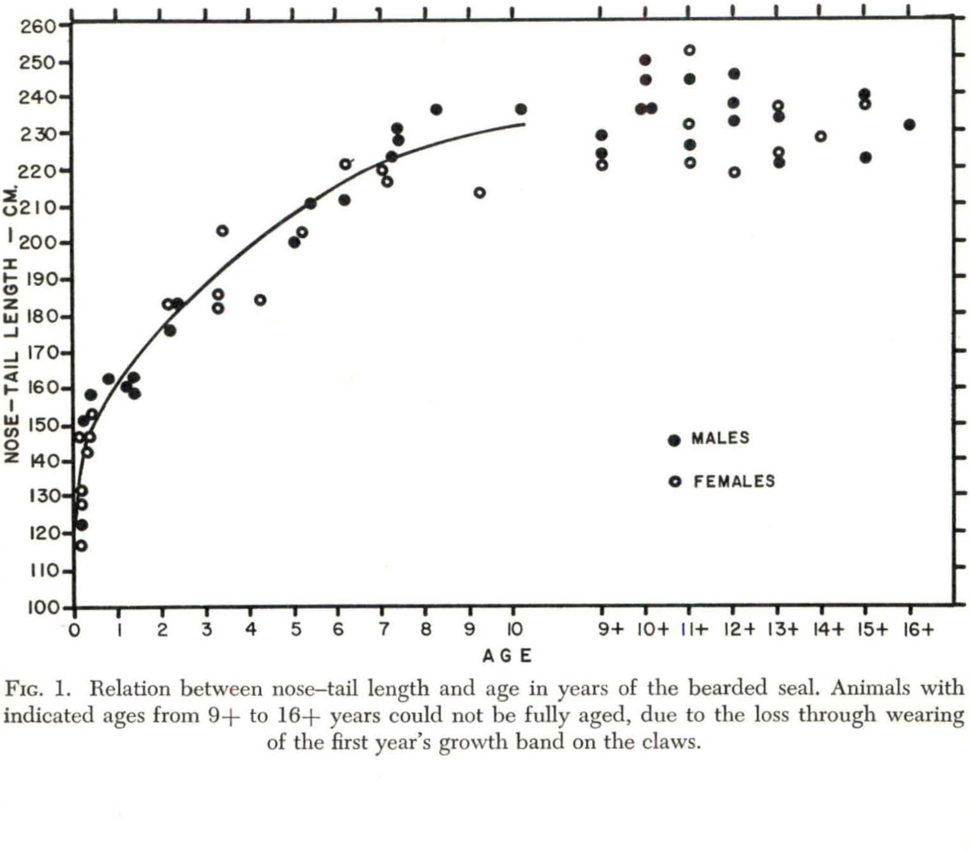

FIG. 1. Relation between nose–tail length and age in years of the bearded seal. Animals with indicated ages from 9+ to 16+ years could not be fully aged, due to the loss through wearing of the first year's growth band on the claws.

included together, since there is no evidence for geographical variation in size. Older seals, whose claws did not permit determination of full age, appear to average about 235 cm. in length. Some authors suggest that the male bearded seal averages somewhat larger than the female, but there is only slight evidence of this in the figure.

REPRODUCTION

Ages at Sexual Maturity

Thienemann (cited by Mohr, 1952) considered bearded seals of four years to be fully grown, and Sleptsov (1943) deduced from size-groupings that both males and females mature after their third year—a few females were supposed to mature at a younger age. Size-groupings of Pinnipedia have been found to be of little value in indicating age, in the light of recent studies in which the animals have been aged from their teeth.

The testis of a five-year-old seal on April 3 was small and inactive, although a few spermatids were detected. A larger testis was secured from a seal which was six years and two months old on July 2. This testis was quite active, with enlarged epididymis and testis tubules, but there was no evidence of spermia or their degenerate remains, as found in older testes at this season; the specimen probably represents the limited sexual activity of adolescence. An eighth-year testis on August 9 contained large numbers of spermatids, and the associated epididymis was filled with colloidal matter, degenerate cell remains, and spermotogenetic cells; the condition resembled that of older males at this season. Another testis of the same age on August 29 was similarly active. Table I summarizes the

Table I. Spermatogenetic activity, length and width of testes in millimetres, and diameters of testis and epididymis tubules in microns, of bearded seals of various ages. Twenty-five tubules from each specimen were measured to determine the mean. Not all tubules could be measured, due to distortions of preservation, but the spermatogenetic stages in such tubules could be evaluated. An "X" indicates the presence of spermatids or spermia in the situation indicated.

Age	Testis length	Testis width	Diameter of testis tubules	Diameter of epididymis tubules	Spermatids in testis	Spermia in testis	Spermia in epididymis
years	*mm.*	*mm.*	μ	μ			
0.2	24	15	61	75			
1.3	25	15	67	87			
1.4	28	18	65	68			
2.2	35	24	...	...			
2.4	38	15	77	89			
4.9	32	18	88	187	X		
6.2	44	22	121	136	X		
7.3	43	28	149	213	X		
7.4	54	37	122	...	X		
7.4	46	33	...	...	...		
8.3	60	40	...	...	...		
10.1	64	38	193	322	X	X	X
Age 9+ to 16+ (av.)	56.4	34.8	142.9	184.8	X[a]	X[b]	X[c]
Specimens examined	19	19	14	10	14	14	12

[a] Spermatids present in all 14 specimens.

[b] Spermia present in 5 of 14 specimens.

[c] Spermia present in 3 of 12 specimens.

activity of testes of various ages, as this is reflected in stages of spermatogenesis, sizes of testes, and diameters of testis and epididymis tubules. It is apparent that there is a marked increase in activity in the early eighth year, and that the male probably breeds for the first time when seven years old.

The baculum, or penis bone, exhibits a spurt of growth in the sixth and seventh years (Fig. 2). This bone appears to attain almost its full length when the animal is seven years old, although the weight continues to increase in older seals.

Sexual maturity of the female is attained when the first ovulation occurs. Some development of follicles, both during and outside the breeding season, occurs in the years before maturity. The youngest female with any extensive follicular development was about five years old on July 3. Ovulation is succeeded by the development of the corpus luteum at the site of ovulation. This gland, or its regressed form, the corpus albicans, is thus an indication of maturity. Of four animals between six and eight years old, three were mature. The ovaries of the youngest, a seventh-year animal taken on August 8, showed an abnormal development of seven large follicles, which were from 7 mm. to 10 mm. in maximum

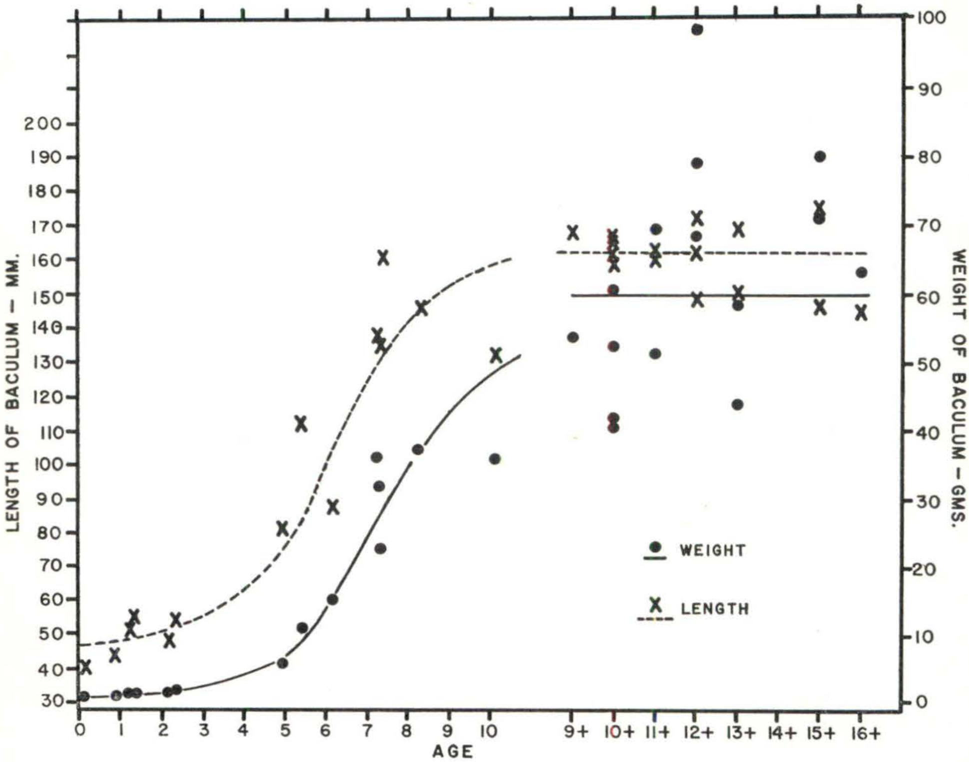

FIG. 2. Relation between size of baculum and age in years of the bearded seal. Animals with indicated ages from 9+ to 16+ years could not be fully aged, due to the loss through wearing of the first year's growth band on the claws.

diameter. Each of these presented the appearance of a small corpus luteum, with plications from the follicle wall and luteinization of the tissue. They were not true corpora lutea, since they had developed deep within the ovaries and could not have ruptured at the surface, nor did they resemble the luteinized follicles described by Laws (1956b) in the elephant seal, *Mirounga leonina*. Whatever their significance, they almost certainly reflect, if abnormally, the hormonal state of maturity. A seven-year-old female on April 29 showed several large follicles, up to 5 mm. in diameter, but no corpus luteum. The ovaries of another of the same age on May 9 were relatively inactive, but a corpus albicans of the previous year's ovulation, which had been unaccompanied by pregnancy, signified maturity. An animal killed in her eighth year on June 30 had been pregnant in her seventh year; one corpus albicans indicated that this pregnancy had probably resulted from her first ovulation.

Thus the limited evidence suggests that the male bearded seal is mature by age of seven and that the female may mature, on the average, when six years old. These are exactly comparable with the ages at maturity in the ringed seal (McLaren, in press). Further collections will undoubtedly establish a range of variation in these ages.

THE BREEDING SEASON AND THE SEXUAL CYCLE

The young bearded seal is, according to most accounts, born in April or May. Some variation in the timing of birth may be related to latitude. Thus Mohr (1952) considers that the birth season is earlier in northern European waters and off Newfoundland than in the higher arctic seas, and Sleptsov (1943) suggests that pupping occurs in March-April in the Okhotsk Sea, or even earlier in the southerly Tartar Straits. May 1 may be considered to be the average birth date in the eastern Canadian Arctic. The mating season according to some authors (Kumlien, 1879; Chapsky, 1938) occurs shortly after the period of birth. Sleptsov (1943), who amassed considerable material, believes that the bearded seal mates a full three months after the birth season, at the end of the moulting period.

The season of male rut is less subject to variation in timing than the season of ovulation, for the females of several species have been known to ovulate outside the breeding season (Hamilton, 1939; Rand, 1954; McLaren, in press). Five adult male bearded seals have been taken with spermia in the testes—on May 30, June 19 (2), July 2, and July 3. The epididymis of the May 30 specimen was unfortunately not collected, but scattered spermia in the *ductuli efferentes* suggest that the animal was potent. The epididymis tubules of one of the June 19 specimens were not fully packed with spermia, and the epididymis of the other was aspermous. Only scattered spermia were mixed with the spermatogenetic cells and degenerate products in the July 3 specimen, while the epididymis of the July 2 male was devoid of spermia. No other testes taken between July 3 and October 8, including three taken in mid-July, were active. It is apparent that the series represents a decline in spermatogenetic activity and that the peak of male potency occurs before June.

Measurements of testes and diameters of tubules demonstrate this same decline in activity in early summer. These measurements are displayed on Figure

3, and the freely drawn curve suggests the best estimate of the period of rut in May, shortly after the pupping season.

Chapsky (1938) and Sleptsov (1943) both suggest that the bearded seal produces one pup every second year. Neither speculates on the mechanism by which this two-year cycle, which is unique among the Phocidae, is established. The limited material of the present study suggests that the female may forego ovulation until after the breeding season of the male, when she has recently given birth to a pup. Thus, two specimens whose tracts showed placental scars of recent pregnancy were taken on May 30 and June 19. The ovaries opposite to those which controlled the previous pregnancies contained large follicles (the largest were 14 mm. and 11 mm. in the respective specimens) which had not yet erupted. Another recently pregnant female on July 6 had a very new corpus luteum; the granulosa cells of the follicle wall were streaming into the unfilled centre, and little luteinization of these cells had taken place. Other females in which no embryos were found were taken in July to September, with corpora lutea in various stages of development. Some were quite recent in appearance, while others were older and approached those of pregnant seals in degree of vascularization and connective tissue development. One specimen on July 29 was pregnant, with a very recently implanted embryo. Its corpus luteum was rather free of vascular tissue, suggesting that those females in which no embryos were found, and whose corpora lutea were of more advanced appearance, were pseudopregnant.

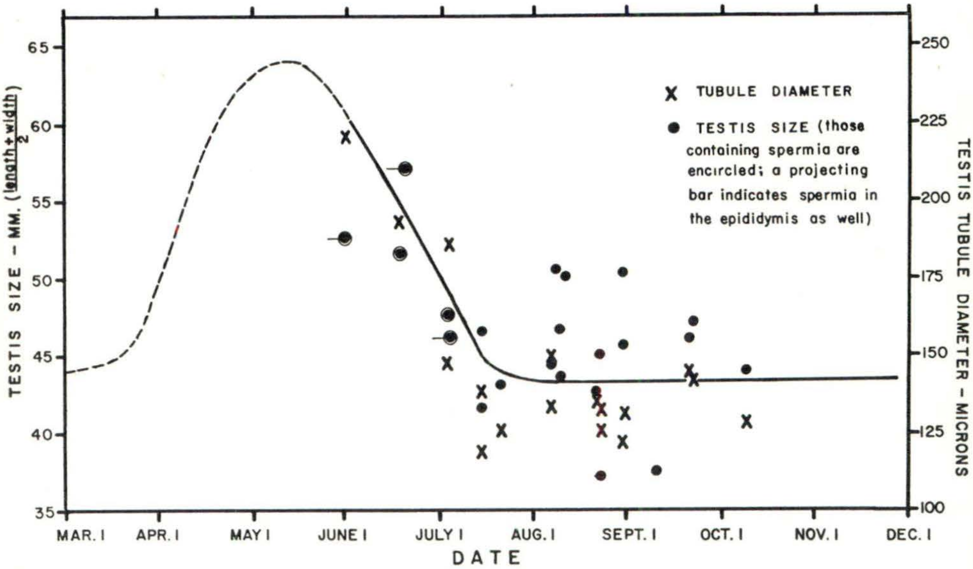

FIG. 3. The seasonal variation of testis size and testis tubule diameter in the bearded seal. The curve is drawn to indicate the presumed peak of sexual activity in May.

Embryos were removed from nine females in late July to late October, and these are listed in Table II. If we consider, from this small series of specimens, that the embryo implants around the beginning of August, a delay in implantation of about 2½ months is implied. Embryos of less than 1 mm. on July 29 and of 2–3 mm. on September 17 suggest that the period covering implantation is at least 1½ months. This probably reflects the length of the breeding season.

TABLE II. Size of embryos of the bearded seal in July to October. Embryos were measured in millimetres from tip of nose to tip of tail along curvatures and flexures.

Date	Geographical origin	Length
		mm.
July 29	Northern Foxe Basin	Newly implanted
August 22	Southwest Baffin Island	14.5
August 28	Northern Foxe Basin	120
August 29	Southampton Island	109
September 2	Ungava Bay	114
September 17	Northern Foxe Basin	2.5
September 20	Southampton Island	222
September 21	Northern Foxe Basin	86
October 29	Northern Foxe Basin	240

Sleptsov (1943) did not acknowledge delayed implantation of the embryo of this species, contrary to the findings of Chapsky (1938). Although Sleptsov dealt with a very large series of animals, he appears to have made some errors in his analysis of the material. He observed one case of apparent copulation on July 7, although active ovulation, as indicated by the presence of corpora lutea, had occurred in all specimens taken after the commencement of seal collecting in late May. He states that between June 1 and 31 the testes of all adult males were swollen, but emphasizes that only small quantities of spermia were observed in the ducts, while suggesting that this should not be taken as an indication that breeding has already occurred. To justify this view, he considers that there is probably never much ejaculate in the ducts of Phocidae in general, an assumption which is certainly not borne out by recent studies. It is quite apparent that Sleptsov's male specimens were passing out of rut, and that his female specimens had ovulated before the peak of supposed breeding activity in the second half of June to the second half of July. The large series of embryos which he removed in early stages of development indicates an average implantation time around the beginning of July, a full month before the suggested implantation time in the eastern Canadian Arctic. A delay in implantation of 2½ months would place the peak of the breeding season in the beginning of April; this coincides with his statements that the pup is produced in March or April in the Okhotsk Sea area.

Sleptsov reaffirmed his views on the timing of the breeding season of other Pinnipedia in a later paper (1948). In this study he examined female harp seals, for which there is very well documented evidence of ovulation shortly after the birth of the pup, and considered that this species, too, mated considerably later than had been supposed; obviously his views on reproduction of this species are also untenable.

RELATIONSHIPS BETWEEN GROWTH AND SEXUALITY

At the time of Laws' (1956a) preliminary analysis of growth and sexuality in marine mammals, little information was available from published accounts of this species. Laws makes use of the findings of Chapsky (1938), whose seal ages were based on length-groupings, and subject to the inaccuracies of this technique.

Laws found that, on the average, 86% of the final length is attained at puberty in the females of the species which he studied. For the bearded seal, he gives figures of 79 inches (201 cm.) at puberty and 98 inches (249 cm.) at physical maturity; thus 81% of the final adult length is reached at the age of sexual maturity. It has been shown in the present study that the female ovulates for the first time when she is about six years old, when she would be (from Figure 1) about 210 cm. in length. It may be considered that females older than nine years have reached physical maturity; the average length of such females is about 230 cm. Thus, in the present material, the female at puberty appears to have reached fully 91% of the final adult length, a figure considerably in excess of that suggested by Laws.

Laws also relates the increase in length in the first year of life of the females of several species to their ages at sexual maturity. These are inversely proportional, the regression line plotted by Laws indicating that females maturing at the age of two years increase their length in the first year by about 80%, while females maturing at the age of six years have a length increment of about 20% in the first year. The female bearded seal, as suggested in Figure 1, increases from about 120 to 160 cm. in the first year, an increment of about 33%. This suggests an age of maturity at five years, whereas the actual age of sexual maturity observed in the small collections available is at six years.

SUMMARY

1. The material on which this study is based was collected from 113 specimens of bearded seals in the eastern Canadian Arctic.

2. The method of aging from dentinal annuli in the canine teeth cannot be applied to the bearded seal, whose teeth are degenerate. Bands on the claws give a valid indication of age, up to 9 to 16 years, and 62 specimens were aged by this technique.

3. The bearded seal grows from about 120 cm. in nose–tail length at birth to a final adult length of about 235 cm., with little sexual difference.

4. The male matures at seven and the female at six years of age.

5. The pup is produced in April and May, averaging around May 1 in the eastern Canadian Arctic. The males are going out of rut in June and are probably most potent in mid-May. Females which have produced a pup probably forego ovulation until after the season of sexual activity of the males, thus establishing a two-year cycle of pup production.

6. The embryo implants during a period of at least 1½ months around the beginning of August, after a delay in development of about 2½ months.

7. The female at puberty has reached 91% of her final adult length, a somewhat greater development than the average of 86% which has been suggested for

other Pinnipedia. The females of other Pinnipedia have been used to establish a relationship between growth in the first year and age of sexual maturity. Females maturing at the age of six are expected to exhibit a length increment of about 20% in the first year; the bearded seal increases its length by 33%, and is thus somewhat at variance with the theory.

ACKNOWLEDGMENTS

The author is grateful to several people who collected material in the course of other field programs in the arctic, particularly A. W. Mansfield and members of the *Calanus* Expedition of 1956, who brought back important collections of reproductive and aging material.

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THE DETERMINANTS OF PRODUCTION IN NORTHERN SEAS: A STUDY OF THE BIOLOGY OF THEMISTO LIBELLULA MANDT.

"CALANUS" SERIES NO. 14[1]

M. J. Dunbar

Abstract

The level of production in the sea is determined not only by the extrinsic factors of the environment, but also by the intrinsic response of the organism to those factors, temperature in particular. In cold seas, the degree of adaptation to low temperature as regards activity, metabolism, growth rate, and the onset of maturity is therefore of great importance. This matter is reviewed and discussed here, and illustrated by a study of the growth rate, breeding cycle, and longevity of a dominant arctic pelagic amphipod, *Themisto libellula* Mandt.

Themisto libellula, in Hudson Bay, Hudson Strait, and the waters of southeast Baffin Island, is shown to have a normal length of life of 2 years, although a 1-year or 15-month life cycle is a possibility in a small proportion of the population. Material from the months of November and December is lacking, but it appears that spawning extends from September through the winter until some time in May or June. If a temperature stimulus is involved in the onset of breeding, it appears to be a fall below, not a rise above, a critical point, since the temperatures during most of the breeding period are below −1.5° C. The spawning in the autumn, however, suggests that temperature is in fact not involved.

The alternating, or two-phase, breeding cycle is confirmed in this species, but the evidence shows that dislocations in the cycle (owing to the possibility of maturation after approximately one year in some individuals) may destroy the supposed reproductive isolation between adjacent year-classes.

Introduction

This paper is a contribution to the study of production in northern waters, production being described in terms of (1) the rate at which organic stuff is made in the seasonal cycle, and (2) the size and density of the resultant standing crop at the height of the seasonal cycle. These, in different trophic levels, depend on a variety of factors, some of them probably still unknown. There is no reason to assume that diatoms, dinoflagellates, zooplankton, fishes, in fact all the poikilothermal elements in the biomass, should be influenced in the same way by the determining environmental factors, or that the production at each level is used to the full by the level above. A large and fast production of phytoplankton, for instance, will make possible a large production of planktonic Crustacea, but it does not follow that the crustacean production will in fact be large, or that it will use the phytoplankton production to the greatest degree possible. There is normally a considerable wastage of plant food by the animals when the former is in great abundance, and a greater or smaller proportion of the plant food will always die unconsumed. The element of wastage was recognized by Volterra (1928 (44)), amongst others, who introduced into his equation for the growth rate of

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Can .J. Zool. 35 (1957) **F.R.B. No. 502** predator populations a coefficient of food utilization, and Riley (1953 (32)) describes the faecal pellets of zooplankton as being green with discarded and unused plant material following the phytoplankton bloom.

In *terrestrial* polar and mountain environments there is another element which apparently operates so that the maximum possible density of wildlife population is seldom if ever reached, namely the constant or intermittent adverse effects of the climate (Wynne-Edwards, 1952 (47)). In describing the redpoll population in the region of Clyde River, eastern Baffin Island, Wynne-Edwards writes: "Except perhaps among carnivorous predators, competition between individuals for space and nourishment seems commonly to be reduced to a low level among members of the arctic flora and fauna; they live somewhat like weeds, the secret of whose success lies in their ability to exploit transient conditions while they last, in the absence of serious competition. In the arctic the struggle for existence is overwhelmingly against the physical world, now sufficiently benign, now below the threshold for successful reproduction, and now so violent that life is swept away, after which recolonization alone can restore it". This factor, if it applies at all in marine environments, might be expected to take effect only in transition areas between the main zones (arctic, subarctic, boreal), where sudden changes in marine climate might have drastic and possibly differential consequences on parts of the system.

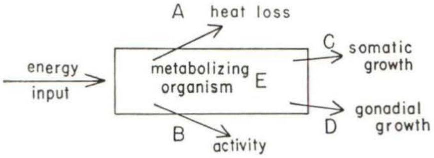


FIG. 1. See text.

Apart from this strictly extrinsic factor, the extent to which the basic (plant) production is used, and therefore the size to which the animal production develops, will depend upon the manner in which the energy obtained from the food itself is used. The energy input fed into an animal (Fig. 1) has to be shared between a number of processes, the relative demands of which, upon the energy capital, are not the same in all environments, or in all animal groups, or at all times of year. It has long been recognized that the activity, for example, of poikilotherms living in very cold circumstances is very much greater than our knowledge of temperature effects upon activity in warmer regions would lead us to expect. There must therefore be regulation, or adaptation, of the determinants of activity which allow the unexpectedly high level in cold regions. Such regulation may be, for all that is at present known about it, either genetically established or a matter of individual ontogenetic adaptation, but it is not difficult to imagine the high probability of the true evolution of such regulation, and its high selective value, since a minimum of activity is required for the business of food-getting and of escaping from predators which are not bound by this temperature condition (homotherms, especially large homotherms).

Regulation in activity with respect to temperature has led zoologists in the past to expect a corresponding, perhaps an enabling, regulation in standard metabolism, and there is evidence that this in fact occurs in many instances. The literature has recently been reviewed by Bullock (1955 (8)). Among the pioneers in the field are Fox (1936 (17*a*), 1939 (17*c*)), Wingfield (1939 (4*b*)); also Fox and Wingfield (1937 (18)) in England, and Thorson (1936 (43*a*), 1950 (43*b*), 1952 (43*c*)) and Spärck (1936 (41)) in Denmark. Thorson, studying the metabolic rates (measured by oxygen consumption) of inshore molluscs in east Greenland, Denmark, and the Persian Gulf, found that the rates were approximately equal in the same species or in closely related species living in the three regions, each being measured at its normal environmental temperature; thus if the arctic individuals were placed in water of normal Danish range of temperature, their metabolic rates were considerably higher than those of the Danish form, and the same, *mutatis mutandis*, for the Danish and Persian Gulf populations. Regulation thus appears to be common, or at least present in a number of species studied.

The work of Fox and Wingfield did not agree with that of Thorson, or of Spärck. Fox (1936 (17*a*)), working on the oxygen consumption of pairs of species (each pair being in the same genus) of echinoderms, annelids, and crustaceans, found that "for seven pairs of species inhabiting respectively English waters and more northern seas (Kristineberg in Sweden), the oxygen consumption of the warmer-water species is greater than that of the colder-water species (measured at the normal temperatures at which each species lives) although the locomotory activity of the former is apparently no greater". Fox suggested "that the similar locomotory activities of the two species require approximately equal amounts of oxygen, but that the non-locomotory oxygen consumption of the warmer-water species is higher than that of the cold-water species". The same results were found for two species of prawns (Fox and Wingfield, 1937 (18)). In this 1937 paper there is a note on the work of Spärck and Thorson, which appeared at the same time. Fox and Wingfield, in commenting on the disagreement between their results and the Danish work, point out that Spärck and Thorson were working on lamellibranchs, which were not used in the English work. Thorson (1952 (43*c*)), and also Berg (1953 (3)), have shown that the animals used in Fox's work were not truly comparable, on account of differences in size and age, and that if these factors are taken into consideration, then metabolic adaptation in the Kristineberg populations was in fact demonstrated.

Wingfield (1939 (46)) showed the danger of drawing too determined conclusions in this matter from comparisons of two different species (which has been the method used by many), by demonstrating that if the polychaete *Pectinaria granulata* from east Greenland is compared with *P. auricoma* from Millport it does not show metabolic regulation, but if compared with *P. koveni*, also from Millport, it does show regulation. Finally Scholander, Flagg, Walters, and Irving (1953 (38)), using this same technique of comparing groups from tropics and arctic which are more or less closely related taxonomically, found that in certain Crustacea there is evidence of metabolic adaptation, the arctic forms showing somewhat higher metabolism than that which would have been expected simply by extrapolation from the tropical performances.

The species which have been studied are mainly shallow-water benthonic forms; there are as yet no data for the metabolic rates of holoplanktonic species in cold water. Research in this field is now urgently needed and is in fact being planned for the next *Calanus* expedition.

In poikilothermal vertebrates, Fry (1951 (19)) and his collaborators have shown that the speckled trout (*Salvelinus fontinalis*) is capable, individually, of a certain limited metabolic acclimation with respect to temperature, but there is no evidence yet that an established regulation exists in populations living in very cold water. Power (unpublished data), working on metabolic rates of the speckled trout at the northern limit of its range in northern Quebec, has so far found only very low rates which show little or no adaptive regulation. On the other hand Scholander, Flagg, Walters, and Irving (1953 (38)), comparing tropical with arctic fishes in this respect (interspecific and intergeneric comparison) found a considerable adaptation, the arctic species and genera lying in an intermediate position as regards oxygen consumption between the tropical fish and the "expected" or extrapolated position for fishes living at 0° C. Peiss and Field (1950 (29)) compared the oxygen consumption of excised brain and liver tissue of the polar cod (*Boreogadus saida*) with that of the golden orfe (*Idus melanotus*), and found that the Q_{10} values for the cod tissue remained steady over the whole temperature range of 0–25° C., whereas the values for the orfe tissue increased markedly below 10° C. This resulted in oxygen consumption values for the polar cod which were several times as great as in the orfe at low temperatures, clearly advantageous in the adaptation of the polar cod to cold environments. These experiments, however, showed a breakdown in metabolic adaptation in the orfe, the warm-water form, at low temperatures, rather than metabolic regulation in the cod.

There remains the question of growth rates. Both Bullock (1955 (8)) and Dehnel (1955 (9)) have observed that if growth in marine poikilotherms shows adaptation with respect to temperature, as has been shown to be the case for the metabolism in some species, then the high production of certain northern waters would be in large part explained. (It should be emphasized, however, that the high production is in the subarctic waters, not in the coldest, or arctic, regions.) Orton seems to have been one of the first to draw attention to the possibility of adaptation in growth rates. Writing in 1923, he refers to his earlier paper (Orton, 1920 (28*a*)) as drawing attention to the lack of evidence bearing on theories (those of Murray and Loeb, for instance) "to explain (*a*) the abundance of life in polar regions, and (*b*) the occurrence of several generations of species living side by side in polar waters". This latter point, the coexistence of several generations, can now be explained by the prevalence of two-phase or polyphase breeding cycles, such as have been demonstrated for euphausids, the chaetognath *Sagitta elegans* and the amphipod *Themisto libellula* (Ruud, 1932 (35); Dunbar, 1940 (11*a*), 1941 (11*b*), 1946

(11*d*) and this paper). Orton urges "(*a*) that we know nothing about the rate of growth of organisms in polar regions, and (*b*) that the kind of metabolism of animals in polar regions and in deep-sea situations is not necessarily the same as that in temperate and tropical regions".

Orton (1923 (28*b*)) found that sea urchins (identified as *Echinus miliaris*) observed in west Spitsbergen showed a rate of growth of the same order as is found in related forms in Plymouth waters in the English Channel. Again, this is the comparison of different species, not of populations of the same species. Thorson (1936 (43*a*)), studying lamellibranchs in east Greenland inshore waters, found slow growth rates, and generalizing from his work on the lamellibranchs, concluded "that the bottom invertebrates in the northeast Greenland seas will on the whole have a slow growth, a long life, and a late maturity which means that the production must be extremely small". He adds that this generalization is provisional, and that investigation of more species is necessary. Later (43*b*), finding that larval growth in arctic waters appears to be fast, he treats adaptive regulation of both metabolism and growth as a generally accepted phenomenon, and on those grounds dismisses Wimpenny's (1941 (45)) paper on "Organic polarity" as being out of date, since Wimpenny assumed that life cycles were shorter in tropical than in polar waters. He makes the observation that the *larvae* of benthonic invertebrates, northern as well as tropical, "seem on the average to spend a similar time (about three weeks) in the plankton", at the temperatures to which they are normally exposed, but he adds that in arctic regions abnormally low temperatures can have an adverse effect, and that "wastage caused by temperature, like that due to starvation, seems mainly to be an indirect one: low temperatures postpone growth and metamorphosis, and give the enemies a longer time to feed on the larvae".

Dehnel (1955 (9)) compared the growth rates, expressed as instantaneous relative rates, of the larvae of gastropod molluscs in southeastern Alaskan and southern Californian waters, and found that the rates for the northern populations were from two to nine times greater than for the southern populations of the same species over given ranges of temperatures. This comparison was intraspecific, populations of the same species being used. In spite of the fact that species with yolky telolecithal egg masses were chosen, to minimize the importance of food availability on growth, it is still possible that factors other than temperature were responsible for the fast growth of the Alaskan embryos, as Dehnel himself points out. Two other comments on these very interesting results are relevant here: (1) the surface temperatures of the southeastern Alaskan waters are not low when compared to arctic or even subarctic regions (the annual range at Sitka is from about 4° C. to 15° C.); and (2) the growth measured was embryonic and larval. It has been pointed out by several workers, including Thorson (1936 (43*a*), 1950 (43*b*)) that there are special problems for the colder-water benthonic forms, in that it is essential, for survival, that metamorphosis be accomplished within a certain short time after hatching, the time being determined by the length of the high production period in the phytoplankton, which is usually short in cold regions, owing to the great stability of the surface waters in summer. Most arctic benthonic molluscs have solved this problem by eliminating the pelagic larval stage.

A high growth rate in embryonic development was also found by Fox (1938 (17*b*)) in sea urchins, those of British waters developing faster than those of the Mediterranean, at given temperatures.

The growth rates of larval and embryonic stages, however, are only a very small part of the problem. From the point of view of the student of production in the northern seas, the important thing is the time taken to reach maturity and breeding. Moreover, there is no reason to assume that what is found in the molluscs and in the echinoderms is true of all groups; and finally, the benthonic and littoral forms may behave quite differently in this respect from the holoplanktonic. Dehnel (1955 (9)) writes: "Generally, the assumption is made that species of marine poikilotherms which inhabit the colder waters of the higher latitudes grow more slowly, grow to a larger size, and have a greater longevity than individuals of the same or closely related species from warmer waters". In fact, this is much more than an assumption, as Dehnel indicates later in his paper. There is a great deal of evidence in the literature for the slowing down of growth rates in cold water as compared with warm, not only in the comparison of different species within one genus but also in the comparison of different populations within one species. Thus Schneider (1891 (37)) concludes that several of the common gammarid amphipods of the Tromsö coast have a 2-year life cycle, some even longer, and comments that increase in life-time, and time taken to reach maturity, with increasing geographic latitude is a well-known phenomenon in insects. In the Lepidoptera, for instance, many species have a 1-year life cycle in Germany and a 2-year cycle in Norway. Schneider mentions also the tiger-moth, *Arctia caja*, which lives 1 year in the Oslo area but which requires 2 years to reach maturity at Tromsö.

In the chaetognath *Sagitta elegans*, Russell (1932 (34)) recorded four, possibly five broods, produced in 1 year at Plymouth, each brood being parental to the next. In the same species in Baffin Island waters, Dunbar (1941 (11*b*)) found the normal life cycle to be probably as long as 2 years before spawning. Bogorov (1940 (5)) found a 2-year life cycle for both *S. elegans* and *Eukrohnia hamata* in the Barents Sea. In the Euphausiidae, Macdonald (1928 (23)) recorded a breeding cycle in *Thysanoessa raschii*, in the Clyde Sea area, which appeared to involve a 1-year life cycle. Einarsson (1945 (13)) also found a 1-year cycle for the same species in southern Icelandic waters, but concluded that in northern Iceland and in west Greenland *T. raschii* took 2 years to reach maturity. Bogorov (1940 (5)) recorded a 2-year cycle for *Thysanoessa inermis* and *T. longicaudata* in the Barents Sea. In the deep-water shrimp *Pandalus borealis*, Hjort and Ruud (1938 (22)) concluded that maturation (to maleness) occurred in the second summer of life in Norwegian waters; in the same species Rasmussen (1942 (30)) described a 3-year maturity age in Spitsbergen.

The copepod *Calanus finmarchicus* has been exhaustively studied. The researches have recently been reviewed and consolidated by Marshall and Orr (1955 (25)), who write (p. 64): "As is natural, the lower the temperature the slower is the rate of development, and the later does the first spawning occur". In the Clyde Sea area, where the temperature at the time it is homothermic in March is about 7° C., *Calanus finmarchicus* spawns at least three times during the period between mid-February and late July. Thus the life span in spring is about 2 months. The winter stock may live up to 7 months. In east Greenland (Digby, 1954 (10*b*)), where the winter temperature is about −1.5° C. for a considerable period, the same species spawns only once a year, in midsummer, and the individual normal life span is therefore 1 year. There is evidence that a proportion of the population may survive a second winter. In Ungava Bay, Fontaine (1955 (16)) found 1-year life cycles in *Calanus finmarchicus* and *Pseudocalanus minutus*. Other planktonic copepods follow the same pattern. Digby (1954 (10*b*)) comments that in view of this, copepods in the arctic cannot be considered to be particularly well adapted to living in cold seas. There is, however, some likelihood that the availability of food may be an important factor, besides temperature, in determining the growth rate.

An exception to this apparent rule of slower growth in colder water was reported by Moore (1934 (26)), who found that the common barnacle, *Balanus balanoides*, has a faster growth at Herda, in Norway, than at Port Erin in the Irish Sea, where the growth was in turn faster than at St. Malo in France.

In vertebrate poikilotherms the evidence is confusing, as indeed it is also in the invertebrates. The arctic char (*Salvelinus alpinus*) in Frobisher Bay, Baffin Island, takes 12 years to reach maturity in the female (Grainger, 1953 (20*a*)). The Atlantic cod (*Gadus callarias*) of Port Burwell, Ungava Bay, grows considerably more slowly than the cod of west Greenland, Newfoundland, or Nova Scotia (Dunbar, unpublished). In these instances there is no evidence that the food supply is involved. In the Amphibia, however, the work of Moore (1939 (27*a*), 1942 (27*b*), etc.) has shown that the embryonic development of species of *Rana* is faster, the colder the environment, the northern *Rana sylvatica* developing at about twice the rate of the southern *Rana catesbeiana*. Differences in the type of life cycle are probably at the root of the ultimate (as opposed to the proximate) causes for the differences between groups in this respect, which, as has been suggested above is the case between the benthonic invertebrates and the holoplanktonic forms.

Material and Methods

The hyperiid amphipods have been given scant attention biologically. The tropical and temperate species are difficult taxonomically and appear to be of secondary importance in the economy of the seas. The cold-water species, however, *T. libellula* in particular, are abundant and often dominant. As a group the hyperiids are well suited to studies of the present sort, being large, easily caught, holoplanktonic or holopelagic, with direct development.

Themisto libellula is a dominant species of the plankton of the waters of Hudson Strait, north and east Baffin Island, and Hudson Bay. Its ecological position farther north is not yet known (it is not abundant in Foxe Basin), but it appears to be arctic rather than subarctic, being not common in the west Greenland waters except in their northern part. It extends, however, into the subarctic on the Canadian side, decreasing in abundance southward along the Labrador Current. In the subarctic it can be relied upon as an indicator of arctic water. It has been recorded from all arctic seas explored, except that information from the Arctic Ocean itself is lacking. The most southerly records are the Strait of Belle Isle (Bousfield, 1951 (6)), off Cape Farewell and the southeast coast of Iceland (Stephensen, 1923 (42)), the Norwegian, Barents, and Murmansk seas, Kara Sea, Bering and Okhotsk seas (Behning, 1939 (2)).

The species figures prominently in the food of the arctic char (Grainger, 1953 (20)), and especially of the ringed seal (Dunbar, 1941 (11*c*)). It forms the most important link in the food chain between the copepods and other smaller planktonic forms on the one hand, and the vertebrates on the other, and in fact it takes the place, in cold water, of the euphausids in this respect.

The material used in the present paper was collected on the *Calanus* Expeditions of 1947 to 1955, the details of the collection being shown in Tables I and II. Open plankton nets were used, and most of the *Themisto* were taken in horizontal hauls. The nets were the 1- and 2-meter stramin nets, a half-meter No. 6 net and No. 5 net of the same size, and 1-meter No. 0 and No. 00 nets. Depths of hauling are approximate only, being calculated from the wire angle and the length of wire. An error of about 10% can be expected in the depth calculations. Material was also obtained from stomachs of the ringed seal (*Phoca hispida*) in the waters of southwest Baffin Island (Cape Dorset) and from Igloolik in Foxe Basin; and from stomachs of arctic char at the head of Frobisher Bay.

TABLE I

COLLECTION DATA FOR THE *Themisto libellula* MATERIAL (IN THE "NET" COLUMN, NUMBERS REFER TO THE BOLTING SILK GRADE, EXCEPT THAT "STR. 1" MEANS "1-METER STRAMIN; "STR. 2", "2-METER STRAMIN")

Year	Date	Station	Depth, m.		Net	Time, E.S.T.	Duration, min.	Numbers	
			Station	Haul				Taken	Measured
1947	24/6	1	18–31	5	6	1420	25	7	7
	29/6	3	28	2	Str. 1	1100	30	2	2
	29/6	3	28	4–5	6	1104	25	9	9
	29/6	3	28	5–7	0	1104	25	42	41
	13/7	13	46–55	6	0	1000	30	80	80
	17/7	18	84	17–21	0	1240	30	50	50
	10/8	33	15	11–13	Str. 1	0810	30	2	2
	10/8	33	15	11	0	0810	30	9	9
	11/8	37	3–4	0	6	1040	30	1	1
	11/8	37	3–4	0	Str. 1	1048	30	1	1
	17/8	41	240	27–35	6	1300	60	1	1
	17/8	41	240	200	0	1300	60	15	15
	17/8	41	240	54	Str. 1	1300	60	Several hundreds	2
	19/8	44	80	70	0	1330	40	1	1
	19/8	44	80	70	Str. 1	1334	36	18	18
1949	26/6	101	18	6–8	Str. 1	1045	30	8	8
	26/6	101	18	1	6	1055	30	3	3
	6/7	103	145–275	90	00	—	20	20	20
	6/7	103	145–275	200	Str. 1		45	14	14
	14/7	103	145–275	105	Str. 1	0930	45	44	44

Year	Date	Station	Depth, m.		Net	Time, E.S.T.	Duration, min.	Numbers	
			Station	Haul				Taken	Measured
1949	7/8	103	145–275	5–10	00	1120	12	9	9
	10/8	123	15	1–7	5	1515	35	1	1
	10/8	123	15	5–10	00	1645	22	3	3
	21/8	125	18	0	Str. 1	—	90	1	1
	23/8	126	70–90	2–10	Str. 1	1057	35	37	37
	24/8	128	185	27	00	1445	70	43	43
	24/8	128	185	137–162	Str. 1	1455	70	25	25
	25/8	129	–	16–19	Str. 1	1340	60	3	3
	25/8	129	–	3	00	1340	60	3	3
	25/8	129	–	13–15	6	1345	50	4	4
1950	28/6	201C	80–100	1	00	0935	55	11	11
	28/6	201C	80–100	20	Str. 1	0955	20	13	13
	15/7	206	55–90	3	Str. 1	1020	45	60	60
	20/7	209	183	75	Str. 1	1305	25	78	78
	3/8	222	80–90	8	5	1800	20	42	42
1951	4/7	303	120	–	Str. 1	1715	30	64	64
	28/7	309	165	75–87	Str. 1	2000	30	43	43
	14/8	326	550–640	225	Str. 1	1015	60	139	139
	21/8	329	183	150	Str. 1	1153	50	47	47
	26/8	335	320	50	Str. 1	1715	15	55	55
	26/8	335	320	92	Str. 1	1715	15	11	11
	26/8	335	320	155–215	Str. 1	1855	30	90	90
	26/8	335	320	0	0	2016	15	24	24
	26/8	335	320	50	Str. 1	2016	15	77	77
	26/8	335	320	92	Str. 1	2016	15	115	115
	26/8	335	320	0	0	2312	15	192	192
	26/8	335	320	50	Str. 1	2312	15	72	72
	26/8	335	320	92	Str. 1	2312	15	67	67
	26/8	335	320	154	Str. 1	2352	30	86	86
	27/8	335	320	0	0	0209	15	207	207
	27/8	335	320	50	Str. 1	0209	15	48	48
	27/8	335	320	92	Str. 1	0209	15	46	46
	27/8	335	320	20–25	Str. 1	0250	15	105	105
	27/8	335	320	250	Str. 1	0407	15	30	30
	27/8	335	320	0	0	0505	15	7	7
	27/8	335	320	50	Str. 1	0505	15	10	10
	27/8	335	320	92	Str. 1	0505	15	3	3
1952	29/7	407	228	115	Str. 1	1010	15	12	12
	29/7	407	228	10	5	1122	15	12	12
	2/8	411	83–91	0	18	0920	12	48	48
	5/8	414	275–365	105	Str. 1	1810	35	216	216
	6/8	416	275–285	115	Str. 1	1535	20	37	37
	6/8	416	275–285	175	Str. 1	1620	45	512	512
1953	13/7	502	22–27	20	0	1615	10	21	21
	21/7	503	65–90	35	0	1520	25	86	86
	21/7	503	65–90	17	Str. 2	1700	15	53	53
	31/7	514	20	9	0	1703	30	15	15
	4/8	520	137	87	0	1250	30	55	55
	4/8	520	137	40–52	Str. 2	1615	15	Several hundred	121
	9/8	527	355–415	62	0	1110	20	43	43
	11/8	531	183	62	0	1710	25	16	16
	17/8	535	140–155	7	5	1320	15	66	54
	4/9	549	75	7	5	1210	20	63	63
	4/9	549	75	46	Str. 2	1345	15	43	43
	8/9	512	21	14	Str. 2	1440	25	32	32
	8/9	512	21	15	0	1545	20	49	49
1954	24/7	603	90–110	40	Str. 2	1600	30	6	6
	27/7	603	90–110	26	Str. 2	1721	15	Several hundred	76
	5/8	606	99	26	Str. 2	0000	30	87	87
	5/8	606	99	43–65	Str. 2	0140	15	265	265
	12/8	613	189	78–115	Str. 2	0955	30	175	175

TABLE II

COLLECTION DATA FOR *Themisto libellula* MATERIAL FROM STOMACHS OF RINGED SEAL (*Phoca hispida*)

Year	Date	Location	Number measured
1953	23/8	Cape Dorset	230
1954	22/3	Cape Dorset	315
1954	13–19/7	Cape Dorset	184
1955	27/10	Igloolik	112
1956	31/1	Igloolik	3
1956	27/2	Igloolik	17
1956	28/2	Igloolik	10

The 1947 and 1949 material comes entirely from Ungava Bay; the 1948 material consists of a collection of *Themisto* taken from the stomachs of arctic char at the head of Frobisher Bay (see map Fig. 2). The 1951 collection is in the main from Frobisher Bay, 1952 from Cumberland Sound. (For the identification of the stations in Table I, see the station lists already published (Dunbar and Grainger, 1952 (12); Grainger, 1954 (20*b*); Grainger and Dunbar, 1956 (21).) The 1953 and 1954 material is from northern Hudson Bay and the western end of Hudson Strait. Collections from ringed seal stomachs in 1953 and 1954 are from the region of Cape Dorset, southwest Baffin Island (August 1953, March and July 1954), and the material from October 1955 to March 1956 is taken from ringed seals off Igloolik, in the north of Foxe Basin.

Measurements were made with a low-power binocular microscope, the specimens being placed on a thin glass slide over a half-millimeter scale. The over-all lengths, from the front of the head to the tip of the longest uropods, were read to the nearest quarter-millimeter and then grouped on integer centers, all individuals from $x\cdot5$ to $(x+1)\cdot25$ being grouped under $(x+1)$ mm. The length frequencies of the samples are presented in the histograms (Figs. 3 to 5 and 11 to 13).

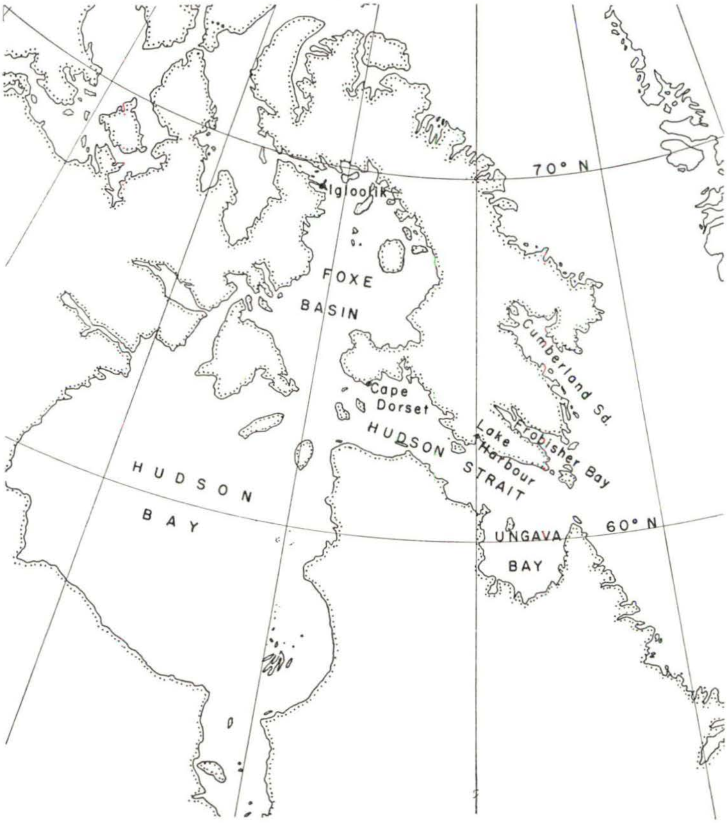


FIG. 2.

The Environment

The detailed hydrography of the area will be published in a paper to appear shortly in this series. Hudson Bay, Foxe Basin, and the western part of Hudson Strait are arctic areas in which the influence of Atlantic water is minimal if indeed it is present at all. Frobisher Bay, although probably containing a small proportion of west Greenland water, with Atlantic admixture, in the summer, is nevertheless predominantly arctic. Ungava Bay, on the other hand, shows considerable Atlantic influence, both hydrographically and in its fauna. It is an unstable region with very large tidal intervals and is slightly warmer below 25 meters than the rest of the region considered here. July temperatures in Hudson Bay and Hudson Strait (western part), below 25 meters, are normally below −1° C., whereas they range from −1.5° C. up to about +1.5° C. in Ungava Bay. In August, the 50-meter water may be up to 2° warmer in Ungava Bay than in the rest of the region, including Frobisher Bay. The 100-meter water in August in Ungava Bay is similar in temperature range to the water at the same depth in Froblisher Bay, between 0° and −1° C., and about 0.5° warmer than the Hudson Bay level, where the 100-meter water is below −1.0°. Hudson Bay, being highly stratified in summer owing to the influx of fresh water from the large land area it drains, is distinctive in having the surface water warmed up to the level of about 10° C. As far as the present paper is concerned, however, these exceptional temperatures are of no significance, since *Themisto* is apparently inhibited by them from invading the surface layers.

Growth Rate and Breeding Cycle

In an earlier paper on *Themisto* in Baffin Island waters (Dunbar, 1946 (11*d*)) it was shown that the size frequencies of the samples were strongly bimodal, the two size-groups being statistically quite separate and therefore representing two separate broods. The same bimodal distribution is demonstrated in the present material, shown in Figs. 4, 5, 11, and 12. The division between the two groups occurs, in the summer period of collecting, at about 20 mm.

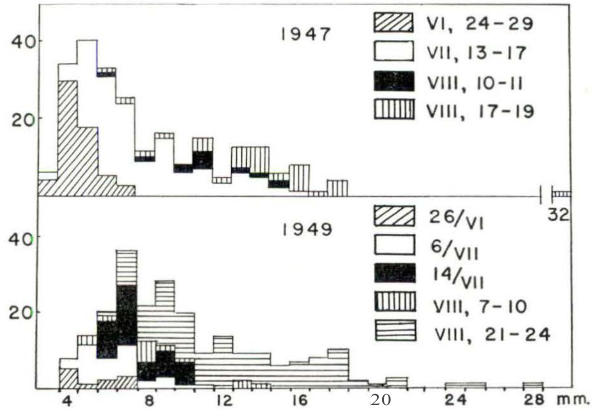
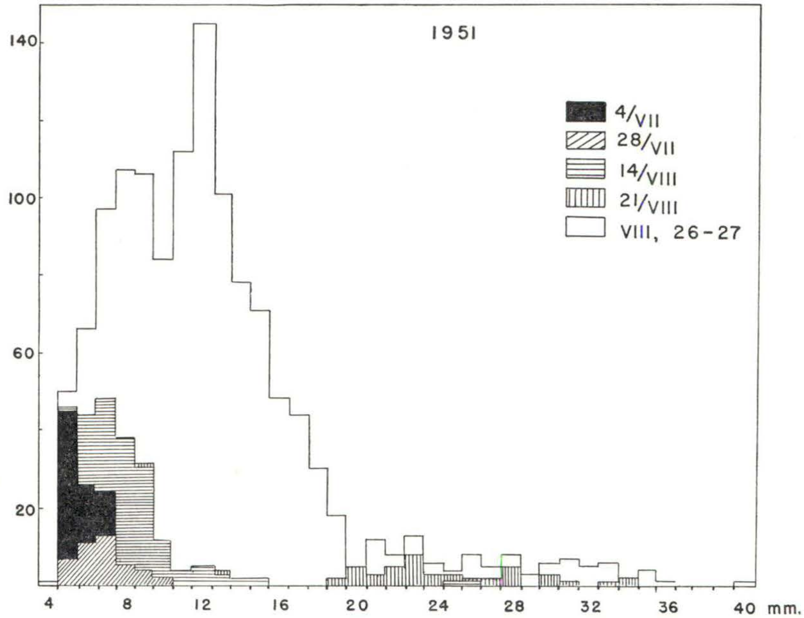


FIG. 3. Size distribution in *Themisto libellula* taken at different times during the summer seasons of 1947 and 1949, Ungava Bay.

In the separation of the broods for statistical treatment, the lowest point in the distribution has been taken, and this point is seen (Fig. 12) to coincide with the point at which, in the ascending series of length, adolescent individuals begin to appear, in contrast to the juvenile population to the left of the low point.

Figs. 3, 4, and 5 show the material from 1947 and 1949 (Ungava Bay), 1951 (Ungava Bay, Lake Harbour, and (predominantly) Frobisher Bay), and 1953 (northern Hudson Bay, and the western end of Hudson Strait), arranged according to date of collecting, to demonstrate change in size during the sum-



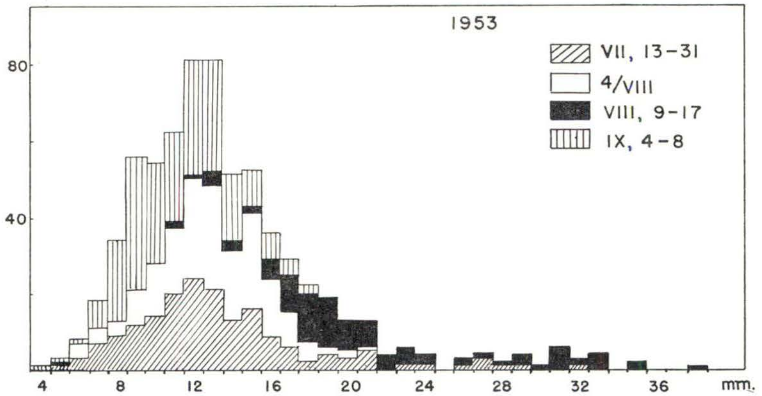
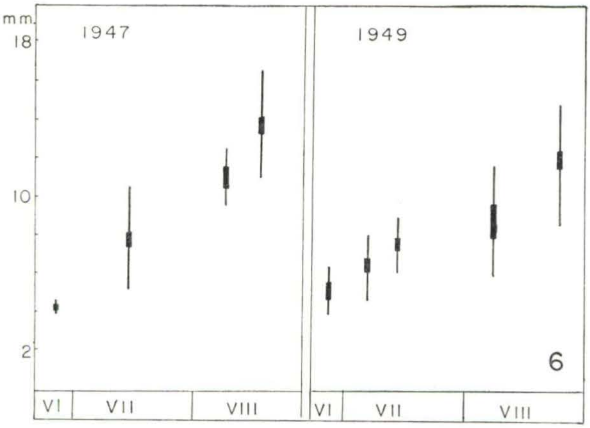
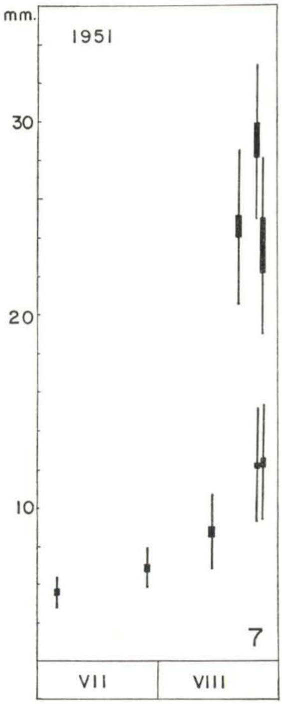


FIG. 4. Size distribution in *Themisto libellula* taken on 5 days in 1951, in Ungava Bay (4/VII), Lake Harbour (28/VII), and Frobisher Bay.

FIG. 5. Size distribution in *Themisto libellula* taken at different times during the summer season of 1953, in northern Hudson Bay and the western entrance of Hudson Strait.

mer season. In Figs. 6, 7, and 8 the increase in body-size in the populations is shown graphically on either side of the mean by lines representing one standard deviation (thin lines) and one standard error (thick lines), the total length of each line being therefore two standard deviations.





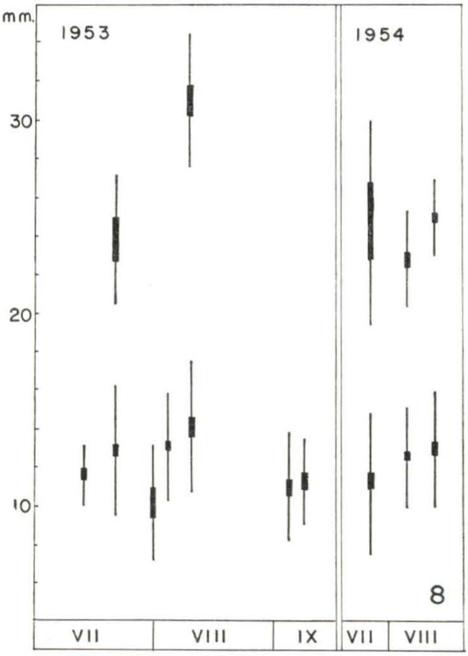
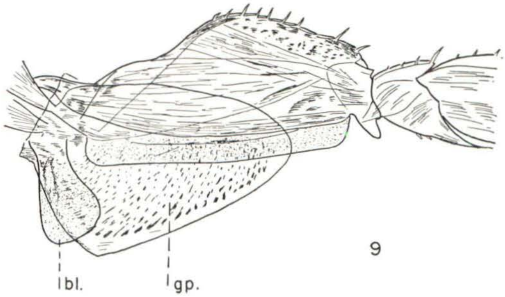


FIG. 6. Changes in mean individual size, Ungava Bay, 1947 and 1949. The total length of the vertical lines represents two standard deviations, that of the broad section two standard errors. Months on the horizontal axis.

FIG. 7. Changes in mean individual size, Ungava Bay (early July), Lake Harbour (late July), and Frobisher Bay (August). (For details see Fig. 6.)

FIG. 8. Changes in mean individual size, 1953 (northern Hudson Bay and west entrance of Hudson Strait), and 1954 (Hudson Bay). (For details see Fig. 6.)



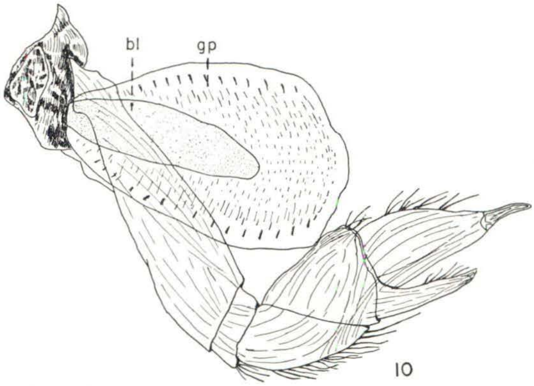


FIG. 9. Part of the fifth peraeopod of a female in the stage referred to as "adolescent" in the text.
Abbreviations: bl., brood lamella; gp., gill plate.

FIG. 10. Second leg of a female in the "maturing" stage, in which the brood lamella (bl.) is increasing in size.
Abbreviation: gp., gill plate.

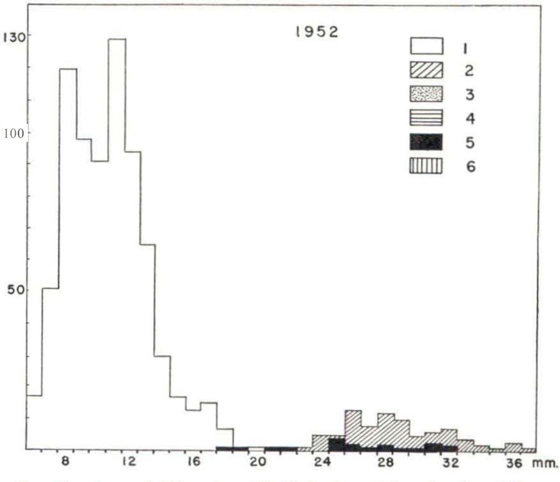


FIG. 11. Size distribution of *Themisto libellula* from Cumberland Sound, 1952, showing maturity stages.
The key refers to Figs. 11, 12, and 13; (1) immature; (2) "adolescent" females; (3) "maturing" females; (4) mature females; (5) adolescent males; (6) mature males. Vertical axis, numbers of individuals; horizontal axis, length in mm.

The material from 1952 (Cumberland Sound), 1954 (Northern Hudson Bay), and from stomachs of the ringed seal (Cape Dorset area, 1953, 1954, and Igloolik, 1955) has been divided into maturity stages, and the results shown in Figs. 11, 12, and 13. The stages are based on the development of the brood lamellae, or oostegites, in the female, and on the growth of the antennae in the male. Mature specimens were not taken in the net hauls, and the seal stomach material was too far digested to allow the use of the ovaries and testes. The delimitation of the stages is as follows:

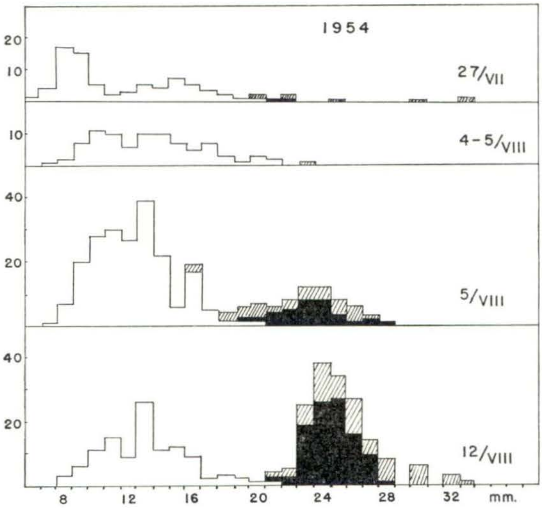


FIG. 12. Size distribution of *Themisto libellula* from northern Hudson Bay, 1954, taken on various dates, showing maturity stages. (Details as in Fig. 11.)

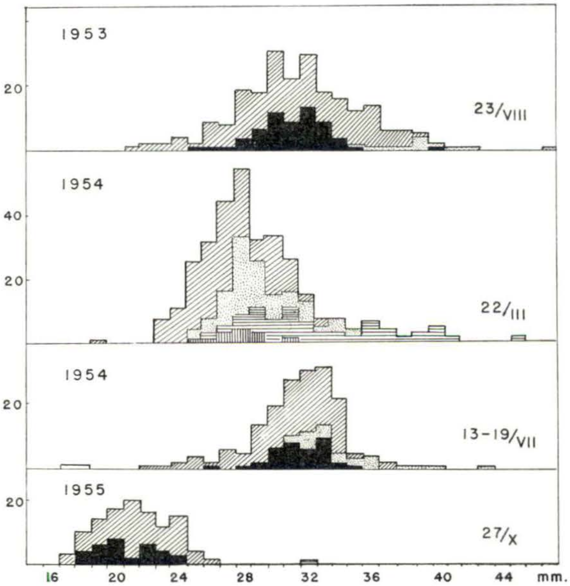


FIG. 13. Size distribution of *Themisto libellula*, with maturity stages, from ringed seal stomachs. 1953, 1954: Cape Dorset; 1955: Igloolik.

Immature: Antennae very short, no sign of development of oostegites.

Adolescent female: Oostegites present, but rudimentary, as in Fig. 9. Ovaries small, usually less than 5 mm. in length, cells very small.

Maturing female: Oostegites increasing in size from the "adolescent" condition (Fig. 10). Ovaries larger, with cells about 0.2 mm. in diameter or larger.

Mature female: Oostegites fully developed, almost twice the length of the gill plates. Specimens often with eggs or young in the brood pouch.

Adolescent male: Antennae increasing in length (Dunbar, 1946 (11*d*), Fig. 5).

Mature male: Antennae fully developed, the first antennae reaching to the hind margin of the first pleonal segment, the second antennae reaching beyond the hind margin of the last pleonal segment.

It has been demonstrated (Dunbar, 1946 (11*d*)) that in *Themisto libellula* there is an alternating or two-phase breeding cycle, such that two generations, or broods, exist at the same time, the two broods being apparently isolated from each other so far as reproduction is concerned, unless the cycle goes out of phase or unless a few individuals breed twice. During the breeding period itself, three broods are present, the breeding group, the adolescent group, and the very young group which is being produced at the time. Breeding cycles of this sort have also been shown to be the rule in certain other cold-water pelagic forms. It was not clear, however, from the earlier work, whether there were breeding periods in the fall and in the early part of the year (March–May), in which case the length of life would be 1 year, or whether there was only one breeding period, in which case the length of life would of necessity be 2 years at least.

Figs. 6, 7, and 8 are not growth curves; they show the manner in which the size-frequencies of *Themisto* in the plankton samples change as the summer advances. It will be seen that in 1947 and 1949 (Ungava Bay) and in 1951 (predominantly Frobisher Bay) there is an orderly progression of advancing average size in the youngest, or juvenile, group. This increase is less clear in the 1954 material, and in 1953, also from Hudson Bay, the slope is definitely reversed by the reduction in average size of the population in September. Fig. 5, dealing with the same 1953 population, shows that this effect in September is caused by the entry into the sample of numbers of very small individuals, down to 4 mm. in length, recently freed from the parental brood pouch. A similar arrival of very small specimens, this time in late August, is also shown in the Frobisher Bay collection of 1951 (Fig. 4), but here the average size of the juvenile population is not reduced compared to samples from earlier in the season owing to the presence of large numbers of larger juveniles, up to 19 mm. in length. There is no such late appearance of small individuals within the collecting season (June–August) in Ungava Bay (Fig. 3).

Another important difference between the Ungava Bay samples on the one hand and those from Frobisher Bay, Hudson Bay, and western Hudson Strait on the other is the almost complete absence of the larger (adolescent) group in Ungava Bay. In the net plankton, only one individual taken in 1947 belonged to the adolescent group, and only nine in 1949. The ringed seal

(*Phoca hispida*) feeds habitually on the larger individuals of the *Themisto* population (Dunbar, 1941 (11*c*)) yet of 36 ringed seals taken in the 1947–1950 seasons, only 10 had *Themisto* in the stomach, and those 10 had a total of only 36 specimens between them. Of these 36 specimens, only one half were over 20 mm. in length, and the largest was only 25 mm. This is in strong contrast to the seal stomachs taken at Lake Harbour, Frobisher Bay (Dunbar, 1941 (11*c*)), and in the Cape Dorset area (McLaren, in press), which were frequently found to be full of *Themisto libellula*, often to the exclusion of other food organisms. A swarm of adolescent individuals was observed and sampled in 1948 at the western end of Ikeresak, or McLelan Strait, which separates the island upon which Port Burwell is situated from the mainland of Labrador, but in that highly turbulent region it is impossible to determine where the swarm came from or whether it represented a permanent population. The evidence is in favor of the conclusion that *Themisto* does not breed in Ungava Bay, that the juvenile population is brought into the bay from the northwest, in the Hudson Strait outgoing current, and that it is swept out of the bay again before it reaches adolescence; or that it does not survive within the bay for some other reason. There are in fact certain hydrographic differences between Ungava Bay and the rest of the area examined here which are referred to above and which might be adequate to explain the matter.

Not one mature specimen, male or female, was taken in the plankton nets in any season. The maturity stages of the net catches of 1952 and 1954 are shown in Figs. 11 and 12, and they are typical of all years. Nor were there any mature specimens taken in seal stomachs in summer. As shown in Fig. 13, however, seal stomachs taken in March 1954, in the Dorset area, contained mature males and females, and mature females occurred in stomachs taken in February 1956 at Igloolik. Stomachs examined in August 1953 and July 1954 contained females in the maturing condition. The absence of maturing females from the net hauls is unexplained. It is improbable that individuals of this size can escape a 2-meter stramin net hauled at 3 knots, especially at night; it may be, however, that the maturing females maintain a lower level of vertical distribution than the others, although the net was lowered close to the bottom on several occasions and hauled obliquely, still without taking the maturing individuals.

Mature females, with and without eggs and young in brood pouches, were taken only in late January, February, and March. The young are released at a size of 2 to 3 mm. In the present series no collecting was done earlier in the winter than the end of January, and summer field work was carried out only between late June and early October. However, since the juvenile samples taken in June and early July show a fairly wide range of body length, and include individuals of only 4 mm., it may safely be assumed that the breeding period extends over a considerable period and that new broods are still being shed in the first half of June. The absence of spent individuals in spring and summer is evidence that each individual breeds once only (see below). We do not know how long the young are retained in the brood pouch.

One mature male was taken in the stomach of an arctic char in Frobisher Bay in August 1948 (precise date in August not given). This was an individual 31 mm. in length with antennae fully developed (first antenna 17.5 mm., second antenna 20.5 mm.), with sexual papillae developed, and with the testes silvery, rounded, and swollen and the seminal duct darkly pigmented. Another male 22 mm. in length had a second antenna 11 mm. long, first antennae missing. The females in the char stomach material from the same month were not mature, but some were in the "maturing" category, up to 32.5 mm. in length.

The presence of the mature male in August, the maturing females in seal and char stomachs in July and August, the one mature female taken in a seal stomach in October 1955 at Igloolik (Fig. 13), and the recruitment of very small juveniles into the stock in late August 1951 (Fig. 4) and early September 1953 (Fig. 5)—all indicate that breeding begins in the late summer and early fall. It is possible that this autumn breeding period is less important than the breeding period in the early part of the year. However, the lack of material in November, December, and January makes it impossible to rule out the possibility of a sustained breeding period throughout the winter, from September perhaps to June, and indeed for the greater part of the year.

Themisto libellula does not appear to be abundant in Foxe Basin, but there is a little material from ringed seal stomachs taken at Igloolik in January and February 1956, which is helpful. From January 31 there are three measurable specimens, 28, 30, and 31 mm. long, all with fully developed oostegites, and parts of 13 other specimens of similar size. From February 27 there are 20 specimens, one male of 27.5 mm. with the antennae broken but clearly well developed, and 19 females of which three are not measurable. The remaining 16 range from 20.0 to 35 mm. in length, and they all have fully developed oostegites, some with eggs and early young. The small size of the smaller of these specimens (20–21.5 mm.) suggests that at least some of the juveniles of each year may come into breeding condition the following winter. From February 28 there is a collection of 11 specimens of which nine are mature females ranging from 26 to 36 mm., one is a mature female of similar size with the head missing, and one is a juvenile of 11 mm. Clearly spawning has started by the month of February if not before, and although it is improbable that many of the juveniles of the year breed in the following winter, some apparently do, as shown by the small specimens taken on February 27, 1956. Most of the breeders each winter, however, must be the adolescents of the previous summer; indeed, the strong bimodality of the size-frequencies in summer makes it impossible that many of the juveniles should breed the winter after they are produced. This means that the life cycle of the individual is between 18 months and 2 years, but that a life cycle of 1 year is not impossible. This argument is illustrated in Fig. 14, and rests on the assumption that each individual breeds only once. The fact that a 1-year life cycle is possible means that the reproductive isolation of the two coexisting year-classes is not complete.

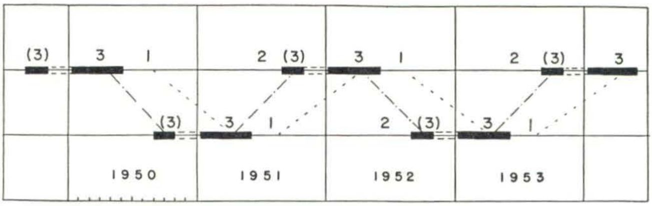


FIG. 14. Schematic diagram representing the probable breeding cycle of *Themisto libellula*. The two horizontal lines represent the time-continua of the two populations which exist together in the same space, between which reproductive contact is probably quite small, or absent. The heavy black portions represent the breeding periods; (1) immature group; (2) adolescent group; (3) mature breeding group. The possible extension of breeding throughout the long winter is indicated by the horizontal dotted lines. The diagonal lines represent the cases in which the alternating cycle may go out of phase either by the holdover of breeding until the fall, or by the precocious maturation of small individuals (Group 1).

Discussion

1. The question of whether *Themisto libellula* breeds more than once in its life is obviously highly important in reaching an understanding of the breeding cycle. The evidence on this point is not entirely conclusive, and in the past there has been some difference of opinion on this point as regards the amphipods as a group. Schneider (1891 (37)) quotes three authorities on the question and gives some observations of his own. Thus Siebold and Stannius (1854 (40)) describe the brood lamellae or oostegites of the female amphipod as developing rapidly at the approach of the breeding season and later disappearing or becoming atrophied. Bate (1856 (1)) considered that there was no evidence for the loss of the brood lamellae. Bruzelius (1859 (7)) was willing to allow the possibility of decrease in size of brood lamellae after breeding, but did not believe that they disappeared completely. Schneider himself pointed out that all three authors appeared to have assumed that amphipod individuals breed more than once, but that there was no evidence of that. He suggested that the absence of spent specimens, and of large females without oostegites, could most simply be explained by supposing that breeding only once per lifetime was normal, as it is in insects.

Blegvad (1921 (4)) records "*Gammarus locusta*" (probably *G. zaddachi*) as breeding seven or eight times per female in Danish waters, within a short time in one breeding season, and finds that the stock produced after the month of May can breed in two seasons; that is, after breeding once in late summer they may survive the winter and breed again the following spring. In Segerstråle's (1950 (39)) paper on the amphipods of Finnish waters, on the other hand, there is no indication that *Gammarus zaddachi* (or its "*salinus*" form) breeds more than once; the cold-water *Gammarus oceanicus*, similarly, appears to breed only once per individual.

In the present study it has been concluded that the *Themisto libellula* individual breeds once and dies. There is no evidence whatsoever to the contrary. No spent specimens of either sex were taken, except in March at the height of the breeding season.

2. The stimulus for the final ripening of the gonads and the onset of the breeding, if it has anything to do with temperature at all, appears to involve a fall rather than a rise in temperature. Orton (1920 (28)) suggested that "Most animals under normal conditions begin to breed either at a definite temperature, which is a physiological constant for the species, or at a definite temperature change, namely at either the maximum or the minimum temperature of the locality", and added that many continued to breed so long as the temperature remained above or below a certain figure, critical for each species, and that a given species might be a winter breeder in warmer situations and a summer breeder in colder areas, a situation which appears to be illustrated in the invertebrate fauna of Norwegian waters, where the northern elements breed in the winter and the southern elements in the summer (Ekman, 1953 (14)). Orton took the argument further: "It follows that in those parts of the sea where temperature conditions are constant or nearly constant, and where biological conditions do not vary much, marine animals will breed continuously". He suggested that this condition might be found in the arctic. In the abyssal depths of the sea, where there may well be no seasonal variation in temperature, breeding all year may well be the case, as is stated, apparently on rather slim evidence, by Reibisch (1927 (31)), although even in the abyssal region there must be a seasonal variation of the food supply, which comes from the surface layers. On the other hand, year-round breeding is known to occur in species where habitats certainly do show considerable seasonal temperature variation, as in *Gammaris zaddachi zaddachi* on the coast of Finland (Segerstråle, 1950 (39)). In arctic waters, however, Orton's prognostication has not been realized. All arctic and subarctic forms so far studied have shown well-marked breeding periods, often extending over only a short part of the year. Indeed, year-round breeding appears to be far more common in *tropical* waters, not in the arctic.

There is to begin with a significant variation in the annual temperature cycle at the depths in which the animals of the arctic and subarctic continental shelf live. Thus in Godthaab Fjord, a decidedly subarctic region as opposed to arctic, the annual range of temperature at 75 meters is of the order of 1° C. to 2.75° C. (Dunbar, 1946 (11*e*)). Surface temperatures of course show a wider range, but they are not ecologically significant in the present argument. In Scoresby Sound, east Greenland, Digby (1953 (10*a*)) recorded, at 50 meters, −0.95° C. at the beginning of October, −1.78° in January, and −1.47° at the end of July. From November to May inclusive the temperature was not above −1.72° C. at 50 meters depth. In the waters of northern Baffin Island, Ellis (1956 (15)) measured, again at 50 meters, temperatures of −0.90° C. in September and October, −1.00° in November, −1.05° in December, −1.70° to −1.75° in April and again in June, −1.65° in late June, and −1.45° in July. A similar cycle was recorded at Igloolik by the *Calanus* wintering expedition of 1955–56: from November through the winter and spring to June, the temperatures at 50 meters were below −1.70° C., in July rose to −1.63°, in August to −0.07°, and in September the temperature measured was −0.24°. Hudson Bay conditions are essentially similar. In the area between Southampton Island, Coats Island, and Mansel Island temperatures at 50 meters in July and August range from −1.50° to about 0.05°, and in the months of April, May, and June they are below −1.70° down to −1.80° C. Winter temperatures in Frobisher Bay and Ungava Bay are not known, but the upper 50–75 meters in Ungava Bay in summer are both warmer and less stable, temperatures as high as 2.16° C. having been recorded.

The coldest time of the year, therefore, in the depths at which *Themisto libellula* lives, in arctic regions, is from November to June inclusive, when the temperature is close to its "floor" level of about −1.70°. From July to early October temperatures are about 2° higher. Therefore, if temperature controls the onset of breeding, and since *Themisto* breeds in the coldest part of the year, it is indicated that the stimulus is a fall below certain threshold value and not a rise above it. However, the fact that breeding begins, apparently, in September, close to the warmest part of the year in the water, suggests that the temperature threshold is not the overriding or efficient stimulus, but that some other factor such as light is involved. It is possible that the autumn breeders should be considered as "hold-overs" from the end of the previous winter, breeding late for one reason or another, and that they are not in the normal physiological condition. More information is needed on the winter biology of the species.

It is well known that arctic species which extend south into the boreal region tend to breed during the winter, but it is not yet established that winter breeding in the arctic itself is a common habit. As a winter breeder of egregiously arctic affinities, *Themisto libellula* contrasts with another important member of the arctic pelagic fauna, *Sagitta elegans arctica* Aurivillius, which breeds in the summer (Dunbar, 1941 (11*b*)), and with the planktonic copepods (Fontaine, 1955 (16); Digby, 1954 (10*b*)). Samter and Weltner (1904 (36)) reported of *Mysis relicta* in Europe that it produced eggs only in cold water, below 7° C., and that the chief production was in the winter, at temperatures between 0° and 3° C.

The appearance of large numbers of very small amphipods released from the parental brood pouches in the dead of winter raises the question of what they eat. The density of the visible or sedimentable phytoplankton during the winter is extremely low, and the first sign of phytoplankton development at Igloolik during 1955–56 did not appear until the first half of May (Grainger, unpublished). Two possibilities remain: either the young feed almost entirely on detritus, perhaps close to the bottom or on it, or else there must be a continuing production of microplankton which, as Rodhe (1955 (33)) suggests for subarctic lakes in Sweden, becomes heterotrophic in the winter, using dissolved organic matter. Indeed, dissolved organic matter, in the form of leptopelic detritus, may play an important part in the direct diet of the young amphipods.

Acknowledgment

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