THE BIOLOGY OF THE ATLANTIC WALRUS
ODOBENUS ROSMARUS ROSMARUS (LINNAEUS)
IN THE
EASTERN CANADIAN ARCTIC

BY

A. W. MANSFIELD

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE
REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY
IN McGILL UNIVERSITY

April 1958

TABLE OF CONTENTS

PAGE

LIST OF TABLES. v

LIST OF FIGURES vi

LIST OF APPENDICES. x

ACKNOWLEDGEMENTS. xi

INTRODUCTION 1

General Remarks. 1

Previous Work. 2

Nomenclature 3

METHODS AND MATERIALS 5

Field Localities 5

Northern Hudson Bay 5

Northern Foxe Basin 7

Travel 8

Counts 9

Marking. 10

Materials Collected. 12

Treatment of Materials 14

AGE DETERMINATION 16

Methods. 16

Body length measurements. 16

Tusk and baculum measurements 18

Claws 19

Teeth 20

PAGE

Application of Methods to the Atlantic Walrus. . . 21
    Tusks 21
    Molariform teeth. 27
    Determination of age in the female. 31
GROWTH. 33
  The Male 33
    Body length 33
    Increase in weight. 34
    Growth of tusks 36
    Growth of the baculum 36
  The Female 37
  Sexual Dimorphism. 38
  External Appearance. 40
    The calf. 40
    Immature males and females. 41
    The adult female. 42
    The adult male. 43
  Dentition. 44
    Deciduous and permanent teeth 44
    Tooth wear. 47
NUTRITION 49
  Food Preferences 49
  Method of Feeding. 53
  Aberrant Diets 56

PAGE

Fasting. 57

THE MOULT 59

THE MALE REPRODUCTIVE CYCLE 62

Sexual Maturity. 62

Growth of the baculum and testis. 62

Histology of the testis and epididymis. 63

The Testicular Cycle in the Adult Male 65

Chronology of Events in the Adult Male 66

THE FEMALE REPRODUCTIVE CYCLE 68

Sexual Maturity. 68

Ovulation in nulliparous females. 69

Ages at first ovulation 69

Birth Rate 72

The Ovarian Cycle. 73

Development of the follicles and ovulation. . . 73

The corpus luteum 77

Implantation and Growth of the Embryo. 80

Birth and Care of the Young. 83

Chronology of Events in the Adult Female 84

DISTRIBUTION AND ABUNDANCE. 87

Relation to the Land 88

Relation to Sea Ice. 91

Local Movements and Migrations 93

SUMMARY 97

BIBLIOGRAPHY. 101

LIST OF TABLES

TABLE PAGE

I Weights of Various Internal Structures of an Adult Male Atlantic Walrus 35
II Comparative Sexual Dimorphism in the Walrus. 39
III Observed Variations in the Dentition 46
IV Food Organisms taken from Stomach Contents. 50
V The Moult. 60
VI Sexual Maturity in the Female. 71
VII Calculated Average Gestation Period derived from Lengths of Eleven Foetuses . . 82

LIST OF FIGURES

FIGURE		TO FOLLOW PAGE
1	Map of Southampton Island showing position of <u>Uglit</u> and Limit of Winter Fast Ice. . . .	5
2	Map of Foxe Basin showing Bathymetry and Limit of Winter Fast Ice	7
3	Stainless Steel Tag used in marking Walrus. . .	11
4	Frequency Analysis of Body Length Measurements in Inches.	17
5	Comparison of Tusk Growth in a Foetal, Two Year Old and Adult Male Walrus	21
6	Comparison of Male and Female Tusk Lengths in the First Three Years of Growth	23
7	Photograph of the Tusk of a 21-Year-Old Male to show Root Ridges and Medial Depressions .	24
8	(a) Illustration of the Root Ridges on an Old Male Tusk after exfoliation of the Cementum.	
	(b) The Dentine and Cementum Layers on the Tusk Root in Longitudinal Section	27
9	Longitudinal Section of the Lower Canine Tooth of a 7-Old-Female (x 3.5).	28
10	Part of a Transverse Section of the Lower Canine Tooth of a 21-Year-Old Male (x 15).	32
11	Deposition of Cementum on the Roots of Molariform Teeth in Males and Females	32

FIGURE | TO FOLLOW PAGE

12 Growth in Length of the Body of Males and Females. 33

13 Increase in Weight of the Body (the weights of 4 males and 6 females of unknown age are taken from Loughrey, 1955). 35

14 Growth in Length of the Tusks 38

15 Growth of the Baculum 40

16 Head and Shoulders of an Adult Male Walrus showing Epidermal Tubercles and Scars from Tusk Inflicted Wounds. 44

17 Head of an Old Adult Male Walrus showing Worn Tusks and Vibrissae. 44

18 Dentition of the Full-Term Foetus A 11 (Teeth indicated by bracketed numbers were not observed in the specimens available, but were inferred from Fay's account of the Pacific walrus). 45

19 Percentage of Stomachs containing Food. 58

20 Development of the Testis (the specimens in breeding condition are indicated by black dots). 63

21 Section through the Seminiferous Tubules of the Immature 6-Year-Old Male A 111 (x 600). . 64

FIGURE — TO FOLLOW PAGE

22 Section through the Epididymal Epithelium of the Immature 6-Year-Old Male A 111 (x 600) 64

23 Section through the Epididymal Epithelium of the Mature Male A 97 (x 600) 65

24 Section through a Seminiferous Tubule of the Adult Male IW 10, taken on November 30: Type A (x 600) 65

25 Section through a Seminiferous Tubule of the Adult Male A 97, taken on June 17: Type B (x 600). 65

26 Section through a Seminiferous Tubule of the Adult Male A 62, taken on September 18: Type C (x 600) 65

27 Seasonal Fluctuation in Diameter of the Seminiferous Tubules in Adult Males (the two Specimens indicated by black dots are in an active state of Spermiogenesis). 66

28 Relation between Age of the Female and Number of Corpora Lutea in the Ovaries 77

29 Section of the Corpus Luteum of the Pregnant Female A 42, taken on August 7 (x 600) . . . 79

30 Section of the Late Pregnancy Corpus Luteum of Female A 9, taken on May 26 (x 600) 79

31 Section of the Regressing Corpus Luteum of Female A 43, taken on August 17 (x 600) . . . 80

FIGURE — TO FOLLOW PAGE

32 Section of a <u>Corpus Luteum Spurium</u> from the Barren Female A 77, taken on October 2 (x 600) 80

33 Growth of the Embryo and Placenta. 81

34 Growth of the Human Embryo (after Arey, 1954) 82

35 Map of the Eastern Canadian Arctic 93

LIST OF APPENDICES

APPENDIX		PAGE
I	Body and Tusk Length Measurements of 83 Male and 39 Female Walrus of Known Age	107
II	Development of the Testis in Immature and Mature Males	111
III	Development of Follicles and Corpora Lutea in the Ovaries of 59 Atlantic Walrus	113
IV	Growth of the Human Embryo (after Arey, 1954)	120
V	Comparison of Mean Body Length and Mean External Tusk Length in Male Atlantic and Pacific Walrus	121

ACKNOWLEDGEMENTS

The initial part of the laboratory work on which this study is based was carried out in the Department of Zoology, McGill University. I am most grateful to Professor J. Stanley for supplying laboratory facilities, and to Dr. M. J. Dunbar for initiating the program of research and offering much useful advice and criticism during its completion. Since April 1956 the work has been supported by the Fisheries Research Board, Arctic Unit, and I wish to thank Dr. H. D. Fisher and his staff for much valuable assistance.

Research on the Atlantic walrus was begun by the Fisheries Research Board in 1953 as part of the general study of the marine resources of northern waters. I am grateful to Dr. Dunbar for directing the research initially, and for designing the tag used in marking experiments.

Dr. E. H. Grainger began the tagging program at Coats Island in 1954, and also made the first substantial collection of reproductive material. Further collections were made from C.G.M.V. Calanus during the period August 1955 - September 1956 and I am indebted to Dr. Grainger for his valuable efforts in the field. Mr. I. A. McLaren contributed specimens from Hudson Strait, and made detailed analyses of their stomach contents. I much appreciate his help and advice throughout the study, and also his criticism of the manuscript.

I would also like to thank Dr. D. V. Ellis for analyzing the collection of stomach contents from northern Hudson Bay and Dr. D. E. Sergeant for reading and correcting the manuscript.

The two summer seasons spent at Southampton Island were made most pleasant by the friendliness and hospitality shown by the residents at the settlement: Mr. and Mrs. A. T. Swaffield and Mr. and Mrs. R. Cruickshank of the Hudson's Bay Company, and Mr. and Mrs. J. Whitford of the Department of Northern Affairs. I am particularly grateful to Father J. Choque, O.M.I., for providing accommodation during this time and for being helpful in so many ways.

At Igloolik, Mr. W. Calder, the Post Manager of the Hudson's Bay Company, provided hospitality which was much appreciated.

During the three seasons' work, Eskimos were my constant travelling companions, and without their help no collections could have been made. I have much pleasure in thanking Paniuk, Joe Curly, Angutialuk and Mikkitok of Southampton Island, and Kramanik of Igloolik for their friendliness and cooperation in all phases of the field work.

For help in the laboratory, I wish to thank Mrs. P. J. Thompson and Mr. R. Szavay for preparing histological sections, and Miss Berit Arnestad for drawing the diagrams.

Special thanks are due to Mr. J. Pollock of the Department of Zoology for photographing and preparing copies of the drawings.

The arduous task of typing the manuscript was undertaken by Mrs. E. O'Brien whom I would also like to thank for her efforts.

Finally I would like to express my gratitude to the Trustees of the McGill Carnegie Fund and to the Fisheries Research Board for providing adequate finances to enable the program to be carried out.

INTRODUCTION

General Remarks

The walrus, Odobenus rosmarus, is a circumpolar species of arctic and sub-arctic waters and is geographically isolated into three or more morphologically distinct groups. The Eastern Canadian Arctic and West Greenland group ranged as far south as Sable Island and the Gulf of St. Lawrence in historic times, but unrestricted commercial exploitation led to a serious decline in numbers and a withdrawal of the group to the more northern and inaccessible parts of its range. The advent of the rifle into the Eskimo economy with consequent wasteful methods of hunting caused further serious reductions in the walrus herds and necessitated the introduction of restrictive hunting measures. In 1931 a Department of Fisheries Act was passed which limited the taking of walrus to Eskimo families and certain white residents in the north and, in addition, the exporting of raw, unworked ivory was forbidden.

In the post-war years the increased interest of the Government in the economy of the native peoples has led to the undertaking of basic research into the natural resources of the arctic. In 1952 the Department of Northern Affairs and National Resources initiated a preliminary two year investigation into the present status of the walrus in northern Hudson Bay (Loughrey, 1955). In 1953 members of Eastern Arctic

Investigations aboard C. G. M. V. Calanus began a study of the walrus herds frequenting this area as part of their general program of research into the marine resources of northern waters (see Dunbar, 1956). In 1955 the present author began a full time study of walrus biology with financial assistance from the McGill Carnegie Fund. In 1956 the work was supported by the Fisheries Research Board, Arctic Unit (formerly Eastern Arctic Investigations) with whom the author is now employed.

Previous Work

The vast early literature was reviewed by Allen (1880) in an exhaustive and authoritative monograph of the North American pinnipeds. The first really important information on the biology of the walrus was given by Chapskii (1936) on the population frequenting the Kara Sea. Belopolskii (1939), Freiman (1940) and Nikulin (1940) contributed detailed analyses of the life history of the Pacific walrus in the Chukchee Sea, and Vibe (1950) gave the most complete record of feeding habits. Unfortunately, many of the conclusions of these workers concerning the problems of growth and sexual maturity were based on ages assumed from frequency analyses of tusk and body length measurements. It is now known that body length is a very variable factor in several species of pinnipeds, and the results of the foregoing authors must be viewed with some reservation.

A new method of age determination in mammals, with special reference to pinnipeds, was discovered by Scheffer (1950a) and Laws (1953a), and both authors suggested its possible application to the walrus. Mohr (1952) pointed out the significance of cementum layers in the molariform teeth as a possible guide to age, and Brooks (1954) and Fay (1955) attempted to apply the method to the Pacific walrus. Brooks recognised the regularity with which the cementum layers were formed, but was unable to correlate this with an annual cycle. Fay determined immature age groups by analysing the frequency distribution of external tusk lengths and found no correlation between cementum layers and age determined by this method. In mature males, however, there appeared to be a good correlation, and Fay was able to offer a better interpretation of growth and age than had previously been given.

The most recent study on the Atlantic walrus was a preliminary investigation made by Loughrey (1955) on the population frequenting northern Hudson Bay.

Nomenclature

The early literature on the systematics of the walrus was reviewed by Allen (1880) who postulated the existence of two species in the genus _Odobenus_. Of recent authors, only G. M. Allen (1942) and Anderson (1946) have supported Allen's suggestion, while Nikulin (1940) has assumed that the Atlantic and Pacific forms are of subspecific rank only: namely Odobenus rosmarus rosmarus and Odobenus rosmarus divergens. Nikulin also refers to a theory of Chapskii (1940) who suggests that walrus inhabiting the Laptev and East Siberian Seas form a separate group, morphologically distinct from the Atlantic and Pacific forms.

In the present work, it has been possible to compare material from northern Hudson Bay and northern Foxe Basin with the data published by Fay (1955) and Chapskii (1936). Reference to Table II shows that the Pacific and Atlantic forms are morphologically distinct, with the Kara Sea walrus comprising an intermediate group more akin to the larger Pacific form. Nothing is known of the fourth group which inhabits the Laptev and East Siberian Seas.

The true relationships between the groups will only be established when their morphometry has been studied in much greater detail, but until then the two subspecific names in current usage appear to be acceptable.

METHODS AND MATERIALS

Field Localities

Northern Hudson Bay (fig. 1). Field work in this area was initiated in the summer of 1953 by members of C. G. M. V. Calanus under Dr. E. H. Grainger. In the following year, work was continued on the walrus census about Seahorse Point and Coats Island, and quantitative bottom samples were taken at selected points off the coast to provide data on walrus feeding. During late July and early August, Dr. Grainger spent a period of three weeks on Coats Island carrying out a preliminary tagging program and collecting a series of specimens for study of the reproductive cycle.

The author began his field work at Southampton Island in March 1955, and was joined by the 'Calanus' on August 14. The ship helped in collecting specimens and tagging animals at Coats Island and Seahorse Point, and then left for Igloolik on September 4. The author finished the 1955 field season in mid-October and returned the following year in late May, remaining until October 27.

Walrus are occasionally taken at the edge of the fast ice to the south of the settlement in the spring months, but the main hunting takes place in the fall, when they haul out on land. The hauling-out sites or uglit are reoccupied

Figure 1. Map of Southampton Island showing Position of <u>Uglit</u> and Limit of Winter Fast Ice.

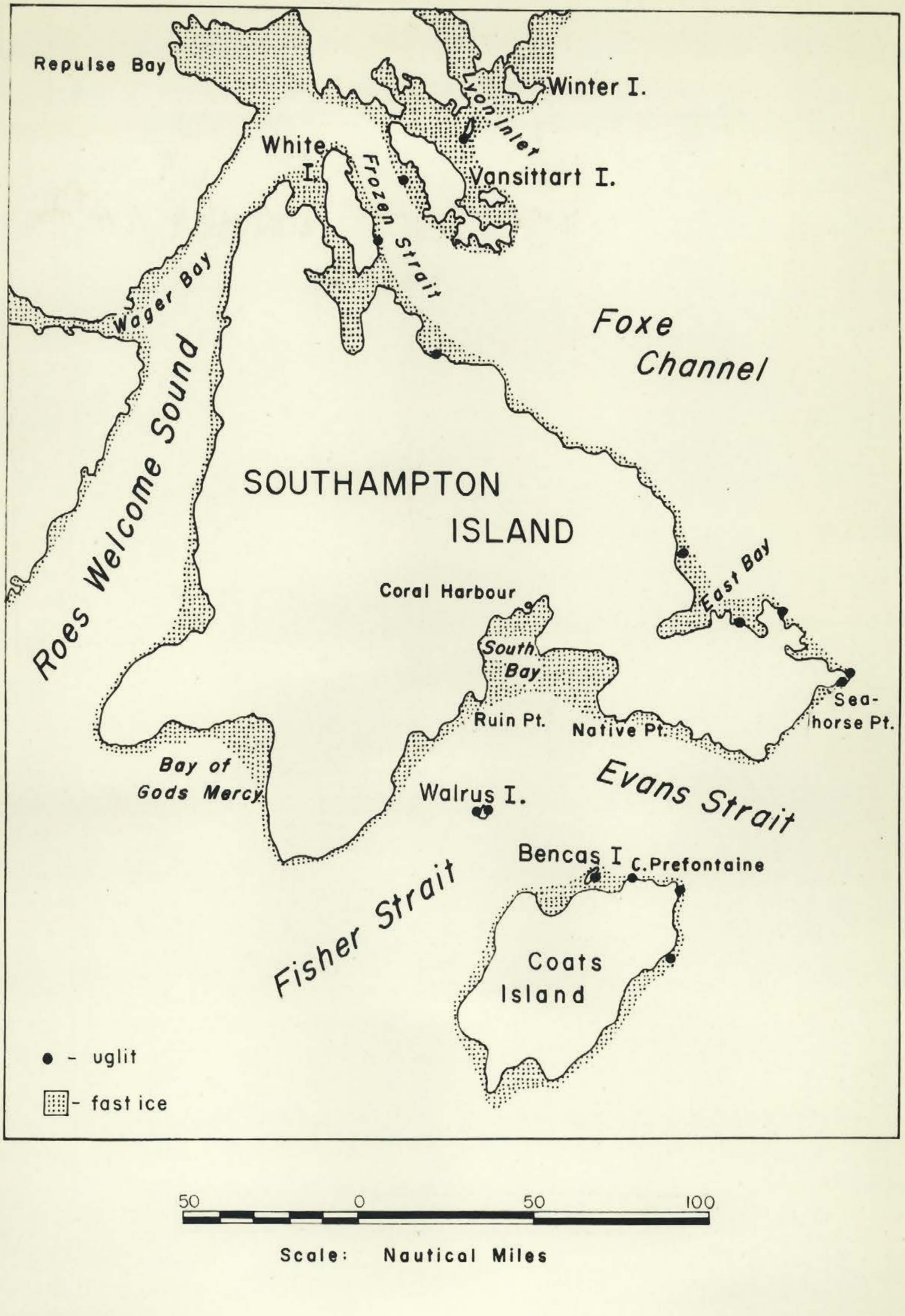

Repulse Bay
Winter I.
Lyon Inlet
White I.
Frozen Strait
Vansittart I.
Wager Bay
Foxe Channel
Roes Welcome Sound
SOUTHAMPTON ISLAND
East Bay
Coral Harbour
South Bay
Ruin Pt.
Native Pt.
Sea-horse Pt.
Bay of Gods Mercy
Walrus I.
Evans Strait
Bencas I
C. Prefontaine
Fisher Strait
Coats Island
● - uglit
▨ - fast ice
50
0
50
100
Scale: Nautical Miles

Figure I

year after year, and they are grouped closely enough on Bencas and Coats Islands to provide both the hunter and field worker with a conveniently restricted locale.

The southern coastline of Southampton Island is uniformly flat and desolate and consists of low raised beaches of fragmented limestone. The bays and indentations in the coast are very shallow and the fast ice is able to remain close to the shore until mid-July. Strong currents combined with high average wind speeds keep the ice constantly moving in Fisher and Evans Straits, and the fast ice in South Bay is rarely able to extend south of a line from Ruin Point to Native Point.

Walrus Island (Akpatorardjuk) in Fisher Strait rises to 160 feet above sea level and is composed of large blocks of black basaltic rock. The coastline is steep and in certain years the island is a favoured hauling-out ground for as many as two thousand walrus (Manning, 1942).

The featureless flat limestone country forms most of the coastline of Coats Island (Akpatordjuark). In the northeast the Precambrian crystalline rocks rise to over 500 feet and provide a welcome relief to the landscape. Bencas Island (Krekektaugaluk) to the north of Coats Island forms a low lying outcrop of the Precambrian rocks.

There are four uglit on these two islands (fig. 1) and they are confined to the Precambrian rocks. Walrus are not known to frequent other places in this area, and they never haul out on the limestone beaches. The ecological factors affecting this choice of hauling-out sites will be discussed in a later section.

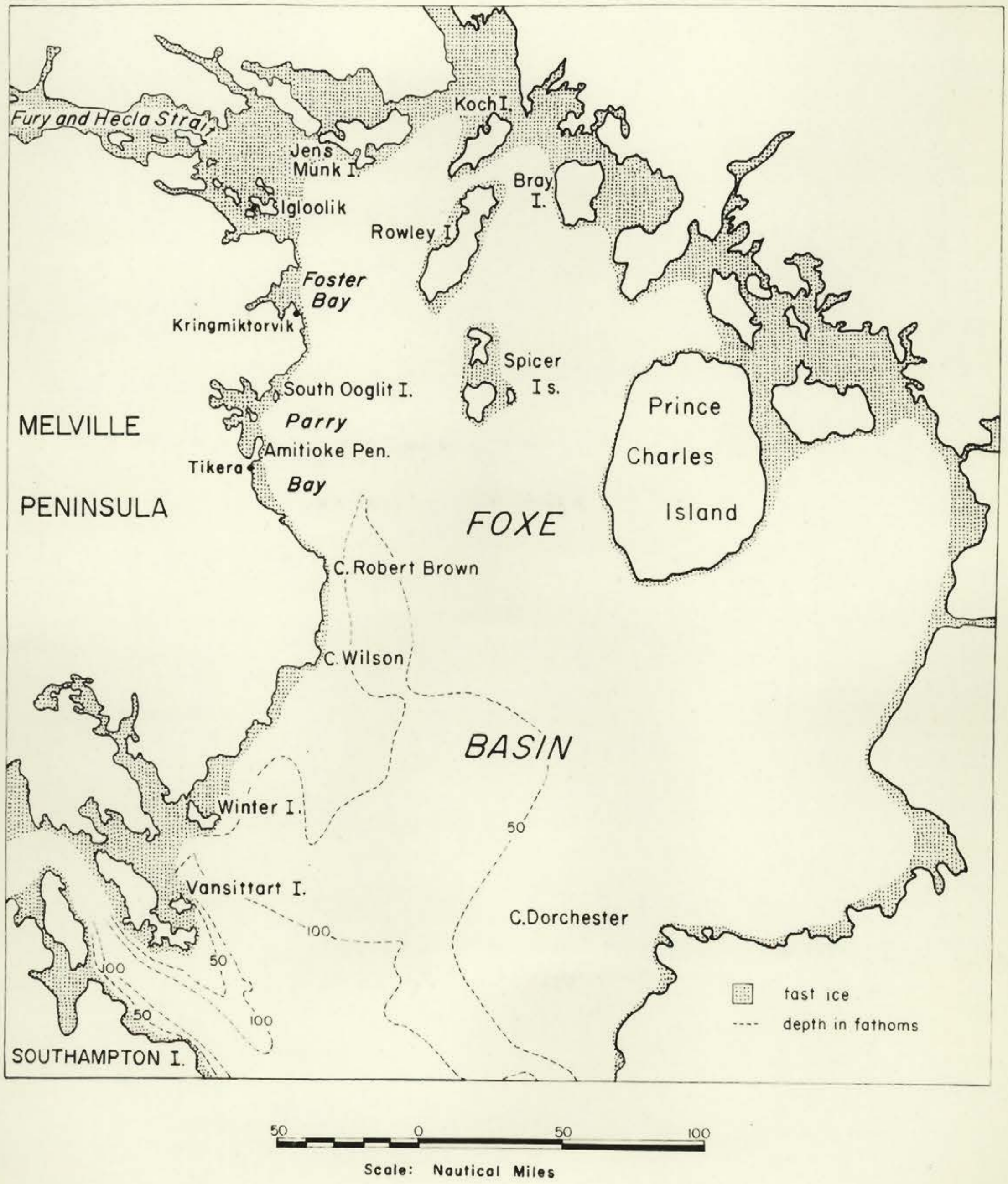
Northern Foxe Basin (fig. 2) C. G. M. V. Calanus reached Igloolik in October, 1955, and remained fast in the ice throughout the winter. During the following summer, work was confined to the northwestern region of Foxe Basin, and the ship was finally beached at Rowley Island in the fall. In the winter of 1955 and the spring of 1956, Dr. Grainger was able to make some collections of walrus material, and these were augmented in the summer by the efforts of several field parties from the ship. In the summer of 1957 the author's field base was located on Amitioke Peninsula, about five miles north of the small Eskimo community at Tikera (68° 03'N, 82° 06'W).

In July and August, the greatest concentrations of walrus are found in the pack ice to the east and north-east of this area, and the hunters from Tikera are generally more successful in securing their winter meat supplies than their nearest relatives at Kringmiktorvik. In September the walrus appear to move north and the hunters from Igloolik are able to make their best catches then.

From October until May, when the fast ice extends all along the coast of Melville Peninsula and to the east of Igloolik Island (fig. 2), special conditions are needed for

Figure 2. Map of Foxe Basin showing Bathymetry and Limit of Winter Fast Ice.

Fig. 2



Fury and Hecla Strait
Koch I.
Jens Munk I.
Bray I.
Igloolik
Rowley I.
Foster Bay
Kringmiktorvik
Spicer Is.
South Ooglit I.
Prince Charles Island
MELVILLE PENINSULA
Parry Bay
Amitioke Pen.
Tikera
FOXE
C. Robert Brown
C. Wilson
BASIN
Winter I.
50
Vansittart I.
C. Dorchester
100
100
50
100
50
SOUTHAMPTON I.
fast ice
depth in fathoms
50
0
50
100
Scale: Nautical Miles

hunting to occur. In east and southeasterly winds the Foxe Basin pack closes in to the edge of the fast ice along the coast, and the hunters are then able to travel out onto the moving ice and look for walrus in the leads of open water.

From Amitioke Peninsula northwards to Igloolik the coast is formed of featureless raised beaches of fragmented limestone. The two major indentations of Foster Bay and Parry Bay retain unbroken fast ice until late in July, and a narrow coastal strip of ice, seldom exceeding a mile in width, connects them. East of Igloolik Island the edge of the fast ice turns northeastwards towards Jens Munk Island.

Walrus are not generally found anywhere on land in this region, though the Eskimos suggest that they come ashore on South Ooglit Island in the fall. At this time the island is usually inaccessible from the mainland owing to the formation of new ice.

Travel

At Southampton Island in the spring months, the hunters haul their canoes and flat-boats across the fast ice on South Bay and look for seals and walrus in the loose ice. The large 22 foot freight canoe fitted with an outboard motor is easily transported by dog sledge, and rapid forays can be made away from the ice edge in fine weather. It is a fragile craft however, and the Eskimos exercise the greatest caution when hunting walrus. In the late summer and fall, motor whale-boats, trapboats and several fully decked 42 foot Peterhead boats are used for the long journeys to the hauling-out sites.

The author accompanied the Eskimos in both canoe and Peterhead boat, and supplemented these hunting trips with several journeys in a whaleboat belonging to the Fisheries Research Board, Arctic Unit.

In northern Foxe Basin, a similar whaleboat was used for the summer's work. In May, 1957, it was hauled to the edge of the fast ice to the east of Igloolik Island and sailed down to the camp site on Amitioke Peninsula. This journey was impeded by unusually difficult ice conditions and little hunting could be done.

Counts

At Coats and Bencas Islands during the summer and fall months, counts were made at the uglit and also while travelling to and from suitable anchorages. On the relatively few fine days when work at sea was possible, walrus were found to be grouped close to each uglek, and few were seen along the coast. On several occasions, most of the uglit were visited in one day, and a large proportion of the walrus frequenting the area were probably accounted for in the observations.

With practice, it became possible to distinguish between adult males and females, but precise numbers of each sex could seldom be obtained owing to their habit of lying so close together.

Counts made from the 'Calanus' in 1954 suggested that the total population frequenting the Coats Island and Seahorse Point area numbered approximately 3,000 animals (Dunbar, 1956). This figure was confirmed by an aerial census of the hauling-out sites made on August 20, 1954, by Loughrey (1955). He was able to fly over all the known *uglit*, and observed an estimated total of 2,900 animals.

Limited local observations from other areas have been made available through R. C. M. P. files, and some verbal reports have been received from Post Managers of the Hudson's Bay Company and Oblate Fathers of the Roman Catholic Mission. The Atlantic Oceanographic Group aboard H. M. C. S. 'Labrador' has contributed further observations from the ship's marine mammal log.

Marking

The seasonal appearance of the walrus, particularly at the traditional hauling-out sites in northern Hudson Bay and Hudson Strait, has led some observers to believe that a definite migration occurs. The paucity of animals in the winter months has been taken as partial proof of such a movement away from their summer haunts, but the lack of animals seems to be more apparent than real. There is little doubt that local movements do occur, but these are more probably in the nature of a dispersal as winter conditions set in.

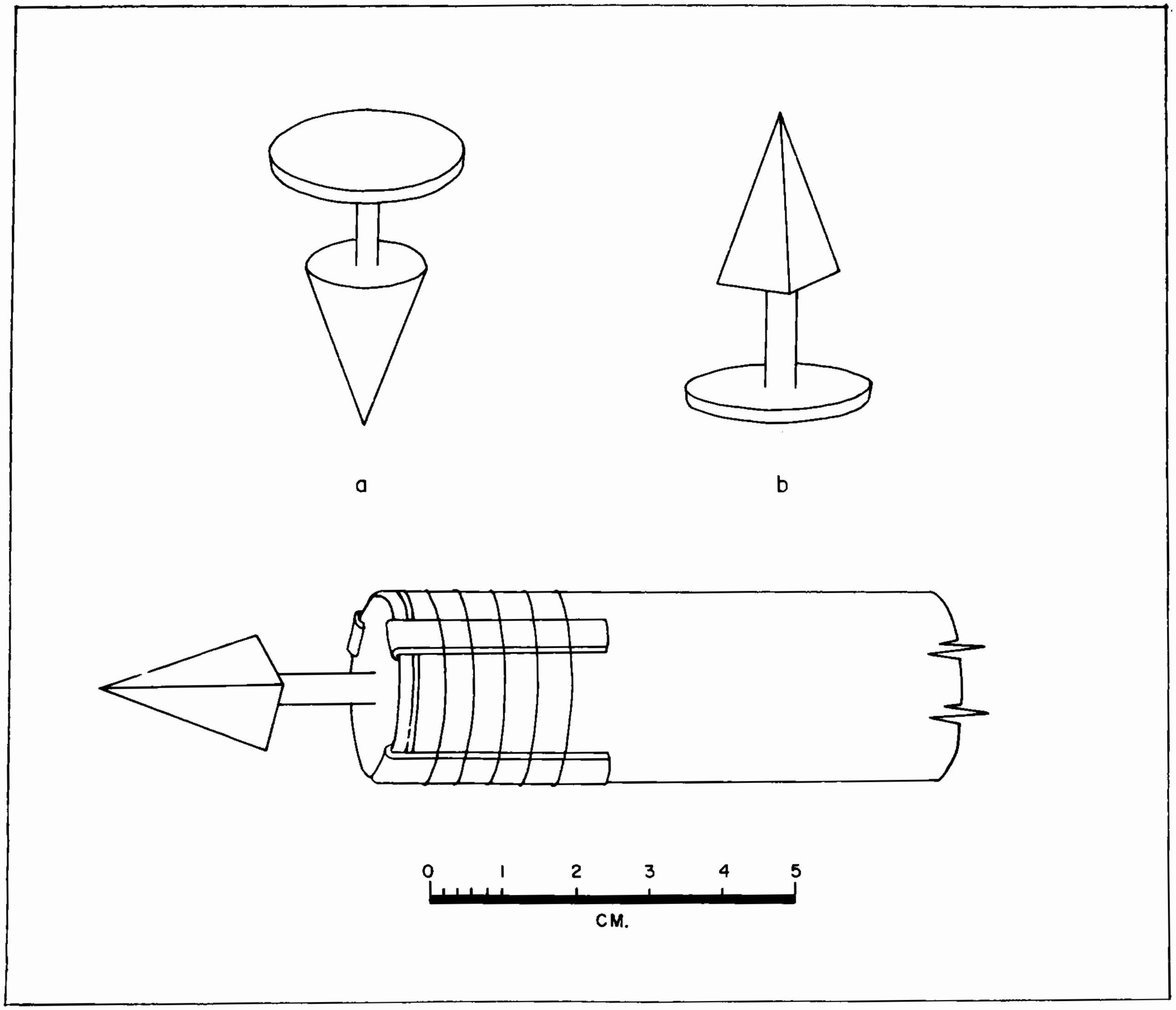
In order to provide data on migratory movements, a tagging program was begun in 1954 at Coats Island by Dr. E. H. Grainger of the Fisheries Research Board (see Mansfield, 1955). Simultaneously, another tagging program was being carried out at Bencas Island and Seahorse Point by a member of the Canadian Wildlife Service (Loughrey, 1955).

The stainless steel tag (fig. 3a) was designed to pierce the epidermis and lodge in the blubber layer, the numbered basal disc remaining on the outside of the skin like a button. Originally, the tag was provided with a conical head, and it was assumed that this would be sharp enough to penetrate the thick epidermis. Then, when the tag was driven fully home, with the disc flush against the skin, the edge of the puncture wound would close around the shaft of the tag and hold it tightly in place. In practice this did not happen, for it was impossible to stick the tag into the skin, even with the long and heavy harpoon then being used. To aid penetration of the tag, four cutting edges were ground onto the point, and further attempts at marking the animals were successful. These modified tags were used in 1955, but failures were high through bending of the shaft on impact with the skin. In 1956 a tag with a stouter shaft was used, and this proved to be the most successful pattern (fig. 3b).

In 1954 and 1955 most of the tagging was done in the

Figure 3. Stainless Steel Tag used in marking Walrus.

Fig.



water from a motor whaleboat. The following summer, most of the animals were tagged on the land at the uglit on the east coast of Coats Island, and this was found to be the simplest method.

115 animals have been marked so far, but no recoveries have been reported. Since the Eskimos at Coral Harbour are well acquainted with the work, the effectiveness of the method is open to doubt. It seems probable that many of the tags must either fall out, or be rubbed off when the animals are hauled out on the ice or land.

Perhaps the most effective method of marking would be by capturing calves and attaching metal straps to their flippers (see Brooks, 1954), but this would necessitate diverting the attention of the temporarily bereaved females. A possible solution would be to immobilize the female by use of a suitably administered alkaloid drug, a method which has proved successful in the management of some larger terrestrial mammals (Crockford et al., 1957). Such a technique might allow both the cow and calf to be tagged and result in an overall saving of much time and effort.

Materials Collected

The present series of specimens comprises samples of 104 male and 72 female walrus. Of these, 48 males and 50 females were taken in northern Hudson Bay, Hudson Strait and Frobisher Bay, and the remaining 56 males and 22 females from northern Foxe Basin (see Appendix I).

Lower jaws, molariform teeth and tusks were collected to provide data on ageing, and whole skulls were taken when possible. These were dried in the wind after removal of the brain and most of the flesh.

The stomachs of most specimens were examined for food contents, and whole or sub-samples were washed in sea water and preserved in 10 percent formalin.

In male specimens, the testes were weighed after removal of the epididymis and measured to the nearest millimetre. A 2 cm. slice from the centre of the testis and epididymis was removed and preserved in Bouin's fluid or 10 percent formalin. It was found that Bouin's fluid was better than formalin as a fixative for testis material since there was less distortion of the tubules and the histological results were better.

Bacula were collected, and were skinned and then wind dried.

In the female specimens the reproductive tract was usually removed entire and examined at leisure while the hunters were butchering the carcass. The sites of old placental scars were noted, and embryos were collected and stored in 10 percent formalin or 60 percent alcohol. The body wall and cranium of larger foetuses were slit to allow penetration of the preservative.

Ovaries were preserved whole in Bouin's fluid or 10 percent formalin and, when time permitted, samples of uterine mucosa and vagina were collected. Pieces of mammary gland were taken from a few mature females.

Samples were either placed in separate numbered jars, or wrapped in squares of muslin with an appropriate label and packed together in larger jars.

Ectoparasites and skin samples were collected together and preserved in Bouin's fluid. A complete intestinal tract was preserved in 10 percent formalin for study of parasitic Acanthocephala.

During the fall hunting at Coats Island in 1956, 11 male and 8 female walrus were weighed. The larger animals were cut into seven or eight pieces during the butchering and each piece was hoisted on the boom, to which was attached a 500 pound Chatillon ice balance.

Complete sets of body measurements were taken on as many animals as possible. These, together with detailed skull measurements, will be used in a later taxonomic study. The standard length (direct, nose to tip of tail) and external tusk length are the only measurements of importance to the present study.

Treatment of Materials

Sections of molariform teeth, several millimetres thick, were cut with a 3 inch diameter jeweller's saw. These were ground down to a thickness of approximately 100 μ with the apparatus described by Fisher and Mackenzie (1954). The sections, both transverse and longitudinal, were examined under a binocular microscope in reflected and refracted light. An optical micrometer was used to measure the width of incremental zones in both the dentine and cementum. Small segments of tusk sections were examined in a similar way.

Stomach contents were identified to species as far as possible, and numbers of each organism were counted and tabulated.

Small pieces of testis and epididymis were embedded in paraffin wax and sectioned at 8 to 10 μ. The sections were stained with Delafield's Haematoxylin and alcoholic Eosin, and were examined for stages of spermatogenesis. Average diameters of testis and epididymis tubules were obtained with an optical micrometer.

Bacula and skulls were cleaned and degreased by boiling in a strong solution of caustic commercial floor cleaner.

Preserved ovaries were sliced into sections 3 or 4 mm. thick and examined for developing follicles and corpora lutea of recent and former pregnancies. Small pieces of corpora lutea and developing follicles were embedded, sectioned at 8 to 10 μ, and stained in Delafield's Haematoxylin and Eosin.

Samples of dried diaphragm muscle were sent to the Department of Health, Toronto, for analysis of trichinosis infection.

AGE DETERMINATION

Methods

Rational exploitation of a stock of wild animals demands a knowledge of population dynamics, and this in turn must be based on a study of individuals of known age if conservation is to be practised to the greatest advantage. Numerous methods have been utilised to determine the ages of particular animals, but few have been precise enough to enable more than rough generalisations about growth and mortality to be made.

Body length measurements. Perhaps the most obvious indicator of age in any animal is the body length, and this measurement has been used as the standard parameter of growth in most species examined. Freiman (1940) was able to measure about 800 walrus and attempted to separate age groups in both sexes. The frequency distribution of nose-tail lengths in the male revealed six distinct peaks at 145, 195, 250, 290, 305 and 350 cm., and Freiman concluded that these represented five immature year groups and a sixth adult group. All the older animals were included in the latter group since variations of size with age were obscured by individual variability.

The females were represented by distinct peaks at 145, 195, 225, 255 and 285 cm., which Freiman interpreted as four immature year groups and the adult animals.

In the series of specimens from the Eastern Canadian

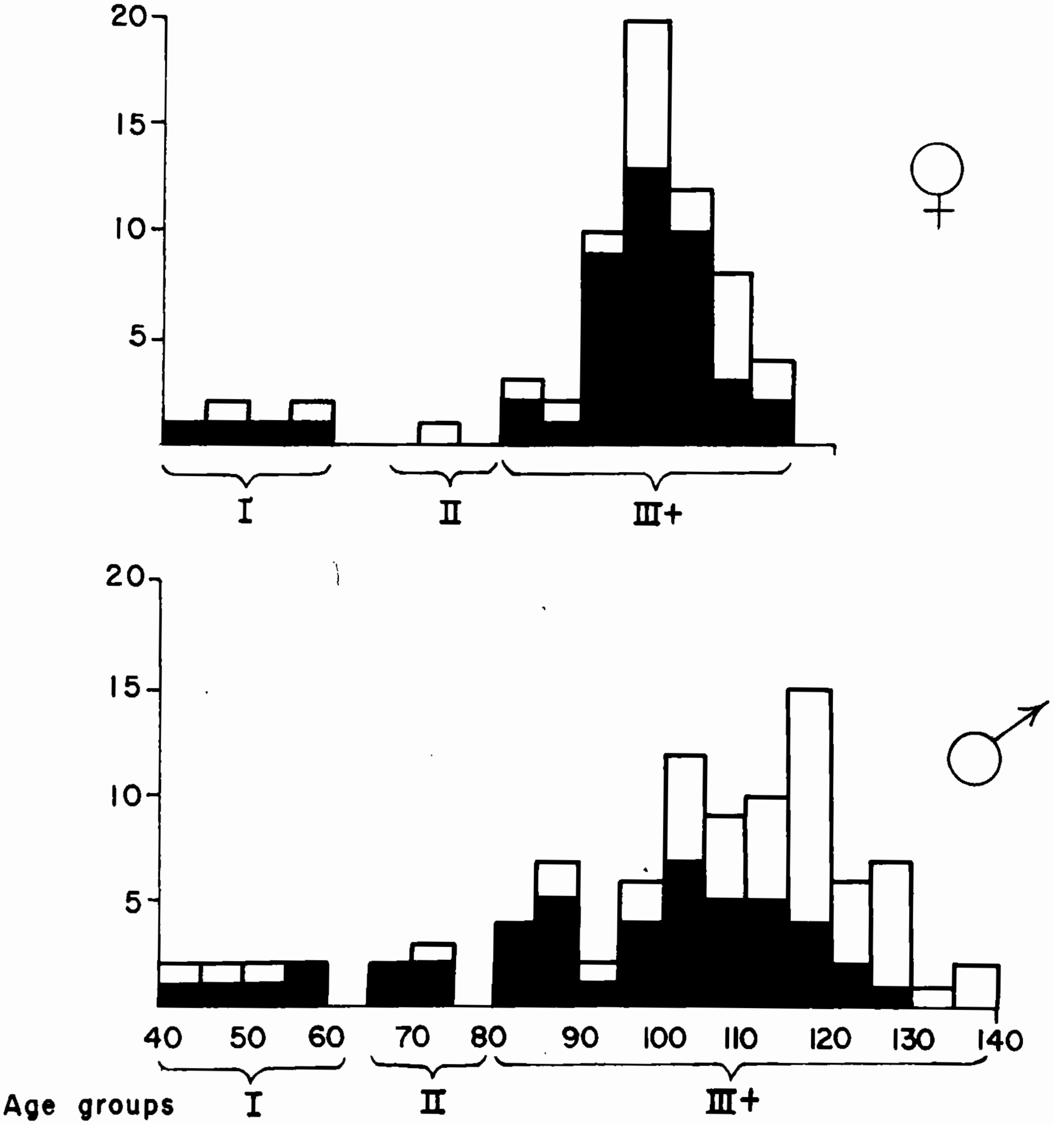
Arctic, measurements of body length were available for 94 males and 66 females. Analysis of these data (fig. 4) shows that only the first two year groups can be distinguished with any certainty, and at greater ages, individual variability masks variation with age. Chapskii (1936) has reached a similar conclusion from his analysis of data collected in the Kara Sea.

Fay (1955) has pointed out that an analysis of frequency distributions is only valid when the samples are obtained within a short space of time. Since Freiman's material was collected between the months of June and October, his interpretation of the data is open to question. Even if sampling methods are adequate, there is good reason for doubting the value of length frequency analyses in determining all but the youngest age classes. Thus, in a detailed study of the southern elephant seal, Mirounga leonina, Laws (1953b) analysed the frequency distribution of nose-tail lengths of 160 males and 142 females, but was unable to distinguish with certainty more than the first two age groups in the female and the first three in the male. Though the early groups were apparently distinct, the ages from the teeth belied the length frequency groupings, and showed that there was an extensive overlap.

Perhaps a further argument against such analyses is the difficulty in measuring a pinniped accurately. The variation in length depending on the position in which the animal is lying when examined, and perhaps also on seasonal

Figure 4. Frequency Analysis of Body Length Measurements in Inches.

Fig. 4.



20
15
10
5
♀
I
II
III+
20
15
10
5
♂
40
50
60
70
80
90
100
110
120
130
140
Age groups
I
II
III+

fatness, must influence the results to some extent. For this reason the measurements recorded in Figure 4 were grouped in class intervals of five inches.

If age groups are to be established from linear measurements with any degree of certainty, then sampling should be adequate, and measurements accurate within small limits. The latter condition can be satisfied by measurements of tusks in both sexes, and further data can be acquired from the bacula (penis bones) of the males.

Tusk and baculum measurements. Analysis of such data yields no more precise information than can be obtained from body-length measurements. Chapskii (1936), using external tusk length and length of the baculum, was able to confirm only the age groupings determined from the body measurements. Belopolskii (1939) utilised only tusk lengths in his analysis of specimens collected from the Bering and Chukchee Seas, but unfortunately he ignored the very real sexual dimorphism and lumped male and female samples together.

Fay (1955) has analysed a series of 128 male tusks of the Pacific walrus collected within a period of six weeks during the summer, and has grouped the lengths into four initial classes. These he interprets as the first four years of growth, and attempts to justify his conclusions by seeking Eskimo opinion. Fay states that "the Gambell men readily classify specimens up to four years of age on the basis of OEL (observed external tusk length), and their concepts of these are approximately as indicated in (the frequency analysis)."

Moreover, corresponding body lengths also agree with the first four age groups determined from Freiman's body-length data.

Certainly, Eskimos will readily classify an animal's age when asked to do so, but their knowledge is not based on any sound criteria, except in the youngest age classes considered. Calves, yearlings and two-year-olds are easily recognised from their association with the cow, but after that distinction is lost and age classification becomes merely a matter of opinion and nothing more. Unfortunately, the interpretation of the tusk length frequency groupings also appears to be a matter of opinion, and the present author feels that the "series of reasonably prominent modes" described by Fay has little basis in fact.

Fay analysed a sample of 107 female tusks in the same way, but the frequency histogram showed no model regularity comparable to the males. However, Eskimo opinion was used again to establish the first four year classes, and these agreed closely with those depicted by Freiman.

Fay also found that baculum length was a crude guide to age, but was of no further help in distinguishing age classes. This is in agreement with the present author's findings for specimens from the Eastern Canadian Arctic.

Claws. Plekhanov (1933) suggested that the conspicuous and regular bands on the claws of several species of phocids could be used to determine the ages of individual seals. Recently, McLaren (in press) has been able to establish the validity of the method in the ringed seal, *Phoca hispida*, by comparing the number of bands on the claws with the age determined from incremental zones in the dentine of the canine teeth.

In the present study claws were collected during routine examination of specimens, but no more than three visible bands were ever found. Fay (1955) found a similar number of bands on the claws of the Pacific walrus, and suggested that the frequency with which animals haul out and move about on the ice (and land) leads to attrition of the claws by breakage and wear.

Teeth. The most important method of age determination applicable to the *Pinnipedia* is that discovered independently by Scheffer (1950a) and Laws (1953a). Scheffer found that visible growth ridges on the canine teeth of the northern fur seal, *Callorhinus ursinus*, corresponded in number with the known age in years, determined from branding and tagging experiments. Laws studied the southern elephant seal and found that the marked periods of fasting and feeding which this animal undergoes were reflected in a differential deposition of dentine, visible macroscopically as alternate opaque and translucent bands in cross-sections of the canine teeth. Root ridges were also present on the canine teeth, and these could be correlated with the bands in the dentine. It was found that one ridge was formed each year, as in the northern fur seal.

Fisher (1954) and McLaren (in press) have applied the methods to the harp seal, Phoca groenlandica, and the ringed seal respectively, though in these two species root ridges are not present on the canine teeth and only the dentinal annuli can be used. Brooks (1953) and Fay (1955) have studied the problems of growth in the tusks and molariform teeth of the Pacific walrus and have found the methods of Scheffer and Laws to be partly applicable, at least to the males.

Application of Methods to the Atlantic Walrus

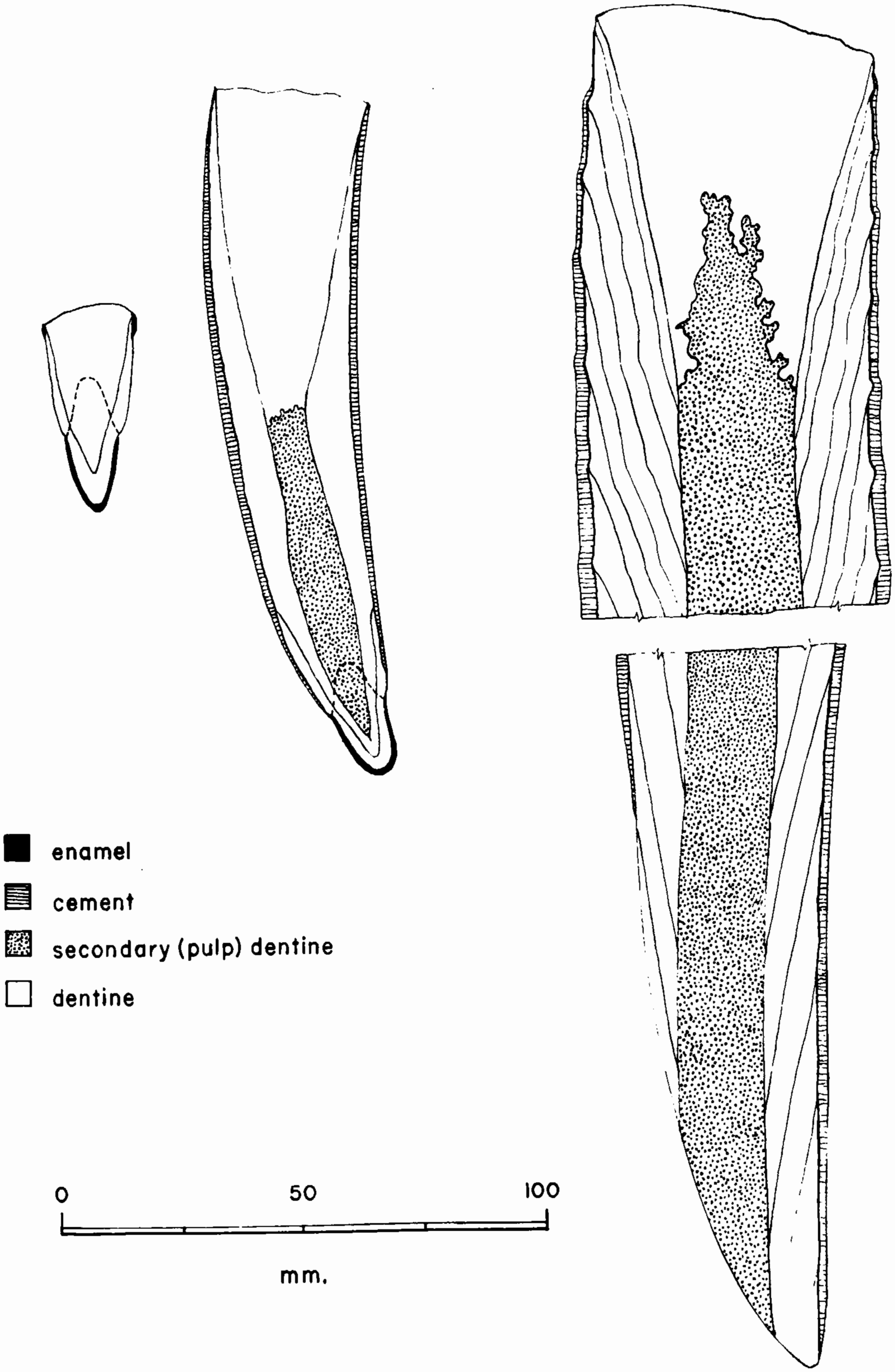
The limited value of measurements of the body, tusks and baculum has been pointed out in the previous section, and no additional useful data can be obtained from the claws. Apart from the value of the numbers of corpora lutea in the ovaries as a rough indicator of age in the female, the teeth provide the only accurate method of determining the age of individual animals.

The peculiarities of the dentition are discussed in a later section, and here only the form of the tusks (modified canines) and molariform teeth (incisors, lower canines and post-canines) need be explained.

Tusks. In the full-term foetus, A 11, taken on May 26, the tusk is a hollow cone of dentine 42 mm. long, with an enamel cap measuring 32 mm. from tip to 'notch'; a few millimetres of the root are covered with a 2 mm. layer of cementum (fig. 5). The whole of the tooth is embedded in the alveolus at birth, and eruption does not occur until later in July and

Figure 5. Comparison of Tusk Growth in a Foetal, Two Year Old and Adult Male Walrus.

Fig.



August. Initial growth is rapid, and is well shown in Figure 6, in which the foetal tusk is compared with the tusks of calves, yearlings, and two and three year olds. Scale drawings of the tusks have been superimposed, and the position of the gum line in relation to each specimen is indicated by appropriate marks. The gum line for the foetal tooth is not included since it appears below the level of the tip.

By October 7 (A 130), the tusk is 72 mm. long and projects 21 mm. from the alveolus. In the second year the tusk has increased in length up to 13 cm. by August 7 (A 41), and projects 4 cm. from the alveolus. Both the yearlings A 41 and A 109 are easily distinguished from the calves by appearance alone, but their age can be confirmed when the reproductive history of the mother is known, for parturient cows do not become reimpregnated until the following breeding season. Thus the immature male A 10, found in company with the gravid female A 9 on May 26, has evidently just reached the end of its second year. Its tusks are noticeably larger than those of other yearlings and project much further from the alveolus. There is a little distal wear on the tusks, suggesting that the animal has only recently begun to feed in the adult manner.

The only other specimen with tusks of comparable length is female A 76 taken on September 19. Slight wear has occurred at the tips of the tusks, suggesting that the animal has been feeding independently for only a short while. Its body size confirms that it is in its third year.

The ages of the other two immature specimens shown in Figure 6 are more difficult to assess if tusk length alone is used, but both are tentatively placed in the group 'three years plus'. The tusks of A 37 show more wear than those of A 10, and the enamel cap is almost obliterated. While body size is little greater than that of A 10, the greater length of the tusks and the larger molariform teeth suggest that the animal belongs to a later age group.

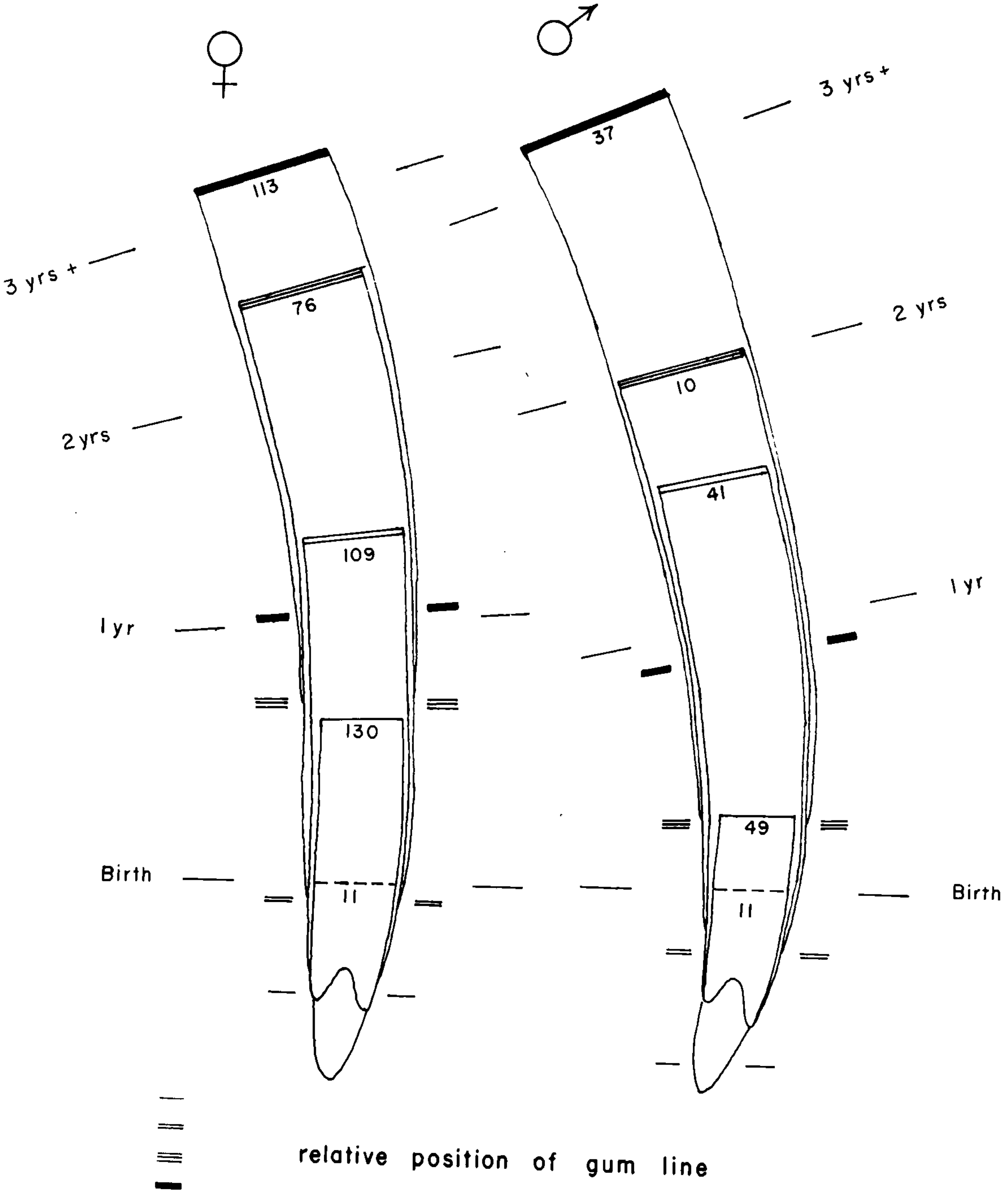
The age of A 37 is confirmed by examination of the cementum layers in the molariform teeth (see p.28), but the same method when applied to A 113 shows that this specimen is five years old. We may conclude, therefore, that tusk length is only reliable as an indicator of age up to two years in the female, and two or possibly three years in the male.

The manner in which the dentine is laid down is illustrated diagramatically in Figure 5. The odontoblasts lining the pulp cavity give rise to regular incremental layers, resembling thin truncated cones. As the tusk elongates, the more distal portion of the pulp cavity becomes filled with secondary dentine. In young animals the pulp cavity is large, but in very old animals it becomes almost entirely obliterated.

At birth, the hypercalcified foetal dentine is replaced by dentine of more normal appearance, the change being readily visible in macroscopic sections of the tusk. In the few immature animals examined, the dentine is fairly uniform in texture and bears only faintly discernible microscopic

Figure 6. Comparison of Male and Female Tusk Lengths in the First Three Years of Growth. (The number at the root of each tusk is the 'A' series field number. The assumed tusk length at the end of each year is indicated by an appropriate mark).

Fig. 6.


♀
♂
3 yrs +
2yrs
1yr
Birth
113
76
109
130
11
3 yrs +
2 yrs
1 yr
Birth
37
10
41
49
11
relative position of gum line

striations which probably reflect changes in calcium metabolism associated with feeding. These microscopic striations are found in adult dentine, and are overlaid by a larger-scale pattern, particularly in the males. When light is reflected at a suitable angle from the polished surface of a tusk section, the pattern is revealed as a series of faintly marked zones consisting of darker, hypercalcified dentine which gradually shades into lighter coloured dentine. The transition between the zones is abrupt, and is indicated in Figures 5 and 8b by a series of thin lines. These changes in dentine deposition are sometimes accompanied by pronounced ridges on the tusk roots (fig. 7). The ridges are particularly well developed in old males, and may be seen most clearly where the cementum is exfoliated (fig. 8a).

In addition to the root ridges and major zones in the dentine, a number of less pronounced but still well defined intermediate zones are visible externally (fig. 8a). The width of the zones between any two ridges is fairly constant, suggesting a regular periodicity in growth. It is known that nutrition plays a most important part in the formation of dentine and that irregularities in diet may result in imperfect deposition of calcium (Schour & Massler, 1945). However, the regularity of the zones and their comparatively small number (about 15 to 20 per root ridge interval) indicates that something other than irregular feeding must account for their formation. It is suggested that the zones result from a periodic readjustment of the periodontal

Figure 7. Photograph of the Tusk of a 21-Year-Old Male to show Root Ridges and Medial Depressions. (The tusk is considerably foreshortened in the picture).

Fig. 7.

fibres which anchor the tusk in the socket. After a definite period of growth of dentine and extrusion of the tusk, the fibres rupture and new ones are rapidly formed. The temporary cessation of growth which results is then reflected as a change in rate and type of calcium deposition.

Formation of the major root ridges cannot be explained in such mechanical terms, and the period of slow growth which they appear to represent must result from some pronounced change in the metabolic activity of the animal. Both the northern fur seal and the southern elephant seal are known to undergo partial or complete fasts each year, and Scheffer (1950a) and Laws (1953a) have correlated this cessation of feeding with the root ridges formed on the canine teeth.

Vibe (1950) has observed that walruses taken in Melville Bay in June during their spring migration have empty stomachs, and real feeding does not commence at the mollusc banks about Saunders Island, northwest of Thule, until early July. Fay (1953) has found that root ridges on the tusks of the Pacific walrus are formed in spring and this is coincident with the breeding season as well as the middle of the migratory period. Animals following different migratory routes along the Siberian and Alaskan coasts, where feeding habits may be expected to differ, have tusks which are indistinguishable. These in turn do not differ from the tusks of an adult male, apparently from the herd resident in Bristol Bay. From these observations, Fay concludes that each ridge represents a breeding season with presumably a period of fasting, and each intervening layer the remainder of the year's growth.

Insufficient factual data on feeding habits in the winter and spring months are available for Foxe Basin and Hudson Bay, and it can only be assumed that mature males and females are fasting for part of that time. Examination of a small series of male tusks showing well defined root ridges indicates that ridge formation has just been completed in early June, and that throughout the summer and fall, growth is rapid. Even in immature animals there appears to be a period of reduced growth during the winter and spring, and visual estimates from the tusks illustrated in Figure 6 show that during the five months June to October, the rate of growth is nearly twice as much as it is during the remainder of the year. Ridges are not formed on the tusk roots of immature animals since the rate of growth, even in winter and spring, is relatively fast. Thus in the first year, the tusk may lengthen by 6 cm., but this rate of increase declines as maturity is reached. The youngest mature males show only faintly marked growth ridges, and the maximum distance apart in any specimen is 3.5 cm. In the oldest males, the root ridge interval may become as small as 0.5 cm. There can be little doubt from this comparison and the foregoing observations that ridge formation does occur in the spring, and that the distance between the root ridges does represent a year's growth.

The tusk is firmly fixed in the alveolus by the periodontal fibres which penetrate the cementum from the surrounding periodontal membrane. Sections of tusk roots from mature males and females reveal that the cementum is divided into well-defined concentric layers (fig. 8b). Each layer consists of a darker inner band of hypercalcified cementum which gradually merges into a translucent outer band. The transition between the layers is abrupt and is often emphasised by the distribution of cementoblast lacunae.

Sections of old male tusks with well defined root ridges show that the translucent zones in the cementum are formed at the end of the period of slow spring growth. The onset of rapid summer growth after breeding is accompanied by an increase in the number of cementoblasts and apparent hypercalcification, which results in a marked dark zone being formed. The distinction between spring and summer growth is more pronounced in older animals, particularly males.

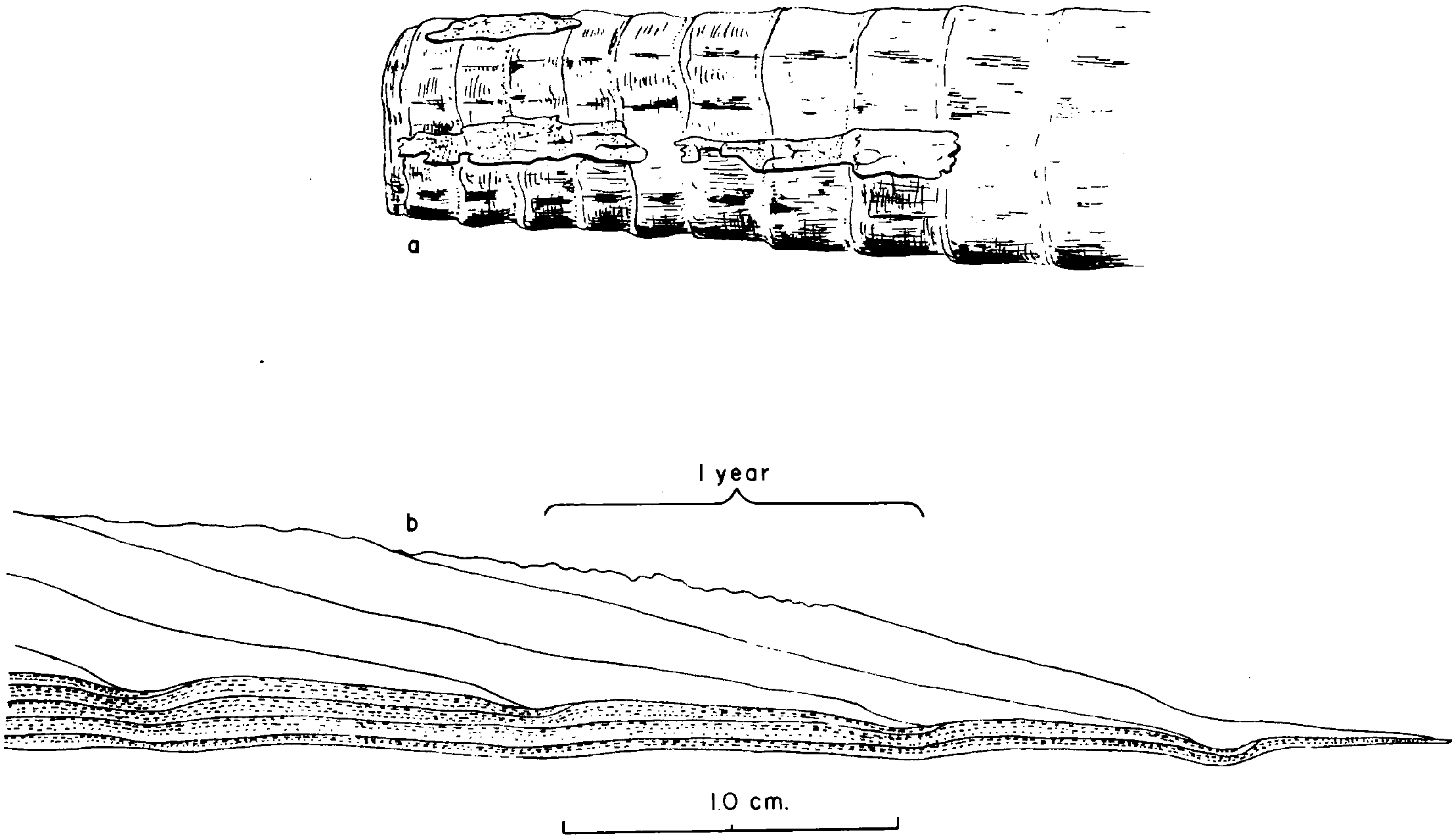
The cementum layers are narrower where they overlie the root ridges, and this tends to smooth out the external contours of the tusk (fig. 8b). In old weathered tusks from which the cementum has become exfoliated, the root ridges are most conspicuous (fig. 8a).

Molariform teeth. In the full-term foetus A 11, the incisors, molars and lower canine teeth are short, hollow cones of dentine, 10 to 15 mm. from root to tip, and capped by a large enamel crown; there is little or no cementum. By the end of the first summer, the teeth have lengthened to 16 - 25 mm., and the cementum averages 0.38 mm. in thickness (A 130).

Figure 8 a. Illustration of the Root Ridges on an old Male Tusk after exfoliation of the Cementum.

Figure 8 b. The Dentine and Cementum Layers on the Tusk Root in Longitudinal Section.

Fig. 8.



In the yearling A 134 most of the teeth are longer than 25 mm., and in the two year old A 76 they average at least 35 mm. in length. At this age the layer of cementum has increased to 1.0 mm. in thickness. The teeth increase in length by the addition of hollow truncated cones of dentine which are sometimes visible externally as shallow ridges (fig. 9); internally the dentine layers are similar to those found in the roots of adult male tusks.

As the tooth lengthens, the pulp becomes filled with secondary dentine, until finally the whole pulp cavity is obliterated. Closure is a variable factor and may occur before or after maturity is reached. This is shown most clearly in the longitudinal section of a molariform tooth from female A 46, which is pregnant for the first or second time (fig. 9). When dentine deposition finally ceases, the cementum becomes continuous over the base of the tooth, and slight extrusion from the socket continues to occur.

Examination of the complete dentition from several immature and adult animals shows that the same relative amount of cementum is laid down on each tooth and tusk. In the first summer cementum is even in appearance, but in the following spring a lighter zone may be laid down (A 134). In the immature male A 10, which is nearly two years old, the lighter zone separating the cementum into two nearly equal layers is not clearly defined in all parts of the sections examined, which indicates that the processes underlying cementum deposition are not regular as yet. In the three year old A 37, the

Figure 9. Longitudinal Section of the Lower Canine Tooth of a 7-Year-Old Female (x 3.5).

Fig. 5.

annual growth increments in the dentine are plainly indicated by ridges, and each ridge is accompanied by a translucent band of cementum, the innermost of which is not as well defined as the outer two. In adult animals, especially old males, the cementum is separated into more clearly defined layers, wide bands of darker cementum alternating with narrow translucent bands; the number of bands is constant for all the teeth in one dentition.

The bands are much more sharply defined than those found on the tusk roots, and this is attributed to the comparative lack of periodontal fibres. In the tusk cementum, the large numbers of fibres and their periodic readjustment to tusk growth give the cementum layers an uneven contour which sometimes complicates interpretation.

Comparison of the tusks and molariform teeth in individual old males shows that the narrow translucent zones of cementum are laid down at the same time of year. It may be assumed that the spring months are times of moderate feeding, for the translucent cementum is evidently hypocalcified. This is shown by the exfoliation which occurs in teeth exposed to the weather for long periods, for the cementum separates off into layers which break along the narrow zones.

The first formed layers are wide and they become progressively narrower as their number increases; there is no indication, in the males at least, that deposition of cementum ever ceases. When the width of cementum layers is plotted against the assumed age in years, a normal exponential growth curve is obtained (fig. 11), and this bears a satisfactory relation to the straight line representing the rate of deposition of cementum in the first two years. Thus it is assumed that after the second year, one well-defined layer of cementum is laid down annually, and this continues throughout the life of the animal.

In the Pacific walrus, Fay (1955, fig. 31) tested the relationship between tusk length and number of cementum layers and concluded that the layers were as good indicators of age as tusk lengths; in fact they were probably better in later years. However, in the earlier age groups, there appeared to be no correlation of age with the number of layers, and Fay assumed that deposition of cementum was irregular in the first six to seven years. This certainly does not apply to the Atlantic walrus, for the foregoing analysis shows that there is a good correlation between age and well-defined cementum layers at all ages after two years.

In view of the doubtful basis on which Fay's first four year classes were erected and the more subjective nature of his analysis, it is impossible to make any direct comparison between the estimated growth rates of the two forms. However, if it is assumed that cementogenesis is similar in both the Atlantic and the Pacific walrus, then linear measurements can be compared directly. Such measurements have been extracted from Figure 31 in Fay's report and they are tabulated in Appendix V; the values are necessarily approximate since they are derived from a mean curve. Similar values are also recorded for the Atlantic walrus and the significance of these measurements is discussed in the section on growth.

The cementum layers on the tusk root cannot be used for determining age since they represent only part of the animal's life history. In general, even fewer years of life are represented by the root ridges, but in some tusks an approximate estimation of age can be made by plotting the distance between the ridges and then extrapolating the curve exponentially to the limit of the tusk. When distal wear is accounted for, an estimation is arrived at which closely agrees with the age determined from the cementum layers in the molariform teeth.

Determination of age in the female. Growth of the tusks in the female follows a basic pattern similar to that of the male, but certain differences occur which render interpretation of the chronology of dentine and cementum deposition difficult. Few adult tusks bear growth ridges on the roots, and when present they are rarely well defined. Cementum deposition on the root is irregular, and it has not been possible to correlate definite layers with the ridges, as in the male. However, on all tusk roots sectioned, the number of cementum layers increases in a regular manner from the open end to the gum line, and this suggests that deposition occurs exactly as in the male.

In the molariform teeth, the cementum has a slightly less proportionate bulk than in the male, and rate of deposition appears to be more irregular. Banding of the cementum occurs in all animals older than two years, but in only a few specimens does the pattern approach that of the males in clarity and regularity of deposition (fig. 10). It would appear that in both males and females the same seasonal influence regulates cementum deposition, but this may be sometimes over-shadowed by the physiological demands of pregnancy and the long lactation period. In the female Pacific walrus, Fay (1955) has found that the relationship between the observed external tusk length and the number of cementum layers in the molariform teeth appears to be radically different from that in the males, and may have little or no practical application in determining age. However, observations on the Atlantic walrus show that tusk length in the females is very variable owing to rapid wear and breakage and is of less value in determining age than the cementum layers.

In Figure 11, the width of cementum layers is plotted against assumed age in years, and normal exponential growth curves result. Comparison with the limiting curves for the adult males shows that the cementum layers in the female are generally narrower, and this is entirely as expected when the maximum size of the adult animals is considered.

In some specimens older than ten years, the outermost incremental layers are very narrow, and age interpretation becomes difficult. The ages of the older animals recorded in Figures 12 and 14 and in Appendix I should therefore

Figure 10. Part of a Transverse Section of the Lower Canine Tooth of a 21-Year-Old Male (x 15).

Fig.10.

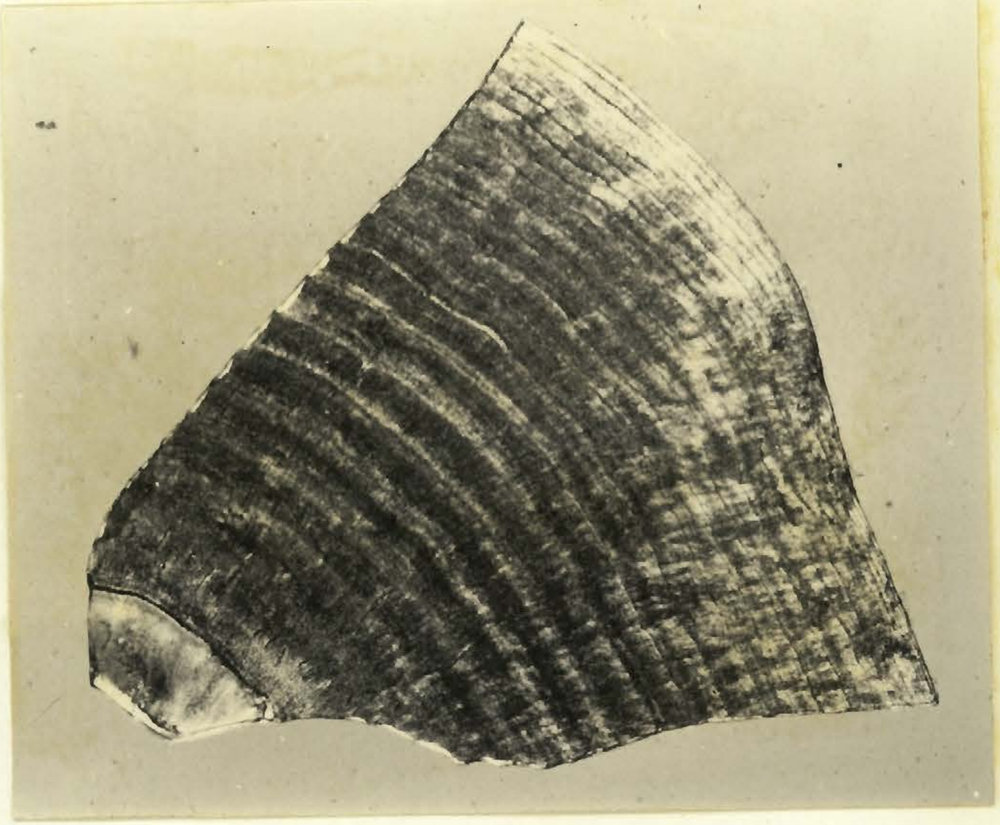
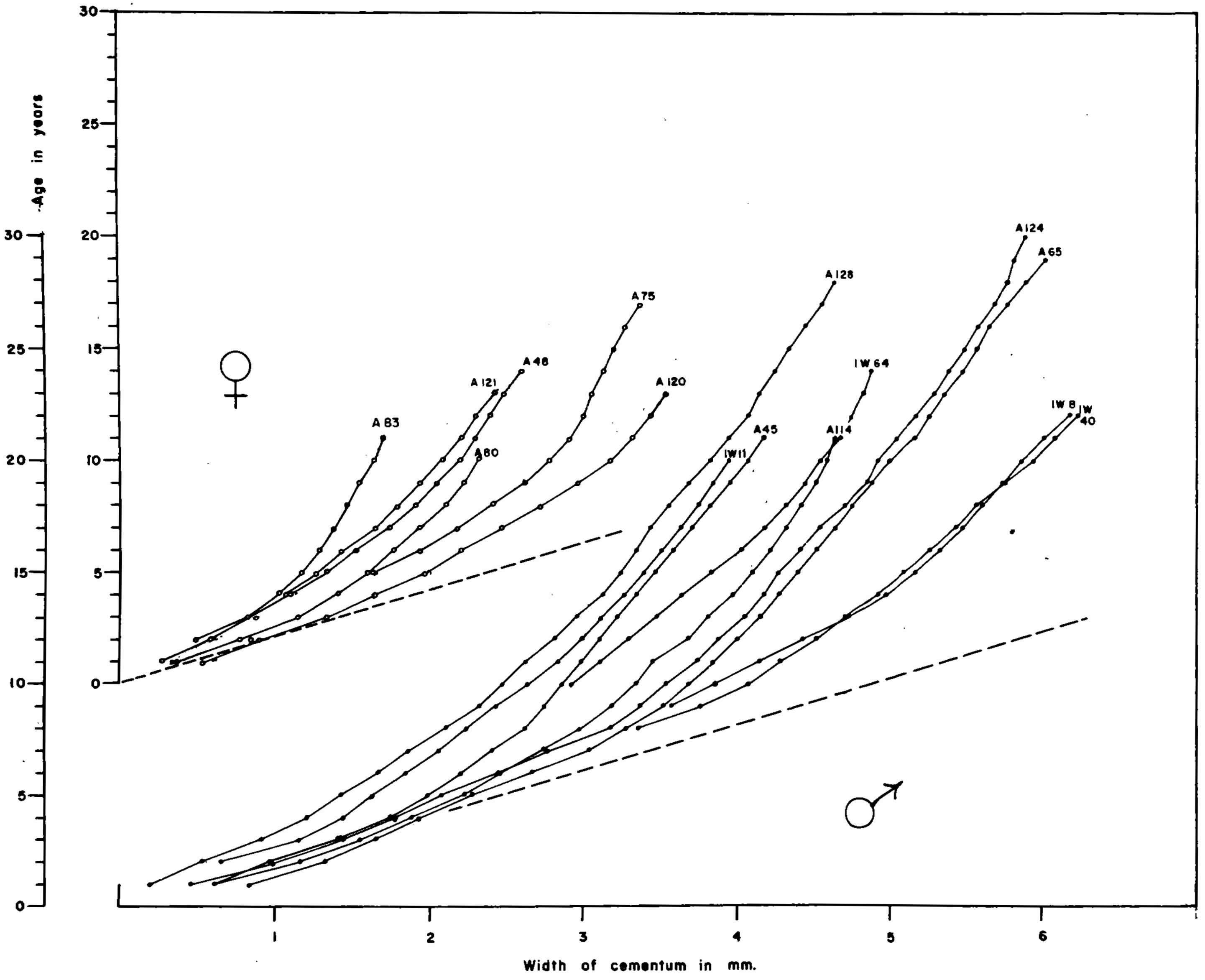


Figure 11. Deposition of Cementum on the Roots of Molariform Teeth in Males and Females.

Fig. 11.


Age in years
0
5
10
15
20
25
30
0
5
10
15
20
25
30
Width of cementum in mm.
1
2
3
4
5
6
♀
♂
A 83
A 121
A 46
A 80
A 75
A 120
A 128
A 45
IW11
IW 64
A114
A124
A 65
IW 8
IW 40

be regarded as minimal.

GROWTH

The Male

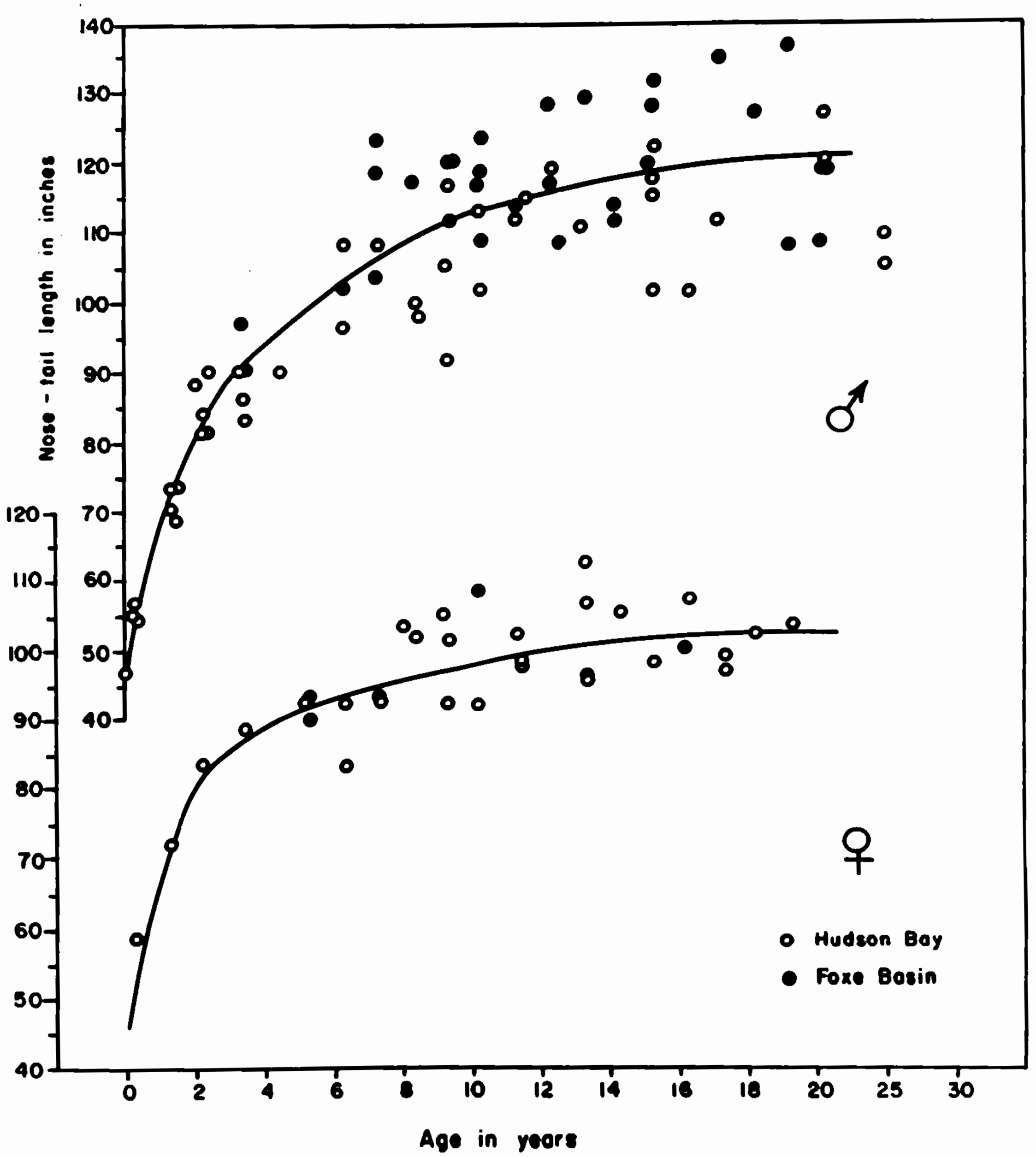
<u>Body length</u>. No new-born calves are available in the series of specimens from Hudson Bay and Foxe Basin, but the foetus A 11, taken on May 26, was evidently full-term and its body length of 47 inches may be considered to represent that of the new-born animal. The body length of calves taken in August and September averages 56 inches, and this compares closely with measurements of the Pacific walrus (Fay, 1955).

The increase of body size with age is recorded as a scatter diagram in Figure 12. The specimens collected in northern Foxe Basin were measured along the ventral curve of the body and the resulting figures have been decreased by ten percent to make them comparable to the Hudson Bay specimens which were measured in a direct line from nose to tail. The average growth curves were sketched in by eye with guidance from a series of regression lines calculated from the method of least squares. Growth in length ceases between 20 and 25 years when an average maximum size of 120 inches has been attained.

The figure shows that walrus from Foxe Basin tend to

Figure 12. Growth in Length of the Body of Males and Females.

Fig. 12.


Nose - tail length in inches
140
130
120
110
100
90
80
70
60
50
40
120
110
100
90
80
70
60
50
40
0
2
4
6
8
10
12
14
16
18
20
25
30
Age in years
♂
♀
○ Hudson Bay
● Foxe Basin

be larger in average size than those from northern Hudson Bay, a fact which has long been known to the Eskimos of Southampton Island. This difference may be merely the expression of a cline in size with latitude, but the little evidence available on distribution and migration suggests that discrete breeding populations are most probably represented.

The Pacific walrus is slightly larger than either of these two forms, and grows to a mean body length of 135 - 140 inches (Fay, 1955; Freiman, 1940). Since these measurements were all taken along the ventral curve of the body, they must be decreased by ten percent to make them comparable to the standard lengths of Hudson Bay and Foxe Basin specimens. The final adjusted mean value of 124 inches reveals a slight but probably real difference in overall length. Comparison of growth rates in immature Atlantic and Pacific walrus is difficult since ageing techniques differ, but some assessment of changes in the adults may be made if lengths are considered only in relation to the number of cementum layers in the molariform teeth. The data in Appendix V then show that after the eighth layer is formed, the Pacific walrus gradually gains a slight ascendancy in size.

Increase in weight. The few data available from weighings are set out graphically in Figure 13 and a mean curve has been fitted by eye to the points; the data suggest that slow growth continues throughout life. Since no new-born calf was taken, the weight of the full-term foetus A 11 is included for comparison.

The dismembered animals were weighed with a 500 pound spring balance (accuracy approximately plus or minus ten pounds) and no allowance was made for loss of blood. No detailed weights of internal organs were recorded, and the figures set out in Table I are taken from Loughrey (1955).

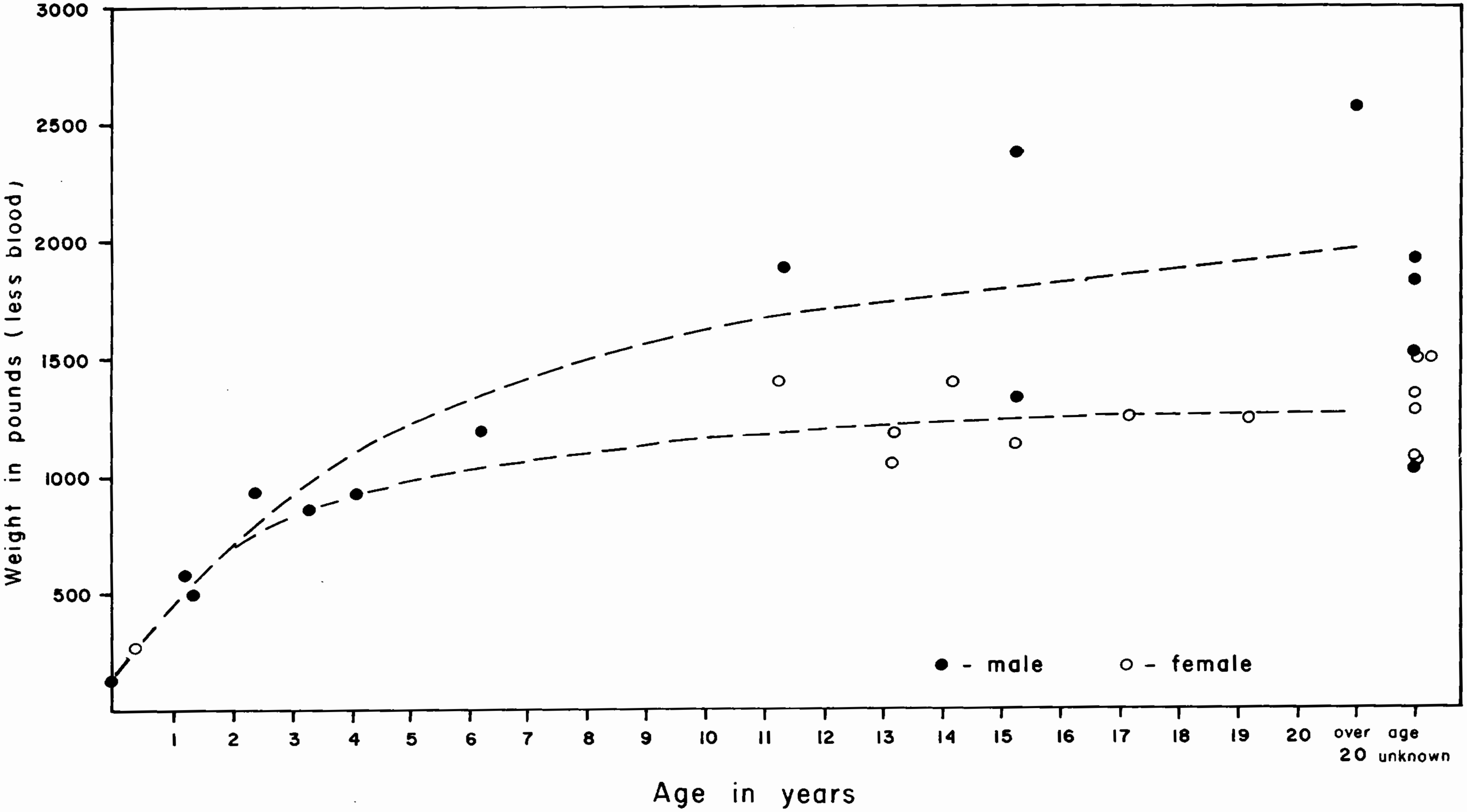
TABLE I

Weights of Various Internal Structures of an Adult Male Atlantic Walrus (Loughrey, 1955).

Structure	Weight in pounds	Percent of total body weight (2084 pounds)
Skin and blubber	632	30.32
Heart	11	0.53
Blood	160	7.68
Lungs	51	2.45
Liver	61	2.92
Stomach, spleen, pancreas and intestine	76	3.65

Figure 13. Increase in Weight of the Body (the weights of 4 males and 6 females of unknown age are taken from Loughrey, 1955).

Fig. 15.



Weight in pounds (less blood)
3000
2500
2000
1500
1000
500
Age in years
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
over 20
age unknown
● - male
○ - female

The maximum weight recorded is approximately 2600 pounds (less blood), but estimated weights of other specimens, and visual observations of body size in very large males, suggest that 3000 pounds may be reached occasionally. The maximum weight of the Pacific walrus recorded by Fay (1955) is 2800 pounds.

Growth of tusks. Although the walrus of northern Foxe Basin appear to be slightly larger on the average than those taken in northern Hudson Bay (fig. 12), there is little evidence of a difference in tusk size. However, when these two populations are together compared with the Pacific walrus, a great disparity in tusk size is shown, and serves to confirm the view that two morphologically well-defined groups exist.

The values of external tusk length are set out in Appendix V, with the number of cementum layers in the molariform teeth forming the basis of comparison. At five years of age there is little difference in tusk length, but after this the values begin to diverge. At twenty years, the tusk of the Atlantic walrus has almost ceased to lengthen, indicating that distal wear is becoming equal to the annual increment of dentine at the root. In the Pacific walrus, the growth rate does not show any appreciable change until after twelve cementum layers have been laid down. However, growth still continues at a greater rate than in the Atlantic walrus, and does not appear to cease until at least thirty cementum layers have been added to the teeth.

Growth of the baculum. Bacula were first prepared by boiling in a strong caustic soap solution and then left to dry in a warm room for several weeks. The weights and length measurements of 40 specimens in the present collection have been plotted in Figure 15 and the curves show that there is no sudden increase in the rate of growth at maturity, as in several species of phocids (Fisher, 1954; Laws, 1953b; McLaren, in press). The strongly sigmoid growth recorded in the Pacific walrus (Fay, 1955) is not apparent in the specimens examined.

The Female

Throughout lactation, growth of the calf is maintained at a rapid rate, and little decrease is shown until nutritional independence is gained. In the third year, a marked change in rate occurs and the male and female growth curves begin to diverge. At 20 years, the adult female attains a maximum average size of 102 inches and weighs approximately 1600 pounds.

Difference in the body and tusk growth rates of the Atlantic and Pacific females cannot be evaluated since Fay (1955) was unable to correlate age with cementum layers at any stage of the life history. Only the oldest adult animals can be compared and these show that a slightly larger size is attained in the Pacific walrus. Thus the average maximum body length is 108 inches (corrected) and the weight 1700 pounds.

Tusk growth in the female Atlantic walrus is slightly slower than in the males. After twelve years, correlation of tusk length and age is usually impossible since rapid wear and breakage of the narrower tusk leads to very variable measurements; thus in Figure 14, two sixteen year old females are shown which have tusks shorter than one of the six year olds. The maximum tusk length recorded is 14 inches, and Fay gives 18.5 inches for the female Pacific walrus. This small difference may indicate that the females are less divergent in tusk characteristics than the males, though it could result from a size limit imposed by greater wear and easier breakage in the females of both forms. While the male tusk is also exposed to strong wear, its greater thickness keeps the effect to a minimum and allows growth to occur until late in life.

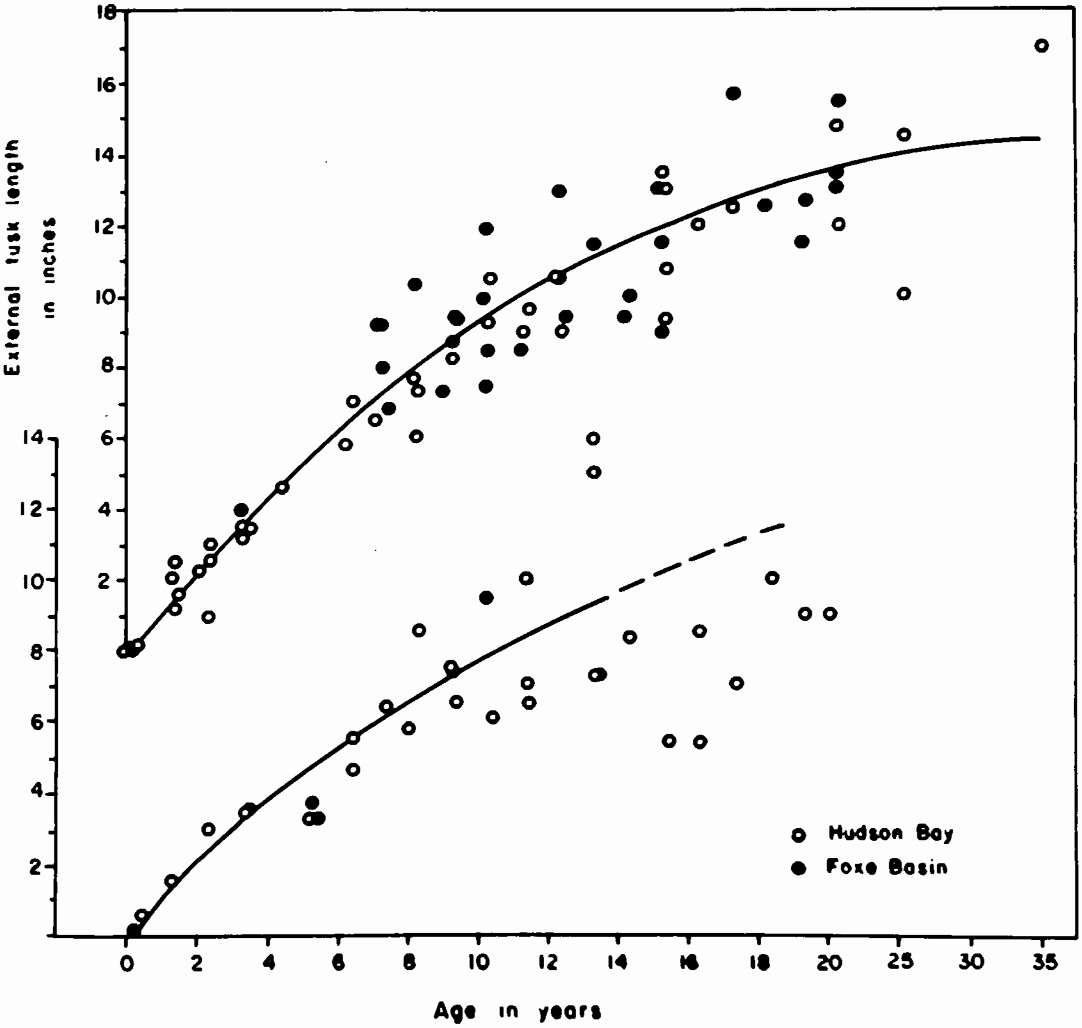
Sexual Dimorphism

The marked difference between the sexes in tusk and body lengths and total weight are summarised in Table II. Body length data for the Pacific walrus are taken from Fay (1955, fig. 21), and the measurements have been decreased by ten percent to give approximate direct nose-tail lengths. The body length data of the Kara Sea walrus are those given by Chapskii (1936) and are evidently direct nose-tail length measurements.

The tusk measurements indicated are the mean lengths at sexual maturity, and body measurements are the maximum average lengths of adult animals. The ratio of male to female

Figure 14. Growth in Length of the Tusks.

Fig. 44.



External tusk length in inches
18
16
14
12
10
8
6
4
2
14
12
10
8
6
4
2
0
2
4
6
8
10
12
14
16
18
20
25
30
35
Age in years
○ Hudson Bay
● Foxe Basin

TABLE II

Comparative Sexual Dimorphism in the Walrus

	Tusk length in inches		Body length in inches		Male body size as percent of female	
	M	F	M	F	Length	Weight
PACIFIC	11	8.5	124	108	120	150
E. CANADA	7	5	120	102	120	150
KARA SEA	10	8	125	104	120	-

body size for the Pacific walrus is taken from Fay's data and represents average values from several authorities.

The gregarious habits and marked huddling behaviour of the walrus are similar in some respects to the behaviour of the polygynous harem breeders such as the northern fur seal and the southern elephant seal. However, harem breeding is characterised by dominance hierarchies in which sexual selection for size and fighting ability in the males is actively maintained. Comparative figures for the polygynous species (Fay, 1955) show that male body length varies from 130 - 165 percent of the female, and weight from 380 - 500 percent. The figures for the different groups of the walrus set out in Table II indicate that, while sexual dimorphism has occurred, it is not pronounced enough to suggest a polygynous habit.

External Appearance

<u>The calf</u>. There is little difference in external appearance between the full-term foetus A 11 and the two month old calf A 39, and the following description is considered applicable to the newly born animal.

The skin is slate gray in colour, particularly when wet, and is covered with a coat of short silver-gray hair from 5 to 10 mm. length (the precise colour is hard to describe. In field notes it is given as 'ash-blond'). This hair covering evidently corresponds to the embryonic pelage (<u>lanugo</u>) of

Figure 15. Growth of the Baculum.

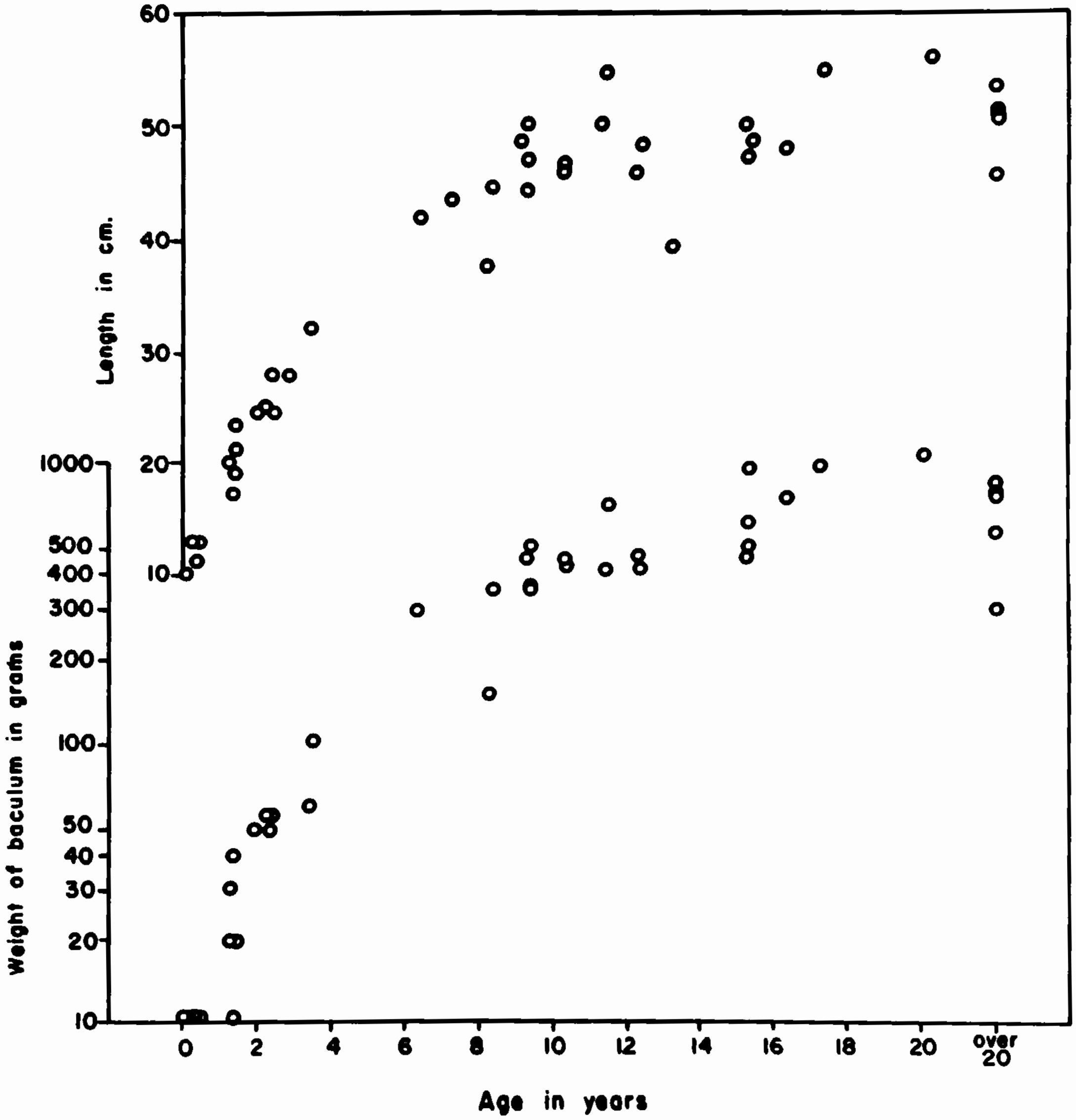

60
50
40
30
20
10
Length in cm.
1000
500
400
300
200
100
50
40
30
20
10
Weight of baculum in grams
0
2
4
6
8
10
12
14
16
18
20
over 20
Age in years

Fig. 13.

phocids, for it has been found in foetuses of the Pacific walrus taken in November and December (Fay, in litt.). Nikulin (1940) has described the appearance of sixty calves taken in June and July, and states that during that time an intensive loss of embryonic hair was occurring. Most of the later calves were bald, but Nikulin gives no indication of when the first hair coat was formed. In the calves taken from northern Hudson Bay in the summer and fall, it is apparent that the natal pelage has been replaced by a thinner coat of shorter and stiffer hairs, 1 to 2 mm. long.

The umbilical cord is probably lost shortly after birth, and the navel scar is healed at the end of three months. The upper canine teeth do not pierce the gums until two months after birth, and by late October they may attain a length of 2 cm. The mystacial bristles are short and inwardly curved, the longest attaining a length of 5 cm. in a two-month-old calf. Both fore and hind limbs are proportionately large.

<u>Immature males and females</u>. There is evidence that an annual moult occurs in the summer months (see p. 59) and the old hair, which has by this time reached a length of 2 cm. and has attained a reddish-brown colour, is shed, and a new and sparser coat of silver-gray hair develops. The skin colour is still a slate-gray, but the patchiness of the hair adds a brownish tinge to the overall colour. Animals which have been hauled out on ice or land for a long time may be stained a light brown colour with faecal matter, and this may be partly responsible for the final colour of the moulting hair.

Scars are usually small in number and appear to result from wounds caused by sharp edges of ice or tusks of other animals. Occasionally, heavy scarring occurs and a possible explanation has been suggested by Soper (1944). A young (probably first year) male was taken on October 24 at Cape Dorset and the whole of the back was covered with small circular wounds and shallow scratches. "The Eskimos were of the opinion that its mother had died, whereupon the orphan had been bullied and abused, until it was frightened and discouraged, and had left the herd to shift as best it could in solitude."

It is impossible to distinguish the sexes of immature animals up to three or four years of age when observing them from a distance, but older sub-adults can usually be accurately sexed if a clear view of the head is obtained. The broader muzzle and thicker tusks of the male are apparent, and the tusks of the female are often sharply pointed as a result of their more rapid antero-lateral wear.

<u>The adult female</u>. The oldest females are usually heavily scarred along the back and about the neck, and it is assumed that many of the wounds are received from the male during copulation. This is known to be a characteristic feature of mating in the northern elephant seal, <u>Mirounga angustirostris</u>, (Bartholomew, 1952) and the southern elephant seal (Laws, 1956a and personal observation). Occasional individuals are observed with a pronounced crown of whitish scar tissue, and this may result from the forceful method commonly used to keep open breathing holes in young ice.

Similar scarring occurs on the heads of the males, and also on the heads of some old bearded seals. Constant abrasion on ice and rocks results in the underside of the body becoming almost pink in colour, and an overall mottled effect is produced which is very difficult to describe adequately.

The tusks may become almost as long as those of the males in a few individuals, but their slender structure usually results in more rapid wear and a sharply pointed profile. The greater degree of twist and curvature may almost cause them to join or even overlap at the tips, if wear has been minimal. The vibrissae are longer than those of the male, the lateral ones attaining a length of 10 - 12 cm.

The adult male. The thick powerful tusks and broad muzzle at once distinguish the adult male, and these characteristics are most pronounced in old age. At sexual maturity, the neck, chest and shoulders become covered with large epidermal tubercles. These are hard, white, fibrous protuberances up to 8 cm. across and 4 to 5 cm. thick, and they are undoubtedly a secondary sexual character (Nikulin, 1940; Fay, 1955). In the Pacific walrus, the skin is much thicker (Fay, in. litt.) and the protuberances in the neck region may reach a thickness of 7 cm. (Brooks, 1954). The lumpiness of the skin about the shoulders, and the development of powerful neck muscles to move the heavy skull, give the male a characteristic depth in outline which is unmistakeable. The tubercles increase in size during life, and in old age the skin over the neck and shoulders assumes a pronounced pinkish-white mottled appearance (fig. 16). Scars from tusk inflicted wounds add to the overall blotchiness, and this may account for the 'albino' males which are sometimes reported (Brooks, 1954). The hair covering is sparser in old animals and rarely exceeds 1 cm. in length. Most of the colour changes associated with increasing age can be attributed to the skin, for moulting hair is usually a reddish-brown colour and the new hair a silver-gray. However, some individuals have light golden-brown hair, and this may result from a missed moult and subsequent fading of the retained hair. This is known to occur occasionally in the southern elephant seal (Laws, 1956a) and may also explain the straw-coloured crabeater seals, Lobodon carcinophagus, sometimes observed (personal observation).

The mystacial bristles become worn with advancing age (fig. 17), the more medial ones sometimes becoming flush with the skin. There seems little doubt that the wear can be attributed to the constant friction involved in feeding. Mohr (1940) is obviously mistaken in implying that the animals with short whiskers taken in European waters in the 20th century are immature. They were most probably all old males.

Dentition

Deciduous and permanent teeth. Only two complete young skulls and an additional lower jaw are available for

Figure 16. Head and Shoulders of an Adult Male Walrus showing Epidermal Tubercles and Scars from Tusk Inflicted Wounds.

Fig. 16.

Figure 17. Head of an Old Adult Male Walrus showing Worn Tusks and Vibrissae.

Fig. 17.

examination (foetus A 11; calf W3; calf W2).

The deciduous dentition appears to be:

$$\mathrm{I}\ \frac{1\ 2\ 3}{1\ 2\ 3}\quad \mathrm{C}\ \frac{1}{1}\quad \mathrm{Pm}\ \frac{-\ 2\ 3}{1\ 2\ 3}$$

this may be reduced by prenatal resorption (fig. 18). Fay (1955) identified a fourth upper premolar, but this has not been found in the two skulls available.

The full set of successional teeth is present at birth, but does not begin to erupt until the calf is two or three months old. The formula observed is:

$$\mathrm{I}\ \frac{2\ 3}{}\quad \mathrm{C}\ \frac{1}{1}\quad \mathrm{Pm}\ \frac{1\ 2\ 3\ 4}{1\ 2\ 3}\quad \mathrm{M}\ \frac{1}{1}.$$

Fay has found that the second and third lower incisor and the second lower molar are present, giving a complete formula of

$$\mathrm{I}\ \frac{2\ 3}{2\ 3}\quad \mathrm{C}\ \frac{1}{1}\quad \mathrm{Pm}\ \frac{1\ 2\ 3\ 4}{1\ 2\ 3}\quad \mathrm{M}\ \frac{1}{1\ 2}.$$

All the data relating to the adult dentition are summarised in Table III. Many of the skulls examined were found at old Eskimo camp sites, and usually most or all of the teeth were missing. Thus in some of the skulls the presence of the normally vestigial teeth was not directly observed, but it was inferred from the development of the alveolus. Although no skull was observed with more than two tusks, rare specimens are known in which a second tusk is developed on one side.

Figure 18. Dentition of the Full-Term Foetus A 11. (Teeth indicated by bracketed numbers were not observed in the specimens available, but were inferred from Fay's account of the Pacific Walrus (1955)).

Fig. 8.

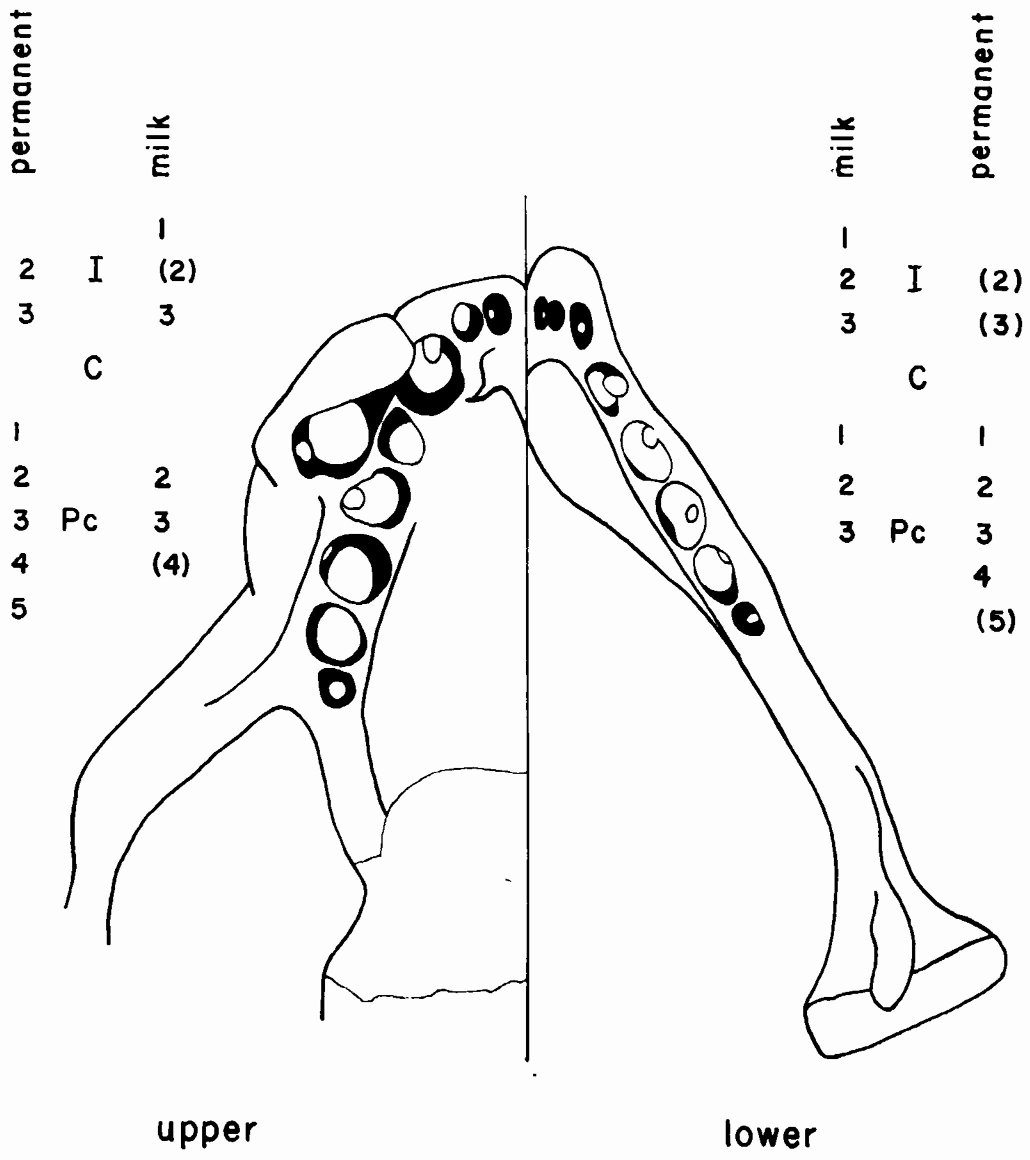

permanent
milk
1
2
I
(2)
3
3
C
1
2
2
3
Pc
3
4
(4)
5
milk
permanent
1
2
I
(2)
3
(3)
C
1
1
2
2
3
Pc
3
4
(5)
upper
lower

TABLE III

Observed Variations in the Dentition

			Incisors			Canine		Post-canines					
	Sex		0	1	2	0	1	0	1	2	3	4	5
UPPER	M	L	1	27	8		36				34	1	1
		R	1	26	9		36				31	4	1
	F	L	2	23	8		33	1			25	6	1
		R	2	25	6	1	32	1			25	6	1
LOWER	M	L	36	2			38				28	10	
		R	37	1			38			1	27	10	
	F	L	34	2			36		1	3	26	6	
		R	34	2			36		1	3	26	6	

The figures in the top line refer to the number of teeth of each type present, and not to the position in the skull. The figures in the body of the Table are number of specimens examined.

From Table III it will be seen that the second and third lower incisor, and the first upper and second lower molar usually remain vestigial and may become resorbed, while the second upper incisor, the fourth upper premolar and the first lower molar occur in up to 26 percent of the skulls examined.

The normal adult dentition may be considered as:

$$\mathrm{I}\ \frac{1}{0}\quad \mathrm{C}\ \frac{1}{1}\quad \mathrm{Pm}\ \frac{3}{3}\,.$$

<u>Tooth wear</u>. Most of the apical wear of the molariform teeth results from occlusal abrasion, though some is undoubtedly caused by the tongue and opposing gingival tissue. Fay (1955) has pointed out that sand and gravel are often found in stomachs and observed about holes in the winter ice where clam shells have been spat out, and he assumes that much of the abrasion results from the ingestion of this material while feeding. This view appears to be confirmed by molariform teeth from the Atlantic walrus, for close inspection of the opposing surfaces reveals that many bear minute pittings and scratchings.

Most tusk wear is antero-lateral, and is undoubtedly associated with the method of feeding. In mature animals of both sexes, shallow medial depressions are often observed below the level of the gum-line and these are evidently caused by some mouth activity (fig. 7). Fay has found that in the males, the distance between the depressions is equivalent to the root ridge intervals, and in very old animals only a broad deep trough is found. The females often show series of widely spaced deeper troughs as well as the shallow depressions, and Fay has associated these with an enormous increase in feeding during lactation. The evidence for these assumptions is that the distances between the deepest troughs are comparable to the total tusk length increments (Absolute Total Length) between pregnancies. Though few tusks are available in the series of specimens from Hudson Bay and Foxe Basin, the pattern of medial tusk wear in the male agrees with that found in the Pacific walrus, but no valid deductions can be made from the female material. The depressions evidently result from a periodicity in growth, and this probably depends ultimately on seasonal changes in feeding habits. The wear appears to be caused by the lateral movements of the lower jaw during feeding, for the skin of the outer lip is very rough to the touch. However, Fay (1955) quotes Eskimo opinion which favours the possible expulsion of materials (presumably water and food detritus) from the mouth, though this would appear to occur too infrequently to result in such wear.

Further distal wear and fracture may result from the use of the tusks while hauling out onto ice or rocks. Though this pattern of behaviour has resulted in many controversial statements in the literature, it has been observed frequently enough by the author to suggest that it is a potent cause of tusk wear. Fighting, or mere exchange of blows between individuals in a disturbed herd is common, but it is doubtful whether the tusks suffer much in such encounters.

NUTRITION

Food preferences

The lactation period of the walrus probably lasts for two years in the majority of animals, and may be extended into the third year if the adult female does not give birth to another calf. The stomachs of calves and and yearling animals taken in northern Hudson Bay were always empty or contained only milk, and this is in agreement with the observations of other authors. Nikulin (1940) records the finding of milk in the stomachs of 2 two-year-old animals, and quotes a similar observation of Freiman (1940) who found both milk and the remains of molluscs in a two year old.

The adult mode of feeding is assumed to begin in the third year, since distal tusk wear is first apparent then. However, Brooks (1954) has suggested that the immature animal remains with the cow, and may rely upon her to rake up its food.

The adult walrus feeds almost exclusively on the molluscs which form the greater part of the Macoma calcaria community (Vibe, 1950), though annelids, crustaceans, holothurians and tunicates may be eaten occasionally (table IV). Foraging depths range from 15 to 80 metres, and the walrus is rarely found over water deeper than this.

TABLE IV

Food Organisms taken from Stomach Contents

Areas of Occurrence

A - Bencas Island and northeastern Coats Island (12 stomachs).
B - Seahorse Point, Southampton Island (2 stomachs).
C - East of Cape Dorset, Hudson Strait (1 stomach).
D - Loks Land, Frobisher Bay (1 stomach).
E - Northwestern Foxe Basin (3 stomachs).

Foods marked with an asterisk could not be identified further than the groups recorded.

Food species	No. of organisms	No. of stomachs containing organisms	No. times dominant	Areas of occurrence
Pelecypods (siphons) *	224	7		A, E
" (feet) *	13	3		A
Shell fragments *		4		A
Mya truncata	2193	14	8	A,B,D,E
Cardium spp.	221	7	1	A,B,E
Saxicava arctica	350	10	2	A,B,E
Astarte borealis	58	1		B
Pecten sp.	140	4	2	A
Holothuroidea				
Cucumaria sp.	47	4		A
Thyonidium sp.	14	5		A,B,C,E
Gastropoda *	19	2		B,E
Opercula *	253	4	1	A,B,C,E
Buccinum sp.	50	2		C,D

TABLE IV (continued)

Natica sp.	60	1		D
Sipho sp.	2	1		D
Decapoda *	11	1		D
Eggs *	31	1		D
Paguridae *	191	1	1	D
Eupagurus Kröyeri	93	1		D
Hippolytidae	5	1		D
Sclerocrangon sp.	1			D
Spirontocaris sp.	1			D
Eualus sp.	1			D
Isopoda				
Mesidotea sabini	20	1		E
Polychaeta *	1	1		B
Ascidiacea *	2	1		E
Priapulus caudatus	11	3		A,E
Squid beaks *	12	3		A,C
Fish otoliths *	25	1		C
Nematoda *	65	1		C
Phoca hispida - skin and blubber	2 lb.	1		A

Vibe has shown from a detailed qualitative and quantitative survey of the walrus banks of northwestern Greenland that the two species of *Cardium* are most frequently eaten at depths from 15 to 35 m., and *Mya* and *Saxicava* from depths between 40 and 80 m.. Since the latter two bivalves are common in the bottom fauna at the shallower depths, it is evident that the walrus selects the larger *Cardium* species by foraging over large areas of the bottom. At greater depths, *Cardium* are scarce, and few are found in stomach contents. Vibe suggests that this partly results from the minimal feeding time available; expediency is necessary, and the walrus forages over as little of the bottom as possible.

No similar data are available for Foxe Basin, but one Eskimo (Kramanik) has confirmed that *Cardium* is generally more abundant in stomachs of animals taken at Amitioke Peninsula, where hunting is usually done in shallow water. East of Kringmiktorvik, where hunting takes place over deeper water, the siphons of *Mya* and *Saxicava* form the principal food elements.

In the Pacific walrus the sexes appear to show differences in feeding habits, for Brooks (1954) has found that the males seem to select *Mya*, *Clinocardium* and *Molpadia*, while the females and immature animals favour the smaller molluscs, *Astarte* and *Macoma*.

During local dispersals and more pronounced migratory movements, walrus may pass over less suitable foraging grounds in which molluscs are not dominant. It is then that the other benthonic organisms already referred to play an important part in feeding (table IV).

It was formerly believed that the walrus was partly vegetarian in diet (Allen, 1880), but no significant amounts of plant material have been found in any stomach contents examined. Brooks (1954) has noted that the food is often covered with algal slime and suggests that it may play a nutritional role in supplying vitamins.

Method of Feeding

The following observations on feeding largely confirm the excellent account given by Vibe (1950).

In adult animals, most tusk wear is antero-lateral. When considered together with the vibrissal wear, this strongly suggests that the walrus forages in sand and mud by standing on its head and rotating its tusks from side to side in the substrate. Adult animals with a broken tusk, or one missing from a congenital defect, are sometimes seen but they appear to feed normally. Brooks (1954) has observed an old and apparently healthy male with both tusks absent, which suggests that the mystacial pads may still be effective in food gathering. Though the vibrissae must be to some extent tactile and of some use when feeding occurs at depths below the limit of vision, they are nevertheless worn very short as the animal grows older, and perhaps become of limited use then. In spite of the broad muzzle, the lips are probably very sensitive and able to select the food organisms required.

The great breadth and depth of the molariform teeth was long considered to be an adaptation for crushing the hard-shelled molluscs on which the walrus feeds (Cobb, 1933). This viewpoint seemed to follow logically from the known fact that hypercementosis in human teeth results from increased occlusal stress. However, the hooded seal (*Cystophora cristata*) exhibits a high degree of hypercementosis, though it is evident from the pelagic nature of this species that the diet must consist of relatively soft-bodied food organisms such as fish, squids or crustacea, which would require little crushing. Fay (1955) has found that all sizes of teeth, irrespective of function, have corresponding amounts of cementum, and suggests that hypercementosis results from an overall physiological function related to tusk growth, rather than from a purely mechanical compression. The strong wear on the molariform teeth may then be explained by normal occlusal abrasion aided by the small particles of grit and sand taken in with the food.

The walrus is able to select not only small individual food items, but can readily separate the more edible parts of them. Thus the species *Serripes*, *Cardium*, *Clinocardium*, *Macoma* and *Astarte* are represented by the feet alone, while only the siphons of *Mya* and *Saxicava* are taken. Since other parts of the bivalves are rarely included in the stomach contents, the walrus must remove the fleshy feet and siphons by squeezing them off with the opposing anterior surfaces of the upper and lower jaws. There is good evidence that the feet of Serripes (Cardium) groenlandicum are comparatively slow in retracting, for Mikulich (1949) has found that they are extensively eaten by a small fish (Pleurogrammus azonus), closely related to the greenlings. After the foot has been removed, the clam dies, and the rest of the body is then eaten. It may be concluded that the walrus is also capable of removing the feet before they have had time to contract into the shell.

This is probably not the only method of feeding, for Vibe (1950) has observed that quantities of intact and connected bivalve shells are sometimes found about the breathing holes of the walrus in thin ice. From this evidence, he suggests that the animal is able to suck out the soft parts of the bivalve before squeezing off the siphons.

Gastropods such as Buccinum and hermit crabs (Paguridae) are also eaten, but no shell fragments are found in the stomach contents. Vibe notes that Buccinum has a thin shell which is often open at the top, and suggests that the soft body of the gastropod is easily sucked out. There seems little doubt that the hermit crabs are removed in a similar fashion since their soft bodies are more numerous in the stomach contents than the anterior thoracic segments and large appendages.

In only one species, Pecten, in which the adductor muscle alone is removed, is it most likely that the whole shell is crushed. In this instance, both shell fragments and the softer body parts are probably separated by the tongue before expulsion.

Aberrant Diets

Chapskii (1936) and Nikulin (1940) record the only two observations of stomach contents which were largely composed of fish. In each case, only the polar cod (Boreogadus saida) was represented. The record of otoliths in one walrus stomach from Cape Dorset (table IV) indicates that the fish-eating habit is probably resorted to when the normal molluscs are in short supply. Further indirect evidence is available from the intestine of an adult male A 127, which contained a large number of Acanthocephala of a species normally infesting fish as a second intermediate host (Dr. Paul Montreuil, verb. comm.).

Fragments of the skin and blubber of several species of pinnipeds and cetaceans are occasionally found in stomach contents. The ringed seal is most often represented, but the bearded seal, hooded seal, narwhal (Monodon monoceros), white whale (Delphinapterus leucas) and bowhead whale (Balaena mysticetus) have all been reported. In the series of specimens from the Eastern Canadian Arctic only one stomach out of 35 contained pieces of ringed seal as food. The rancid nature of the blubber suggested that the food had been dead for a long time before being eaten. However not all food of this sort is carrion, for numerous and well substantiated accounts show that certain adult walrus actively prey on seals. These adult animals are rogues, for the Eskimos from northern Hudson Bay and Foxe Basin state that they are all males which are solitary at the time of capture.

The causes of the carnivorous habit are obscure. According to Fay (1955), the Alaskan natives say that the rogues are orphaned young which never learned to feed on the bottom, but this ignores the fact that only males become rogues. It is not known whether seal meat is eaten to the exclusion of other foods, but the tusks, yellowed with grease and often heavily scratched, suggest that this is so. Such a diet is paralleled only by that of the polar bear (<u>Thalarctos maritimus</u>), and it is of interest to note that the liver of rogues is regarded as unfit to eat by the Eskimos. Rodahl (1949) has described hypervitaminosis A in polar bear liver and its toxic effects on human beings, and this may explain the Eskimos' distaste of rogue walrus liver.

Fasting

The writings of earlier authors concerning the hauling-out habits of the Atlantic walrus have been well summarised by Allen (1880), and Nikulin (1947) and Fay (1955) have contributed detailed studies of the Pacific walrus. From these accounts, it appears that at all times from April to December, and probably throughout the whole year, the walrus hauls out onto land or ice during periods of fine weather and remains relatively inactive between feeding excursions.

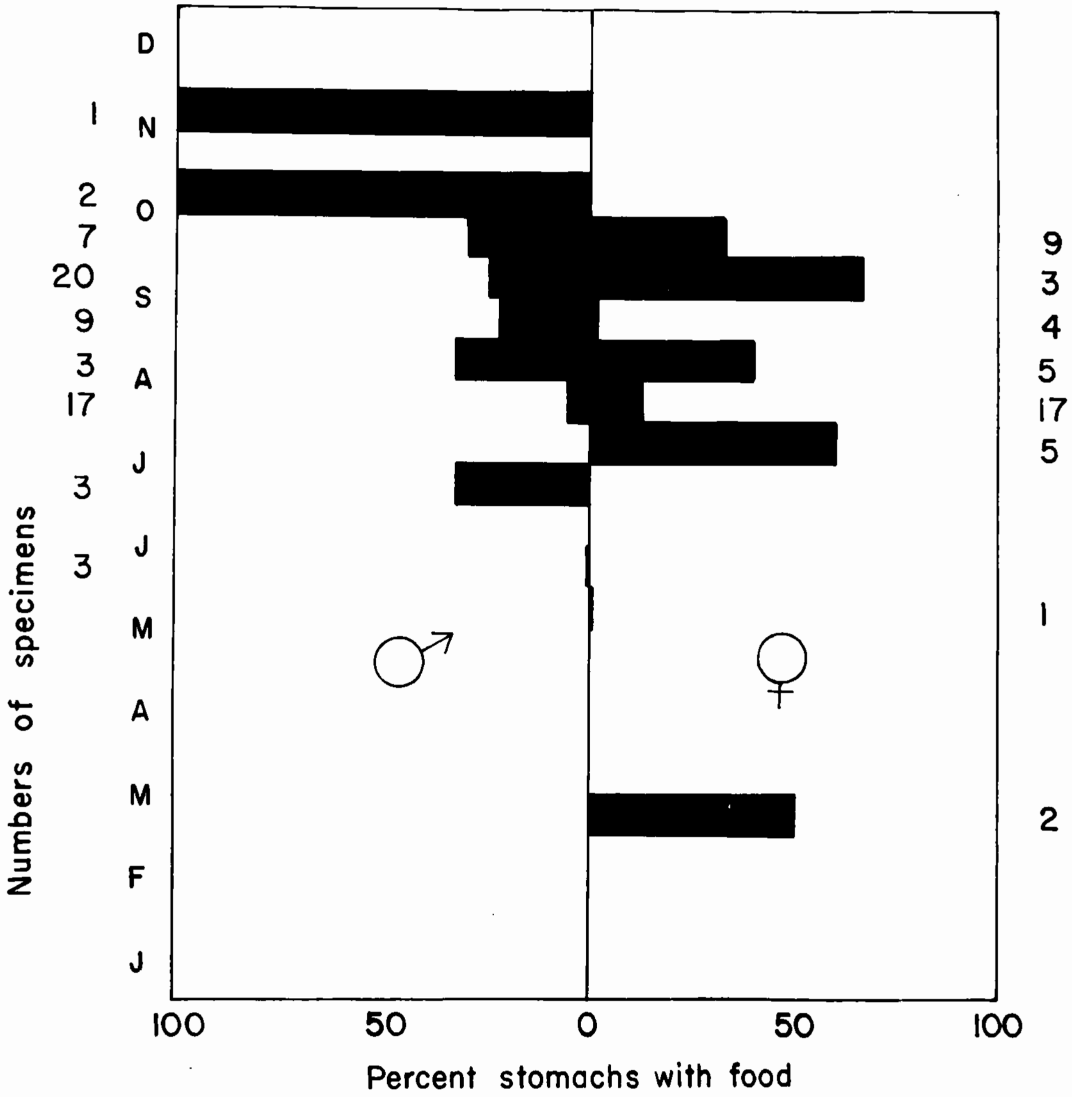
Allen (1880), in quoting an account of Shuldham written in 1775, states that during the spring, walrus at the Magdalen Islands used to remain ashore for periods as long as fourteen days provided the weather was fair. Fay (1955) has observed that during November and December the Pacific walrus may remain on shore at Big Diomede Island for as long as a week, and Nikulin's account (1947) gives five days as the maximum time. At Coats and Bencas Islands, the present author found that walrus did not remain ashore for longer than six days, owing to the frequency of bad weather. Though feeding appears to be intermittent at all times of the year, it is probably more intensive during winter.

Of 111 stomachs examined in the field, only 35 contained food of any sort. During the period July to October, slightly more females than males have food in their stomachs (fig. 19), but the difference is not significant. No observations have been made in the spring months during the breeding season, and it has been assumed that feeding is then at a minimum, particularly in the males.

A few stomachs containing small quantities of stones have been found, but there is no correlation of these with absence of food. The stones may satisfy hunger pangs occasionally (see Laws, 1956a) but the small amounts swallowed suggest that they are accidently ingested with the food.

Figure 19. Percentage of Stomachs containing Food.

Fig. 19.


Numbers of specimens
D
1
N
2
O
7
9
20
3
S
9
4
3
A
5
17
17
J
5
3
J
3
M
1
♂
♀
A
M
2
F
J
100
50
0
50
100
Percent stomachs with food

THE MOULT

The calf is born with a coat of soft, fine, silver-gray hair, 5 to 10 mm. in length. According to Nikulin (1940), this embryonic pelage is shed soon after birth and by the end of July most calves are devoid of hair. In August the new coat begins to form and by the end of the first year attains a length of 6 mm. (see table V).

In succeeding years an annual moult occurs in the summer months, though it is a much more variable and prolonged process than the moult of phocids. The new hair covering is a silver-blond colour when dry and accounts for the many light-coloured individuals seen in the fall and early spring.

In the summer months the old hair is a reddish-brown colour and can be easily pulled out. During periods when the animal is hauled out, shedding of the old hair is aided by friction of the skin on the rocks or ice, and by deliberate scratching. At the uglit, this moulted hair falls between the rocks and fills the cracks with a dense felt.

Mohr (1952) has presented evidence for an annual renewal of the vibrissae, but it has been impossible to confirm her observations. Examination of the mystacial pads of the specimens recorded in Table V shows that there is an even gradation of wear, and this suggests that the vibrissae are retained throughout life. In individuals with short vibrissae, the length appears to result from wear alone rather than replacement.

TABLE V

THE MOULT

When old and new hair are present, 'fast' and 'pulling' refer to the old hair only. A full hair coat is indicated by the symbols xxxxx. A dash indicates 'no observation recorded'; a blank means 'nothing observed'.

Field No.	Date	Sex	Age	Length of old hair in mm.	Amount	Fast or Pulling	Length of new hair in mm.	Amount
A 11	26 May	M	0	5 - 10	xxxxx	f		
A 39	2 Aug	M	1				1 - 2	xxxxx
A 96	17 Jun	M	13	10	-	f		
A 97	17 Jun	M	7	10	-	f		
A 37	1 Aug	M	3	-	-	p	-	-
A 38	2 Aug	F	13	6	xx	-	1 - 2	xxxx
A 40	6 Aug	M	10	12	xxxxx	p		
A 109	6 Aug	F	1	6	xx	-	3	-
A 41	7 Aug	M	1	-	xxxx	p	-	-
A 42	7 Aug	F	10	12 - 18	xxxx	p	-	-
A 110	10 Aug	F	20	12	xx	-	6 - 12	xxx
A 111	12 Aug	M	6	10	xxx	p	2	-
A 112	13 Aug	F	9				6 - 12	xxx
A 43	17 Aug	F	-	-	xxx	p	3 - 6	xxx
A 44	17 Aug	F	-	12	-	f	2 - 3	-
A 45	20 Aug	M	21	12	x	p	3 - 12	xxx
A 46	20 Aug	F	7	12	xxx	-	3	x

TABLE V (continued)

A 113	21 Aug	F	3	-	-		6 - 12	xxxx
A 48	22 Aug	F	15	-	-	-	1 - 10	xx
A 114	22 Aug	M	20				6 - 12	xxxx
A 115	22 Aug	F	10	-	x	p	6 - 12	xxx
A 116	23 Aug	M	4				6	xxxx
A 151	2 Sep	M	-	18	xx	p	2 - 17	xxx
A 152	2 Sep	M	-	10 - 13	-	p	2	-
A 118	10 Sep	M	1				6	xxxx
A 119	10 Sep	F	15	-	x	p	6 - 12	xxxx
A 61	18 Sep	M	2	6 - 12	-	-	3	-
A 72	23 Sep	F	16			f	-	-
A 78	2 Oct	F	6			f	6	-
A 79	2 Oct	F	6	12	x	p	2 - 12	xxxx
A 80	4 Oct	F	10			f	6 - 12	-
A 81	5 Oct	F	4				6 - 12	-
A 127	6 Oct	M	15	12	x	-	12	xxxxx
A 129	7 Oct	M	6	12	xxx	p	6	x
A 131	7 Oct	M	3				12	-
A 132	7 Oct	F	20	-	x	-	-	xxxx
A 133	7 Oct	F	23	-	x	-	6	xxxx
A 136	10 Oct	F	11	-	xxx	-	-	xx

THE MALE REPRODUCTIVE CYCLE

Most of the male material available from the Eastern Canadian Arctic is not representative of the breeding season. Fortunately, Fay (1955) has been able to collect a sufficiently large sample of male Pacific walrus in the late spring months, and the reproductive cycle can thus be established with some accuracy.

Sexual Maturity

Perhaps the best criterion of maturity in the male is the presence of sperm in both the seminiferous tubules and the epididymis, and this can only be demonstrated effectively by histological examination of preserved material. Gross changes in the size of the genitalia are known to occur at maturity in several other pinnipeds, and bacula and testes of the walrus have been examined to see if similar increased growth occurs.

Growth of the baculum and testis. Fisher (1954) has found that in the harp seal, the maturation of the gonads is accompanied by an increased rate of growth of the baculum and testes in the eighth year. A similar acceleration of growth in these organs at maturity has been recorded in both the ringed seal (McLaren, in press) and the southern elephant seal (Laws, 1956b).

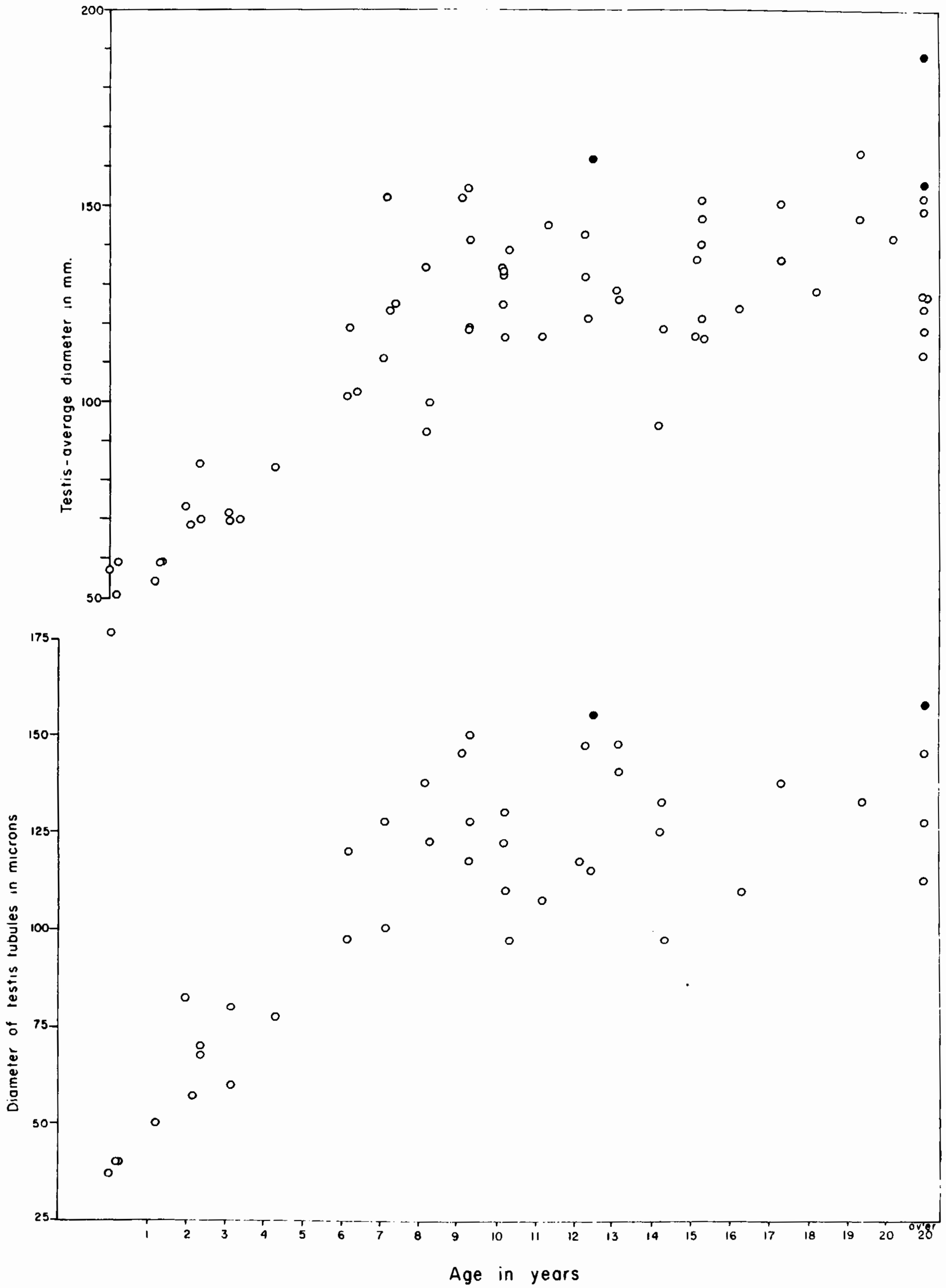
In the northern fur seal the baculum and testes develop fairly steadily throughout life (Scheffer, 1950b) and do not show any accelerated growth during late adolescence. Fay (1955) has shown that steady development of these organs occurs in the Pacific walrus, and this agrees with the findings of the present author for the Atlantic walrus (figs. 15 and 20).

Histology of the testis and epididymis. The initial growth of the seminiferous tubules is rapid, and in yearling animals they become packed closely together and form the bulk of the testis. Each tubule consists of a basal layer of undifferentiated cells, with spermatogenic cells scattered throughout the central cytoplasmic syncytium. This appearance is maintained until the end of the second year, when the layer of cells adjacent to the basement membrane becomes clearly differentiated into Sertoli cells and spermatogonia. The loose syncytium contains large numbers of spermatocytes with resting nuclei and pale cytoplasm.

In the next three years, this picture of steady growth is maintained. The number of spermatogonia in the basal layer increases steadily, and the spermatocytes become much larger and fill most of the tubule. In the two specimens taken in their seventh year, the spermatocytes have become more peripheral in distribution, and a few tubules have patent lumina. Active cell division is observed in many spermatocytes, up to four layers of cells being formed above the basal layer of spermatogonia and Sertoli cells

Figure 20. Development of the Testis. (Specimens in breeding condition are indicated by black dots).

Fig. 20.


Testis-average diameter in mm.
200
150
100
50
Diameter of testis tubules in microns
175
150
125
100
75
50
25
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
over 20
Age in years

(fig. 21). There is spermatid formation in a small number of tubules, but no spermia are present. In later age groups the testis tubules show the features typical of post-oestrus adults, with large lumina, sloughed spermatids and spermatocytes, and giant cells.

In the epididymis, there is the same picture of steady development up to the time of maturity. The low, cuboidal epithelial cells lengthen into tall columnar cells in the yearling animal. In the third year, a brush border of long cilia develops, and lobing of the epithelium occurs in the following year. There is no secretory activity at this stage. The fifth year animal shows little further development, though there is some cellular detritus in the duct. In the seventh year, many of the tall cells bear terminal vacuoles in the cytoplasm, indicating the beginning of a phase of secretory activity (fig. 22).

In older animals the epithelial cells are more heavily vacuolated, and secretion is present in some sections of the duct (fig. 23). There is a greater amount of cellular detritus consisting mainly of whole and fragmented spermatids and spermatocytes.

The condition of the seminiferous tubules and epididymis in the six-year-old animals clearly indicates that maturity is reached in that year. However, a larger sample of specimens might well reveal a range in the ages at maturity, with a peak age at six or possibly seven years.

Figure 21. Section through the Seminiferous Tubules of the Immature 6-Year-Old Male A 111 (x 600).

Figure 22. Section through the Epididymal Epithelium of the Immature 6-Year-Old Male A 111 (x 600).

Fig. 21.

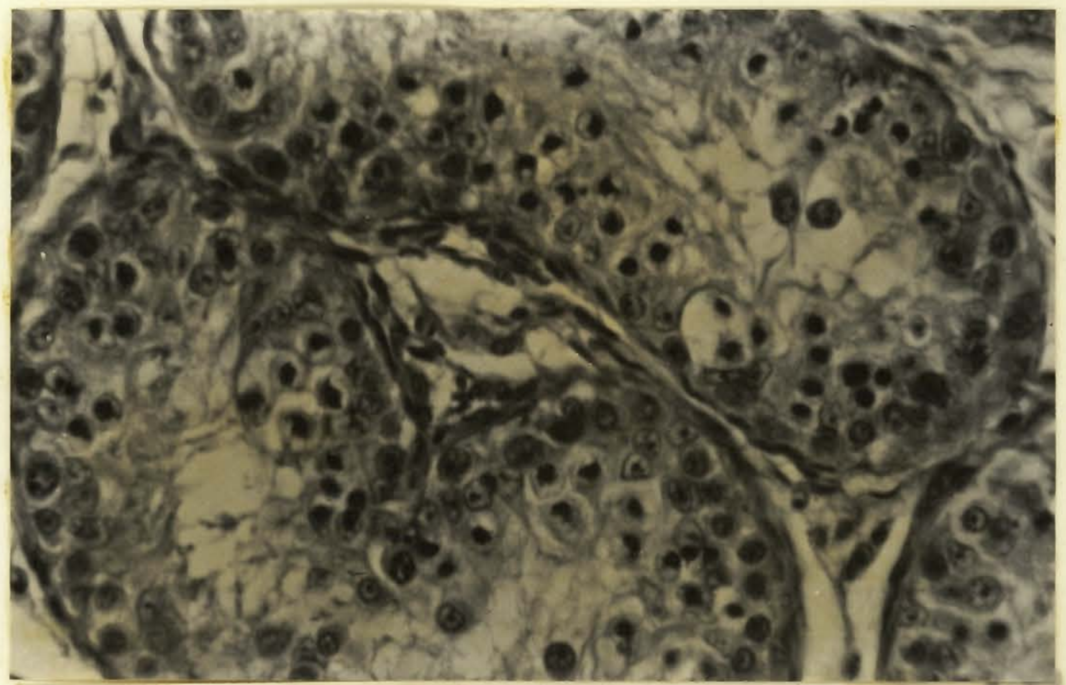
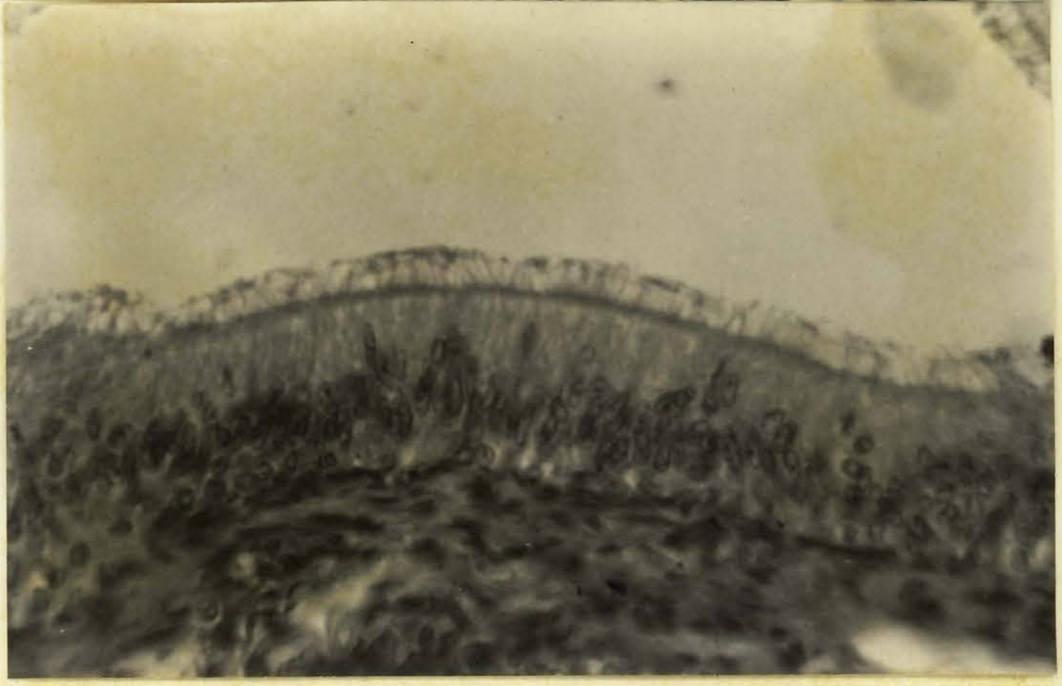


Fig. 22.



The Testicular Cycle in the Adult Male

The most complete account of the testicular cycle in a mature pinniped has been given by Laws (1956b) in a paper on the physiology of reproduction of the southern elephant seal. He recognised seven phases of tubule activity, and these have been described in great detail.

For the present study, it was found that tubules could be divided more suitably into three easily recognisable types, depending on their state of activity. These types are as follows: (A) - Sertoli cells elongated with maturing spermia attached to their free ends; small lumina (fig. 24). (B) - Sertoli cells withdrawn towards the basal layer, with columns of spermatids and spermatocytes occupying most of the epithelium; no spermia visible; large lumina containing sloughed spermatids, and multinucleated giant cells formed from the fusion of spermatids or spermatocytes (fig. 25). (C) - Only a few spermatocytes remain, together with a peripheral layer of spermatogonia and Sertoli cells. In a few tubules the latter terminate in an apparent cytoplasmic syncytium which fills most of the centre (fig. 26).

The state of development of the testes in the adult male is summarised in Appendix II, the three tubule types being given in the order of frequency of occurrence. There is slight evidence of a seasonal variation in the diameter of the seminiferous tubules and this is illustrated in Figure 18. When additional specimens can be obtained from the winter months,

Figure 23. Section through the Epididymal Epithelium of the Mature Male A 97 (x 600).

Figure 24. Section through a Seminiferous Tubule of the Adult Male IW 10 taken on November 30: Type A (x 600).

Fig. 23.

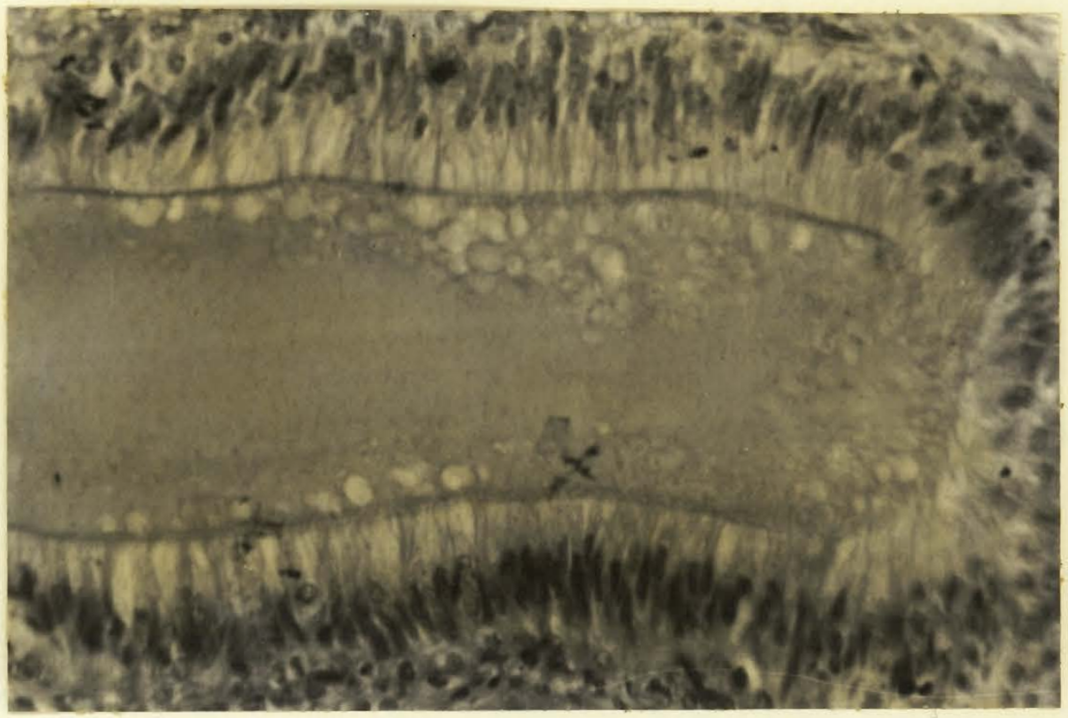


Fig. 24.

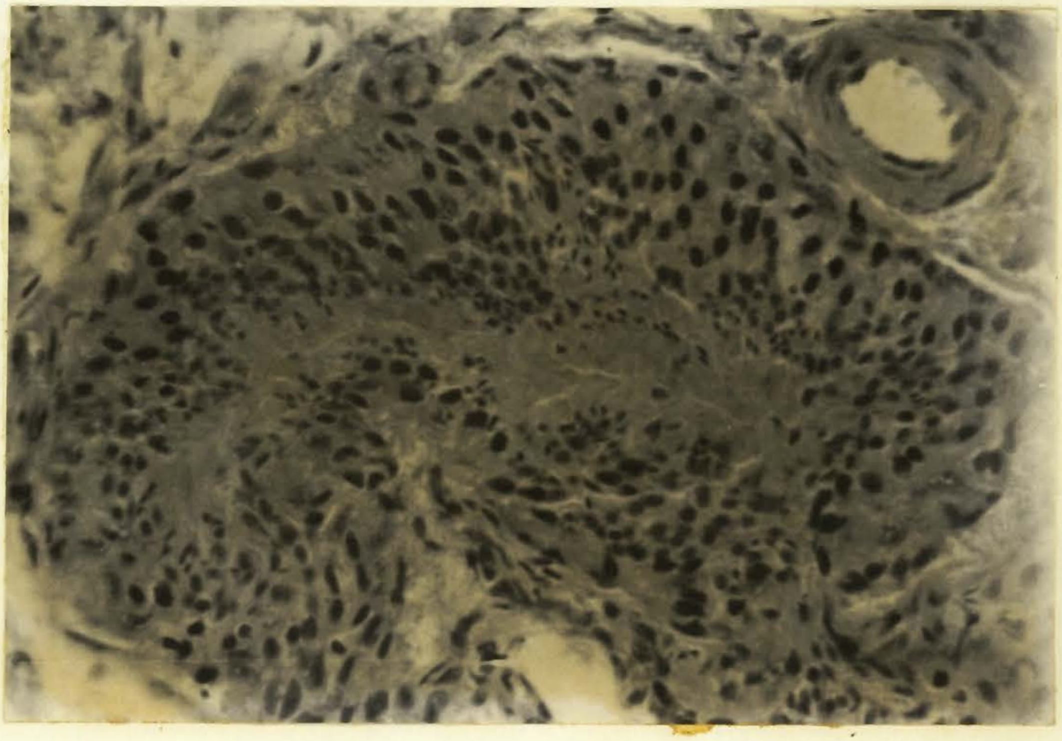


Figure 25. Section through a Seminiferous Tubule of the Adult Male A 97 taken on June 17: Type B (x 600).

Figure 26. Section through a Seminiferous Tubule of the Adult Male A 62 taken on September 18: Type C (x 600).

Fig. 25.

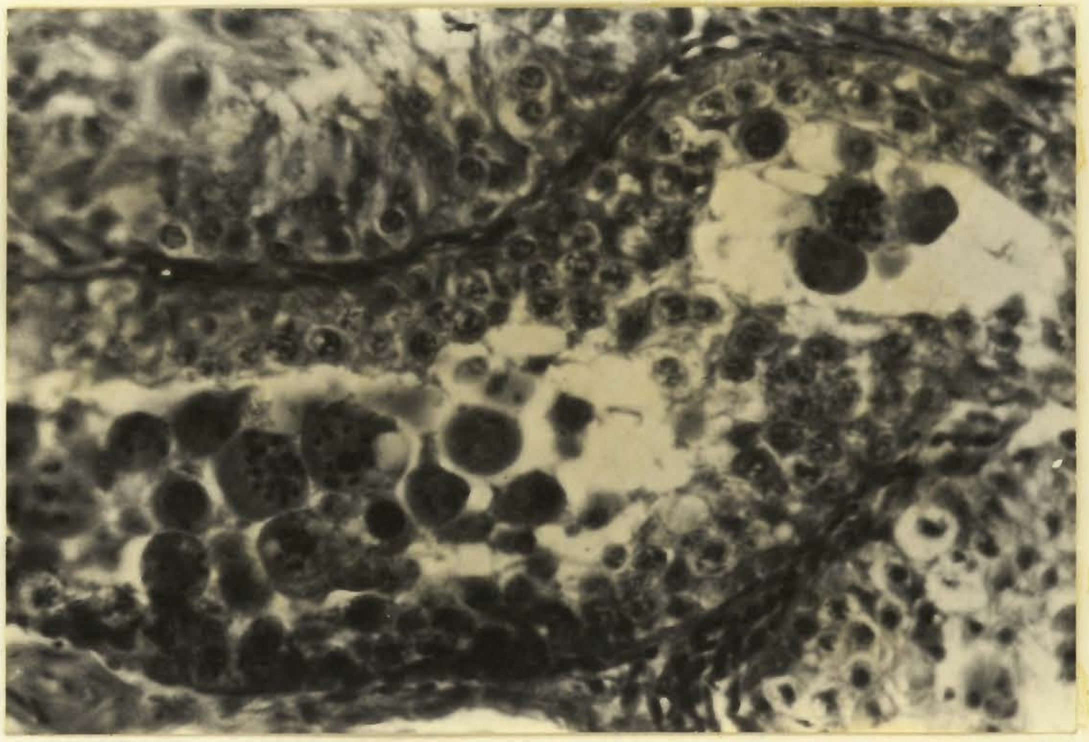
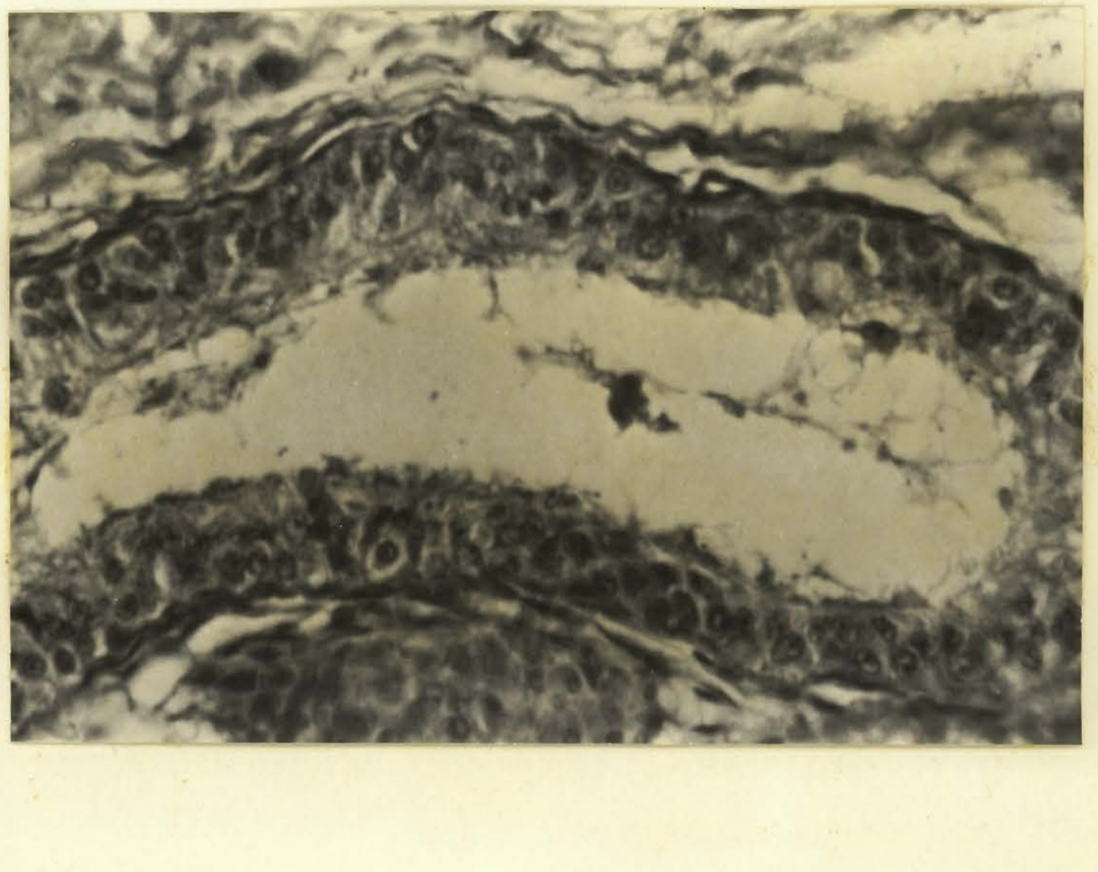


Fig. 26.



the tubules will probably show a more pronounced cyclical fluctuation than is suggested by the graph.

Chronology of Events in the Adult Male

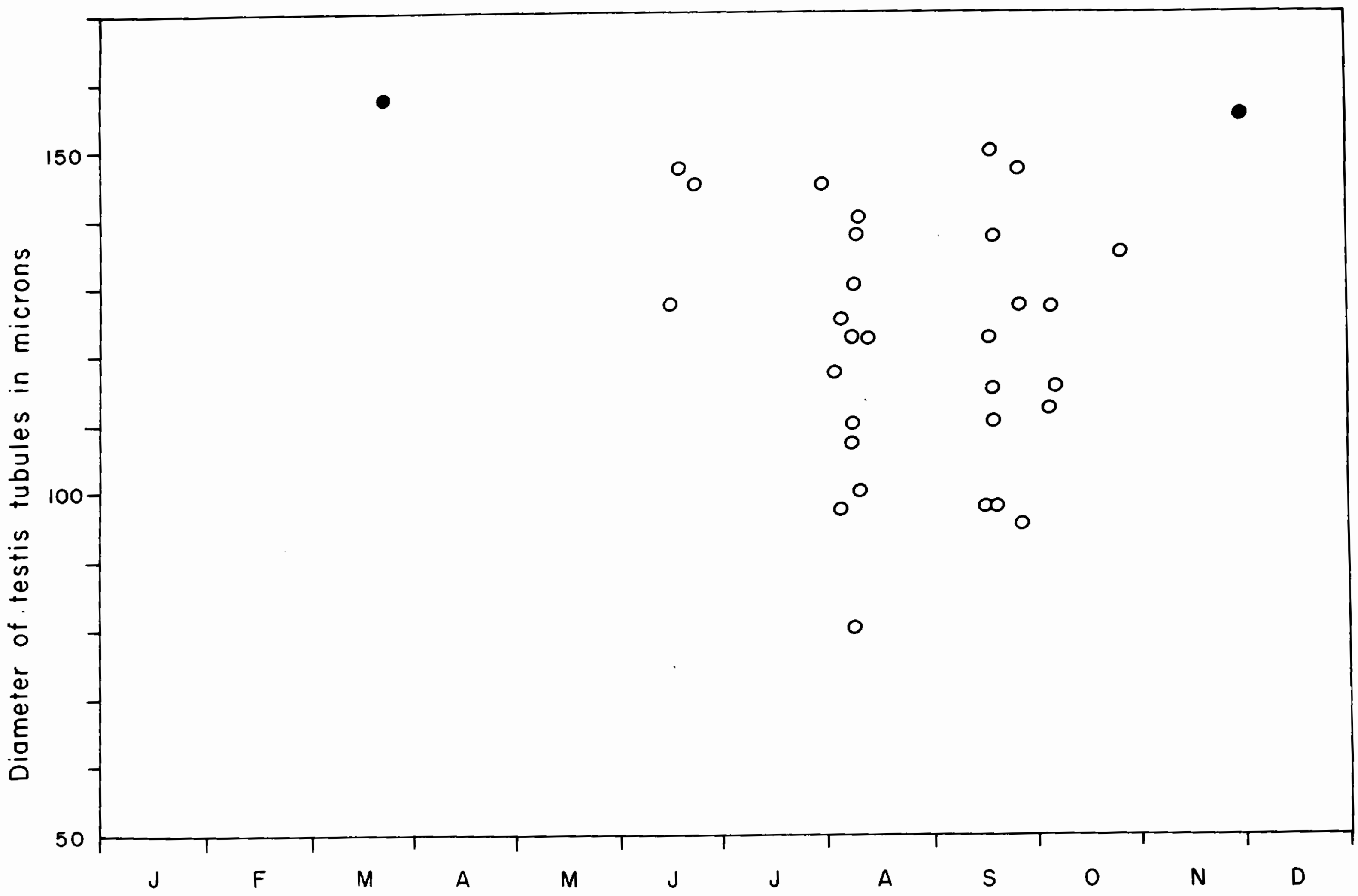
Although only two specimens of the Atlantic walrus have been found in an active state of spermiogenesis (fig. 27), the larger amount of data on the Pacific walrus collected by Fay (1955) has enabled the annual cycle of the adult male to be fixed with some certainty.

Fay found that between April 20 and June 8, 94 percent of the 5 to 10 year olds and 16.5 percent of the older animals were fecund. The seminiferous tubules of the apparently non-breeding older males were found to contain abundant Sertoli cells, which Fay suggested might be associated with sterility. There is no suggestion of a comparative sterility with age in the Atlantic walrus, for mature males up to 28 years of age show normal post-oestrus changes in the testis. It seems highly probable that Fay has misidentified these normal post-oestrus changes (particularly type C), and that all his adult males are either sexually active or beginning to enter the quiescent phase. His comparison between the two age groups may well mean that the older males terminate the breeding season earlier and more abruptly.

Since all the Atlantic walrus taken in June are post-oestrus adults, the season of rut may be assumed to end about the middle or end of May. Throughout the summer months, the

Figure 27. Seasonal Fluctuation in Diameter of the Seminiferous Tubules in Adult Males (the two specimens indicated by black dots are in an active state of spermiogenesis.

Fig. 27.


Diameter of testis tubules in microns
150
100
50
J
F
M
A
M
J
J
A
S
O
N
D

tubules remain in phase B. A few may enter phase C, but this never becomes a general condition, even as late as the end of October. By late November the tubules are once again in a state of active spermiogenesis. Fay (in. litt.) has confirmed this early commencement of rut and its continuation into mid-winter, and cites the following specimens as evidence: "A 16-year-old male taken on November 28 had much spermatogenic activity in the testes, and the epididymal tubes were packed with sperms. Two 8 year olds, one taken December 6 and the other January 26, were in the same condition. Two 6 year olds (November 6 and December 12) appear to be in the early stages of spermatogenesis, but no sperms are present and the epididymides contain only sloughed spermatids and some half-developed spermia."

This long period of rut is comparable with that of the southern sea lion (Otaria byronia), though the seasonal limits are not so well defined in that species (Hamilton, 1939). There is good evidence from the reproductive cycle of the female that breeding occurs only in the months of April, May and June, and observations of copulation in the Pacific walrus suggest that this is so. Thus Brooks (1954) states that mating occurs on the ice in April and the first part of May in the Bering Sea and is occasionally observed in Bering Strait in late May and early June. There is also one observation of copulation at Point Barrow in early July. The only evidence available from the Eastern Canadian Arctic is from northern Foxe Basin. In April the walrus are in the northern part of their territory, and mating has been seen on rare occasions by Eskimo hunters from Igloolik. There is no record of copulation occurring in the water, though this is probably quite frequent.

The short breeding season is probably limited by the ovarian cycle of the female and the marked gregarious behaviour and sexual segregation of the herds. These factors are considered in greater detail in the section dealing with the chronology of events in the female (see p.84).

THE FEMALE REPRODUCTIVE CYCLE

Sexual Maturity

Freiman (1940) was unable to distinguish more than five age groupings in his frequency analysis of body and tusk measurements of the female Pacific walrus, and from this and other data he concluded that sexual maturity was attained at three or four years of age. Fay (1955) adopted a similar method of age grouping and supposed that the majority of females were first impregnated when four or five years old.

The present study, based on more objective methods of age determination, shows that there is probably a wider variation in the ages of females ovulating for the first time. This is not a unique occurrence in the <u>Pinnipedia</u>, for Fisher (1954) has shown that in the harp seal, the female may become mature between the ages of three and eight years with a peak at six years. Similarly McLaren (in press) has found that the ringed seal becomes sexually mature from four to seven years of age, with the peak again at six years.

Ovulation in nulliparous females. Macroscopically visible follicles do not occur until the female is five years old, though further specimens would probably indicate follicular development at an earlier age. The immature appearance of the gonads is still found in one of the seventh year females however, and this may possibly extend to later age groups.

The female is considered to be sexually mature when one of the follicles has ripened and liberated its ovum with the formation of a corpus luteum at the site of ovulation. If conception follows ovulation, the corpus luteum persists throughout pregnancy, and then degenerates into a fibrous corpus albicans after the birth of the calf. Regression may be gradual over a period of years until the corpus albicans is finally reduced to a small dense white scar. When conception does not occur, the corpus luteum evidently regresses more quickly and may reach a small diameter in a relatively short time. It is suspected that the resulting corpora albicantia may not persist for more than several years (see p.80)

Ages at first ovulation. Only four mature females with a single corpus luteum in the ovaries have been collected, and the condition of their reproductive tracts shows that they have not borne young before. Two are five year olds (IW 43, IW 48), one is a six year old (A78) and the other is a nine year old (A112), and each one has ovulated too late in the season for impregnation to occur.

The formation of corpora lutea without subsequent conception (corpora lutea spuria) is not unique among the Pinnipedia, for McLaren (in press) has found that at least thirty percent of ringed seals ovulating for the first time do not conceive. He suggests that the unseasonal ovulations may reflect a polyoestrus cycle in the young females, and the regular cycle only becomes fixed by the advent of full maturity. This probably explains conditions in the walrus, though there is no evidence of more than one corpus luteum being produced in a year.

The twelve females with two corpora lutea (including corpora albicantia) in the ovaries show a varied reproductive state. All have borne young, and four are definitely pregnant for the second time (A9, A42, A110, A120). The data are set out in Table VI with the corpora lutea separated into two columns representing the assumed first and second ovulations. In the first column, a corpus luteum of pregnancy (corpus luteum verum) is only indicated when there is definite evidence of an old placenta, or when the female is accompanied by a yearling or two-year-old calf. The ages in the final column have been adjusted to correspond with these assumed first ovulations, the minimum age difference being allowed when the history of the assumed first ovulation is unknown.

TABLE VI

Sexual Maturity in the Female

The classes of females are as follows: 'M' - mature, nulliparous; 'P' - pregnant; 'B' - barren; 'c' - with calf; 'y' - with yearling.
A question mark indicates that the history of the assumed first ovulation is unknown.

Field No.	Reproductive condition	Assumed 1st. ovulation	Assumed 2nd. ovulation	Age of specimen	Age at 1st. ovulation
IW 43	M	c.l. spurium	-	5	5
IW 48	M	"	-	5	5
A 78	M	"	-	9	9
A 112	M	"	-	6	6
A 46	P	?	c.l.verum	7	6
A 73	Bc	?	"	7	5
A 9	Py	c.l. verum	"	8	5
A 42	Py	"	"	8	6
A 115	Bc	?	"	9	7
A 80	P	?	"	10	9
SD 141	Bc	?	"	11	9
A 83	Bc	?	"	11	9
A 82	P	?	"	11	10
A 125	B	?	"	11	9
A 110	Py	c.l. verum	"	13	11
A 120	P	"	"	13	11

The wide range of ages and the lack of a definite peak in the age distribution suggests that the older animals have undergone ovulations which are no longer recorded in the ovaries. Until more specimens have been examined, it is difficult to assign an age at which the majority of females attain sexual maturity, but a figure of seven years may be adopted provisionally.

Birth Rate

In order to arrive at an unbiased estimate of the birth rate, only those adult females can be considered which were not deliberately selected to represent a certain phase of the reproductive cycle. The total number of mature females from Foxe Basin and northern Hudson Bay is 31, and of these 9 are pregnant. This represents a birth rate of 0.29 calves per female per year, but there is little doubt that the value is an underestimate. During most of the year there is marked segregation of the sexes, and occasional groups of old females are found. One such group, containing several old barren females, is included in the Foxe Basin catch, and this has resulted in the low figure for the birth rate.

At Southampton Island the walrus usually haul out at the uglit in the summer and fall, and the sexes appear to mix together quite freely. Seventeen females were collected in the fall hunting, and six were pregnant, giving a birth rate of 0.35. This figure is considered to be more representative, and will be used in preference to the lower value. According to Freiman's (1940) data, the crude birthrate in the Pacific walrus is between 0.37 (Table 3) and 0.43 (Table 2), and Brooks (1954) has found a value of 0.33. Both Chapskii (1936) and Loughrey (1955) give a higher figure of 0.5, but this is evidently based on series of selected animals.

The birth rate indicates that the reproductive cycle is basically biennial, but a varying number of missed pregnancies, particularly in older animals, leads to calf production more nearly once in every three years.

The Ovarian Cycle

Ovaries were prepared for macroscopic examination by cutting them into longitudinal slices 2 - 3 mm. thick with a sharp long-bladed pocket knife. Follicles were classified into size groups by setting a pair of dividers at 3 and 6 mm. and applying them to the longest diameters. Larger follicles were measured in two planes and listed individually (see Appendix III). Selected parts of follicles and corpora lutea were embedded in paraffin wax, sectioned at 8 μ and stained in Delafield's Haematoxylin and Eosin.

Development of the follicles and ovulation. In all the phocids and otariids so far investigated, the developing embryo remains in the blastocyst stage for several months before implanting in the uterine mucosa and undergoing normal development. In the Odobenidae, however, development is direct, and no delay in implantation occurs (Fay, 1955). This has been confirmed in the series of specimens collected from Hudson Bay and Foxe Basin, and the different pattern of development is reflected in the cycle of follicular activity.

Enders, Pearson and Pearson (1946) have found that in the northern fur seal, the corpus luteum of pregnancy suppresses follicular growth in that ovary throughout the development of the embryo until several months after parturition. In the other ovary, there is a progressive development of follicles during pregnancy, until they become numerous at parturition. In the walrus the overall suppression of folliculation during pregnancy is clear, but there is a limited activity, particularly in the ovary containing the corpus luteum. The specimens suggest that follicular development is by no means an even process, and females taken in August may have ovaries with no follicles larger than 3 mm., or as many as 16 in one ovary (A 46). The fact that the females taken earliest (W 7) and latest (A 82) in the season show no development of follicles, suggests that the peak in August is real (A 46) and would continue to be shown by a larger number of specimens. The picture of development in later pregnancy is uncertain for the ovaries of the only female with a full-term foetus are in a low state of follicular activity.

There is no evidence of renewed follicular activity and subsequent ovulation in the period during and after parturition, though Fay (1955) has observed this in 2 (9 percent) out of 23 post-partum females examined. Such follicular development is evidently abnormal, for no newly pregnant females with calves have ever been found. This continued suppression of ovarian activity in the period following birth of the calf is in marked contrast to conditions found in the majority of phocids and otariids, where a new phase of follicular proliferation results in post-partum oestrus and a new pregnancy (Fisher, 1954; Laws, 1956b; McLaren in press; Rand, 1954).

From July to October, after the birth of the calf, the effect of the corpus luteum has declined. There is a renewal of follicular activity, which is mainly confined to the non-pregnancy ovary, but this is once again markedly uneven. Numbers of follicles larger than 3 mm. fluctuate between one and twenty nine, the largest follicle attaining a mean diameter of 10 mm. There is no evidence that development beyond this stage occurs at this time, for corpora lutea spuria have not been recorded from females with calves.

In the following spring a small proportion of females ovulate and are impregnated before the males go out of rut. The remaining females show a varied state of follicular activity throughout the summer and fall months, and in all but four specimens, (A 121, W 14, IW 38, IW 39) ovulation has occurred with the formation of a corpus luteum spurium.

In IW 38 and 39, there are numerous follicles over 3 mm. in diameter, and at least one healthy 8 mm. follicle in each pair of ovaries. Most of the follicles are atretic, but the usual type of cystic atresia has not occurred. Instead the cavity of each follicle has become invaded by a marked proliferation of theca lutein cells. The resulting body bears a close resemblance to the corpus luteum atreticum described by Maximow and Bloom (1948) for the human female. Luteinised follicles are found in the barren adult female A 121, and in an immature female IW 25, both of which seem capable of ovulating soon.

McLaren (1958) has recorded similar large follicles in the ovaries of an immature six-year-old bearded seal, and concludes that they almost certainly reflect the hormonal state of maturity. It seems reasonable to assume that in the walrus such follicles indicate impending ovulations, though it must be pointed out that this is probably an abnormal development.

The mechanism by which folliculation is suppressed in the year following the birth of the calf is unknown. The only other pinniped in which a biennial reproductive cycle occurs is the bearded seal, but in that species ovulation appears to follow the birth of the pup. However, in females, ovulation is delayed until the males are out of rut, and only corpora lutea spuria are formed (McLaren, 1958).

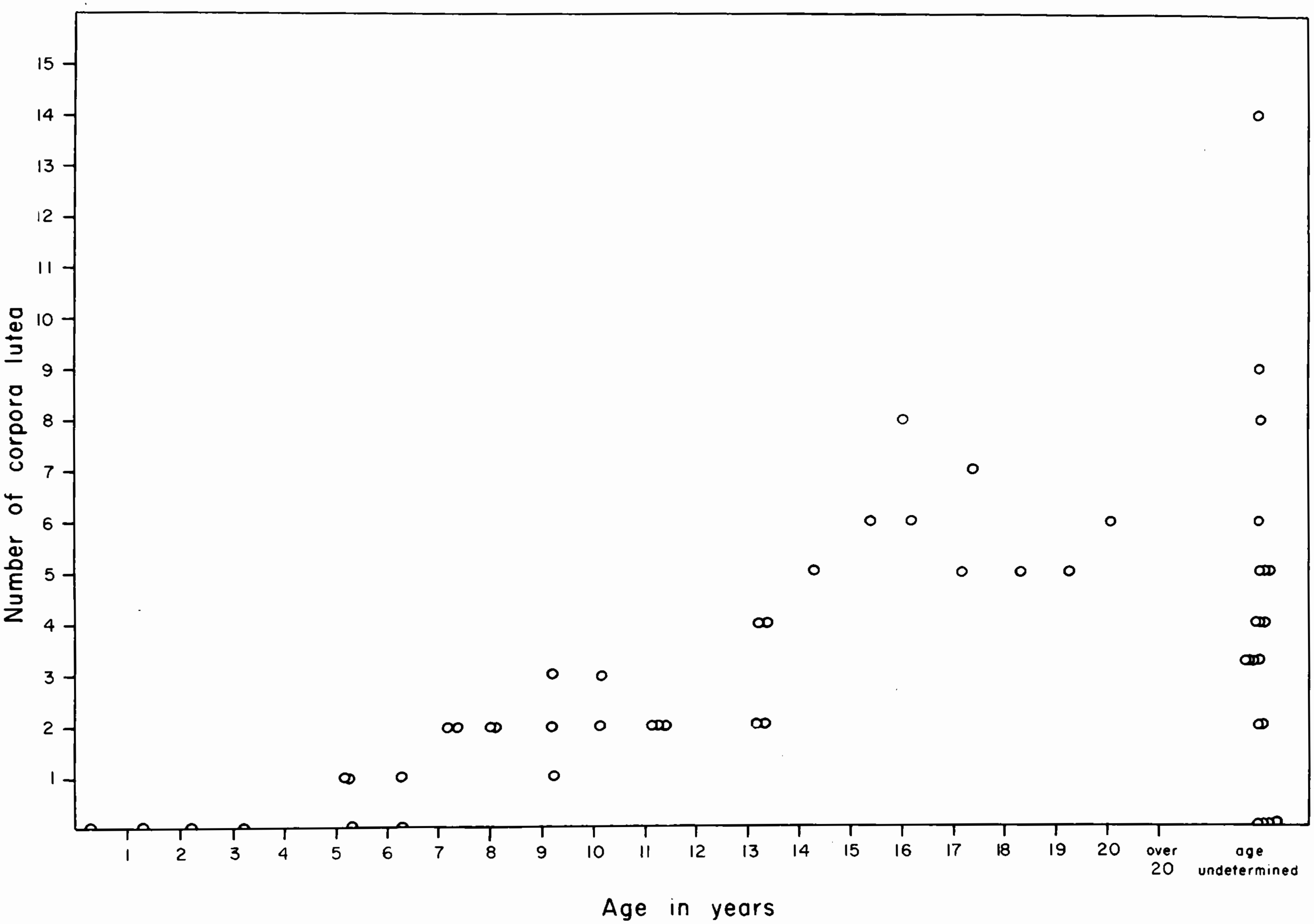
No specimens are available for the winter and spring months, but Fay (in litt.) gives details of a barren female taken on December 4, in which five follicles greater than 5 mm. in average diameter are present in the ovaries. The largest follicle is 11 mm. in diameter, which suggests that ovulation might occur within a few weeks. Since conceptions do not appear to take place in the winter and spring months when the males are known to be sexually active, there must be some effective barrier to copulation. Perhaps segregation of the sexes, which is known to occur at other seasons of the year, may be the limiting factor.

The rapid onset of post-partum oestrus in those phocids and otariids with an annual breeding cycle tends to effect an alternation in function of the ovaries, though this is never complete (see Laws, 1956b; McLaren, in press; Rand 1954). Where the corpus luteum persists as a fibrous corpus albicans throughout succeeding pregnancies, the alternation in function may be easily shown by the balance of corpora lutea in right and left ovaries. Thus in those pairs of ovaries in which the numbers of corpora lutea are the same, or differ by only one, the alternation is perfect. This occurs in 73 percent (30) of the walrus examined, and a further 15 percent (6) show a difference of only two corpora lutea.

<u>The corpus luteum</u>. The final development of the follicle and its transformation into a <u>corpus luteum</u> are not represented in the limited collection of material available. A ripening follicle, 16 mm. in diameter, is present in the right ovary of the barren female IW 45 taken on August 5, and may well represent the initial stage in the development of a <u>corpus luteum spurium</u>. This is the largest healthy follicle recorded, though a cystic follicle 29 mm. in size is present in the right ovary of the barren female A 125 taken on September 27. Since there is no evidence to suggest that cystic follicles reach a greater size than healthy follicles, it is

Figure 28. Relation between Age of the Female and Number of Corpora Lutea in the Ovaries.

Fig. 28.



Number of corpora lutea
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
Age in years
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
over 20
age undetermined

assumed that 29 mm. more nearly represents the average diameter at ovulation. This is supported by the occurrence of 30 mm. follicles in the Pacific walrus (Fay, 1955).

There is probably little difference in the size of the ripe follicle and the corpus luteum which will soon form. This is in marked contrast to conditions in the Phocidae in which the mature follicle attains only 65 percent of the diameter of the fully grown corpus luteum (Fisher, 1954; Laws, 1956b; McLaren, in press). In this family however, the corpus luteum is maintained at a small size until implantation of the embryo when final rapid growth occurs.

After collapse of the follicle, luteinisation is rapid, and maximum development of the corpus luteum is attained at some time before August 3 (W 7). There is some suggestion that a slow growth is maintained throughout the gestation period, since the largest corpus luteum (A 9) is found just prior to parturition, but this may be the result of sampling error. At this time, the gland shows degenerative changes which are similar to those found in most other species of pinnipeds.

There is great variation in the sizes of corpora lutea taken in August which might indicate a wide spread in the dates of conception. However, the structure of the glands is similar and the size difference probably results from individual variation in follicular size at ovulation. At this stage, the luteal cells are oval or polygonal, 20 - 40 μ in diameter, with large eccentric pale-staining nuclei (fig. 29); up to 20 percent contain one or more clear vacuoles which may be large enough to fill most of the cell. According to Laws (1956b), similar vacuoles in the luteal cells of the southern elephant seal contain lipoid material, and Harrison (1948) has emphasised the point that they are not necessarily indicative of degeneration, but probably represent a resting period during the establishment of the placenta.

In late pregnancy, signs of degeneration have already appeared (fig. 30). A few luteal cells have enlarged to 55 µ in diameter, and most show peripheral vacuolation and shrinkage. The amount of fibrous interstitial tissue is increased and the luteal cells become separated into small groups.

No specimens are available for the early post-partum period, but by early July the corpus luteum has regressed by nearly a third of its size (SD 141) and there is a great increase in fibrous tissue. The luteal cells are mostly fragmented, and the spaces which they formerly occupied are being invaded by cords of interstitial cells from the periphery of the gland (fig. 31). Regression is apparently maintained for a number of years following parturition, and the fibrous corpus albicans gradually shrinks to a compact white scar.

The corpora albicantia collect in the ovaries, and as many as fourteen have been found in one old female (fig. 28). Bertram (1940) has suggested that the corpora albicantia in Weddell and crabeater seal ovaries persist for the life of the individual animals, and Harrison, Matthews and Roberts (1952) have agreed with his observations, though they state that there is no definite evidence that the corpora albicantia

Figure 29. Section of the Corpus Luteum of the Pregnant Female A 42 taken on August 7 (x 600).

Figure 30. Section of the Late Pregnancy Corpus Luteum of Female A 9 taken on May 26 (x 600).

Fig. 30.

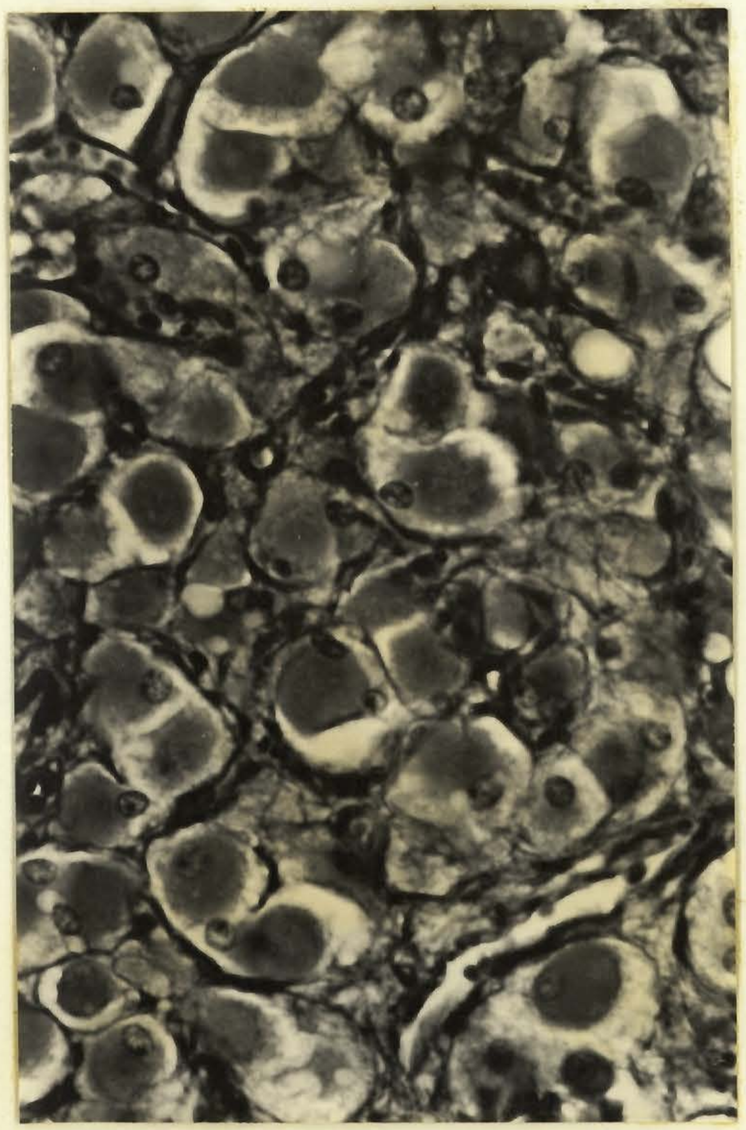
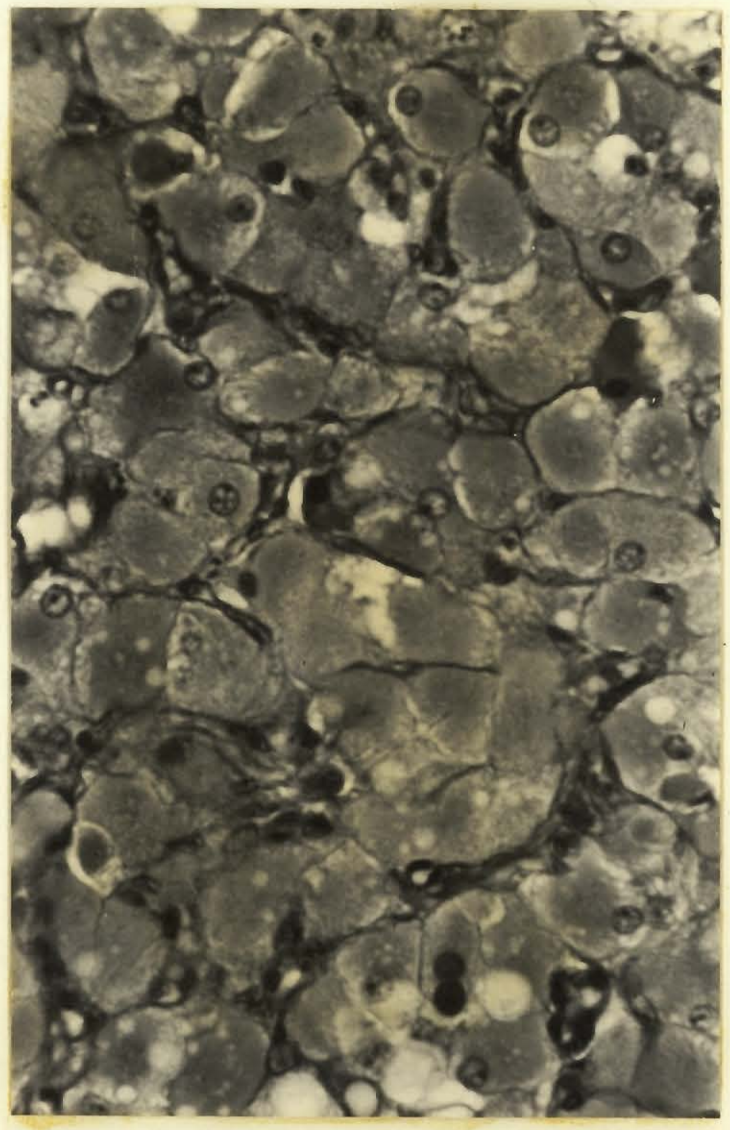


Fig. 29.



do not disappear. More recent work on the Weddell seal (Mansfield, in press) suggests that their retention is variable, and Fisher (1954) has shown that in the harp seal, the corpora albicantia remain visible for only about five years in animals up to twenty years.

In the adult walrus, the corpora albicantia in each ovary can be arranged in a descending order of size, with a minimal value of 2.5 mm.. The smaller corpora albicantia are always accompanied by several larger ones and this indicates that regression is gradual over a period of years. The rate of regression is not constant however, for in <u>corpora lutea spuria</u>, fibrous connective tissue is poorly developed (fig. 32) and the resulting corpora albicantia probably reach the minimal diameter in a relatively short time. Histological examination shows that the process is only quantitatively different from the regression of normal corpora lutea of pregnancy, and the resulting corpus albicans does not differ in any way except in size.

Implantation and Growth of the Embryo

Since no free blastocysts or recently implanted embryos have been recorded in the material from the Eastern Canadian Arctic, data from the Kara and Bering Seas (see Fay, 1955) have been used in compiling the composite growth curve shown in Figure 33. It is clear that foetal lengths recorded from all three areas do not differ significantly, and the same

Figure 31. Section of the Regressing Corpus Luteum of Female A 43 taken on August 17 (x 600).

Figure 32. Section of a Corpus Luteum Spurium from the Barren Female A 77 taken on October 2 (x 600).

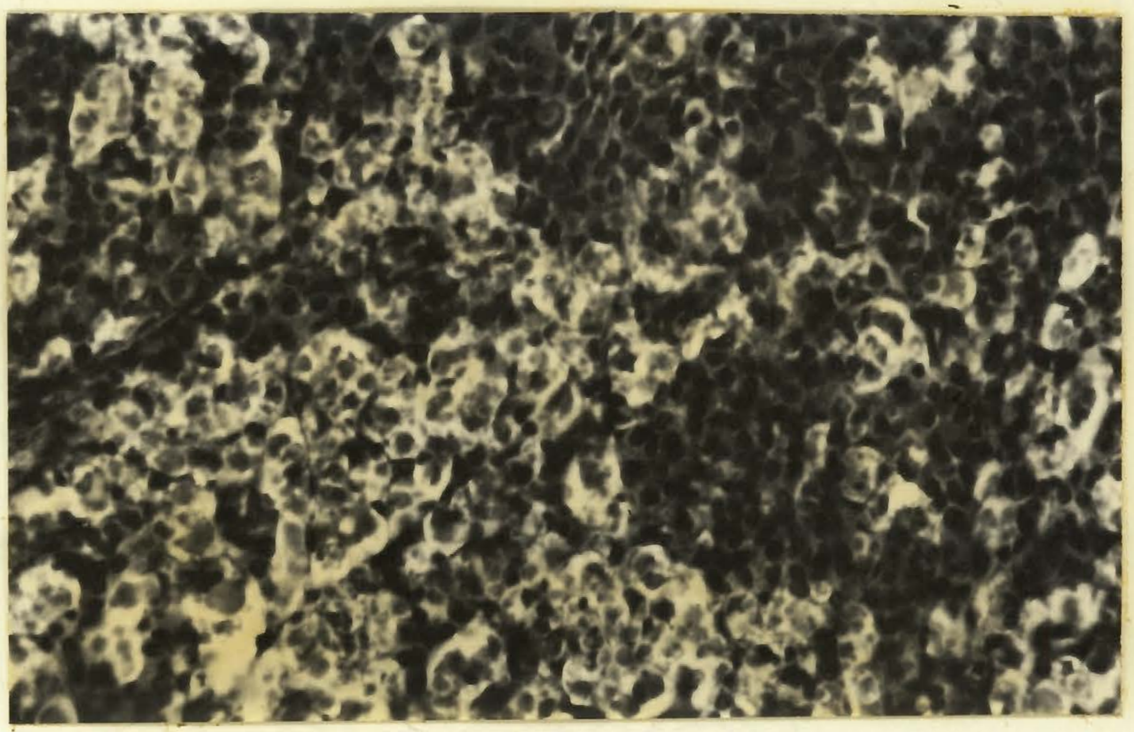


Fig. 31

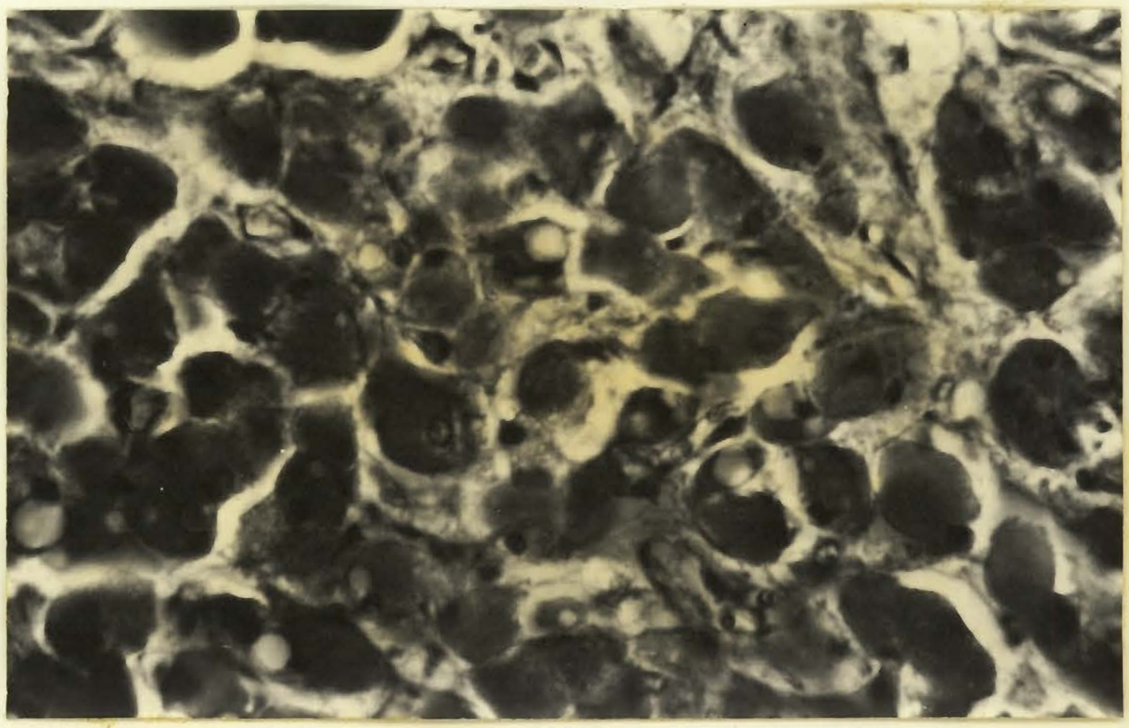
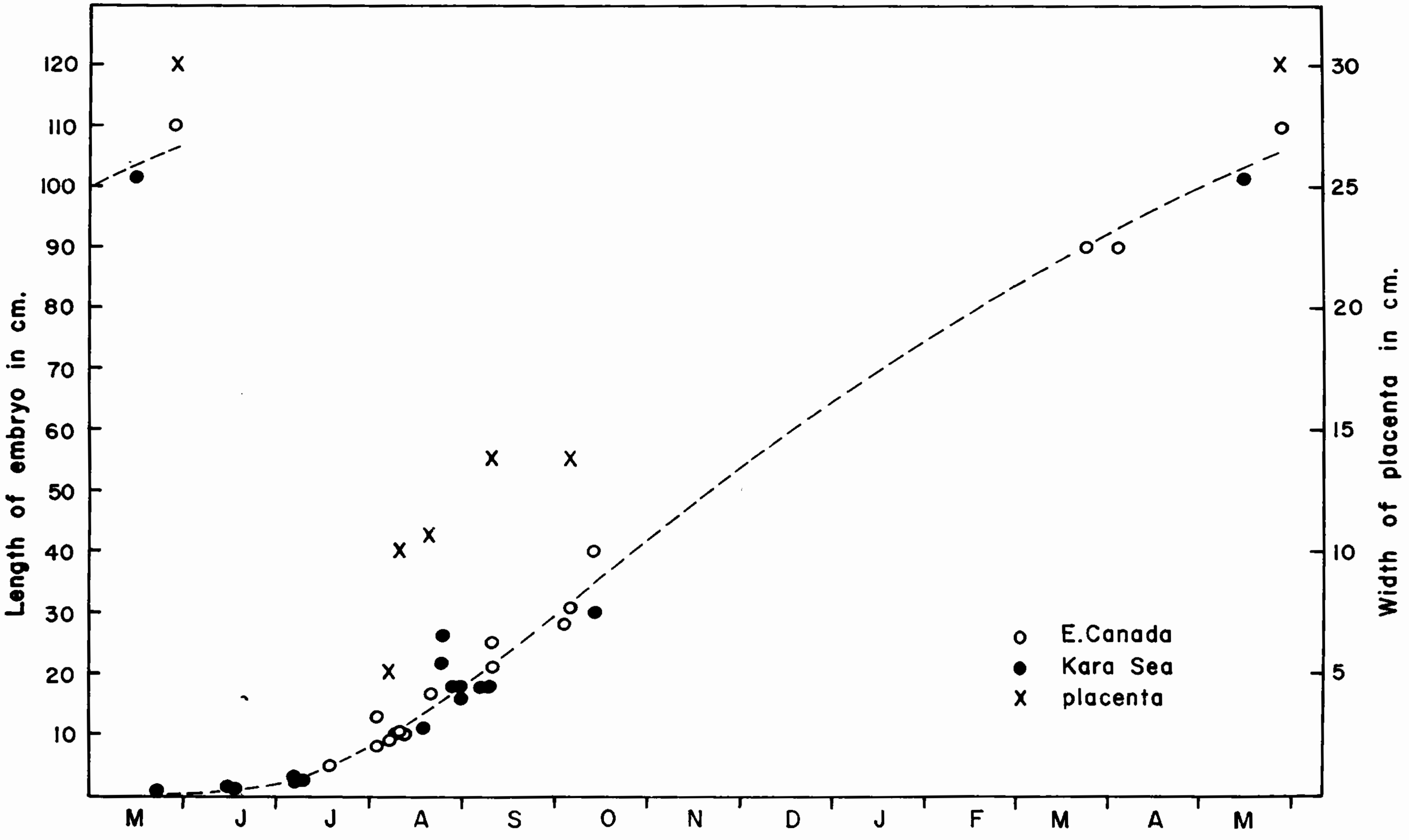


Fig. 32.

Figure 33. Growth of the Embryo and Placenta.

Fig. 33.


Length of embryo in cm.
10
20
30
40
50
60
70
80
90
100
110
120
Width of placenta in cm.
5
10
15
20
25
30
M
J
J
A
S
O
N
D
J
F
M
A
M
○ E.Canada
● Kara Sea
X placenta

curve has been fitted to all the data. Implantation evidently occurs about the middle of May on the average, and this is confirmed by the following calculations.

Development of the embryo is assumed to parallel that in humans, and a direct comparison may be made by drawing a curve of equivalent foetal lengths (see Fay, 1955). This is illustrated in Figure 34, and the numerical data from which it is derived (Arey, 1954) are listed in Appendix IV.

In order to calculate the average gestation period, it is necessary to assume a mean birth date. Since the foetus A 11, taken on May 26, was near full-term, this date may be used as a convenient beginning. This may be somewhat late, however, for Fay has observed that full-term foetuses are rare in the experience of Eskimo hunters in Bering Strait in late May and early June.

The lengths of eleven foetuses and the corresponding gestation periods calculated are set out in Table VII. The average gestation period is 376 days, but this is probably a slight underestimate since measurements were taken from embryos which had shrunk during preservation. A better figure perhaps is 380 days, which gives a mean conception date of May 11. Fay assumed a mean birth date of May 14 and found that the calculated mean gestation period was 366 days. When allowance is made for the difference in average birth dates chosen, the results do not appear to differ significantly.

TABLE VII

Calculated Average Gestation Period derived from lengths of Eleven Foetuses

(a) The length of the full-term foetus A 11 is 110 cm.
(b) This is derived directly from the curve in Figure 21.
(c) The birth date is taken as May 26.

Field Number	Date	Crown-rump length in cm.	Percent full-term crown-rump length (a)	Percent gestation complete (b)	Days to birth (c)	Calculated total gestation
W 6	3 Aug	13.2	12.0	24.5	296	390
W 7	3 Aug	7.8	7.1	21.5	296	374
IW 50	6 Aug	8.7	8.0	22.5	293	376
A 42	7 Aug	10.0	9.1	23.0	292	380
A 110	10 Aug	11.4	10.4	24.0	289	380
W 14	11 Aug	10.6	9.6	23.5	288	374
A 46	20 Aug	17.0	16.4	28.0	279	387
A 119	10 Sep	24.8	22.5	32.5	258	379
A 120	10 Sep	20.8	18.9	30.0	258	369
A 80	4 Oct	28.5	26.0	35.0	234	360
A 82	5 Oct	31.0	28.2	37.0	233	369
				Average gestation period		376 days

Figure 34. Growth of the Human Embryo (after Arey, 1954).

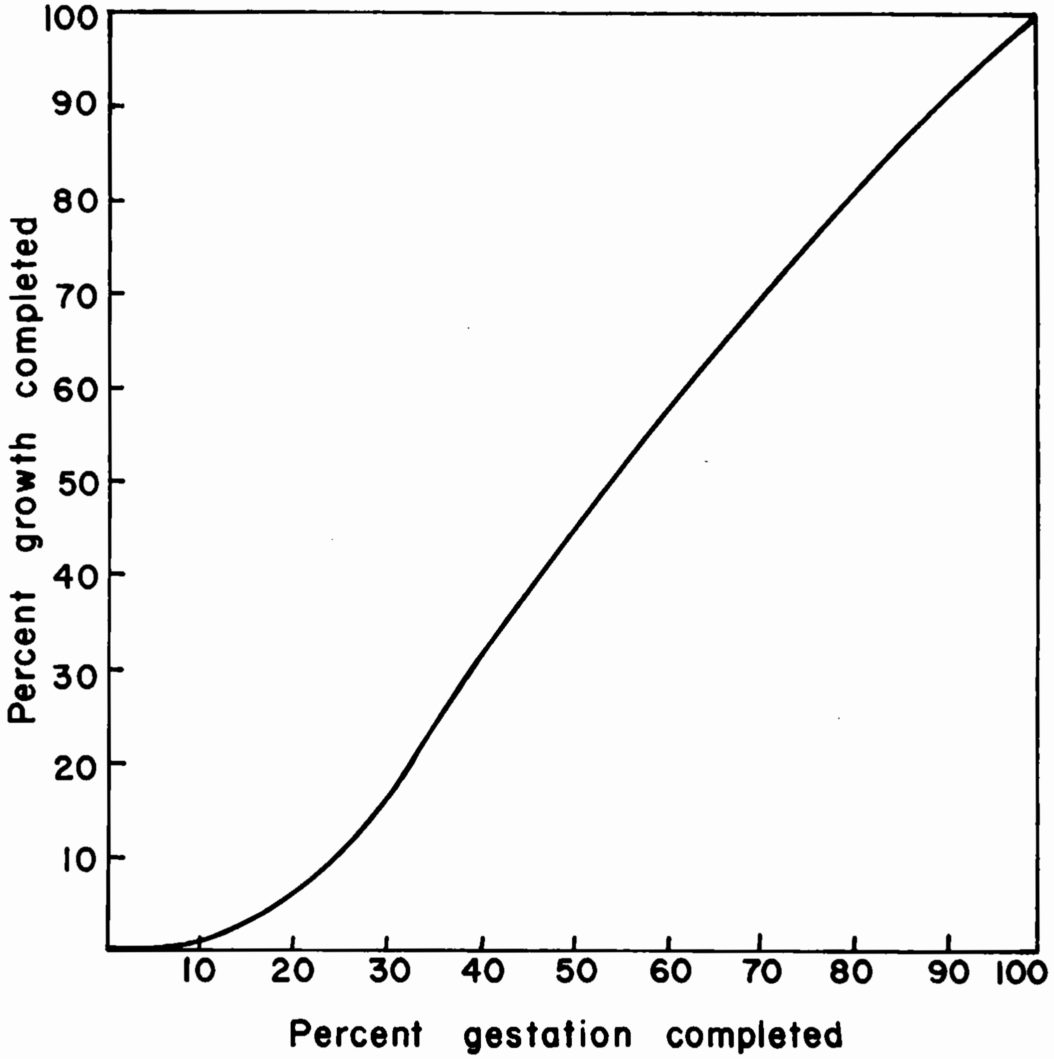

100
90
80
70
60
50
40
30
20
10
Percent growth completed
10
20
30
40
50
60
70
80
90
100
Percent gestation completed

Fig. 34.

Birth and care of the Young

The range of foetal lengths indicates that breeding extends over a period of about two months, which is comparable to conditions in the Phocidae (Laws, 1956a) and the Otariidae (Rand, 1954). Occasional unseasonal births occur in these families and are also characteristic of the Odobenidae. Thus Fay (1955) records a calf of not less than two months taken on May 13, which was regarded as a curiosity by the hunter who captured it. Perhaps the most notable example is that cited by Freuchen (1935) who records a cow walrus with a new-born calf caught in Frozen Strait (see fig. 1) on January 31; an Eskimo also caught a similar calf from which the umbilical cord had not yet been shed. Such untimely births probably result in a great disadvantage for the calf, in spite of the solicitous care of the cow, and it is doubtful if many new-born young can survive at this early season.

The appearance of the calf has been described on page 40, and evidence for the exceptionally long lactation period is given in the section on nutrition. Numerous and well documented accounts of the behaviour of cow and calf are available in the literature (see Allen, 1880; Fay, 1955) and need not be considered here in detail. What should be stressed, however, are the strong ties between mother and young which are of great survival value where the reproductive potential is so low. Great protection is afforded during the critical period before weaning, and the calf or yearling is able to learn both swimming and feeding techniques while remaining in close contact with the cow. The particular pattern of behaviour in which the young animal clings to the mother is very striking, and even a two-year-old animal has been seen to ride the back of an adult male in this way.

Strong social ties link the breeding females with the young and immature animals (Freiman, 1940) and help to provide even greater measures of protection. There seems no reason to doubt that orphaned young are adopted by other females, though this has not been definitely observed in the specimens taken from the Eastern Canadian Arctic.

Only one calf is produced at birth and the process has been accurately described by Ryder (1954) in Fay's account of the Pacific walrus (1955); it does not differ appreciably from parturition observed in other species of pinnipeds (Laws, 1956a; Mansfield, in press). Twins have never been recorded, and according to Fay, "none of the Alaskan natives contacted ... had knowledge of this phenomenon."

Male calves appear to outnumber females at birth, and Brooks (1954) has recorded a sex ratio of 1.2 to 1 in 234 calves examined.

Chronology of Events in the Adult Female

The calculated average gestation period of 380 days shows that development of the embryo begins in mid-May at a time when the males are still in rut. It is highly likely, therefore, that the blastocyst implants in the uterus only a short time after mating. Observations by native hunters in Foxe Basin, and by Brooks (1954) in the Bering Sea, confirm that copulation occurs at this time of year.

Parturition takes place approximately two weeks later in the following spring, and is followed by sexual quiescence in the majority of females. When post-partum oestrus does occur (see p. 74), ovulation is probably delayed until the males are out of rut, for no pregnant females with calves have ever been found. Increased follicular activity in the following spring results in the development of ripe follicles, but only a small proportion of females manage to ovulate before the breeding season is over. The remainder ovulate later in the summer with the development of <u>corpora lutea spuria</u>. There is no indication that females remain barren for a third year following the birth of the calf, and it is assumed that they ovulate sufficiently early in the next season for impregnation to occur.

Fay (1955) has suggested that the initial pregnancies are biennial and that a progressive delay in the time of ovulation results in a series of missed pregnancies in the ten to fifteen-year-old animals. A similar pattern of reproduction may occur in the Atlantic walrus, though the evidence suggests that barrenness is mainly confined to the older animals.

The small number of unseasonal births suggests that ovulations are rare in the winter and early spring. It may be argued that winter births are more common than is supposed and are offset by a high calf mortality, but examination of the ovaries fails to reveal any indication of this.

Senility has been observed in some old seals (Laws, 1956b; McLaren, in press), but the oldest walrus specimens available show that normal ovarian function may continue to a late age.

The social ties between adult females and the young and immature animals are evidently strong enough to cause a general segregation of the sexes throughout the year (Fay, 1955). The gravid female may seek an isolated floe away from the main herd when calving is imminent (A 9 on May 26), but observation suggests that she soon returns to the other animals once her calf is born. Though old males occur in these groups of adult females and young, their presence does not imply a polygynous social structure; rather, the very nature of the habitat suggests that breeding is promiscuous.

DISTRIBUTION AND ABUNDANCE

The morphological evidence for the formation of discrete populations has been discussed in the section on growth, and the data are summarised in Table II. Though the marked differences in tusk length and resulting facial proportions between the Atlantic and Pacific forms may be regarded as characters of subspecific rank, the status of the Kara Sea walrus is uncertain. It has long been supposed that the walrus inhabiting the shores of northeastern North America, Greenland, Spitzbergen, Franz Josef Land and northwestern Asia represent a uniform stock, distinct from the Pacific walrus, but the summary of morphological characters indicates that this is not so; rather, it would appear that the Euro-Asiatic walrus is more akin to the Pacific walrus, and the Eastern Canadian Arctic population is distinct from either of these stocks. Whatever the relationships, it is clear that the Pacific and eastern North American forms have been separated for a long period of time.

Recently, Davies (1958) has reviewed the distribution of the northern pinnipeds and suggests that the separation of O. r. divergens and O. r. rosmarus dates from the penultimate or an earlier glacial maximum in the Pleistocene. This implies that effective mingling of the stocks did not occur during the ice-free period preceding the last glaciation, a fact which Davies finds hard to explain in view of the imminence of contact along the Siberian shelf at the present day. However, Davies assumes that the Euro-Asiatic walrus is closely related to the eastern North American stock and remains distinct from the Pacific walrus. If we accept the morphological evidence and adopt the alternative view that the walrus of the Kara Sea is little different from the Pacific walrus, then the pattern of speciation is more easily understood. Indeed, the geographical evidence alone suggests that this is the more probable development.

Within the proposed subspecies O. r. rosmarus which occupies the Eastern Canadian Arctic, some slight differentiation in body form has taken place. This suggests that isolated breeding populations occur, a view that is supported by Loughrey's detailed discussion of the geographical distribution in this region (1955). The formation of such discrete groups can only be fully appreciated when the ecological factors effecting distribution are fully understood. Vibe (1950) has given the most detailed account of these so far, and the following observations are included to supplement his work.

Relation to the Land

The numerous accounts of walrus hunting in the past four centuries abound with descriptions of the terrestrial habits of the animal, for it was at the hauling-out sites on the land that the principal killings were effected. The evidence suggests that the walrus was essentially a sedentary animal where abundant feeding areas occurred, and made use of ice when it appeared, rather than seeking it out in definite migratory movements. In places such as Sable Island and the Magdalen Islands, where the spring months were often ice-free, the breeding cows took to the land to bear their young (Allen, 1880). In the early summer, the hauling-out sites remained populated, evidently by members of both sexes.

In the higher latitudes of Bear Island and Spitzbergen, walrus were found ashore in large numbers in July and August when there was little pack ice about, and they presumably frequented the land until the onset of winter conditions. Thus the land haul-out seemed to result directly from lack of ice, and could occur from as early as April until late October. Observations on the walrus in northern Hudson Bay confirm this pattern of behaviour, for animals are not found on the land until late July, when most of the ice has left the area between Southampton and Coats Islands.

Evidence from the behaviour of the Pacific walrus suggests that this species is more actively migratory (Brooks, 1954), though Nikulin (1947) shows conclusively that sedentary populations do occur where food organisms are plentiful. Walrus remain in these areas of abundant food at least throughout the whole summer, and haul out on shore at established sites. ["With the appearance of drifting ice, they forsake the shore and use the ice for resting as long as it is present in the shallow water zone"] Nikulin stresses the fact that walrus are not adapted to pelagic life like some other pinnipeds and therefore /"cannot maintain themselves in the open water for long periods of time without resting on the ice or on shore"_7.

The walrus is markedly gregarious when hauled out on the land, and large 'pods' of closely packed animals are formed. At Walrus Island in Fisher Strait, an estimated maximum of 1,000 animals has been observed in the fall (W. F. Carrick, personal communication), and further observations quoted by Allen (1880) show that as many as 7 - 8,000 were seen at the 'echouries' on the Magdalen Islands in the late eighteenth century. Nikulin (1947) records that in 1937 - 38, mass settlements of 2 - 3,000 animals were observed at four places on Wrangell Island, and in 1941, 8,000 were seen at the hauling-out ground at Inchovyn on the Chukotsk Peninsula. Similar settlements, but numbering only 500 animals, have been observed by Chapskii (1936) on Novaya Zemlya.

The physical nature of the hauling-out sites at the present time is partly dependent on the presence of man. In former times gently shelving sand bars and wide sand or shingle beaches were commonly used, and localised population pressure often forced the animals to move inland. These sites were probably the most favoured, for the walrus has poor ability to move on land. These past records also show that bays with high bordering headlands were most frequently used, and Fay (1955) has suggested that high promontories associated with hauling-out sites in the Bering Sea may serve as landmarks for coastal navigation. In that region, animals will haul out on anything from boulders to turf, and Nikulin (1941) records that some of the sites may change from year to year.

In northern Hudson Bay, the walrus is never known to haul out on the limestone beaches, and the _uglit_ are restricted to the rocks of the Precambrian shield. Each _uglek_ is situated on a promontory or small islet, and the dip of the rocks allows deep water to be reached a little way from shore. When disturbed, the animals are able to enter the water very quickly and reach a safe depth in their initial plunge from the rocks. The same _uglit_ are used year after year, which indicates that the walrus are able to identify them easily from the water.

Weather conditions play a large part in determining hauling-out behaviour and it has been found that the _uglit_ on Bencas and Coats Islands are only frequented when the wind is offshore and not too strong. In high winds from any quarter, or when the sea is breaking on the rocks and covering them with spray, walrus desert the land and seek more sheltered bays. This movement to calmer waters invariably leads them to one of the other _uglit_.

Nikulin (1947) has found a similar correlation between rough seas and onshore winds and the hauling-out habits of the Pacific walrus.

Relation to Sea Ice

When drifting ice appears in shallow waters during the summer and fall, the walrus deserts the land and hauls out on the floes (Nikulin, 1947; Loughrey, 1955). At Southampton Island this occurs particularly along the coasts of Bell Peninsula, and the uglit in this area are not so frequently occupied as those on Bencas, Coats and Walrus Islands.

In the fall young ice forms in the bays and along the coasts, and the walrus maintains breathing holes by breaking through this thin layer with its head. This habit has been described by Johansen (1910) and probably accounts for the pronounced patch of scar tissue which some adults bear on the crown. As the new ice thickens, the breathing holes become more difficult to maintain, until finally the walrus is forced to retreat to open water at the edge of the fast ice. Vibe (1950) has shown that when the ice edge extends beyond the outer limits of the mollusc banks in certain areas of northwest Greenland, the walrus population disperses to more accessible feeding grounds. There seems little doubt that similar local movements occur during the winter and spring throughout most of the Eastern Canadian Arctic.

Loughrey (1955) quotes observations from numerous sources which tend to support the hypothesis that the majority of walrus populations are local and sedentary. In view of the ecological relationships discussed by Vibe, this seems a more reasonable assumption than the postulation of extensive migrations.

The interaction of seasonal ice movements with the location of suitable foraging grounds does not completely explain the patchy distribution of the walrus at the present time, and other factors such as lack of population pressure and the effects of human predation must be involved. However, these can only be effectively assessed when more data become available.

Local Movements and Migrations

In Foxe Basin, optimal conditions appear to be met with, for feeding shallows are extensive and ice is abundant all the year round. Walrus do not appear to frequent the southern part of the basin where depths are greater than fifty fathoms (see fig. 2), which indicates that this population is effectively isolated from the Southampton Island group. The extensive migrations postulated by Freuchen (1935) appear to have little basis in fact, for the walrus is obviously perfectly adapted to existence amongst the winter ice in this region.

In western Hudson Bay, (see fig. 35), there is a small population along the coast from Eskimo Point to Wager Bay, and recent R. C. M. P. game reports (1956, 1957) suggest that the numbers are increasing. Former <u>uglit</u> are now being reoccupied (see Loughrey, 1955), and observations indicate that the herds remain in the area throughout the winter.

Few walrus have been seen in recent years south along

Figure 35. Map of the Eastern Canadian Arctic.


GREENLAND
Alexandra Fiord
Buchanan Bay
Smith Sound
Thule
Saunders I.
Melville Bay
Jones Sound
Wellington Ch.
DEVON ISLAND
BANKS ISLAND
Barrow Strait
Lancaster Sound
Prince Regent Inlet
Pond Inlet
BAFFIN BAY
VICTORIA ISLAND
Dolphin & Union Strait
Coronation Gulf
Queen Maud Gulf
Spence Bay
GULF OF BOOTHIA
Pelly Bay
Committee Bay
BAFFIN ISLAND
DAVIS STRAIT
Holsteinsborg
Home Bay
Kivitoo
Padloping I.
Hoare Bay
Leybourn Is.
Loks Land
FOXE BASIN
Repulse Bay
SOUTHAMPTON ISLAND
Mill I.
Salisbury I.
Nottingham I.
C. Weggs
Button Is.
Port Burwell
Akpatok I.
Payne Bay
UNGAVA BAY
Chesterfield Inlet
Coats Island
Mansel I.
Mistake Bay
HUDSON BAY
Port Harrison
Sleeper Is.
Belcher Is.
100 50 0 100 200
scale: Statute Miles

Fig. 33.

the coast as far as Cape Henrietta Maria, though at that point, over one thousand animals were seen hauled out in the summer of 1955 (see Loughrey, 1955). The bathymetry in this area suggests that this herd may be associated with others found about the Belcher and Sleeper Islands to the northeast. Little is known of this group, but a scarcity of animals along the northeast coast of Hudson Bay points to its being a resident population.

At the western end of Hudson Strait, in the late summer and fall, walrus evidently remain on the ice coming down from Foxe Channel and feed in the shallows about Nottingham and Salisbury Islands. It is only when most of the ice has gone, usually late in the fall, that they haul out on the rocks at these islands. The small winter catches at Cape Dorset and Amadjuak indicate that some part of the population remains in the area throughout the year.

There appears to be a small gap in distribution along the north side of Hudson Strait until the Middle Savage Islands (62° 08'N, 67° 55'W) are reached. A recent report by F. G. Cooch (in litt.) indicates that several hundred walrus are found about these islands from October until May. After this time their distribution is unknown, though the Eskimos state that they move westwards towards Hudson Bay.

From Hudson Strait northwards to Home Bay, but excluding most of Cumberland Sound, the coastal waters probably form natural reserves at the present time, for limited hunting occurs. In the early part of the century, the biggest hauling-out ground was at Padlei, just south of Padloping Island on the eastern Baffin Island coast, and Bethune (1934) records that one company took over four thousand skins per year. According to recent Eskimo opinion (H. N. Andersen, in litt.), there is a large resident breeding population in this area, and several uglit are known which are used year after year. Reports from the R. C. M. P. establishment at Cape Christian (1955, 1957) indicate that walrus are scarce from the north of Home Bay to Pond Inlet, which suggests that the extensive migration down the Baffin Island coast postulated by Freuchen (1935) does not occur at the present time. A similar limited distribution of walrus is found along the Greenland coast, the animals occurring only between Sukkertoppen and Egedesminde (Allen, 1942). This partial isolation of the Davis Strait herds from those further north in Baffin Bay may result from lack of population pressure, for there is no indication that the intervening coastal areas are unsuitable feeding grounds.

The herds frequenting Kane Basin in the summer and fall almost certainly migrate south through Smith Sound and winter along the coasts of northwest Greenland (Vibe, 1950), and Ellesmere and Devon Islands (R. C. M. P., 1954). This movement is emphasised by the narrowness of Smith Sound, and parallels on a small scale the channeled migratory stream of the Pacific walrus through Bering Strait.

The most difficult group to assess is that found about Akpatok Island in the summer. According to Eskimo opinion these animals spend the winter off the Labrador coast at Hebron (A. W. F. Banfield, in litt.) or in Davis Strait (L. M. Tuck, in litt.), and then migrate into Hudson Strait, reaching Akpatok Island by mid-July. In commenting on the supposed migration, Tuck states that "walrus have not been recorded within the vicinity after the first week or so of August, but this must be treated with caution as I was unable to learn of a single visit to the island by native hunters during late August on."

Tuck's comment is particularly apt since it illustrates the dangers of accepting opinion, even of apparently knowledgeable hunters, without due consideration of all the economic and ecological factors involved.

SUMMARY

The material examined consists of samples taken from 48 males and 50 females in northern Hudson Bay and 56 males and 22 females in northern Foxe Basin.

Body and tusk length measurements were analysed to see if their frequency distributions showed any modal regularity equivalent to presumed year groups. Only the yearling and two-year-old animals could be distinguished by this method, and further age classes were masked by individual variation with age. The teeth were next examined with the object of establishing the periodicity of the incremental layers in the dentine and cementum. No positive proof of their annual nature has been found, but it is highly probable that the layers are formed at the same season each year. A similar method has been used for the Pacific walrus by Fay (1955), but only the adult males can be aged in this way. The number of cementum rings in the immature males appears to be variable, which is surprising in view of the regularity of their formation in the Atlantic walrus. If cementogenesis is equivalent in both the Atlantic and Pacific forms, then the ages assigned to immature Pacific walrus on the basis of frequency modes in the measurement of tusk length are incorrect. In spite of these differences in age determination, it is apparent that the Pacific walrus is slightly larger in body size and much longer in tusk length at sexual maturity than the Atlantic walrus. Comparison of these two forms with the walrus of the Kara Sea shows that the latter group is more akin to the Pacific walrus.

Examination of 69 skulls and 74 lower jaws shows that the normal adult dentition is I 1/0 C 1/1 Pm 3/3. In addition, the second upper incisor, the fourth upper premolar and the first lower molar occur in up to 26 percent of the specimens.

Stomach contents were analysed and 22 food organisms recorded. The feet and siphons of several species of pelecypods form the dominant food, but other benthonic invertebrates are eaten when these are scarce. Blubber and skin of the ringed seal were taken from the stomach of one adult male. Feeding appears to be an irregular process at all times of the year, and there is no direct evidence of any prolonged periods of fasting correlated with the breeding season or the moult. The latter event occurs annually and is a more variable and prolonged process than the moult of phocids.

The males become sexually mature when six years old and the testes show the typical facies of post-oestrus adults in the following summer and fall. There is no accelerated growth of the testes and baculum which characterises the onset of sexual maturity in phocids. Only two adult males with sperm in the testis and epididymis have been found and these indicate that the males are in rut from late November until at least the end of March. More extensive data on the reproductive cycle of the Pacific walrus shows that the testes produce sperm from November until late May, and evidence from the female breeding cycle indicates that copulation occurs principally in April, May and June.

The female is considered to be sexually mature when the first ovulation occurs. Breeding maturity is not generally coincident with sexual maturity, since only 30 percent of the nulliparous females become impregnated at this time. The age at first ovulation varies from 5 to perhaps 10 years, and it is assumed that the majority of females ovulate for the first time when they are seven years old. The reproductive cycle is basically biennial, though missed pregnancies, particularly in the older animals, lead to calf production more nearly once in every three years. The average calf production is 0.35 per annum, which is not significantly different from the estimated birth rate of the Pacific walrus.

In the year following the birth of the calf, folliculation is suppressed in the ovaries, and the female remains barren. In the following spring, only a few females become impregnated, the remainder ovulating later in the season. Corpora lutea vera and spuria are similar to those in other pinnipeds, and they regress to form easily recognisable dense white scars, the corpora albicantia. Their rate of regression is variable, and some may eventually disappear; however, their number does give some indication of the past reproductive life of the individual female.

The curve of foetal growth has been compared with that of the human embryo and used to calculate the average gestation period and average date of conception. No delay in implantation occurs, the embryo forming soon after impregnation on May 11 (average date) and being born at the end of May. The calf remains protected by the female for two years and does not appear to attain nutritional independence until the end of that period.

Morphological evidence shows that within the subspecies O. r. rosmarus occupying the Eastern Canadian Arctic, some slight differentiation of body form has taken place. This suggests that isolated breeding populations occur, and emphasises the sedentary nature of the walrus. During the summer, when ice leaves the normal feeding areas, walrus haul out on suitable rock outcrops. Promontories and small islets with clear descents to deep water are favoured, and the animals are quick to take to the water when disturbed. These uglit are used year after year, except when ice remains in their vicinity during the summer. Local weather conditions determine which uglek is used, the exposed rocks being abandoned during onshore winds and heavy seas. Ice is always preferred as a resting place, and local movements fluctuate as the pack moves with wind and current. The extensive migrations once postulated have not been reliably observed, and they fail to take into account the walrus' adaptation to its environment and its ability to winter in areas where pack ice is extensive.

BIBLIOGRAPHY

Allen, G.M. 1942. Extinct and vanishing mammals of the western hemisphere with the marine species of all the oceans. Amer. Comm. for International Wild Life Protection, Spec. Pub. 11. Lancaster, Pa.

Allen, J.A. 1880. History of North American pinnipeds. A monograph of the walruses, sea-lions, sea-bears and seals of North America. U.S. Geol. Geog. Surv. Terr. Misc. Pub. 12. Washington.

Anderson, R.M. 1946. Catalogue of Canadian recent mammals. Nat. Mus. Can. Bull., 102: 1 - 238.

Arey, L.B. 1954. Developmental Anatomy. W.B. Saunders Co., Philadelphia. 680 pp.

Bartholomew, G.A. 1952. Reproductive and social behaviour of the northern elephant seal. Univ. Calif. Pub. Zool., 47: 369 - 472.

Belopolskii, L.O. 1939. O migratsiiakh i ekologii razmnozheniia tikhookeanskogo morzha [On the migration and ecology of the Pacific walrus]. Zool. Zhurnal, 18 (5): 762 - 778.

Bertram, G.C.L. 1940. The biology of the Weddell and crab-eater seals: with a study of the comparative behaviour of the Pinnipedia. Brit. Mus. (Nat. Hist.) Sci. Rep. Brit. Graham Land Exped. 1934 - 7, 1 (1): 1 - 139.

Bethune, W.C. 1934. Canada's Eastern Arctic. Its history, resources, population and administration. Dept. of Interior, Lands, N.W.T. & Yukon Branch, Ottawa.

Brooks, J.W. 1953. A study of the Pacific walrus in the Bering Straits and the Arctic Ocean adjacent to north-western Alaska. Alaska Cooperative Wildlife Research Unit, 4 (3).

Brooks, J.W. 1954. A contribution to the life history and ecology of the Pacific walrus. Alaska Cooperative Wildlife Research Unit, Spec. Rep. 1.

Chapskii, K.K. 1936. Morzh karskogo moria; resultati issledovaniia biologii, geograficheskogo rasprostraneniia i zapazov morzha karskogo moria i Novoi Zemli. [The walrus of the Kara Sea; results of the investigation of the life history, the geographical distribution and stock of walruses in the Kara Sea and Novaya Zemlya]. Trudy, Vsesoiuznyi arkticheskii institut, Leningrad, 67, 1 - 124.

-----. 1940. Rasprostranenie morzha v moriakh Laptevykh i Vostochnosibirskom [Distribution of the walrus in the Laptev and East Siberian Seas]. Problemy Arktiki, 6: 80 - 94.

Cobb, W.M. 1933. The dentition of the walrus, Odobenus obesus. Proc. Zool. Soc. Lond., 1933 (3): 645 - 668.

Crockford, J.A., F.A. Hayes, J.H. Jenkins & S.D. Feurt. 1957. Nicotine salicylate for capturing deer. J. Wildlife Management, 21 (2): 213 - 220.

Davies, J.L. 1958. Pleistocene geography and the distribution of northern pinnipeds. Ecology, 39 (1): 97 - 113.

Dunbar, M.J. 1956. The Calanus expeditions in the Canadian arctic, 1947 to 1955. Arctic, 9 (3): 178 - 190.

Enders, R.K., O.P. Pearson & H.K. Pearson. 1946. On certain aspects of reproduction in the fur seal. Anat. Rec., 94: 213 - 218.

Fay, F.H. 1953. The Pacific walrus. A progress report of laboratory work on the specimens collected in the 1952 field season. Arctic Inst. N. Amer., Project No. ONR - 77. MS.

-----. 1955. The Pacific walrus.(Odobenus rosmarus divergens): Spatial ecology, life history and population. Univ. of Brit. Columbia Thesis, MS.

Fisher, H.D. 1954. Studies on reproduction in the harp seal Phoca groenlandica Erxleben in the northwest Atlantic. Fish. Res. Board Can. MS Rep. 588, 109 pp.

Fisher, H.D. & B.A. Mackenzie. 1954. Rapid preparation of tooth sections for age determinations. J. Wildlife Management, 18 (4): 535 - 537.

Freiman, S.I. 1940. Materiali po biologii chukotskogo morzha /Contributions to the biology of the Chukotsk walrus 7. Tikhookeanskii n-i. Inst. Rybnogo Khoziaistva i Okeanografii, Izvestiia, 20: 3 - 20.

Freuchen, P. 1935. Mammals, Part II. Field notes and biological observations. Rep. Fifth Thule Exped., 1921 - 24, 2 (4-5): 235 - 251.

Hamilton, J.E. 1939. A second report on the southern sea lion, Otaria byronia (De Blainville). Discovery Reps., 19: 126 - 164.

Harrison, R.J. 1948. The development and fate of the corpus luteum in the vertebrate series. Biol. Rev., 23 (3): 296 - 332.

Harrison, R.J., L.H. Matthews & J.M. Roberts. 1952. Reproduction in some pinnipedia. Trans. Zool. Soc. Lond., 27 (5): 437 - 531.

Johansen, F. 1910. Observations on seals (Pinnipedia) and whales (Cetacea) made on the Danmark expedition 1906 - 08. Medd. om Grønl., 45: 203 - 224.

Laws, R.M. 1953 a. A new method of age determination in mammals with special reference to the elephant seal (Mirounga leonina, Linn.). Falkland Islands Dependencies Survey Sci. Rep., 2: 11 pp.

-----. 1953 b. The elephant seal (Mirounga leonina Linn.). I. Growth and age. Falkland Islands Dependencies Survey Sci. Rep., 8: 62 pp.

-----. 1956 a. The elephant seal (Mirounga leonina Linn.). II. General, social and reproductive behaviour. Falkland Islands Dependencies Survey Sci. Rep., 13: 88 pp.

Laws, R.M. 1956 b. The elephant seal (*Mirounga leonina* Linn.). III. The physiology of reproduction. *Falkland Islands Dependencies Survey Sci. Rep.*, 15: 66 pp.

Loughrey, A.G. 1955. Preliminary investigation of the Atlantic walrus, *Odobenus rosmarus rosmarus* (Linnaeus). *Dept. N. Affairs and National Resources, Can. Wildlife Service, Ottawa*, MS. 175 pp.

Manning, T.H. 1942. Remarks on the physiography, Eskimo and mammals of Southampton Island. *Can. Geog. J.*, 24 (1): 16 - 33.

Mansfield, A.W. 1955. Eastern Arctic fisheries investigations, 1947 - 55. *Arctic*, 8 (2): 133 - 135.

-----. in press. The breeding behaviour and reproductive cycle of the Weddell seal (*Leptonychotes weddelli* Lesson). *Falkland Islands Dependencies Survey Sci. Rep.*, 18: 41 pp.

Maximow, A.A. & W. Bloom. 1948. *A text book of histology*. W.B. Saunders, Philadelphia. 5th. Ed., 700 pp.

McLaren, I.A. 1958. Some aspects of growth and reproduction in the bearded seal (*Erignathus barbatus* Erxleben). *J. Fish. Res. Board. Can.*, 15 (2).

-----. in press. The biology of the ringed seal (*Phoca hispida* Schreber) in the eastern Canadian arctic. *Fish. Res. Board Can., Bulletin*.

Mikulich, L.V. 1949. Viedanie terpugom krupnich molliuskov / On the eating of large molluscs (*Serripes groenlandicum*) by terpug (*Pleurogrammus azonus*) /. *Tikhookeanskii n-i. Inst. Rybnogo Khoziaistva i Okeanografii, Izvestiia*, 31: 199 - 200.

Mohr, E. 1940. Walrosse als irrgäste in den Europäischen gewässern. *Zool. Anz., Leipzig*, 130: 253 - 255.

-----. 1952. *Die robben der Europäischen gewässern*. *Monographien der wildsaugethiere, XII*. Dr. Paul Schöps, Berlin, 284 pp.

Nikulin, P.G. 1940. Chukotskii morzh [the Chukotsk walrus]. *Tikhookeanskii n-i. Inst. Rybnogo Khoziaistva i Okeanografii, Izvestiia*, 20: 21 - 59.

-----. 1947. [Biological characteristics of the shore aggregations of the walrus in the Chukotsk peninsula]. *Tikhookeanskii n-i. Inst. Rybnogo Khoziaistva i Okeanografii, Izvestiia*, 25: 226 - 228.

Plekhanov, P. 1933. Opredelenie vozrasta tiulenia [Determination of the age of seals]. *Sovetskii Sever*, 4 (1): 111 - 114.

Rand, R.W. 1954. Reproduction in the female Cape fur seal, *Arctocephalus pusillus* Schreber. *Proc. Zool. Soc. Lond*., 124 (4): 717 - 740.

R.C.M.P. (see end of bibliography).

Rodahl, K. 1949. The toxic effect of polar bear liver. *Norsk Polarinst. Skr*., 92: 90 pp.

Ryder, R.A. 1954. *Walrus observations, Bering Sea expedition, spring 1954* (cited in Fay, 1955). Rep. submitted by E.A. Trickey, C.O., U.S.S. Burton Island, MS.

Scheffer, V.B. 1950 a. Growth layers in the teeth of *Pinnipedia* as an indicator of age. *Science*, 112, No. 2907: 309 - 311.

-----. 1950 b. Growth of the testes and the baculum in the fur seal, *Callorhinus ursinus*. *J. Mammal*., 31 (4): 384 - 394.

Schour, I. & M. Massler. 1945. The effects of dietary deficencies upon the oral structures. *Physiol. Rev*., 25.

Soper, J.D. 1944. The mammals of southern Baffin Island, Northwest Territories, Canada. *J. Mammal*., 25 (3): 221 - 254.

Vibe, C. 1950. The marine mammals and the marine fauna in the Thule district (northwest Greenland) with observations on ice conditions in 1939 - 41. <u>Medd. om Grønl.</u>, 150 (6): 1 - 116.

The following annual reports are a selection of those submitted by 'G' Division detachments to the Ottawa Headquarters of the Royal Canadian Mounted Police on June 30 of each year.

R.C.M.P. 1954. Game conditions - Craig Harbour.
1955. " " Cape Christian.
1956. " " Chesterfield.
1957. " " Cape Christian.
1957. " " Chesterfield.

APPENDIX I

Body and Tusk Length Measurements of 83 Male and 39 Female Walrus of Known Age.

Males are designated as either immature - 'I' or Mature - 'M'. The classes of females are as follows: 'I' - immature; 'M' - mature, nulliparous; 'P' - pregnant; 'B' - barren; 'c' - with calf; 'y' - with yearling.
Body length is the direct nose-tail measurement (IW series were measured along the ventral curve of the body and have been corrected by deducting ten percent).
Tusk length is measured in a straight line from tip to alveolar crest; the circumference is taken at the gum line.

A: Males

Field No.	Date.	Age.	Class.	Body Length, Inches.	Tusk Length,	Tusk Circ,
					Inches.	
A 10	26 May	2.0	I	88	2.1	0.8
A 11	26 May	0.0	Foetus	47	0.0	0.0
A 37	1 Aug	3.2	I	90	3.1	0.9
A 39	2 Aug	0.2	I	56	0.1	-
A 40	6 Aug	10.2	M	113	9.3	2.0
A 41	7 Aug	1.2	I	73	2.0	0.6
A 44	17 Aug	8.2	M	100	7.8	1.5
A 45	20 Aug	21.2	M	120	14.8	2.5
A 49	22 Aug	0.3	M	57	0.1	-
A 60	2 Sep	10.3	M	116	-	-
A 61	18 Sep	2.3	I	81	2.5	0.9
A 62	18 Sep	8.3	M	98	7.5	1.9
A 63	18 Sep	9.3	M	105	9.5	1.9
A 64	18 Sep	16.3	M	101	12.0	2.1
A 65	18 Sep	29.3	M	105	14.5	2.4
A 66	18 Sep	10.3	M	102	10.5	1.8
A 67	18 Sep	9.3	M	91	8.3	1.8
A 68	18 Sep	17.3	M	111	12.5	2.5
A 70	23 Sep	15.3	M	122	13.5	2.5
A 71	23 Sep	15.3	M	115	13.0	2.4
A 74	17 Sep	0.3	I	55	-	-

APPENDIX I (continued)

Field No.	Date.	Age.	Class.	Body Length, Inches.	Tusk Length, Inches.	Tusk Circ, Inches.
A 84	5 Oct	12.4	M	107	9.0	1.9
A 96	17 Jun	13.1	M	110	-	-
A 97	17 Jun	7.1	M	108	6.5	1.6
A 111	12 Aug	6.2	I	108	5.8	1.5
A 114	22 Aug	20.3	M	126	12.0	2.4
A 116	23 Aug	8.3	M	96	6.0	1.8
A 118	10 Sep	1.3	I	70	2.6	1.5
A 122	10 Sep	15.3	M	101	9.3	2.0
A 123	10 Sep	4.3	I	90	4.5	-
A 124	17 Sep	35.3	M	122	17.0	2.6
A 127	6 Oct	15.4	M	117	10.8	2.4
A 128	6 Oct	28.4	M	109	10.0	2.8
A 129	7 Oct	6.4	I	96	7.0	1.5
A 131	7 Oct	3.4	I	86	3.5	1.1
A 134	7 Oct	1.4	I	73	1.5	-
A 135	10 Oct	2.4	I	90	3.0	1.0
A 136	10 Oct	11.4	M	115	9.8	2.4
IW 3	24 Sep	3.3	I	97	-	-
IW 4	4 Oct	21.4	M	-	7.4	-
IW 5	26 Oct	19.4	M	108	12.8	-
IW 6	26 Oct	7.4	M	-	6.9	-
IW 10	30 Nov	12.5	M	108	9.5	-
IW 20	22 Jun	9.1	M	121	7.3	-
IW 21	10 Jul	0.1	I	41	0.0	-
IW 35	10 Jul	0.1	I	49	0.0	-
IW 37	10 Jul	0.1	I	52	0.0	-
IW 40	30 Jul	22.2	M	108	13.5	-
IW 41	30 Jul	11.2	M	116	10.0	-
IW 44	5 Aug	6.2	I	103	-	-
IW 51	10 Aug	10.2	M	124	12.0	-
IW 52	9 Aug	15.2	M	128	9.0	-
IW 53	9 Aug	15.2	M	120	13.0	-
IW 54	9 Aug	10.2	M	109	7.5	-
IW 55	9 Aug	3.2	I	90	4.0	-
IW 56	9 Aug	11.2	M	114	8.5	-
IW 57	9 Aug	10.2	M	118	8.5	-
IW 58	9 Aug	8.2	M	117	10.2	-
IW 59	9 Aug	21.2	M	119	15.5	-
IW 60	9 Aug	18.2	M	127	12.5	-

APPENDIX I (continued)

Field No.	Date.	Age.	Class.	Body Length, Inches.	Tusk Length, Inches.	Tusk Circ, Inches.
IW 61	9 Aug	14.2	M	104	5.8	-
IW 62	9 Aug	7.2	M	104	9.3	-
IW 63	9 Aug	7.2	-	123	9.3	-
IW 64	9 Aug	22.2	M	119	13.0	-
IW 65	9 Aug	13.2	M	129	11.5	-
IW 66	9 Aug	14.2	M	114	9.5	-
IW 70	10 Sep	11.3	M	105	7.5	-
IW 72	19 Sep	7.3	M	119	8.0	-
IW 73	19 Sep	12.3	M	127	10.5	-
IW 74	19 Sep	14.3	M	113	10.0	-
IW 75	19 Sep	19.3	M	137	11.5	-
IW 76	19 Sep	17.3	M	136	15.8	-
IW 77	24 Sep	12.3	M	117	13.0	-
IW 78	24 Sep	15.3	M	131	11.5	-
IW 79	24 Sep	9.3	-	121	9.5	-
IW 80	24 Sep	9.3	M	112	9.0	-
W 2	25 Jul	0.2	I	45	0.0	-
W 11	4 Aug	12.2	M	118	10.5	-
W 13	11 Aug	2.2	I	84	-	-
S 2	31 Jul	11.2	M	111	9.0	-
S 52	3 Sep	3.3	I	84	3.5	-
S 54	3 Sep	1.3	I	69	1.1	-
S 55	4 Sep	2.3	I	81	1.0	-

B: Females

A 9	26 May	8.0	Py	103	5.8	1.4
A 13	27 May	20.0	B	-	9.3	1.8
A 38	2 Aug	9.2	Bc	105	7.5	1.4
A 42	7 Aug	8.2	Py	101	8.5	1.4
A 46	20 Aug	7.2	P	94	6.5	1.5
A 48	22 Aug	13.2	Bc	112	14.0	1.8
A 72	23 Sep	16.3	B	107	8.5	1.6
A 73	17 Sep	7.3	Bc	93	-	-

APPENDIX I (continued)

Field No.	Date.	Age.	Class.	Body Length, Inches.	Tusk Length, Inches.	Tusk Circ, Inches.
A 75	19 Sep	17.3	By	99	-	-
A 76	19 Sep	2.3	I	83	3.0	0.9
A 77	2 Oct	18.4	B	102	10.0	1.8
A 78	2 Oct	6.4	M	92	5.5	1.1
A 79	2 Oct	6.4	I	83	4.8	0.9
A 80	4 Oct	10.4	P	92	6.0	1.3
A 81	5 Oct	3.4	I	88	3.4	0.8
A 82	5 Oct	11.4	P	98	6.5	1.5
A 83	5 Oct	11.4	Bc	97	7.0	1.5
A 109	6 Aug	1.2	I	72	1.5	0.6
A 110	10 Aug	13.2	Py	106	13.0	-
A 112	13 Aug	9.2	M	94	6.3	-
A 113	21 Aug	5.2	I	92	3.3	-
A 115	22 Aug	9.2	Bc	101	7.3	1.4
A 119	10 Sep	14.3	P	105	8.3	1.5
A 120	10 Sep	13.3	P	95	7.3	1.5
A 121	10 Sep	13.3	B	96	7.3	1.5
A 125	27 Sep	11.3	I	102	10.0	-
A 126	27 Sep	19.3	Bc	103	9.0	-
A 130	7 Oct	0.4	I	59	0.6	0.4
A 132	7 Oct	15.4	Bc	98	5.3	1.5
A 133	7 Oct	17.4	By	97	7.0	1.5
IW 36	10 Jul	0.1	I	50	0.0	-
IW 42	2 Aug	14.2	-	102	-	-
IW 43	5 Aug	5.2	M	93	3.9	-
IW 45	5 Aug	15.2	-	98	12.0	-
IW 48	5 Aug	5.2	M	90	3.3	-
IW 49	5 Aug	16.2	B	100	5.0	-
IW 50	5 Aug	10.2	Py	108	9.5	-
W 16	11 Aug	0.2	I	52	0.0	-
SD 142	2 Jul	0.1	I	50	0.0	-

APPENDIX II

Development of the Testis in Immature and Mature Males

Field Numbers: 'A' series from Bencas and Coats Islands, 1955 & 6.
'W' series from Coats Island, 1954.
'IW' series from Foxe Basin, 1955 & 6.
S 2 from Seahorse Point, Southampton Island.

Testis: Tubule types as detailed on page 65.
Diameters in microns.
xxx indicates presence of sperm.

Field No.	Date.	Age.	Testis tubules		Epididymis	
			Diam.	Types in order	Diam.	Sperm?
A 11	26 May	0.0	15		31	0
A 39	2 Aug	0.2	16		43	0
A 49	22 Aug	0.3	15		42	0
A 41	7 Aug	1.2	20		54	0
A 10	26 May	2.0	33		-	-
A 61	18 Sep	2.3	28		67	-
W 13	11 Aug	2.2	23		60	0
A 135	10 Oct	2.4	27		60	0
A 37	1 Aug	3.2	24		55	0
IW 55	9 Aug	3.2	32		80	0
A 123	10 Sep	4.3	31		96	0
A 111	12 Aug	6.2	48		96	0
IW 44	5 Aug	6.2	39		92	0
A 97	17 Jun	7.1	51	B	55	0
IW 62	9 Aug	7.2	40	B	-	-
IW 72	19 Sep	7.3	-	B, C	-	-
IW 6	26 Oct	7.4	-	B	80	-
IW 58	9 Aug	8.2	55	B, C	-	-
A 62	18 Sep	8.3	49	C, B	-	-

APPENDIX II (continued)

			Testis tubules		Epididymis	
Field No.	Date.	Age.	Diam.	Types in order	Diam.	Sperm?
IW 20	22 Jun	9.1	58	B, C	68	0
A 63	18 Sep	9.3	60	B	60	0
A 67	18 Sep	9.3	47	B	62	0
IW 80	24 Sep	9.3	51	B	-	-
A 60	2 Sep	9.3	-	B, C	71	0
IW 51	9 Aug	10.2	49	B, C	51	0
IW 54	9 Aug	10.2	52	B, C	78	0
IW 57	9 Aug	10.2	44	C, B	88	0
A 66	18 Sep	10.3	39	B, C	79	0
IW 56	9 Aug	11.2	43	B	80	0
S 2	31 Jul	11.2	-	B, C	-	-
A 136	10 Oct	11.4	-	B, C	-	0
W 11	4 Aug	12.2	47	C, B	52	0
IW 73	19 Sep	12.3	-	C, B	-	-
IW 77	24 Sep	12.3	59	C, B	69	0
A 84	5 Oct	12.4	46	B	75	0
IW 10	30 Nov	12.5	62	A	81	xxx
A 96	17 Jun	13.1	59	B, C	112	0
IW 65	9 Aug	13.2	56	B, C	104	0
IW 61	9 Aug	14.2	50	C, B	83	0
A 145	Sep-Oct	14.3	53	C, B	-	-
IW 74	19 Sep	14.3	39	C, B	-	-
A 64	18 Sep	16.3	44	C, B	59	0
A 68	18 Sep	17.3	55	C, B	78	0
IW 5	26 Oct	19.4	53	B	66	0
IW 4	4 Oct	21.4	45	B, C	60	0
IW 40	30 Jul	22.2	58	B, C	73	0
IW 15	21 Mar	24.8	63	A	-	xxx
A 128	6 Oct	28.4	51	B	73	0

APPENDIX III

Development of Follicles and Corpora Lutea in the Ovaries of 59 Atlantic Walrus

The classes of females are as follows: 'I' - immature; 'M' - mature, nulliparous; 'P' - pregnant; 'B' - barren; 'c' - with calf; 'y' - with yearling.

Follicles are classified as either atretic (A) or healthy (H). Measurements of larger follicles and corpora albicantia represent maximum and minimum diameters of the sections examined. Thus a follicle listed as '7.4' measures 7 mm. by 4 mm. Corpora lutea are measured along three diameters.

Follicles marked with an asterisk are luteinised.

Field No.	Date.	Age.	Class	Ovary	Number of Follicles						Corpus Luteum	Corpora Albicantia
					1 - 3 mm.		3 - 6 mm.		Over 6 mm.			
					A	H	A	H	A	H		
A 9	26 May	8	Py	R	2	12	0	3	0	0	38.37.27	
				L	0	4	0	0	7.4	0	0	13.12
A 13	27 May	20	By	R	2	5	0	4	0	13.9 8.7 7.6 6.6	0	6.6 6.5 5.2
				L	0	2	0	2	14.8	9.7	0	7.7 7.4 5.3
A 38	2 Aug	9	Bc	R	24	0	21	5	12.8 7.5	0	0	9.4
				L	7	0	0	0	0	0	0	25.16 17.5

APPENDIX III (continued)

A 42	7 Aug	8	Py	R	3	0	0	0	0	0	0	19.10	
				L	1	12	0	0	0	0	34.25.39		0
A 43	17 Aug	-	Bc	R	41	38	1	0	10.10	0	0	18.13	
				L	19	52	0	0	15.2 7.5	0	0	9.7	
A 46	20 Aug	7	P	R	1	12	0	0	0	0	0		0
				L	12	49	0	13	0	8.5 8.5 7.6	37.27.34	8.5	
A 48	22 Aug	13	Bc	R	6	10	0	0	0	0	0	32.20	10.6
				L	40	75	2	1	0	0	0	14.8	12.8
A 72	23 Sep	16	B	R	0	14	0	6	0	0	0	9.7 7.5	9.5
				L	5	3	0	3	0	0	21.14.21	12.8	8.4
A 73	17 Sep	7	Bc	R	5	4	0	0	0	0	0	5.4	
				L	1	5	0	0	0	0	0	30.20	
A 75	19 Sep	17	By	R	13	1	0	0	0	0	18.10.16	8.6 3.2	5.2
				L	7	8	0	0	0	0	0	7.4	
A 76	19 Sep	2	I	R	0	0	0	0	0	0	0		0
				L	0	0	0	0	0	0	0		0
A 77	2 Oct	18	B	R	4	4	2	5	0	0	23.17.17	14.4 6.3	11.7
				L	6	14	1	13	0	0	0	9.5	

APPENDIX III (continued)

A 78	2 Oct	6	M	R L	0 0	3 2	0 0	0 0	0 0	0 0	12.10.10 0	0 0
A 79	2 Oct	6	I	R L	0 0	0 0	0 0	0 0	0 0	0 0	0 0	0 0
A 80	4 Oct	10	P	R L	0 0	5 5	0 0	0 1	0 0	0 0	0 32.25.31	13.11 0
A 81	5 Oct	3	I	R L	0 0	0 0	0 0	0 0	0 0	0 0	0 0	0 0
A 82	5 Oct	11	P	R L	0 4	4 17	0 0	0 0	0 0	0 0	0 34.29.29	0 9.6
A 83	5 Oct	11	Bc	R L	9 1	26 11	0 0	1 0	0 0	0 0	0 0	11.4 16.14
A 109	6 Aug	1	I	R L	0 0	0 0	0 0	0 0	0 0	0 0	0 0	0 0
A 110	10 Aug	13	Py	R L	1 0	11 8	0 0	3 0	0 0	7.5 10.8	30.23.23 0	7.6 0
A 112	13 Aug	9	M	R L	20 14	41 61	0 1	3 4	0 0	0 0	0 32.26.24	0 0
A 113	21 Aug	5	I	R L	18 17	31 31	0 0	3 6	0 0	0 0	0 0	0 0
A 115	22 Aug	9	Bc	R L	4 0	26 8	0 0	17 0	8.7 0	0 0	0 0	18.14 29.19
A 119	10 Sep	14	P	R L	3 10	29 4	0 0	1 0	0 0	0 0	38.35.27 0	9.4 9.4 7.5

APPENDIX III (continued)

A 120	10 Sep	13	P	R	0	0	0	0	0	0	0	17.8	
				L	5	22	0	2	0	0	29.28.21		0
A 121	10 Sep	13	B	R	15*	6	3*	5	8.6*	0	0		0
				L	49*	7	3	5	7.6*	0	0	13.7 6.4	7.5 6.4
A 125	27 Sep	11	M	R	0	8	8	13	11.10 33.25	11.8 8.7 7.6	0	5.2	
				L	1	7	3	5	13.12 12.10 12.7 8.7 7.5 7.3	0	0	4.2	
A 126	27 Sep	19	Bc	R	20	8	2	0	0	0	0	22.16 8.3	6.4
				L	26	5	23	0	0	0	0	8.5	6.3
A 130	7 Oct	1	I	R	0	0	0	0	0	0	0		0
				L	0	0	0	0	0	0	0		0
A 132	7 Oct	15	Bc	R	6	12	0	4	0	0	0	10.6 5.4	9.5 3.3
				L	6	31	0	11	0	7.6	0	9.5 4.4	6.5
A 133	7 Oct	17	By	R	2	21	1	6	9.5	7.6 7.5	0	14.8 3.3	8.3
				L	4	13	3	6	0	0	22.19.14	11.4 3.3	5.2

APPENDIX III (continued)

IW 12	12 Mar	-	I	R L	21 38	27 21	5 8	36 6	0 0	0 0	0 0	0 0	
IW 24	10 Jul	-	B	R L	- 2	- 3	9 0	1 4	0 0	0 0	0 22.22.19	7.6 10.5	6.3
IW 25	10 Jul	-	I	R L	63* 58*	10 9	16* 38*	9 7	0 7.5	0 10.10 10.10 9.9	0 0	0 0	
IW 32	10 Jul	-	B	R L	0 -	0 -	0 0	0 13	0 0	0 0	28.24.17 0	12.11 10.10 8.5	8.7
IW 33	10 Jul	-	B	R L	- 0	- 0	3 0	8 1	0 0	7.6 7.5 0	0 29.16.20	13.8 13.7 10.7 6.6	13.7 10.6 10.7
IW 38	10 Jul	-	B	R L	20* 38*	13 14	16* 7*	6 7	13.11 0	8.8 8.8	0 0	16.12 12.6 12.10 11.8 8.8	12.11 12.10 10.9 5.3
IW 39	30 Jul	-	B	R L	17* -	0 -	26* 7*	0 0	8.4 7.6 7.5 0	0 10.6	0 0	14.10 8.6 6.4 13.8 11.4 8.3 6.4	10.8 8.4 6.4 13.8 10.4 6.5 5.3

APPENDIX III (continued)

IW 43	5 Aug	5	M	R	0	31	0	22	0	0	19.24.15.	0	
				L	1	20	1*	10	0	0	0	0	
IW 45	5 Aug	15	-	R	0	2	0	1	9.7*	19.13 7.6	0	15.6 9.8	11.9 3.2
				-	-	-	-	-	-	-	-	-	
IW 46	5 Aug	-	I	R	0	32	0	29	0	0	0	0	
				L	0	44	0	11	0	0	0	0	
IW 48	5 Aug	5	M	R	2	8	0	2	0	0	0	0	
				L	0	27	0	0	0	0	13.17.11	0	
IW 49	5 Aug	16	B	R	0	5	0	2	0	8.7	19.18.17	10.7 5.3	8.6 5.2
				L	0	4	0	5	0	8.7	0	11.6 7.5	10.7
IW 50	5 Aug	10	Py	R	0	8	0	6	0	0	29.20.26	0	
				L	0	11	0	1	0	0	0	16.12	12.7
S1/53	30 Jul	-	B	R	3	40	0	30	0	0	0	9.5 4.4	7.4
				L	0	2	2	14	0	0	30.27.21	14.13	
S 53	3 Sep	-	B	R	1	1	0	0	0	0	31.30.29	11.6	
				L	0	0	0	0	0	0	0	0	
SD/141	2 Jul	11	Bc	R	0	50	0	8	0	0	0	15.7	
				L	0	21	0	0	0	0	0	34.17	
W 1	25 Jul	-	Bc	R	0	2	0	3	8.4	0	0	22.13	7.4
				L	-	-	1	5	0	7.5	0	16.11	8.5
W 4	26 Jul	-	I	R	0	13	0	2	0	0	0	0	
				L	0	17	0	0	0	0	0	0	

APPENDIX III (continued)

W 5	28 Jul	-	B	R	0	1	2	2	0	0	0	13.10	11.10
				L	0	1	1	7	0	0	30.28.18		0
W 6	3 Aug	-	P	R	0	15	0	0	0	0	39.24.31	13.6	13.3
				-	-	-	-	-	-	-	-		-
W 7	3 Aug	-	P	R	5	13	0	0	0	0	33.29.26		0
				L	4	9	0	0	0	0	0	16.11	14.8
W 9	3 Aug	-	Bc	R	1	5	2	0	8.6	0	0	23.10	
				L	0	11	4	10	0	10.6	0	14.14	13.6
												10.10	6.5
												4.2	
W 10	4 Aug	-	-	R	-	-	0	3	-	-	0	11.7	
				-	-	-	-	-	-	-	-		-
W 12	11 Aug	-	B	R	1	18	1	17	0	0	26.21.20	10.4	
				L	15	22	6	17	0	0	0	11.9	9.8
W 14	11 Aug	-	P	R	-	-	0	2	0	9.6	34.29.20		0
										8.5			
										7.3			
				L	5	1	5	0	0	0	0	14.14	
W 15	11 Aug	-	B	R	14	13	9	18	0	7.6	0	14.10	
				L	11	10	4	13	0	0	0	14.14	12.8
W 17	11 Aug	-	Bc	R	2	2	7	0	9.6	0	0	15.11	8.8
				L	2	0	1	0	0	0	22.20.19	13.11	10.6
W 18	11 Aug	-	B	R	7	2	13	13	0	7.5	0	10.8	
				L	8	1	11	7	0	0	30.28.15	14.5	

APPENDIX IV

Growth of the Human Embryo (after Arey, 1954).

No. of days	Crown-rump length in cm.	Percent gestation completed	
		Days	Crown-rump length
7	0.1	2.5	0.03
14	0.2	5.0	0.06
17.5	1.5	6.3	0.43
21	2.0	7.5	0.57
24.5	2.5	8.8	0.71
28	5.0	10.0	1.42
35	8.0	12.5	2.28
42	12.0	15.0	3.42
49	17.0	17.5	4.86
56	23.0	20.0	6.57
70	40.0	25.0	11.43
84	56.0	30.0	16.00
112	112.0	40.0	32.00
140	160.0	50.0	45.72
280	350.0	100.0	100.00

APPENDIX V

Comparison of Mean Body Length and Mean External Tusk Length in Male Atlantic and Pacific Walrus

Age of Pacific Walrus (Fay, 1955; fig. 31)	No. of Cementum Layers in Molariform Teeth	External Tusk Length - Pacific Walrus	External Tusk Length - Atlantic Walrus	Nose-tail Length (adjusted) - Pacific Walrus	Nose-tail Length - Atlantic Walrus
1.0	1		1.0		68
1.3	2		2.1		81
1.7	3		3.2		89
2.0	4		4.3		94
2.6	5	5.4	5.3		98
3.2	6	6.7	6.3		102
3.7	7	8.2	7.2		105
4.4	8	9.6	8.0	108	108
4.9	9	11.0	8.8	112	111
5.5	10	12.1	9.4	114	113
6.1	11	13.3	10.0	117	114
7.0	12	14.6	10.5	118	115
8.0	13	15.5	11.0	121	116
9.0	14	16.5	11.4	123	117
10.1	15	17.3	11.9	124	118
10.9	16	18.0	12.4	125	119
12.0	17	18.8	12.7	126	119
13.1	18	19.3	13.0	126	120
14.0	19	19.8	13.2	127	120
16.0	20	20.8	13.4	128	120
17.0	21	21.1	13.5		
18.0	22	21.4	13.6		
19.0	23	21.9	13.7		
20.0	24	22.2	13.8		
21.0	25	22.5	13.9		
26.0	30	23.7	-		