

THE PACIFIC WALRUS (ODOBENUS ROSMARUS DIVERGENS):
SPATIAL ECOLOGY, LIFE HISTORY, AND POPULATION

by

Francis Hollis Fay

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ABSTRACT

The Pacific Walrus (*Odobenus rosmarus divergens*): Spatial Ecology, Life History, and Population

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The Pacific walrus inhabits the Bering Sea during winter and the Chukchee Sea in summer, generally in close association with sea ice. The year-round northern limit to this range is marked by the southern edge of the relatively unbroken pack ice which, though not impenetrable, is usually avoided. The southern limit appears to be set by air temperatures, regions with monthly means of 50° F or more being unoccupied. Between these two "barriers," the animals frequent waters of less than 50 fathoms depth in which their preferred food, the pelecypods Mya, Saxicava, Astarte, Macoma, and Clinocardium, occur.

Seasonal migrations between the Bering and Chukchee Seas appear to be partly in response to changing physical conditions and partly due to an innate or learned behaviour pattern. Females are the most regular migrants; males are more subject to the inconsistencies of ice drift.

The bull Pacific walrus reaches sexual maturity at six to eight years of age, the cow at four to five years of age. Breeding takes place mostly from April to June as the

animals are migrating northward, and there is no evidence of any organized polygamy or "harem breeding." Gestation is one full year, and twinning is unknown. An individual cow rarely conceives in successive years, the first three pregnancies generally being at 2-year intervals and later ones three or more years apart. Males become senile at about fifteen years of age.

Full adult body size is achieved at four to six years of age by both sexes, though growth continues slowly thereafter. The tusks and other teeth grow at a relatively high rate throughout the life span, and analyses of their structure and size have yielded good techniques for age determination.

The population, upwards of 40,000 animals at present, has declined slightly in the past fifteen years, but it has reached or is approaching equilibrium. The birth rate and death rate are about equal, human predation accounting for most of the latter. Since the population is currently too small to satisfy the Alaskan Eskimos' needs, it is recommended that it be permitted to increase by eliminating some of the wasteful hunting practices which are now in effect.

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COMMITTEE IN CHARGE:

H.F. Angus, Chairman

I.McT. Cowan

P. Ford

P.A. Larkin

G.J. Spencer

W.M. Cameron

S.E. Read

E.S. Carpenter

V.J. Okulitch

W.D. Kitts

External Examiner - M.J. Dunbar
McGill University

LIST OF PUBLICATIONS

Quantitative Experiments on the Food
Consumption of *Parascalops breweri*,
Journal of Mammalogy 35, 107-109, 1954.

The Geographical and Ecological Distribution
of Cottontail Rabbits in Massachusetts,
Journal of Mammalogy 36 (in press), 1955.

THESIS

THE PACIFIC WALRUS, ODOBENUS ROSMARUS DIVERGENS: SPATIAL ECOLOGY, LIFE HISTORY, AND POPULATION

The holarctic distribution of walruses is defined by three primary factors: sea ice, air temperatures, and distribution of certain pelecypod genera upon which they feed. Pronounced migrations occur, partly in response to seasonal variations in these factors.

Quantitative analyses of reproduction, growth, and mortality have been founded upon the development of an age determination technique involving dental morphometry and histology. Tusk growth is the key to aging, since it proceeds at a relatively high rate throughout the life span.

There has been a slight decrease in the number of Pacific walruses within the past fifteen years, but at present the population has reached or is approaching stability. Currently there are too few to supply the maintenance needs of some Eskimo villages, and since human predation is the primary factor controlling population size, recommendations have been given for reducing the kill without affecting the harvest.

GRADUATE STUDIES

Field of Study: Zoology

History and General Principles	W.A. Clemens
Biological Methods and	Zoology
Procedures	Department
Forest and Wilderness Game	I. McT. Cowan
Population Dynamics	P.A. Larkin

Other Studies:

Synoptic Oceanography	W.M. Cameron
Forest Associations	V. Krajina
Biometrics	V.C. Brink
People of the Arctic	G.H. Marsh

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To a large degree, success in the field has been directly attributable to the kind hospitality of Mr. and Mrs. Paul E. Tovey, Mr. William Caldwell, and Mr. and Mrs. Donald G. McLean, recently of Gambell, Alaska. The Eskimos of St. Lawrence Island, most particularly Messrs. Charles

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SUMMARY

The holarctic distribution of walruses is defined by three primary factors: sea ice, air temperatures, and distribution of certain pelecypod genera upon which they feed. Pronounced migrations occur, partly in response to seasonal variations in these factors.

Quantitative analyses of reproduction, growth, and mortality have been founded upon the development of an age determination technique involving dental morphometry and histology. Tusk growth is the key to ageing, since it proceeds at a relatively high rate throughout the life span.

There has been a slight decrease in the number of Pacific walruses within the past fifteen years, but the population (about 40,000) has reached or is approaching stability. At present there are too few to supply the maintenance needs of some Eskimo villages, and since human predation is the primary factor controlling population size, it has been recommended that current wasteful hunting practices be abolished.

INTRODUCTION

Throughout the pages of history it has been a general rule that European man's expansion of his environment has been accompanied by thoughtless exploitation of natural resources for economic gain, some to the point of complete or near extinction. The animal resources of the new fringe areas have usually been the first to suffer because of their accessibility and per capita values, but due to their powers of reproduction, many exploited populations have recovered fully when with a changing economy or restrictive legislation they have been left alone once more. Such has been the fate, notably, of the fur seal and sea otter in North America, though some others have not fared as well. Moderately tapped as early as the 8th and 9th centuries A.D., the world walrus population felt its first real blow from commercial enterprise in the early 1800's, and by 1850 walrus hunting in northern seas had become an extremely profitable business. Harvests from the North Pacific region between 1860 and 1880 averaged about ten thousand animals annually, the fruits of the hunt being mainly oil and ivory for sale in the ports of western North America and eastern Asia. A serious decline in numbers became very evident towards the end of the 19th century, and Clark (1884) predicted that the population would soon be so thoroughly decimated that it would no longer be profitable to seek them.

This prediction became reality within the next forty years, though land-based traders carried on a lively business with Eskimo hunters in some areas until halted by the "Walrus Act" of 1941. Since that time, walruses have been harvested only by Eskimos, presumably only for their own use.

The general opinions of Eskimo and White observers in Alaska from 1935 to the present indicate no major changes in walrus population density; indeed, some observers consider that there has been a slight increase over an all-time low experienced about 1920. What, then, is the size of the present population? What are its characteristics and potentialities for growth? How large an annual harvest can be safely taken without endangering its future status? If this resource is to be maintained for the benefit of the Alaskan natives who are dependent upon it, then these questions must be answered and a sustained-yield management program devised. These are the problems which the writer set out to solve in 1951. Fortunately, at the same time and independently, Mr. James W. Brooks of the University of Alaska was making preparations for a similar investigation, and it has been largely through our cooperative efforts in the field that many of the conclusions in the following pages can be reached. Our empirical data have been pooled where desirable, but the analyses and conclusions have been arrived at independently.

The writer's field work was centered about the region of St. Lawrence Island, Alaska, situated in the north-central

portion of the Bering Sea (Fig. 1). Of the three most suitable localities (St. Lawrence, King, and Little Diomed Islands) it was initially chosen because of its accessibility by air during the spring months. This choice later proved to be a very good one from many other aspects. The spring hunting seasons of 1952, 53, and 54 were spent at the village of Gambell (Sevuokuk) on the northwest extremity of the island where it was possible to take an active part in the annual hunt and to gather much first-hand information and specimens. Occasional visits to Savoonga, a village about 35 miles ESE, also yielded many data and specimens, all of which were collected by local people at the writer's request. In 1952 a survey of other Eskimo villages and coastal waters north to Barrow was made possible by the cooperation of the U.S. Coast Guard (C.G.C. Storis), and much supplementary information was later obtained by questionnaire and vocal communication with teachers and other local observers from nearly all of the coastal villages north of the Alaska Peninsula. Brooks' work covered the villages of Wales, Diomed, and Barrow and the vicinity of the Walrus Islands in Bristol Bay. Thus, between us, we have directly or indirectly investigated nearly every locality where the Pacific walrus occurs east of the International Date Line, and Soviet reports of conditions west of the Line have completed the overall picture.

Most of the field investigations were centered upon problems of general ecology, productivity, growth, and mor-

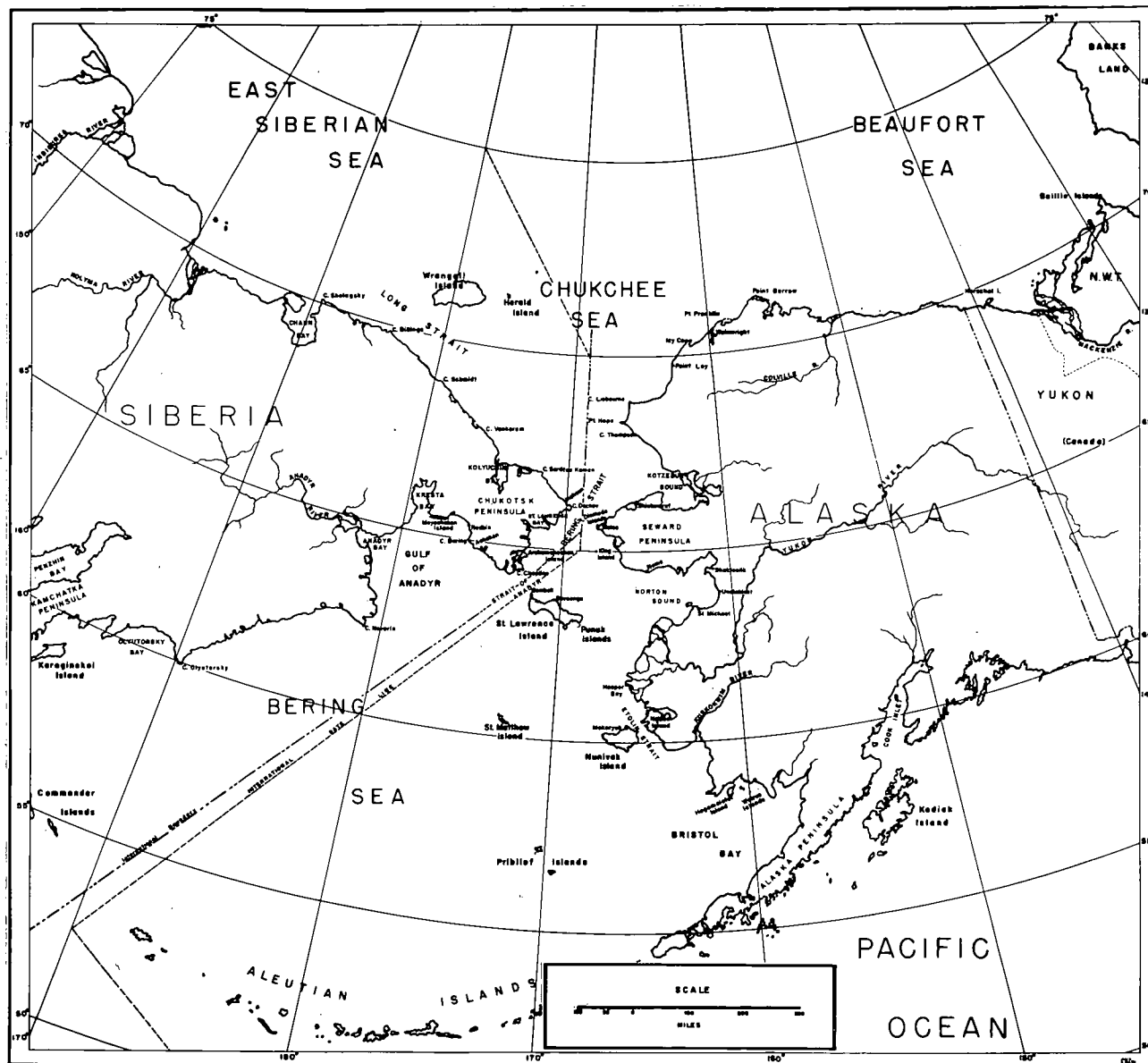


Fig. 1.--A map of Alaska and Siberia showing localities mentioned in the text.

tality, for these are the foundations upon which a population study must be built. Analyses of these data form the bulk of this thesis.

PART I
SPATIAL ECOLOGY

DISTRIBUTION

The general range of the Pacific walrus has been briefly outlined by many writers, varying somewhat with their experience, their survey of previous literature, and their personal interpretation of the data and its implications. Of these, the most complete and authoritative are the discussions by Belopolsky (1939), Brooks (1954), Collins (1940), Heinrich (1947), and Nikulin (1940), each of which has helped to resolve some of the salient features of the distribution, their causes and effects. Generalizing from these and other recent data, it is apparent that in winter the bulk of the population occurs about the Bering Sea between lat. 57°N and 64°N , while in summer it occupies the Chukchee Sea north to lat. 72°N , east to long. 155°W , and west to long. 175°E . To this pattern there have been many exceptions, but most concerned only small groups of wanderers.

The literature concerning this region prior to 1900 suggests that the general features of distribution have been about the same for the past 150-200 years, the principal exceptions being that the outer fringes of the range extended farther and that the population was more dense throughout its range than it is now. The overall shrinkage appears to have occurred mostly in the last half of the 19th century, and it has continued into the 20th.

In order to fully appreciate the design of modern exploitation and population, a brief examination of seasonal movements is necessary. This is presented in the following pages. It is in part a summary and in part a supplement to the earlier works.

January-February

Prior to this writing there has been insufficient material with which to judge the basic character of winter distribution. The earlier records consisted entirely of a few localized observations from the vicinity of several Eskimo villages and negative reports from others. In the winters of 1953 and 1954, however, the writer, through the kindness of the U.S. Navy Electronics Laboratory, Special Studies Branch, was able to obtain a series of significant observations which were secured and recorded by personnel of the icebreakers U.S.S. Burton Island and C.G.C. Northwind in the Bering Sea (Ryder, 1953; R.E. Morell, in litt.). These constitute the bulk of the data shown in Fig. 2.

From early January to mid-March the population appears to be loosely aggregated in a broad undulating band stretching, roughly, from Bristol Bay, Alaska, to the Gulf of Anadyr, Siberia. In January the width of this band probably averages about 150-200 miles, but by mid-February it may be as much as 300 miles, due to the gradual southward dispersal of ice in response to strong northerly winds. Within this loose aggregate appears a well defined pattern of local concentra-

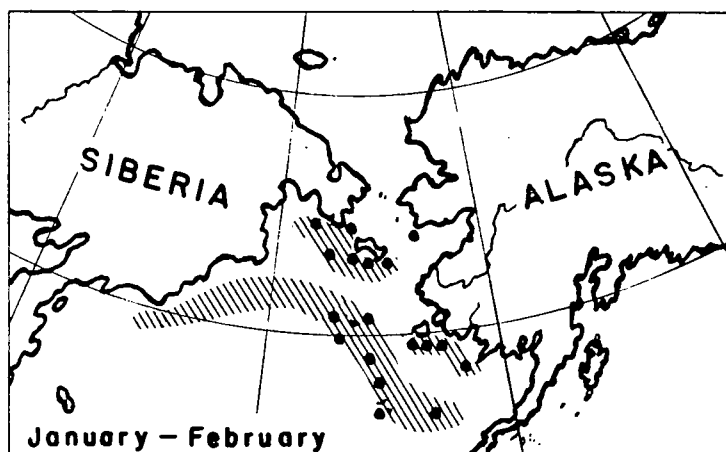


Fig. 2.--Distribution in winter

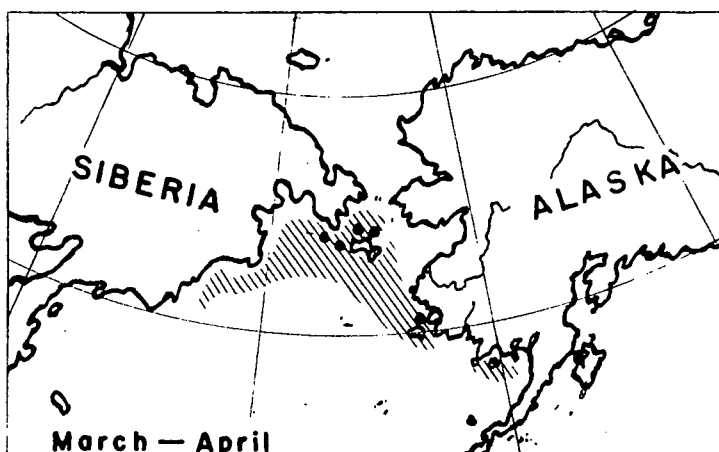


Fig. 3.--Distribution in early spring

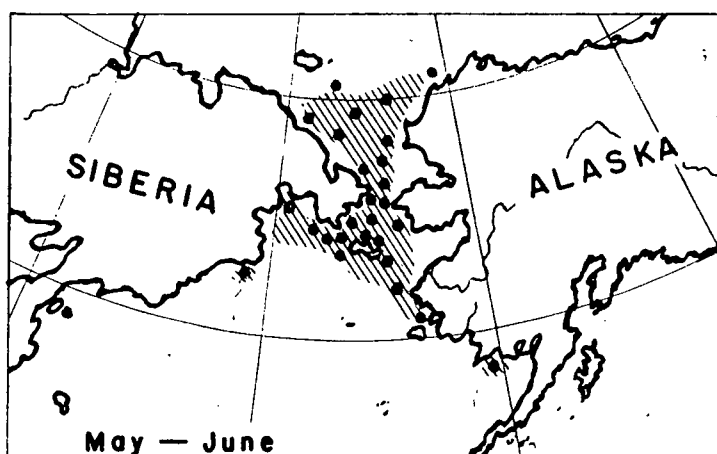


Fig. 4.--Distribution in late spring. Dots are recorded observations; crosshatching represents probable range occupied by the bulk of the population.

tions in two general environments: (a) on the southside of large islands and peninsulas, and (b) along the southern edge of the pack ice. Because of the strong north wind during the winter months and its effect of pushing the pack in a general southerly direction, it would be expected that immediately south of the islands and peninsulas there would be more open leads amongst the ice than elsewhere. This has been verified by the St. Lawrence Island men, who state that the "south-side" is usually quite open in winter, and seals and walruses are more abundant there than they are in the more tightly packed ice to the west and north.

The second area of concentration, along the edge of the pack, is probably occupied for the same reason, i.e. ample open water between the floes. Observers on the C.G.C. Northwind in the winter of 1954 reported that the walruses seen appeared to have been exclusively "in areas of little or no ice pressure" (R.E. Morell, in litt.).

North of St. Lawrence Island the pack ice is essentially entire, for although leads are frequently formed, they quickly freeze over again. In spite of such unfavorable conditions, there is a small(?) proportion of the population which remains there in winter. These "winter walruses" (Heinrich, 1947) are usually lone bulls, and they have been reported occasionally north of St. Lawrence Island and Nunivak Island, near Nome, King Island, Wales, Diomede, and in the vicinity of Point Barrow. Possibly they are sparsely distributed over the rest of the north Bering Sea

and Chukchee at that time, as well. In Muller's account (Golder, 1914) of travels in northeast Siberia there is mention of the natives hunting walruses near Wrangell Island in winter.

March

By March, though the overall pattern remains about the same, there is a definite tendency for a few small herds to begin moving northward, at least through the Strait of Anadyr, between St. Lawrence Island and Cape Chaplino. Nikulin (1940) mentions some which were seen near the latter point at this time, and his distribution maps (op. cit., Figs. 1,9) indicate their presence in the strait and slightly north of it. Airline pilots flying the Nome-Gambell mail route have also reported that the first walruses observed north of the island are generally sighted in the first week of March with a gradual increase in numbers thereafter. These were believed to be mostly males, and the few taken in that month by Gambell hunters are predominantly of that sex.

April

As the southern edge of the pack begins to melt and break up, and the leads south of Bering Strait remain open longer, the northward migration commences. In April herds have been observed in Etolin Strait and on the north-side of Nunivak Island (Lantis, 1946; R.B. Gibson, in litt.), near Cape Chaplino and Arakamchechen Island (Nikulin, 1940), north, east, and west of St. Lawrence Island, and even as far

north as the west side of Bering Strait (Nikulin, op. cit.). This "advance guard" is composed almost wholly of males. The herds are small (2 to 10 individuals) and for the most part are widely scattered, for there are still large unbroken expanses of ice, particularly in the northeast sector of the Bering Sea. In recent years the most southern extremes of range have been recorded at this time (Ryder, 1954). These records, shown in Figure 3, probably represent individuals whose current and wind-propelled ice pan disintegrated, leaving them stranded and separated from the rest of the population. Nikulin also attributes his southernmost records to this phenomenon.

May

The beginning of the major northward surge of females and young is observed in May. By this time the ice north and south of Bering Strait breaks up and begins to melt under the influence of wind, surface currents, and warmer air temperatures. The north wind decreases in force and south, east, and west winds are frequent, serving to more nearly coordinate air and water (and thus ice) movements into a common vector towards the north. The last of the passing herds are seen at Nunivak and Nelson Island early in the month (Lantis, 1946; R.B. Gibson, in litt.), and by the end of the month the movement through Bering Strait is well under way (Fig. 4). The animals passing north between St. Lawrence Island and Siberia throughout this period are

principally females accompanied by juveniles and newborn young, though a few adult bulls are usually seen amongst them. Those found within 15 miles of the north side of the island, however, are predominantly bulls (98 per cent) which appear to be the bulk of the former advance guard now lingering behind the rest of the population.

As noted above, the passage through Bering Strait commences earliest on the west side, and is not evident on the east side until sometime after the middle of May. This is to be expected, for there is an earlier breakup on the Siberian side (Goodman, et al, 1942). "Bimodal" migration through the eastern half (Brooks, 1954, p. 7) is undoubtedly a result of ice conditions between St. Lawrence Island and the Alaskan and Siberian mainlands, for the Strait of Anadyr breaks up earliest, and the distance that herds must travel from there to Bering Strait is much less. Thus the first migrants are animals which have come through the Strait of Anadyr, and the second wave those moving up from Bristol Bay and the St. Matthew-Pribilof region, along the Alaskan coast.

At King Island, Diomedes, and Wales the first animals observed are females with juveniles and young, followed by a mixture of adults and immatures of both sexes, and finally by a few old bulls (Bailey and Hendee, 1926; Brooks, 1954; Heinrich, 1947; W.E. Rasmussen, in litt.; A. Nagozruk, Sr., voc. com.). By the end of the month some may be as far north

as Point Hope (J.D. O'Donahue, in litt.) or Icy Cape, in the case of an early breakup such as was experienced in 1954 (Ryder, 1954; R.F. Gray, in litt.).

Two southern concentrations of bulls are recorded during May, one in the vicinity of Hagemeister and the Walrus Islands in Bristol Bay (Brooks, 1954), and the other deep in the Gulf of Anadyr near Kresta Bay (Belopolsky, 1939). The former was estimated to contain about a thousand animals in 1953, and apparently remains in the same region throughout the summer.

June

By the first week of June the sea south and east of St. Lawrence Island is ice free, but much still remains along the Siberian coast in St. Lawrence Bay, the Gulf of Anadyr, and in patches as far south as Karaginskoi Island (Jackson, 1896; Nikulin, 1940; Transehe, 1925), probably due to the colder coastal waters found in that region (Goodman, et al, 1942). The last of the migrating herds are observed passing the east and west ends of St. Lawrence Island at this time, those to the west being females and those to the north males. Within the second week they have all passed by King Island (W.E. Rasmussen, in litt.), and by the third week most of the final migrants have swum through the east side of Bering Strait (Brooks, 1954; Heinrich, 1947). On the west side the migration is completed by the end of the month when the ice is finally gone

(Nikulin, 1940). Big and Little Diomede Islanders state that the greatest proportion of the herds pass through the west side, and a few late stragglers are sometimes seen in the Strait (both sides) as late as July (Heinrich, 1947; Nikulin, op. cit.). Eskimos at St. Lawrence Island state that many females haul out on the beaches north of Cape Chaplino in June.

To the north, large herds are reported near Wrangell Island and Long Strait by the end of the month, while at Cape Serdtse Kamen and Point Hope the animals are seen for the first time in large quantities near shore (Nikulin, 1940; Rainey, 1947; J.D. O'Donahue, in litt.). This lag between occurrence at sea and observation near land appears to be the rule throughout the entire migration and may be due to less favorable ice conditions inshore. In the southern extremities, in addition to the Bristol and Kresta Bay herds noted above, small groups are sometimes found near Karaginskoi Island, and other larger herds have been reported south of Cape Navarin and along the north side of the Gulf of Anadyr near Cape Bering (Nikulin, op. cit.). Apparently these are all bull herds, though Belopolsky (1939) states that females and young appear with the bulls at Kresta Bay in June and July.

July-August

During July the northward movement is completed in the Chukchee Sea. Most of the migrants (particularly females

and young) have progressed northwestward from Bering Strait and are abundantly distributed (Fig. 5) off the northeast coast of Siberia as far west as Long Strait and amongst the ice south of Wrangell Island (Nikulin, 1940; Transehe, 1925). In the days of heavy commercial exploitation by American ships, this was the preferred hunting area, according to Collins (1940) and Nikulin. As the ice deteriorates and retreats northward in August, the herds advance slightly to the region about Wrangell and Herald Islands, and some have been observed by Nikulin near the mouth of the Kolyma late in the month.

On the Alaskan coast, inshore records are common near Icy Cape, Wainwright, and Barrow in July and early August (Bailey, 1948; Bailey and Hendee, 1926; Brooks, 1954; Collins, 1940; Rainey, 1947; Ryder, 1953a; R.F. Gray, in litt.). At Wainwright the bulls appear first, followed a few days later by the cows (R.F. Gray, in litt.), while at Barrow the animals observed are nearly all bulls (Brooks, 1954). By mid-August the coast is generally ice-free at least to Point Franklin, and walruses are no longer seen near shore. Although herds and individuals were formerly encountered as far east as Banks Land and the Baillie Islands (Anderson, 1937; Clarke, 1944; MacFarlane, 1905; Porsild, 1945), none was observed by vessels operating east of Barrow in 1952 (McAllister, 1953), 1953 (Ryder, 1953a), or 1954 (F. Neave, in litt.).

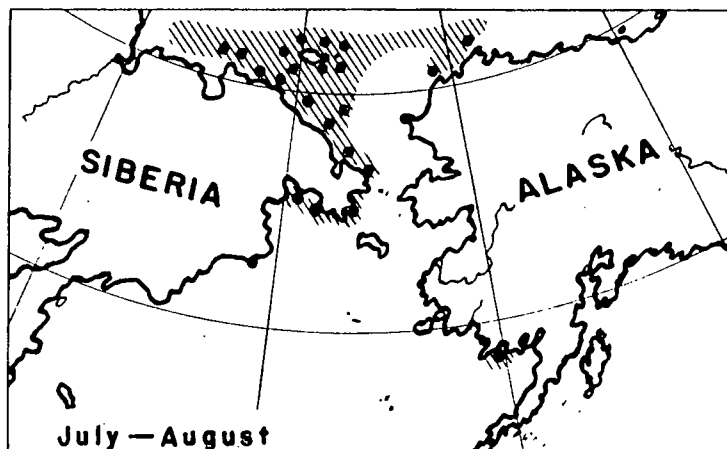


Fig. 5.--Distribution in summer

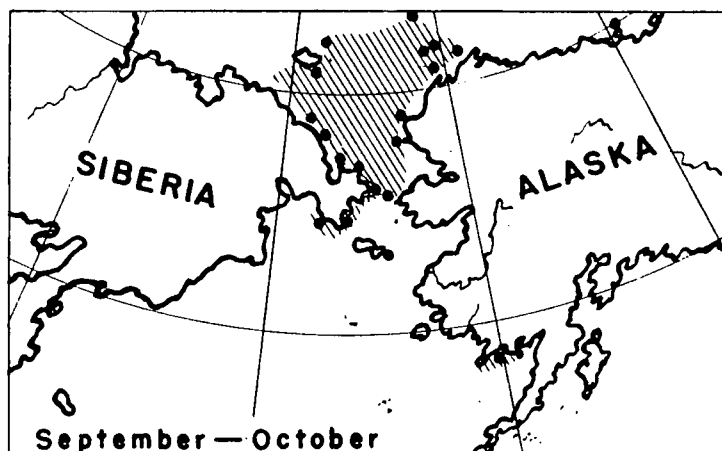


Fig. 6.--Distribution in early fall

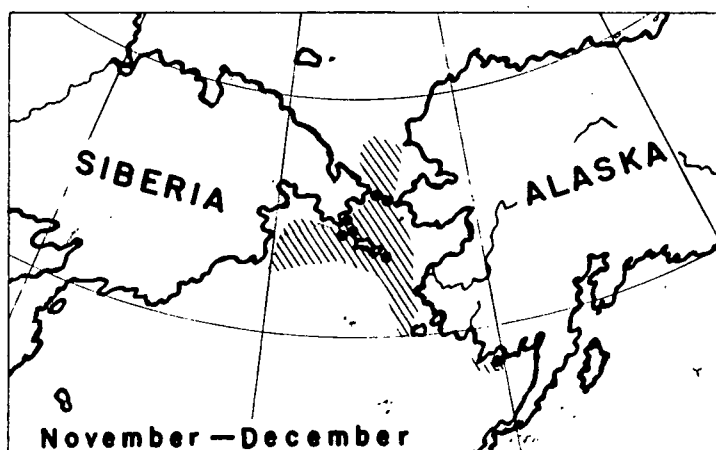


Fig. 7.--Distribution in late fall and early winter. Dots are recorded observations; crosshatching represents probable range occupied by the bulk of the population.

To the south, ice remains along the Siberian Coast from Kresta Bay to St. Lawrence Bay until late July or August (Jackson, 1896; Nikulin, 1940; Transehe, 1925), and with it walrus herds also remain. When this ice finally melts, the Kresta Bay group moves slightly eastward to the beaches at Meyecheken Island and Achchen where they haul out in locations regularly occupied at that time each year. Other regular hauling grounds for semi-stationary summer herds are located at Arkamchechen Island, Cape Inchoun (near C. Dezhnev), and Cape Serdtse Kamen. There is apparently some intercommunication between all of these in the late summer and early fall, while throughout the summer period additional herds and individuals of irregular occurrence are observed along the entire coast from Cape Navarin to Cape Billings, according to Nikulin (1940) and Siberian Eskimos now living at Gambell. On the Alaskan side of the International Date Line a few individual strays are also reported along the coast and about the islands, but the abundance of these, compared to those on the Siberian shores, appears to be relatively insignificant. At present only one regular semi-stationary summering herd (Walrus Islands) is known to occur in Alaskan waters, and like its Siberian counterparts, it is composed wholly of bulls (R. Mahaffey, in litt.). Herds have apparently occupied this same locality throughout historic times though they have varied, quantitatively, during this period.

"Resident" herds such as this formerly occupied regular hauling grounds on the Pribilof and St. Matthew Islands (Elliott, 1882; Hanna, 1920, 1923; Preble, 1923) but were apparently wiped out by the commercial ivory hunters many years ago. None but an occasional lone individual has been seen in either locality in recent summers (Wilke, 1942; C.A. Barnes, voc. com.; E.B. Elliot, voc. com.; R. Rausch, in litt.). Small summering herds (either or both sexes) are said to occur about the Penuk Islands (lat. 63° N, long. 169° W), but none was observed there in 1952 or 1953.

At Capes Thompson and Lisbourne, both near Point Hope, herds of varying sizes and either sex formerly remained in the same vicinity during July, August, and September, according to local Eskimos, and transient herds often stopped there in the fall to rest on the beaches. Within the past four years, however, the summer residents have not been seen, and transients are apparently very infrequent. Local opinion attributes this to an increase in aircraft traffic along the coast.

September

The distribution during September (Fig. 6) resembles that which is observed in August, the main differences being the records of "farthest north" and the beginning, late in the month, of southward migration. The farthest north observation was recorded on September 5, 1951, when two walruses were seen hauled out on the edge of the Arctic pack at lat. $75^{\circ}52'N$,

long. $164^{\circ} 15' W$ (C.A. Barnes, voc. com.). These were probably a cow and calf or yearling, for one was about twice the size of the other. Two other loose aggregations of 30 and 200 animals have been recorded at about lat. $73^{\circ} N$, long. $161^{\circ} W$ by Barnes in 1951 and by observers on the H.M.C.S. Labrador in 1954 (A. Loughrey, in litt.), respectively. In addition to these, a few have been observed between Barrow and Icy Cape by Ryder (1953a) and R.W. Niesz (in litt.), and Nikulin (1940) has indicated "thousands personally observed" off the southeast coast of Wrangell Island. In the last half of the month the vanguard of southgoing herds is sometimes seen near Point Hope (J.D. O'Donahue, in litt.) and even as far south as Bering Strait (Heinrich, 1947).

October

There are few records for this month, except those from the Siberian coast given by Nikulin. O'Donahue indicates that some are occasionally seen near Point Hope in the first half of October, but none was observed anywhere along the Arctic coast of Alaska by personnel of the U.S. Coast Guard icebreaker Northwind, returning from the Beaufort Sea in 1954 (F. Neave, in litt.).

New ice begins to form in the regions north of $70^{\circ} N$ lat. about the middle of the month, and strong northerly winds begin to blow in the Chukchee, driving the new and old ice southward. The general pattern of walrus movements is rather problematical with such a dearth of data, but Nikulin's

suggestion that they proceed southward well off shore, with and ahead of the ice, seems most logical, for they are seldom seen until they reach Bering Strait. When the fall is warm, and the "freezeup" is late, the herds are said to mostly swim south at least as far as Bering Strait, where they sometimes haul out in great numbers at Cape Deznev (East Cape), Big Diomed Island, and other places along the Siberian coast in October and November (Heinrich, 1947; Nikulin, 1940).

November-December

The fall migrations observed from Little Diomed Island by Heinrich (1947) seemed to lack the purposiveness of the spring movement, for herds were seen passing either north or south from September to December, inclusive, and those which went ashore at Big Diomed sometimes basked there for as long as a week. However, a strong southward movement through the Strait was noted in November, during which time the animals were very noisy and mostly in the water, swimming.

The herds usually arrive in the vicinity of St. Lawrence Island late in November (Fig. 7). Bulls are the first to appear (swimming) and they are followed in early December by a mixture of herds, most of which are cows, according to Eskimo informants. At this time the animals are known occasionally to haul out in certain places along the north side and regularly on the Punuk Islands, sometimes in sufficient quantities to nearly cover the north island which

is about 30 acres in area. The latter are said to consist of both sexes, the bulls being particularly vociferous and aggressive. This was interpreted by two informants as breeding behaviour, though it is highly improbable that any breeding occurs in the fall months.

By late December very few are seen passing Gambell, and the winter pack ice is well formed. It is presumed that the regular wintering distribution pattern is achieved by mid-January.

DISCUSSION

General Features of Distribution

The spatial ecology of walruses, judging from the preceding account and what little is known of their occurrence in other parts of the world, can be resolved into four major components, all of which must be present at the same time. These are food, air, haul-outs, and suitable air temperatures. It is quite obvious that food and air must be available at all times for mere existence. Thus, of necessity, the majority of the "Pacific" population is limited to regions south of the relatively unbroken Polar pack ice in summer and south of the Chukchee and North Bering Sea pack in winter, for there are few localities in the northern regions where ice is sufficiently loose to permit access to both sea and air at will. Walruses are capable of making and maintaining breathing holes under

certain conditions (Vibe, 1950) but generally retire to regions of less ice stress when possible.

The need for haul-outs further restricts the range by necessitating close juxtaposition to either land or ice. In the Western Nearctic ice appears to be preferred -- at least it is occupied most frequently. In the Eastern and Palearctic, land seems to play a more important role as a summer hauling ground, but even there Johansen (1910), Neale (1882), and Zalkin (1937) have suggested that ice is preferred when conditions are not unfavorable for its use. These conditions involve the distribution of food. Throughout the holarctic range of walruses, the foods most often utilized consist of six genera of pelecypods (Mya, Saxicava, Cardium, Clinocardium, Astarte, and Macoma) which inhabit Arctic, Subarctic, and certain North Temperate seas at depths ranging from the littoral zone to about 50 fathoms (Allen, 1880; Brooks, 1954; Johansen, 1910; Keen and Frizzell, 1939; Nikulin, 1940; Pratt, 1935; Soot-Ryen, 1939; Vibe, 1950; Zalkin, 1937). This means a drastic reduction in the potential range (Fig. 8), especially in the eastern and Palearctic region, much of which is characterized by precipitous coastlines and deep fjords. Unless ice is in close proximity to the few shallow areas where food species occur, land must be used for haul-outs. Exceptions to this rule occur, but when the animals are located over deeper water, they either starve or feed upon some alternative prey such as the larger

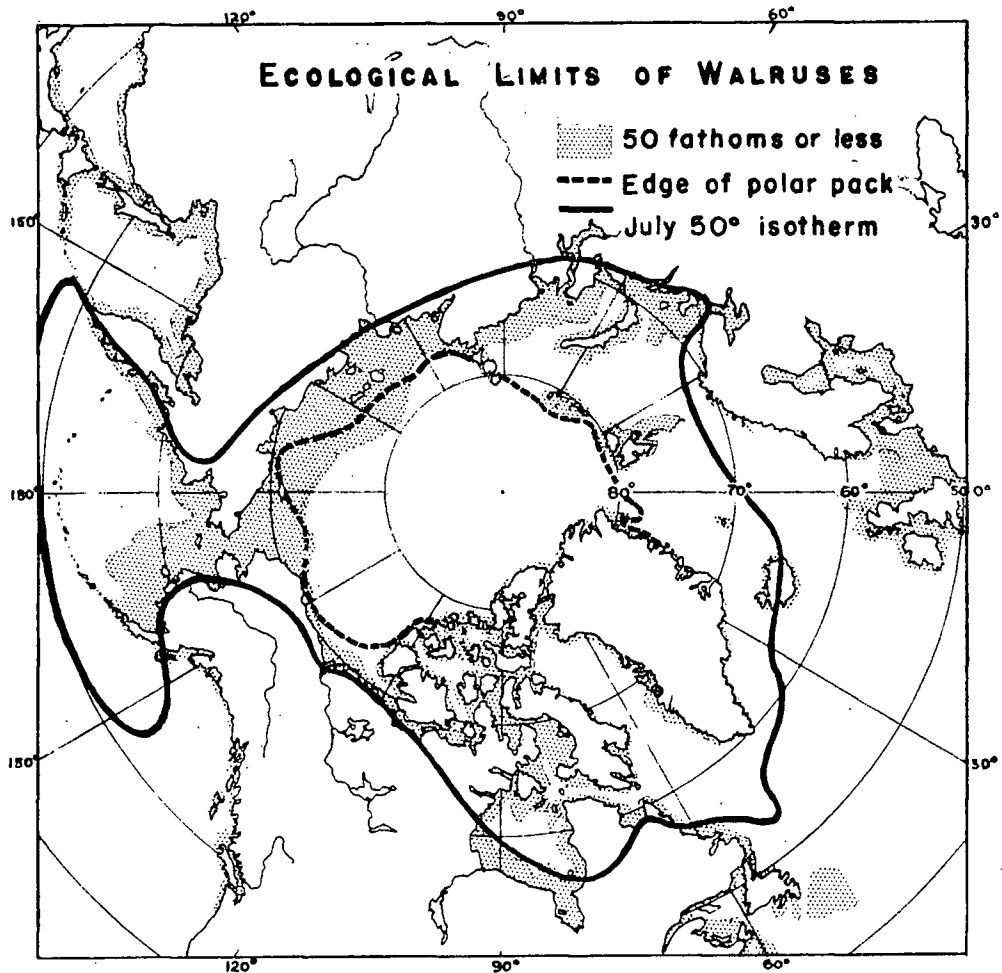


Fig. 8.--The general physical boundaries of holarctic walrus distribution in summer. The potential range lies within waters of 50 fathoms or less, north of the 50°F monthly mean isotherm, and south of the polar pack edge.

plankters and/or other marine mammals (Chapsky, 1936; Vibe, 1950; Zalkin, 1937).

The type of ice used as a haul-out seems to be of little importance except that its upper surface should be close enough (2 feet or less) to the water line for ease of access, and it must be strong enough and large enough to hold its potential occupants. Of the physical properties of land haul-outs, beach materials appear to be of no consequence, at least in the Bering-Chukchee and Kara Sea (Chapsky, 1936) regions. Anything from boulders to sand or turf is suitable. So far as the writer is aware, however, regular land haul-outs are generally located close (0-5 miles) to 10-fathom water and near or adjacent to high promontories. The latter probably serve as landmarks for navigation, since most of the Alaskan west coast north of lat. 60°N is elevated only slightly above sea level and is quite invisible from a few miles offshore. A swimming walrus, whose horizontal line of vision is highly restricted, would, if he were in need of a rest, be expected to swim towards any visible indication of land, viz. a geographical feature jutting above the horizon. Similarly, the consistently close relationship between the hauling grounds and 10-fathom water is probably a matter of convenience, since it is more likely that the animals would find their way back to the same beach if the feeding area was not too far distant from it.

The southern limit to distribution appears to be

defined by temperature, though it is not possible at present to decide whether this is cause or effect. On the basis of food distribution, walruses would be expected to occur southward along the coasts to California, China, France, etc., yet within historic times they have been very exceptionally recorded south of 65° N lat. in Europe (Mohr, 1940), 52° N lat. in the North Pacific (Allen, 1880; Turner 1886; Golder, 1922) and 43° N lat. in eastern North America (Allen, 1880; Dunbar, 1954). An examination of the recent climatological data for Alaska (U.S. Weather Bureau, 1951-54) reveals that the monthly mean temperatures experienced by walruses near the coastal and insular stations are between 0° and 50° F, the mode being about 20° F. Daily extremes of up to 80° F may occur in the southern fringes of their present range (i.e. Bristol Bay), but the majority probably never experience daily temperatures warmer than 50° - 60° F. South of the Alaska Peninsula, particularly along the "Panhandle" and northern British Columbia, monthly mean winter temperatures (15° - 40° F) appear to be well within the range of walrus tolerance, but in summer they are slightly higher (50° - 60° F). If temperature is the limiting factor as it seems to be, then the southern limit of distribution appears to be at about the level of the 50° July isotherm (Fig. 8). Certainly all of the present world populations of walruses occur well within this boundary.

Migrations

The regularity and apparent purposiveness with which

the seasonal migrations occur indicate that there is an innate and/or learned behaviour pattern directing the process. Although ice movements, influenced by winds and surface currents (Fig. 9), tend to parallel the peregrinations of walruses, they evidently are not directly involved in the causative mechanism, for it has frequently been observed that animals will swim towards their goal when ice is in apposition.

Ice is often utilized as a haul-out during migration regardless of the direction in which it is oriented, but the writer's impression from observations at Gambell is that floes proceeding northward in spring are more often occupied than those which are drifting southward.

As Brooks (1954) and Nikulin (1940) have noted previously, females are the most actively migratory, males in general being more apathetic and subject to irregularities of ice drift. Undoubtedly this accounts, in part at least, for the occurrence of bull herds in the southern extremes of summer range, for these lingering animals are found in regions where sea ice persists long after the rest of Bering Sea is ice-free. At St. Lawrence Island, for example, a few bulls can usually be found amongst the brash and floes caught in certain north-side bays two or three weeks after the last migrants and drift ice have passed Gambell. This, most certainly, is the explanation for bull aggregations on the Siberian coast in summer, judging from the literature, and though there are no specific data on this phenomenon for the Bristol

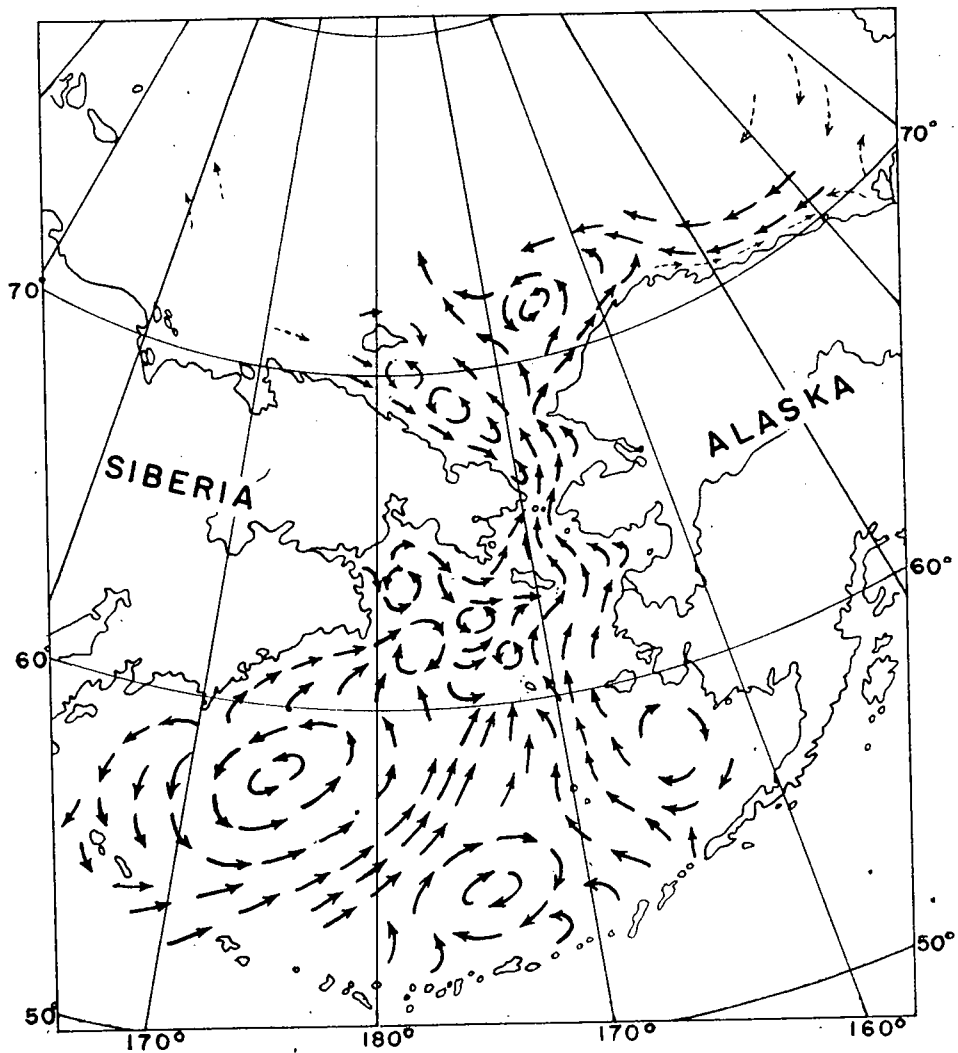


Fig. 9.--Surface currents: Bering, Chukchee, Beaufort, and East Siberian Seas. Data from Goodman, et al (1942), LaFond (1954), Mineyev (1946), and Sverdrup (1928).

Bay herd, it is presumed to be the case there as well. Perhaps the choice of certain land haul-outs after the ice has melted is partly due to learning as well as the other factors mentioned above.

East-west limits of the summer range appear to be governed by the Polar pack, the direction of ice drift, and food. Except in late summer and early autumn, the passages along the Siberian coast at Cape Shelagsky and the Alaskan coast at Point Barrow are largely blocked by the pack. There are open leads and channels through which the animals could pass to the west and east, but in the latter instance offshore currents and food conditions appear to be relatively adverse. Recent oceanographic investigations (LaFond, 1954; W. Cameron, voc. com.) indicate that along the Arctic coast of Alaska there may be a weak coastal current towards the east, but offshore the tendency is for clockwise rotation in the Beaufort Sea with a convergence of easterly and westerly currents at about the region of Point Barrow (Fig. 9). The latter, together with general clockwise drift of the Polar pack (Crary, et al, 1952; Koenig, 1952) would be expected to direct walrus movements towards the north and west, rather than east, once they had reached Barrow. According to the Eskimos of Wainwright and Barrow (R. Gray, in litt.), this is the observed pattern of their movements.

Several observers (Anderson, 1913; Bailey, 1948; McAllister, 1953; F. Neave, in litt.) have noted that birds

and seals are scarce along the Alaskan coast east of Barrow, and surveys in 1950-51 (M.W. Johnson, in litt.) have revealed many more larvae of benthic invertebrates in the Chukchee than in the Beaufort Sea, though this apparent difference is not necessarily a constant one (F. Neave, in litt.). All of these indicate a much lower productivity east of the "Barrow convergence," presumably due to physico-chemical properties of the water (the eastern Chukchee is warm and saline; the Beaufort cold and brackish, according to Tully, 1952).

In the west there appear to be similar current complications (Fig. 9), though Sverdrup (1928) concluded that ice drift along the North Siberian shelf was due entirely to wind and that no permanent currents existed. Walruses, in small numbers at least, do penetrate the East Siberian Sea, according to Nikulin (1940) and Ognev (1935). The pelecypod fauna, however, seems to be rather poor in comparison to the Chukchee (Soot-Ryen, 1939), and may be another factor controlling walrus abundance in that region.

Range Reduction

There has been much speculation upon a cause for the more restricted distribution of the present population as compared to the past. There are three general theories: (a) overall decimation of the population, (b) decimation of the more accessible elements of it, i.e. the southern herds, and (c) climatic changes. In all probability it has been

brought about by all of these and possibly some other more subtle ones. The "shrinkage" is evident in all of the former fringe areas. Some animals are occasionally seen in most of them but they are less abundant than they were 100 years ago, indeed 50 years ago. This of course, points to overall destruction. The disappearance of the Pribilof summering herd was diagnosed by Elliott (1882) as the work of commercial ivory hunters, and no doubt this was the fate of the St. Matthew herd as well. If it were not, they would have been expected merely to decrease in quantity, rather than disappear completely. Finally, climatic changes would bring about alterations in the physical and biological properties of the environment, the effects of which would be most noticeable on the fringes of the range. There are some indications of climatic amelioration during the past 2-300 years (Dunbar, 1954) which may have resulted in a slight northward shift of the southern temperature tolerance limit of walruses.

PART II
LIFE HISTORY

The basic features of life history are fundamental to a study of animal population, for they are the mechanisms of productivity and reflections of environmental resistance. The most significant recent contributions to Pacific walrus life history are those of Brooks (1954), Freimann (1940), and Nikulin (1940), to which might be added the papers of Collins (1940) and Heinrich (1947), whose observations offer many helpful clues to the unsolved problems. Chapsky (1936), Vibe (1950) and others have contributed basic information on Atlantic walruses. These, plus many lesser contributions, are largely supplementary to one another, each adding structural members to the framework of knowledge; yet, among them there is a degree of disunion which renders the structure unstable. In an effort to rebuild and strengthen this framework, the writer expended most of his field time and effort in the pursuit of empirical proof of earlier theories and points of dissension.

Much of the information on breeding and birth has been gained from examining reproductive organs, the bulk of which were collected by Eskimo cooperators prompted by monetary compensation. These specimens have also contributed much to the analysis of growth, supplemented by a large series of other morphometric data secured by the writer and James W. Brooks. Except in the following paragraph, all age

designations are based upon the writer's interpretation which is elaborated in the section on "GROWTH" (p. 77 et seq.).

REPRODUCTION

Sexual Maturity

Males.--The Eskimo hunters at Gambell stated that bulls are sexually mature at four years of age, and Vibe (1950) reports a similar opinion among Greenlanders in the Thule district. Chapsky (1936) suggests maturity at five, while Belopolsky (1939), Freimann (1940), Freuchen (1935), and Murie (in Asdell, 1946) say five or six. Brooks (1954) is non-committal, but doubts that puberty is reached in the fifth year. Perhaps each of these authorities is correct within his own realm, since the basic difference between them lies not in the determination of which bulls are mature but in assigning an age to the animals examined.

The materials utilized in the present approach to this problem consisted of 106 testis pairs, each of which was accompanied by tusk measurements or tooth specimens for age reference. These were prepared in the field by removing the tunica vaginalis and epididymys after which the main testicular body was measured to the nearest millimeter and weighed to the nearest gram. Tissue samples from these, excepting the majority of calves', were fixed in a formol-acetic solution and later sectioned for histological examination. Table 1 lists the resulting data on spermatogenesis.

TABLE 1

A HISTOLOGICAL COMPARISON OF TESTIS
DEVELOPMENT WITH AGE AND SEASON

Spec. No.	Age	Date	Spermatogenic Cell Types*						
			Sptg	P.Spc	S.Spc	Sptd	Spz	Sert	Giant
A- 73	0	May	xxx						
A- 72	1	June 2	xxx						
A- 23	2	May 23	xxx	x					
A- 26	2	May 24	xxx	x					
A- 32	2	May 25	xxx	x					
A-458	3	May 11	xxx	xxx				x	
A-303	3	May 28	xxx					x	
A-324	3	June 2	xxx	xx				xx	
A-106	3	June 8	xxx	x				x	
A-277	4	May 25	xxx	xxx				x	
A-248	5	April 26	xxx	xx	xxx	xxx	xxx	x	
A-272	5	May 15	xxx	xxx	xxx	xx	xx	x	
A-280	5	May 25	xxx	xxx	xxx	x	x	x	
A-318	5	June 2	xxx	xxx	xxx	xx	x	x	x
A-266	6	May 12	xxx	x	xxx	xx	x	x	
A- 14	6	May 21	xx	xxx	xxx	xx	x	x	
A- 28	6	May 24	xx	xxx	xxx	xx	xxx	x	
A-276	6	May 25	xxx	xxx	xx	x		x	
A- 64	6	June 2	xx	xx	xxx	xxx	xxx	x	
A-322	6	June 2	xx	xx	xxx	xx	xx	x	
A-244	7	April 20	xx	xxx	xxx	xxx	xxx	x	
A- 10	7	May 21	xxx	xxx	xxx	xx	x	x	x
A-278	8	May 25	xxx	xxx	xxx	xx	xx	x	
A-279	8	May 25	xx	xxx	xxx	xxx	xx	x	
A-243	9	April 20	xx	xxx	xxx	x	x	x	
A- 31	9	May 25	xx	xx	xxx	xxx	xxx	x	
A-282	10	May 24	xx	xxx	xxx	xxx	xx	x	
A-246	>10	April 22	xx	xxx	xx	x		x	
A-245	>10	April 23	xx	xx				xxx	
A-254	>10	April 24	xx	xxx	xx	x		x	
A-253	>10	April 26	xx	xxx	xx	x	x	xx	
A-260	>10	May 12	xxx	xx	xxx	x		x	
A- 29	>10	May 24	xxx	xxx	xx	x		x	
A-275	>10	May 25	xxx	xx	x			xxx	
A-283	>10	May 25	xx	xxx	xxx	xx	xxx	x	
A-284	>10	May 25	xxx	xx	xxx	x		xxx	x
A-285	>10	May 25	xx	xxx	xx			xxx	
A- 71	>10	June 2	xxx	xxx	xx	x		xx	
A-122	>10	June 6	xxx	xxx	xx			xxx	x

*Sptg - spermatogonia; P.Spc - primary spermatocytes;
S.Spc - secondary spermatocytes; Sptd - spermatids; Spz -
spermatozoa; Sert - Sertoli cells; Giant - giant cells

x = few; xx = common; xxx = abundant

While the presence of sperms in the seminiferous tubules is not necessarily an indication of breeding ability, it at least establishes a limit below which no breeding can occur. The youngest animals with sperms in their testes were the 5-year-olds, though it may be argued that the single 4-year-old specimen is not a sufficient representation of his age class. Ninety-four per cent of the specimens from five to ten years, inclusive, were fecund (fecundity is used here in reference to the presence of spermatozoa, hence the potential ability to produce mature gametes), while those over ten years were only 16.5 per cent fecund -- a highly significant difference in proportions. The seminiferous tubules of the older animals were mainly characterized by empty lumina and abundant Sertoli cells, which are associated with senility and cryptorchidism in humans (Maximow and Bloom, 1948, p. 521). From these data it has been concluded that the potentially effective population of breeding males probably consists of animals under fifteen years of age. Possibly the apathy in migration exhibited by old bulls is correlated with their relatively degenerate gonads. The Bristol Bay summering herd, for example, appears to be mainly old males.

Full maturity appears to occur between six and eight years, judging by Freimann's (1940, Table 5) analysis of progressive development of secondary characters (thickened and "warty" skin), and it is further indicated by the attain-

ment of full adult testis dimensions by age six or seven (Fig. 10 and Table 2). There are no indications of seasonal fluctuations in testis size, though this possibility has not yet been thoroughly investigated.

Females.--The literature is in essentially the same state of disagreement about sexual maturity of the cows as it is of the bulls, but again it is largely a matter of age determinations. The writer's material consisted of twenty-eight reproductive tracts from animals one year old or older, plus a large sample (51) from newborn calves for comparison. In the field the uteri were measured and examined for evidences of placental scars or recent implantations, after which they were discarded. The ovaries were preserved in formaldehyde and were later sectioned in the laboratory into serial 3mm.-thick slices for macroscopic inspection. Brooks supplied twenty-two additional pairs for this phase of the work.

Of all the calf ovaries, only two bore follicles of macroscopic dimensions, those being about 0.5 to 1 mm. in diameter and very sparsely distributed. Two yearling pairs were comparable to the calves', only a few follicles of 1 to 3 mm. diameter being visible. In the four pairs of 2-year-old ovaries considerable advancement was apparent, with large numbers of follicles up to 6 mm. in diameter crowded into the cortex and appearing externally through the tunica as small translucent bubbles. Atresia, indicated by cloudy liquor folliculi (Allen, et al, 1930), was very prevalent,

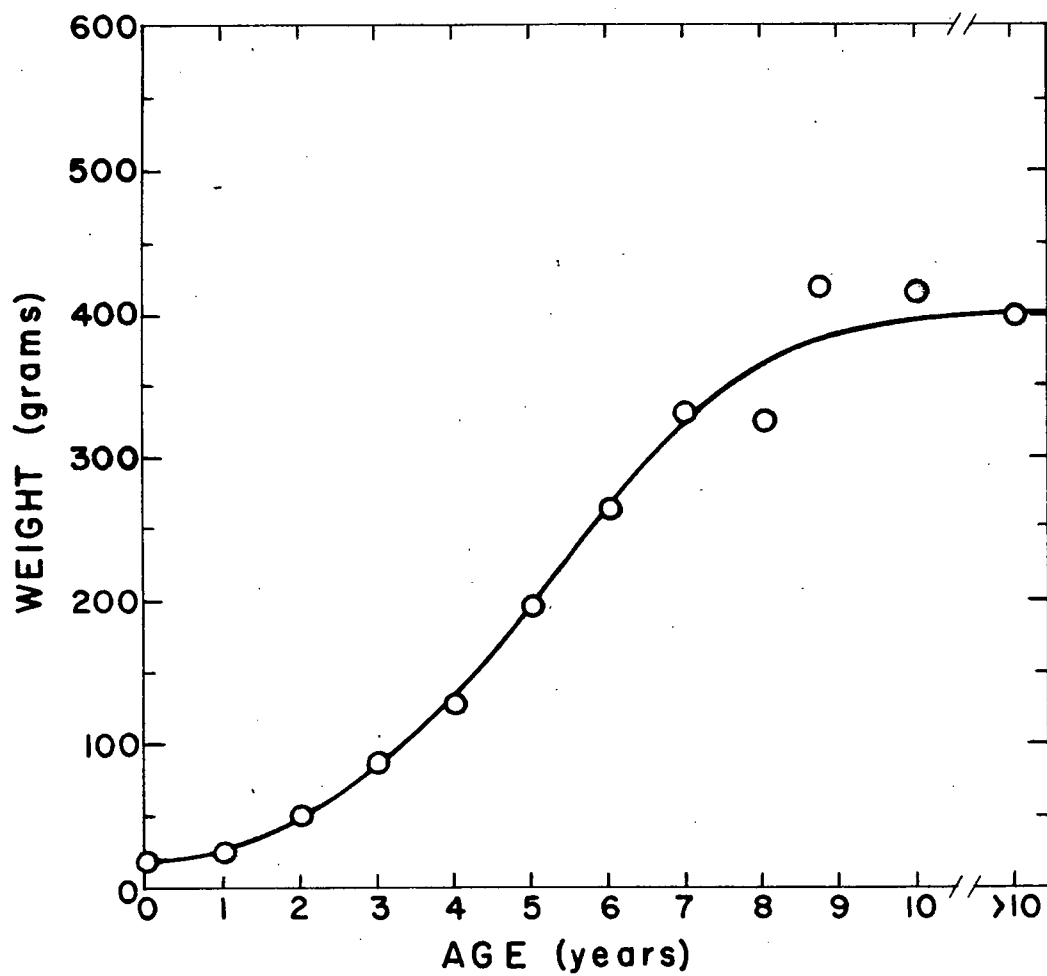


Fig. 10.--Average testis weight growth of Pacific walruses. Open circles are mean values given in Table 2.

TABLE 2
TESTIS LENGTHS AND WEIGHTS

Age (years)	Length (mm.)			Weight (grams)		
	No.	Range	Mean \pm S.E.	No.	Range	Mean \pm S.E.
0	64	60 - 88	73.2 \pm 0.3	64	13 - 26	18.4 \pm 0.1
1	3	73 - 91	82.5 \pm 5.3	2	20 - 29	24.5 \pm 4.5
2	5	105 - 112	109.2 \pm 1.2	5	44 - 58	50.4 \pm 3.0
3	4	113 - 135	127.0 \pm 5.2	4	64 - 98	89.0 \pm 8.4
4	1	130	1	130
5	4	135 - 170	155.0 \pm 8.4	4	115 - 275	197.5 \pm 18.2
6	6	150 - 197	176.5 \pm 7.7	6	191 - 322	265.2 \pm 19.6
7	2	178 - 195	186.5 \pm 8.5	2	250 - 415	332.5 \pm 82.7
8	2	203 - 220	212.5 \pm 8.5	2	325 - 330	327.5 \pm 2.5
9	2	205 - 206	205.5 \pm 0.7	2	408 - 433	420.5 \pm 12.6
10	1	225	1	417
>10	12	153 - 227	190.3 \pm 7.0	12	256 - 565	399.4 \pm 24.5

about one-third of the visible follicles being in various stages of degeneration.

The only pair of 3-year-old ovaries examined by the writer was identical in appearance to the 2-year-olds', the largest follicle measuring 5 mm. in diameter (as opposed to the 10-30 mm. diameter of Graffian follicles in adults). Four others of this age recorded by Freimann (1940, Table 3) bore no embryos in the uterus, and thus had probably not ovulated, though he does not specify this.

Within the 4-5 year group all the animals examined by Brooks and the writer were either newly impregnated or had borne their first calf in the current season. The youngest pregnant animals recorded by Freimann also fall within this group. Thus it is probable that most of the females are sexually mature at 4 years of age, though some may not mature until later.

Lowered productivity in later years has been briefly demonstrated in tabular form by Freimann (1940, Tables 2 and 3) and exemplified by Eskimo reports that "very old" females are occasionally barren. Four animals which fitted the latter's description (i.e., tusks heavy and worn short, yellowed, and cracked) were examined by the writer, two of which had borne calves in the current season, the third had borne one the previous year and was not oestrus, and the fourth displayed a fresh corpus luteum verum in one ovary though no implantation was macroscopically evident. The abundance of

developing follicles in the ovaries of the first was comparable to younger adults; in the second and third they were sparse; and in the last only three could be found, each of which was atretic and measured less than 1 mm. in diameter. These specimens are mentioned only as examples of relative ovarian histology, for the proportion of fertile to infertile animals suggested by them is not representative of old animals in general (see below, p. 57 et seq.). Their non-representation is due to Gambell hunting policy, which stresses the capture of only those cows accompanied by newborn young.

Breeding Season and Location

The only direct observations of copulation are a few recorded by Brooks (1954) for May and June in Bering Strait, and July at Barrow. Russian literature contains no mention of breeding observations. Information solicited by questionnaire from Nunivak Island, Hooper Bay, Shaktoolik, King Island, Point Hope, and Wainwright yielded negative reports, and personal interviews with natives at St. Lawrence Island, Wales, Diomedes, Point Hope, and Wainwright also were negative. Near a herd of cows and young on May 21, 1954, (lat. 67°56'N, long. 168°43'W) Ryder (1954) observed an adult bull which was decidedly more sluggish than others in the vicinity, and which lay on its back on an ice floe until the ship approached to within fifty feet. "Since the penis of this bull was partly unsheathed, ... he may have been spent from breeding efforts, although no females were noted

alongside him."

The indirect evidences of breeding season are, fortunately, more numerous. These may be classified into four groups: (a) testicular development, (b) ovarian cycles, (c) foetal growth, and (d) birth dates.

Testicular development.--During the period April 20 to June 6 there was no significant change in the proportion of fecund to non-fecund males (2:1). Nevertheless, the production of "giant cells" (Maximow and Bloom, 1948, p. 521) in late May and June by a few specimens (Table 1) is believed to be an indication of seasonal degeneracy, a condition further indicated by Brooks' (1954) and Chapsky's (1936) specimens collected later in the summer (June through September). It seems probable that the testes undergo an annual cycle of spermatogenic activity with peak production in the spring months.

Ovarian cycles.--Sixteen pairs of ovaries from oestrus and early post-oestrus females were examined. These (Table 3) show a definite trend of ovulation date variability with age. By June 1, plus or minus a week, the youngest (under ten years) and oldest (over twenty years) animals had already ovulated at least once; all but one had formed a corpus luteum verum; and three had implanted embryos of macroscopic size. Conversely, none of the "middle-aged" females had ovulated in the last week of May. A full discussion of factors affecting age-ovulation sequence is given below (p. 64). In general these data suggest that most of the

TABLE 3
COMPARATIVE OVARIAN HISTOLOGY
BY AGE AND SEASON

Specimen Number	Age	Date	Ovarian Structures			Visible Embryo
			Ripening Follicles	Corpus Luteum Spurium	Corpus Luteum Verum	
B-201	4	May 24		x	x	
B-15A	4	June 2		x	x	
B-214	5	May 30			x	
B-35A	5	June 7			x	
B-34A	5	June 7			x	x
B-123	5-6	May 22			x	
B-12Q	5-6	June 2		x	x	
B-117	7	May 22	x		x	x
B-17A	7-8	June 2			x	x
B-25A	7-8	June 5			x	
A-42	>10	May 26	x			
B-114	13	May 22	x			
B-113	17-18	May 22	x			
B-200	20	May 24	x			
B-102	>20	May 22	x	x		
A-304	>20	May 28			x	

breeding occurs from April to June, inclusive.

Foetal growth.--Belopolsky (1939), Brooks (1954), and Chapsky (1936) recorded the crown-rump lengths of sixteen separate embryos and fetuses taken in summer and fall and estimated the conception dates for a few. Utilizing the measurements given by these authors, the writer has calculated the probable dates of conception (Table 4) by comparison with equivalent stages of human pre-partum growth (Appendix I). The results indicate that most were conceived prior to mid-May. In calculating the mean conception date and length of gestation period, the data from Brooks' specimens have been omitted. His were taken during the breeding season and apparently are representative of only the earliest breeders, for several other fertilized females taken at the same time had no macroscopic embryos.

While there may be serious objections to this technique on the basis of the animals compared (i.e., humans and walruses), its apparent correlation with observed ovarian development suggests that it is at least a close approximation of the truth.

Birth dates.--Though the length of the gestation period has not been precisely established, it has been calculated to be about 367 days (Table 4). On this basis, four newborn young and two full term fetuses examined by the writer could have been conceived about May 8, 11, 18, 19, 21, and 22. But the value of birth dates is mainly found in their chronological frequency which is an indica-

TABLE 4

CALCULATED CONCEPTION DATES OF
ATLANTIC AND PACIFIC WALRUS EMBRYOS

Source	Collection Date	Crown-rump Length (cm)	Per cent Full-term C-R Length ^a	Per cent Gestation Completed ^b	Days from Conception to Birth ^c	Calculated Total Gest. (days) ^d	Calculated Days Since Conception ^e	Conception Date
Brooks(<u>in litt.</u>)	May 22	0.6	0.59	9.2	374	412	35	April 17
Brooks(1954)	June 15	2.3	2.25	14.1	333	388	52	April 24
	June 16	1.7	1.67	13.0	332	382	48	April 30
Belopolsky(1939)	July 7	2.3	2.25	14.1	309	360	52	May 16
	July 7	2.7	2.65	14.9	309	363	55	May 13
	July 8	2.8	2.74	15.0	310	365	55	May 14
	July 18	5.2	5.1	18.2	300	368	67	May 12
Chapsky(1936)	Aug. 19	11.0	10.8	24.0	268	353	88	May 23
	Aug. 23	22.0	21.6	32.3	264	390	118	April 27
	Aug. 24	26.5	26.0	35.2	263	406	129	April 17
	Aug. 28	18.0	17.6	29.4	259	367	108	May 12
	Aug. 29	17.5	17.5	29.3	258	365	107	May 14
	Aug. 30	16.0	15.7	28.0	257	357	103	May 19
	Sept. 6	18.0	17.6	29.4	250	354	109	May 20
	Sept. 6	18.0	17.6	29.4	250	354	109	May 20
	Oct. 12	30.0	29.4	37.5	214	342	137	May 28
	Oct. 12	40.0	39.2	44.5	214	386	162	May 3
Mean of 14 (Belopolsky, Chapsky) ^f						366.6		May 13

- ^a Full term crown-rump length = about 102 cm. (average of 6)
^b Extrapolated from curve of equivalent foetal growth (App. I)
^c Average birth date = May 14
^d
$$\frac{\text{Days to birth}}{\text{Per cent gestation to be completed}} \times 100$$

^e
$$(\text{Mean of d}) \times \frac{\text{Per cent of gestation completed}}{100}$$

^f See text p. 44

tion of the time range during which breeding occurs. Since this subject is discussed in detail below (p. 52) it is sufficient to state here that the majority of births occur during May, but occasionally a few may be as early as February or March and as late as July or August. The mode appears to be slightly before the middle of May.

In summary, the few direct observations suggest that the breeding season extends from May to July, but indirect techniques indicate that most of the breeding occurs from April to June. During the latter period the animals are engaged in their annual northward migration and may be found anywhere between latitudes 60° and 70° N in the Bering and Chukchee Seas.

Breeding Behaviour

The social organization of walrus breeding activity has been speculated upon for a very long time. In most instances it was presumed to resemble that of its otariid cousins, which are characterized by a form of organized polygamy usually referred to as "harem breeding." The principal bases for this assumption were: (a) the apparent disparity in size between sexes, and (b) the occurrence of large on-shore herds at certain localities. Nikulin (1940) notes that "[Among mammals not a single systematic group is known where polygamy does not go hand in hand with sharply defined sexual dimorphism,]" but he failed to recognize that in a relative sense, the dimorphism displayed

by walruses is insignificant when compared to the otariids or to the harem-breeding phocids. The walrus is, in fact, a sort of intermediate between the relative monomorphism of most phocids and the strong dimorphism of otariids and elephant seals. This is demonstrated in Table 5 and is particularly evident in the contrasting forms of their respective growth curves (Fig. 24, p.107).

According to Nutting (1891, p. 103),

...polygamy...can properly only apply to those species in which a single male habitually copulates with several females, and jealously and persistently defends them from the approach of other males.

Bertram (1940) has observed that this polygyny could only exist where the animals are hauled out on land, since it would be impossible to defend a harem from intruders when in the water. Pacific walruses do not haul out on land in the spring when they breed, but are in the process of active south-north migration, spending much of their time swimming and the remainder on the ice. It is obvious that such a schedule does not lend itself to harem maintenance. Furthermore, an ice floe lacks long-term stability and would be difficult to defend unless it was of very broad dimensions. The writer's observations suggest that, in the selection of haul-outs, floe size is of no importance except that it be large enough to support the animals.

Without exception, persons who have been familiar with the Pacific walrus have observed the general tendency for monosexual aggregations, but "harems...have not been

TABLE 5
COMPARATIVE SEXUAL DIMORPHISM AMONG PINNIPEDS

Species	Authority ^a	Male Body Size as Per cent of Female	
		Length	Weight
<i>Phoca vitulina</i>	1,8,10	100 - 130	105 - 110
<i>Phoca hispida</i>	1,10	100 - 120	?
<i>Phoca groenlandica</i>	1,10	110	155
<i>Halichoerus grypus</i> ^b	1,10	130 - 135	?
<i>Erignathus barbatus</i>	1,10	120 - 145	?
<i>Cystophora cristata</i>	1,10	120 - 125	?
<i>Mirounga angustirostris</i> ^b	12	150 - 190	?
<i>Mirounga leonina</i> ^b	9,11	165	about 400
<i>Odobenus rosmarus</i>	1,3	120	?
<i>Odobenus divergens</i>	1,2,4,5	120	150
<i>Otaria byronia</i> ^b	6	130	?
<i>Eumatopias jubata</i> ^b	1,7,11	140	380 - 400
<i>Zalophus californianus</i> ^b	8	135	500
<i>Callorhinus ursinus</i> ^b	11	150	480
<i>Arctocephalus australis</i> ^b	1	135	?

^a 1-Bertram (1940), 2-Brooks (1954), 3-Chapsky (1936), 4-Fay, 5-Freimann (1940), 6-Hamilton (1934,1939), 7-Kenyon (1952), 8-Kenyon, et al (1954), 9-Laws (1953), 10-Mohr (1952), 11-Scheffer and Wilke (1953), 12-Townsend (1912).

^b Known to be polygynous

noticed even by those people who report seeing copulating walrus" (Brooks, 1954, p. 52). Both sexes are highly gregarious throughout the year, the cows forming up into groups whether bulls are present or not. The fact that bulls may encounter and join such groups does not constitute harem formation, for more than one bull may accompany a small cow herd. During the cruise of the U.S.S. Burton Island in May, 1954, Ryder (1954) recorded 57 separate groups of walruses between the Alaska Peninsula and Point Barrow, of which at least 16 were male herds, 18 were female herds, and 12 were bisexual (considering only the adults). The mean ratio of males to females in the latter was about 1:1, except in herds of fifty or more individuals where cows predominated. In the few bisexual groups observed by the writer near Gambell, the adult sex ratio was also estimated as 1:1.

Considering the circumstances under which breeding probably occurs, it seems most likely that males encounter females partly by chance and that no harem organization can exist. The so-called "breeding rookeries" referred to by Hanna (1923) were all-bull herds, while Eskimo and popular reports of breeding at Cape Lisbourne and the Punuk Islands seem untenable, since they occur in late summer and fall during anoestrus.

Under the conditions noted above, a single bull may copulate with several cows, but it is also conceivable that

a cow could be serviced by more than one bull. Thus, unless future investigations of walrus social behaviour prove otherwise, it must be concluded that the Pacific walrus is promiscuous, bordering on polygamous -- an intermediate between phocids and otariids. This social pattern may stem from an ancestral stock of on-shore harem breeders which were more sexually dimorphic than the modern genus. Certainly there is a strong potentiality for that form of behaviour to develop again should walruses be restricted to land haul-outs during the breeding season (e.g. by a warmer world climate).

Copulation has been observed very infrequently, and there are no descriptions of it. Brooks (1954) records one occurrence on the ice and states that the Diomedé Eskimos occasionally witness it in the water. It may seem incredible that the breeding act would be so seldom encountered if it was a common phenomenon during spring migration when the herds are so much in view, but to anyone familiar with these animals, it is no surprise. When they are on the ice, they lie upon, beneath, and between one another in such a mixture of bodies and appendages that it is exceedingly difficult for the observer to distinguish entire individuals, let alone sexes until they are alarmed by shots or by the nearness of hunters. In the melee that follows, the hunter's mind is generally occupied with thoughts of procuring meat and ivory rather than with satisfying his curiosity.

In addition, it is probable that copulation is a

very brief process, the chances being exceedingly slight that it would be observed whether on ice or in the water. In his studies of the northern elephant seal, Mirounga angustirostris, Bartholemew (1952) concluded that the main advantage of a large baculum or os priapi lies in the speed with which intercourse can commence. Because of the structural support offered by the baculum, no preliminary erection is necessary, and sexual contact may be accomplished as soon as a receptive female is found. Coitus is completed in three to seven minutes by the elephant seal (Bartholemew, op. cit.) and about six minutes by the Alaska fur seal, Callorhinus ursinus, (Bartholemew and Hoel, 1953). Since about two-thirds the bulk of a walrus penis is baculum, its copulatory activity may be equally as brief and inconspicuous.

Gestation

Estimates ranging from ten months (Vibe, 1950) to one year (Brooks, 1954, and others) have been suggested as the probable length of the gestation period. The writer's interpretations tend to support the latter. Utilizing data from the sixteen embryos mentioned above (Table 4), the mean calculated gestation is about 367 days. Although delayed implantation seems to be the rule with other pinniped groups (Fisher, 1954), there is no evidence of its occurrence among walruses. Nevertheless, it cannot be ruled out until further data have been obtained to demonstrate its

absence.

The corpus luteum verum remains large and fully luteinized throughout the gestation period. Degeneration and connective tissue invasion appears to begin immediately after parturition.

Birth

Season.--Opinions expressed by previous investigators are in general agreement that the young are mostly born between April and June, with occasional reports for other seasons. These have been mainly based upon implication and Eskimo statements.

The earliest birth recorded by the writer was inferred by the condition of a calf taken at Gambell on May 13, 1953. In color it was dark brown; the umbilicus was completely healed; and the points of the tusks were exerting pressure on the gums. Comparing it to Chapsky's (1936) and Nikulin's (1940) descriptions of young observed in mid and late summer, the animal was considered to be not less than two months old, placing its birth date in late February or early March. Such early births are apparently not common, for it was exhibited as a sort of curiosity by the hunter who had killed it.

Although several full-term fetuses were recorded in April (W. Caldwell, in litt.), no newborn calves were seen near Gambell from 1952 to 1955. Charles Slwooko, a local resident, stated that he heard one barking on April 23,

1953, and Nikulin also reports that a Cape Chaplino Eskimo found evidences of parturition in April. At least two out of twenty calves examined by the writer could have been born in that month.

Newborn young and fresh afterbirths were observed by Ryder (1954) on May 2 and again on May 21 amongst large herds of females, and the bulk of those observed and examined near Gambell appeared to have been born in the first three weeks of May. No full-term fetuses were observed at Gambell after May 26, and they are rare in the experience of Wales and Diomede hunters (late May, early June). Calculated parturition dates of nineteen females taken in May and June range from April 13 to June 1 with a mean of May 14 (Table 6).

Births in seasons other than spring are occasional, but probably cannot be considered common. Vibe (1950) states that the West Greenlanders talk of small calves being seen in any season, though he saw none except in May and June. Diomede Eskimos speak of "fall babies" (Heinrich, 1947), and R.F. Gray (in litt.) reports that "every year there are cases of calving in the summer and fall" noted by the people of Wainwright, Alaska. Heinrich also has "seen one in autumn that was too small to have been born the previous spring," while Zalkin (1937) observed a 96 cm. fetus in July. One taken at Gambell in February, 1953, was judged to be no more than six months old.

The probable explanation for early and late births appears to be closely connected with breeding frequency

TABLE 6
PARTURITION DATES

Specimen Number	Age	Collection Date	Estimated Days Since Parturition*	Parturition Date	
				Range	Median
A-271	5	May 15	5 - 10	May 5 - 10	May 8
A- 15	5	May 22	10 - 20	May 12 - 17	May 15
A- 24	5	May 24	(Foetus)	May 24 - 26	May 25
A-289	7	May 28	30 - 60	March 28 - April 28	April 13
A-258	7	May 12	2 - 5	May 7 - 10	May 9
A-261	7	May 13	0 - 2	May 11 - 13	May 12
A-305	7	May 28	5 - 10	May 18 - 23	May 21
A- 58	7	May 26	2 - 5	May 21 - 24	May 22
A- 59	7	May 26	0 - 2	May 24 - 26	May 25
A- 65	7	June 2	0 - 2	May 31 - June 2	June 1
A-267	8-9	May 15	0 - 2	May 13 - 15	May 14
A-98	9	June 7	10 - 20	May 18 - 28	May 23
A-256	10	May 12	0 - 2	May 10 - 12	May 11
A- 30	11	May 25	(Foetus)	May 25 - 27	May 26
A-102	>20	June 8	30 - 60	April 9 - May 9	April 24
A-273	>20	May 12	0 - 2	May 10 - 12	May 11
A-263	>20	May 13	0 - 2	May 11 - 13	May 12
A-101	>20	June 8	20 - 30	May 9 - 19	May 14
A- 2	>20	May 19	2 - 5	May 14 - 17	May 16
Mean				May 11 - 17	May 14

*Based on post-partum regression of uterine horn plus general condition of the young.

phenomena, discussed below (p. 57 et seq.).

Behaviour at parturition.--Reports from the literature and Eskimo observers lead to the conclusion that birth occurs on the ice, rather than, as Freuchen (1935) suggests, in the water. So far as the writer is aware, the process has been witnessed only once by white observers and very infrequently by Eskimos. This scarcity of records is probably due to the rapidity with which the act is accomplished, the chances for observation being very slight. Matthews (1952, p. 61) describes the birth of a southern elephant seal thus:

I was looking at a pupless cow when suddenly she gave a convulsive heave and the baby shot out like a torpedoe being launched, the mother at the same time lashing her hind end about and swinging the body around so that the umbilical cord was broken leaving about a foot of it attached to the baby. The placenta was born about ten minutes later...

Such brief parturitions are also reported for other pinnipeds by Mohr (1952) and Bertram (1940), while Ryder (1954) describes a walrus birth on the ice as follows:

She sat more or less upright on her front flippers with her body at right angles to the ship... The posterior portion of her body was turned somewhat laterally with the ventral side away from the [observer] ... When first seen, the calf was partly visible, steaming and wet-appearing. As the ship continued to approach, the female squirmed occasionally and looked back at the newborn calf which gradually became more visible. It lay motionless for a minute or so until the mother saw the ship and slid into the brash. The parent promptly surfaced close by the floe and looked at the calf [which]...slowly wiggled to the edge of the floe and fell into the brash and water... No sounds were heard from the cow or calf and no umbilical cord attachment or actual severing of same by the female was observed.

The posture and general features of this account are similar to another description as told to the writer by Phillip Campbell, a Gambell native, who had heard it second or third-hand. His description was approximately as follows:

The female sat upright with her head bent down. When the calf emerged with umbilical cord still attached, the mother cut the cord by rubbing the point of her tusk across it. She then took the baby into the water for two or three minutes to wash it off, after which she placed it on the ice and swam off to feed.

The afterbirth of the walrus is apparently ignored by the mother, as is that of other seals. Ryder (1954) observed that glaucous gulls (Larus hyperboreus) and kittiwakes (Rissa tridactyla) were actively feeding upon such remnants as well as mucous and feces. Possibly Arctic foxes (Alopex lagopus), which are constantly roaming the ice fields, may also forage upon this material.

Twinning.--Among pinnipeds the birth of twins seems to be very rare, in fact Hamilton's (1939) record for the southern sea lion, Otaria byronia, seems to be the only one in existence. Eskimos at Little Diomed (Brooks, 1954) and at Gambell rarely observe two calves attended by a single cow, and they consider such combinations to be the result of "adoption" by the female of an orphaned calf. Belopolsky (1939) states that "[some Eskimo hunters claim to have seen two embryos in one uterus,]" but none of the Alaskan natives contacted by Brooks or the writer had knowledge of this phenomenon.

Uterine dimensions and post-partum regression.--Uteri examined at Gambell were measured in order to obtain a rough index of growth and post-partum regression. Lengths of the cornua were measured along the anterior curved surfaces from the apex of their external division to the ostia (Fig. 11). Diameter was measured at the widest point along the length. From these it was apparent that the uterus reaches full adult size at age three or four, and that complete regression following parturition probably requires 2-3 months (Table 7). The southern sea lion is considered to accomplish this in about four months (Hamilton, 1939) and the Alaska fur seal in less than three (Enders, et al, 1946).

Average breadths of the zonal placenta scars are also recorded in Table 7. The scars may remain evident for more than a year, by which time they become much reduced and take on an orange hue. After two years they cannot be discerned with certainty, if at all.

Breeding Frequency

That walruses are basically biennial breeders has been well established by several earlier investigators, notably Brooks (1954), Chapsky (1936), and Freimann (1940), and their conclusions are upheld by the writer's observations. Bertram (1940) considers that a possible explanation for this phenomenon may be found in the extraordinary length of the gestation period, and that the bulls may become seasonally infertile before the parous cows have time to recover from

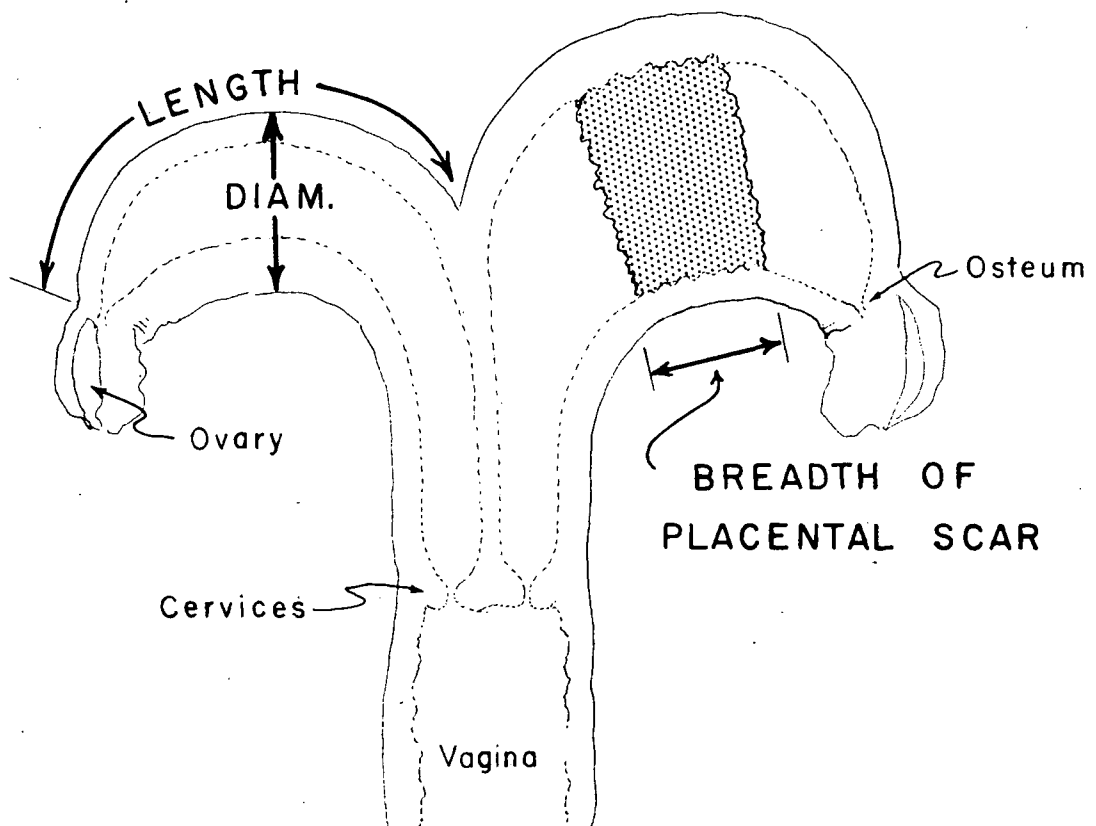


Fig. 11.--A partial diagram of the female reproductive organs showing general internal structure (broken lines) and gross measurements utilized. Lengths and diameters of both uterine horns were recorded.

TABLE 7
POST-PARTUM REGRESSION OF THE UTERINE HORN

Specimen Number	Estimated Time Since Parturition (days)	Horn Length (mm)	Horn Diameter (mm)	Breadth of Placental Scar (mm)
A-263	0-2	150
A-273	0-2	1028	254	100
A-261	0-2	889	203	130
A-256	0-2	864	230	100
A- 59	0-2	870	200	90
A- 58	2-5	840	214	80
A- 2	2-5	813	230	89
A-258	2-5	750	178	110
A-305	5-10	750	170	70
A-271	5-10	698	273	70
A- 15	10-20	610	159	60
A- 98	10-20	60
A-101	20-30	40
A-102	30-60	318	...	35
A-289	30-60	315	95	35
A-249	one year	230	60	25

parturition and develop a new Graffian follicle. R.M. Laws also suggests that this may be the cause of "missed pregnancies" in the southern elephant seal, Mirounga leonina (Lockley, 1954).

According to Dr. A.J. Wood, Animal Nutrition Laboratory, University of British Columbia, most mammals which breed shortly after parturition ovulate either within a few days post-partum or after about two-thirds or more of the lactation period is past. Those species which experience the first ("post-partum") usually are capable of ovulating again at the second ("post-lactis") if fertilization is unsuccessful. Pinnipeds in general seem to fit this pattern rather well, the harem-breeders being fertilized at the equivalent of the first oestrus, pupping and copulating within a week or ten days, and the intermediates and non-harem-breeders at the second. Examination of ovaries from forty adult female Pacific walruses revealed that these animals have three potential oestrus periods: (1) post-partum, a week more or less after parturition, (2) post-lactis I, about one year after parturition (two-thirds the way through the 18-20 month lactation), and (3) post-lactis II, about one month after the latter. The first or post-partum oestrus is very seldom achieved; it had occurred in only two (9 per cent) of the twenty-three parturient specimens examined. Hence, though walruses appear to be potentially annual breeders, there is some retarding influence, possibly nutrition, which

does not often permit it. Perhaps the frequency of annual ovulations is related to calf survival, for it has been observed (Brody, 1945, p. 434) that individual productivity in some mammals varies directly with infant mortality. The only estimate of natal and early post-natal calf mortality which the writer has been able to obtain suggests a rate of about 3-5 per cent per year, similar to the rate of annual ovulations (3-9 per cent, the former from Freimann, 1940).

The second ovulation (post-lactis I) had been or was being experienced by sixteen (94%) of the seventeen non-parturient specimens (Table 3, p. 43). The calendar date at which this ovulation occurs varies with the age and previous history of the animal. Young females in their first oestrus (actually not "post-lactis," but equivalent in time and manner) apparently ovulate earliest in the season (March?), so early in fact that they may not be fertilized, due, perhaps, to a dearth of potent males at that time. Females having one or two previous pregnancies to their credit are next in succession (April-May), and fertilization success appears to be very high (90-100 %). A few of the oldest animals (twenty years more or less) also fall within this group.

Last in succession (late May-June) are the "middle-aged" females, about 10-15 years old, which have experienced three or more previous pregnancies. The proportion of these successfully fertilized is not known, but there are several indications that it is small -- perhaps 25 per cent or less. First, it has been noted above that there are signs of a

decline in male gametogenesis after late May; hence the chances of meeting a fertile bull may decrease rather sharply in June. Second, in the proportions of breeding females recorded by Freimann (1940, Tables 2 and 3), none of the 9 to 13-year-olds was pregnant. Third, in the writer's and Brooks' sample of parturient females there is a notable scarcity of animals between ten and fifteen years of age.

If, for some reason, the post-lactis I ovum is not fertilized, a second post-lactis ovulation takes place about a month later. What proportion of the female population reaches this stage is not known, but the data suggest that it involves mainly the youngest and middle-aged adults, the former because post-lactis I was too early and the latter because it was too late. For the former, post-lactis II occurs at the optimum time in April or May and undoubtedly achieves a high degree of fertilization success, but for the middle-aged females, if it occurs at all, it is probably seldom successful. An idealized schedule of conceptions resulting from all three ovulations is shown in Table 8.

From the above material it is apparent that Bertram's proposed scheme is operative, but its effect is triennial rather than biennial breeding. That is, the middle-aged females, because of their late oestrus, generally "miss" one or two pregnancies and are not fertilized until at least two years after their last (third) parturition. The delay in ovulation is probably associated with the long lactation period, for Espe notes (1941, p. 161) that "...in certain

TABLE 8

IDEALIZED SCHEDULE OF CONCEPTIONS FROM THREE
POSSIBLE OVULATIONS EXPERIENCED BY PACIFIC WALRUSES

Age (years)	Oestrus	Date	Relative Quantity Fertilized
4-5	Post-lactis I ^a Post-lactis II ^a	March-April April-May	Few Most
5-10	Post-lactis I Post-lactis II	April-May May -June	Most Few
10-15	Post-lactis I ^b Post-lactis II ^b	June July -Aug.	Few Very few
20±	Post-lactis I ^b Post-lactis II ^b	April-May May -June	Most Few
any	Post-partum	April-June	Most (?)

^a The initial ovulations, hence not strictly "post-lactis."

^b May actually be 2-5 years post lactis.

species...lactation [may] prolong the life of the corpus luteum, and ovulation ceases." It is apparent that its effect is cumulative (cf. the progressive stages and ages of post-lactis I) and does not result in a "missed pregnancy" until two or three young have been born in successive biennial cycles. With advancing age and approaching senility, other factors may enter the picture, resulting in lowered ovulation frequency. An example of this has been seen (p. 40) in which an apparently healthy elderly female had borne a calf one year previously but showed no signs of ovulating in the current season.

Proof of the above breeding frequency hypothesis is found in the sequence of birth dates (p. 52 et seq.), in the calculated conception dates (Table 4, p. 45), and in the crude birth rate. If breeding was strictly biennial or was partly biennial and partly annual, the crude birth rate should be about 0.5 young per adult female per year. According to Freimann's (1940) data, however, it is between 0.37 (Table 3; 71 animals) and 0.43 (Table 2; 35 animals), while in a series of twenty-one specimens loaned by Brooks it is 0.33. These differ significantly from the expected rate, attesting to the strong tendency for other than biennial breeding.

Unfortunately, because the writer's and Brooks' (1954) data are so sparse and Freimann's are so ill-organized, it is not possible to construct a table of age specific birth rates of the female population.

THE YOUNG

Sex Ratio

Of 139 calves known to have been captured by Gambell hunters in 1952, 53, and 54, the proportion of males to females did not differ significantly from the expected 1:1 ratio. Nevertheless, males slightly outnumbered females in this and other recorded samples (Brooks, 1954; Nikulin, 1940) about 1.2:1.

Morphology

At birth the calf is pale slate gray, and the soles of the fore feet are often blotched with flesh color. The pelage is sparse and fine, the vibrissae long (up to 3 inches) and slender, and the claws pointed, slender, and soft. Generally no teeth are visible, though small bumps indicate their presence beneath the gums in some instances. Five out of sixteen examined by the writer had one or both of the lower canines partially exposed. Except for external genital openings, the sexes are identical in size and general appearance. Body measurements are shown in Table 9.

Within a few days the young walrus changes to a very dark, almost black color. Gradually, as the weeks pass, this is transformed into a rich chocolate brown and is, according to Nikulin (1940), accompanied by a post-natal molt which takes place partly in June and July. These color changes involve skin as well as pelage pigmentation.

TABLE 9
CALF BODY MEASUREMENTS*

Age (months)	Body Length (inches)			Hind Foot Length (inches)		
	No. of Speci- mens	Range	Mean \pm S.E.	No. of Speci- mens	Range	Mean \pm S.E.
Newborn	8	40 - 52 1/4	45.8 \pm 1.4	5	11 - 13 3/4	12.8 \pm 0.5
0 - 1	25	45 - 52 1/4	48.6 \pm 0.4	13	12 1/2 - 14 1/2	13.4 \pm 0.2
1 - 2	21	49 1/4 - 59 1/4	54.0 \pm 0.5
2 - 3	40	49 - 72 1/2	58.3 \pm 0.7

*Data from Brooks (1954), Fay, and Nikulin (1940).

Remnants of the umbilical cord remain attached until July or August (Nikulin, op. cit.; Chapsky, 1936), and by late summer or fall the tusks may begin to erupt. For the first three months body length increases at the rate of about four or five inches per month (Table 9).

Precocity

The young are probably capable of swimming immediately after birth, though they are usually carried by the mother. Calves no more than one or two weeks old have been observed to swim very well indeed when pursued, often with a leaping and diving motion similar to the otariids. Independently they appear to be unable or unwilling to dive more than a few feet below the surface or to remain submerged for more than one or two minutes. Much of their swimming and diving ability in later life may, therefore, be a result of learning.

Parental Care

The strong maternal bond between cow and calf has been elaborated in great detail by many earlier writers, notably Allen (1880). Aside from its remarkable anthropomorphic implications, this inseparability of parent and offspring is of particular significance as a survival mechanism. Food and protection appear to be the primary effects.

Food relationship.--The young feed exclusively upon milk for at least the first eighteen months, and intermittently up to two years, according to stomach analyses performed by Brooks (1954), Chapsky (1936), Freimann (1940), Nikulin (1940), Zalkin (1937), and the writer. Among pinnipeds this is an exceptionally long duration, though some sea lions may nurse as much as one year (Otaria: Hamilton, 1934; Eumatopias: Kenyon, in litt.). In view of the number of walrus calves that have been maintained in captivity on a variety of other diets (Mohr, 1952; Murie, 1872; Nikulin, op. cit.), it is apparent that they are not dependent upon milk as such, so long as their nutritional requirements are met. This suggests that the situation as it occurs in Nature is due, rather, to physical or psychological inability of the young to obtain solid foods. Mitchell (1909) observed that young captives "showed no knowledge of how to extract...[mollusks from the shells], although they would bring...[them] from the bottom of their pool."

An orphaned yearling reported by Brooks (op. cit., p. 59) and another by Heinrich (1947) appeared to be in good physical condition, and the former's alimentary tract contained "stones and animal matter" demonstrating bottom-feeding ability. A third specimen examined by the writer displayed severe gastric inflammation, and except for a few stones and one brachiopod shell fragment, its intestine

contained only mucous and large quantities of bile. This animal was in ill health. Its blubber was only about one centimeter thick, as opposed to 3.5 cm. recorded by Chapsky for yearlings, and its gall bladder was about six times normal size, indicating that no food had been ingested within, perhaps, two weeks or more.

Two-year-old walruses appear to be capable of full nutritional independence, though they mostly remain in close association with female herds even at that age. Nikulin (1940) and others have suggested that this is primarily due to their dependence upon adults to stir up food from the bottom, their own tusks being too short for efficient grubbing. This, however, could be either cause or effect, and it seems more probable, as Brooks has noted, that such a relationship is purely incidental to the social pattern, for tuskless adults reported by him and the Gambell men were in good health.

Protection.--Being born during the spring migration, the calves are faced with a 500 to 1000-mile swim. Whether or not they could or would successfully accomplish this alone is not known, for they are carried most of the way by their mother, either on her back or clasped to her breast. When threatened from above (e.g. by hunters), the cow dives with the calf in her "arms"; when threatened from below (e.g. by killer whales), the youngster climbs high on her shoulders. The latter escape behaviour of the young

is evident up to at least two years of age, though body size probably renders its goal unattainable, hence relatively ineffective, after the first eight or ten months.

The social tie between mother and young is practically unbreakable -- where one goes the other must also go. If one is killed, the other stays with it or carries it away, depending upon which one of the pair survives. If the cow is killed, another cow or even juveniles may "rescue" the calf, and occasionally, orphaned calves are "adopted" by other cows. As the offspring advance in age, the bond weakens and is generally broken at the end of the second year.

When a calf is injured or by some means separated from the herd, it barks incessantly. This penetrating sound has been heard at distances up to two or three miles under certain conditions and appears to be a highly effective device for attracting the attention of older animals. Its efficiency was demonstrated to the writer on May 22, 1952, when a calf was permitted to bark briefly before being dispatched. Prior to this time only two other walruses had been seen in an area of perhaps twenty square miles west of Gambell, yet within five minutes a bull and two cows appeared near the ice floe on which we stood. No others could be found that day in a still larger area of exploration.

The value of these social features is obvious. Each contributes to a high rate of calf survival -- a necessity where the reproductive potential is low.

NUTRITION

Quality

The basic features of nutrition as they affect ecological and maternal relationships have been outlined above, but before proceeding with the discussion of growth, some additional review is desirable. In general, the pelecypods (Mya, Clinocardium, Astarte, and Macoma make up the bulk of the Pacific walrus' spring and summer diet, other genera being largely incidental (Brooks, 1954). There are no data concerning seasonal preferences, except that a large tunicate forms an important part of the fall diet near St. Lawrence Island.

Quantity

Observations suggest that there is no regular daily feeding schedule. Probably food is taken when and where available, regardless of the hour, for daylight rhythms would have little effect upon either the food species or the walrus' ability to find them in the 10-30 fathom darkness. The abundance of empty stomachs, even in regions where a rich bottom fauna exists, suggests that feeding is infrequent, though Murie (1872, p. 461) notes that

the great glandular superficies and correlated large lymphatics point to means of speedy and frequent digestion; and in the walrus these apparatus are extraordinarily developed.

Daily rations for a 6-month-old captive included twenty pounds of mackerel and 3-4 pounds of liquid nutrients

(R. McClung, in litt.), while Chapsky (1936) reports that captives in Hagenbeck's Zoo, Hamburg, consumed up to 15 kg. (33 pounds) of chopped fish per day. A full stomach from an adult male examined by Brooks contained about one hundred pounds of invertebrates.

There is no conclusive evidence of seasonal fasting on the part of either sex (Table 10), except in localities where suitable benthos is absent. Brooks (1954) believes that the bulls feed very little in summer, but growth studies, contrarily, indicate (p.102) that the greatest annual growth increments are achieved in summer and fall; hence feeding cannot be less frequent then than at other times of the year. On the basis of tusk structure, breeding cycles, and comparison with other pinnipeds, fasting, if it occurred at all, would be expected to take place in late winter or spring.

Predation on Seals

Predatory walruses or "rogues" are well-known in Eskimo lore and have been observed and/or reported by many earlier investigators. In the Bering-Chukchee region they occur rarely, perhaps one in a thousand or even less frequently. The universal theory among Alaskan natives is that these animals were orphaned when very young and never learned to bottom-feed; consequently they fed upon whatever animal matter they could get (e.g. seals). The credulity of this tale seems rather doubtful, since all rogues are apparently

TABLE 10
PROPORTION OF FEEDING WALRUSES BY SEASON AND LOCATION

Authority	No. and Sex of Specimens	Date	Location	Per cent with Food in Stomach		
				Male	Female	Both
Fay	12 M 15 F	April-May	Gambell	42	20	30
Brooks(<u>in litt.</u>)	40 MF	June	Bering Str.	--	--	12
Brooks(1954)	71 M	July-Aug.	Barrow	16	--	--
Zalkin(1937)	56 M*	July-Sept.	Franz Jos. L.	43	--	--
Chapsky(1936)	46 MF*	Aug.-Oct.	Kara Sea	--	--	26

*O.r. rosmarus

adult bulls, no females or sub-adults being reported. A more probable solution (viz. that flesh-eating is induced when benthos is unavailable because of too-deep water or other conditions) has been offered by Chapsky (1936) and Southampton Island Eskimos (A. Loughrey, in litt.). Under such conditions Vibe (1950) found seal remains in two out of about one hundred stomachs, the remainder being empty. Males should be most prone to this, for they occur more frequently in the "fringe" areas than females do. Once begun, this type of feeding is evidently continued indefinitely by some individuals whether or not bottom forms can be obtained thereafter.

Seal eaters are generally solitary, according to Heinrich (1947), and are readily distinguishable by their grease-stained tusks and body. In the Bering and Chukchee Seas their importance is questionable, but it is said that they may be detrimental at times by frightening seals away from certain localities (Nikulin, 1940). Their flesh is unpalatable (Freuchen, 1935), and Alaskan natives claim that it causes serious illness when eaten. The described symptoms of the latter correspond to those of hypervitaminosis-A (Rodahl, 1949, 1950), as might be expected.

Feeding Behaviour

The feeding behaviour has been deduced by several writers, but there is little general agreement among their theories. This problem is an intriguing one, since bivalve

flesh in the stomachs consists only of non-masticated feet and siphons; rarely are mantle or shell fragments present.

Mollusks are apparently rooted from the sea bottom by means of the muscular mistachial pads and the tusks. The latter may be used in either a raking, digging, or brushing motion, as observed by Johansen (1910) and indicated by the worn antero-lateral surfaces. Vision probably plays no part in selecting food items, for the eyes are small and appear to be ill-adapted to low light intensities. Thus food is probably selected by touch, using the lips and the vibrissae which are amply supplied with nerve endings of the trigeminal at their bases (Mohr, 1952).

Once a mollusk has been located, one of three possible methods is used to devour it: (a) the exposed siphon or foot is bitten or torn off; (b) the soft parts are sucked out of the shell; or (c) the prey is taken into the mouth and the shell crushed and ejected after certain soft parts have been selected by tongue and lip action. Materials from various sources (Allen, 1880; Brooks, 1954; Cobb, 1933; Mohr, 1952; Vibe, 1950; and others) have given evidence for each of these methods, but the first appears to be by far the most common. The unusual ability of walruses to bite and tear off chunks of flesh without a dental battery adapted for this type of feeding becomes more credulous when the facial structure is critically examined (Figure 12).

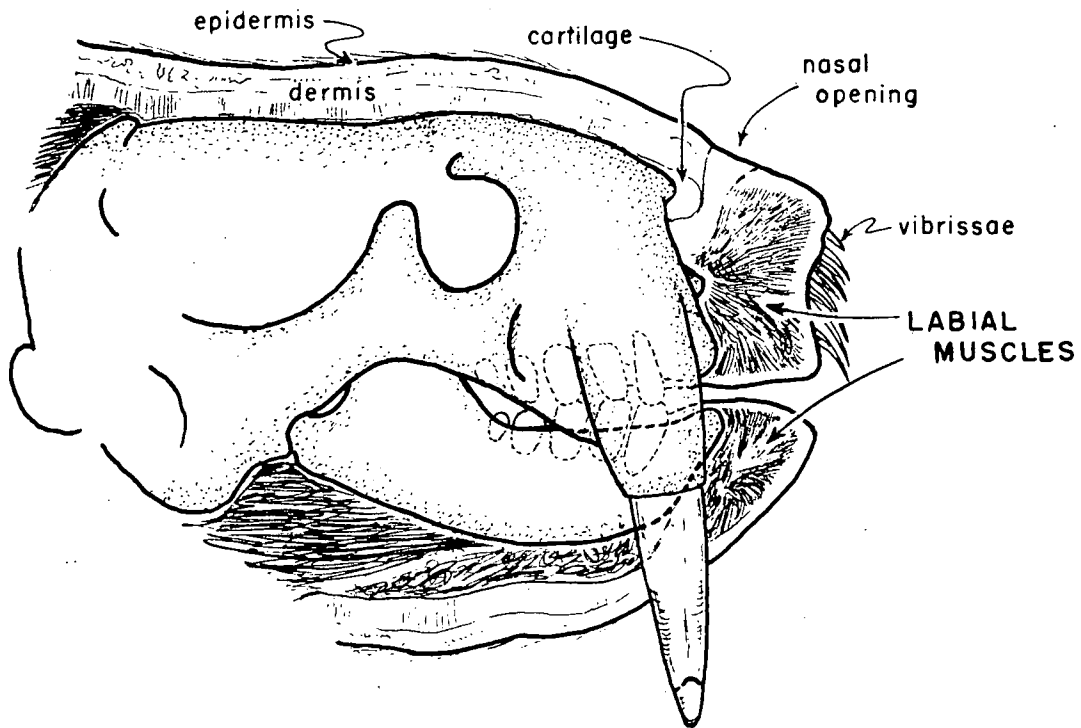


Fig. 12.--Sagittal section of the skin and superficial musculature of a 2-year-old bull walrus (from a photograph). When the teeth are fully occluded, the bony epiphyses of the lower jaw are about one-half inch away from the upper. Tough gingival tissue on both surfaces fills this gap. Pelecypod feet and siphons could be bitten ("squeezed") off, either at that point or by the muscular lips.

GROWTH

To a study such as this one, which has as its goal the assessment of population trends, an empirical system for dividing the animals into groups of like age is indispensable. This must be based upon certain morphological characters whose rate of change can be charted with sufficient accuracy to yield reliable ageing criteria. The search for such characters has led far afield and has unexpectedly revealed many interesting and useful facts in addition to those for which it was originally designed. In the following pages these are presented in their entirety for their value in the present analysis and for the sake of future investigators who may wish to direct studies along similar channels.

Age Determination

The most effective technique for determining age criteria of wild animals is to observe and record the morphological features of known-aged individuals. This may be done by either of two methods: (a) keeping the animals in captivity or (b) marking wild stock at birth and recapturing them at frequent intervals thereafter. Several captive walruses have been raised in the zoological parks of Europe and North America, but few records of their development have been kept. These few (Mohr, 1952; B. Benchley, in litt.; G. Crosby, in litt.; R. McClung, in litt.), though helpful,

are not adequate as a basis for age classification. Eleven wild calves were tagged and released in 1953 by Brooks, but none has been recaptured as yet.

Direct methods.--Scheffer (1950) and Laws (1952) suggested that encircling ridges on the roots of walrus tusks might represent annuli which could be readily counted and yield an accurate age appraisal. Upon investigating this feature it was found that (1) ridges are evident only on the roots of bull tusks eighteen inches or more overall length; (2) the larger, hence older the tusk, the smaller the interval between ridges (Fig. 13); (3) those on any given root represent only a small portion of that tusk's growth history; and (4) each ridge is the outward equivalent of an internal dentin layer pattern. It has not been conclusively established that the ridges or layers are produced at the rate of one per year, but tusks from bulls killed at Gambell, Wales, and Barrow in winter, spring, and summer, indicate that one ridge is formed during late winter and early spring. None is formed before puberty; thus they appear to be associated with an annual physiological rhythm related to reproductive cycles.

Twenty-one juvenile and young adult tusks were longitudinally sectioned in a search for structural clues to pre-pubertal development. Traces of interrupted dentinogenesis were found, but in several instances tusks of equal size and shape did not seem to bear the same or even similar

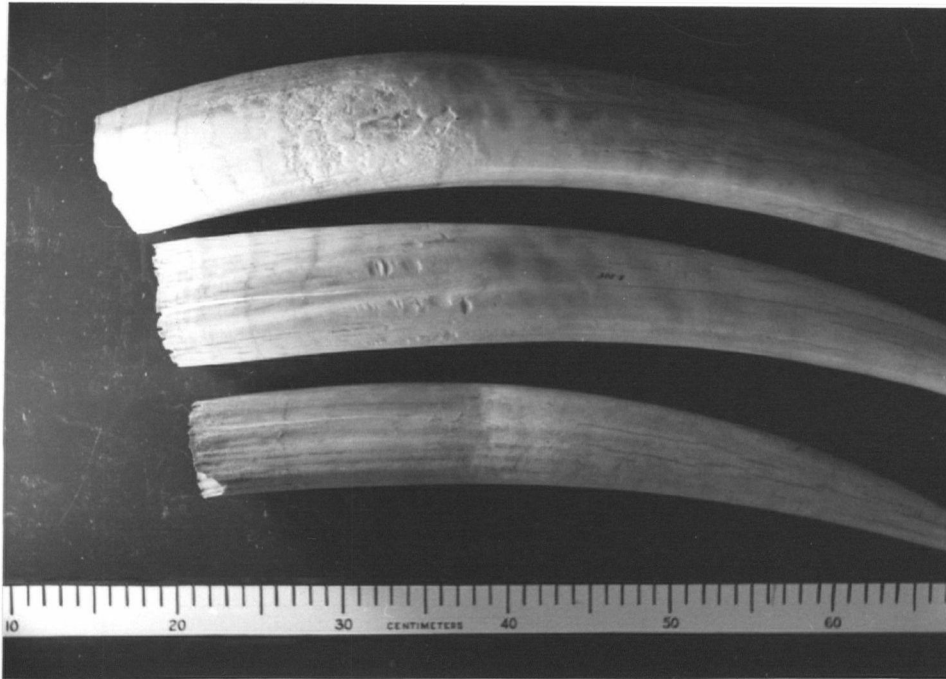


Fig. 13.--Root ridges (left) on male tusks, showing narrower intervals with increasing tusk size.

layer patterns, and some had no visible layers whatever. This line of assault was therefore abandoned.

A similar technique involving the molariform teeth was tested after a preliminary examination revealed regular laminations in the cementum. This promising feature was also independently discovered by Mohr (1952, p. 33) and Brooks (1954) and pursued by the latter. Preliminary conclusions from Brooks' and the writer's studies were similar: (1) the laminae were well defined only in male teeth, and (2) their number seemed to be significant only as a rough indication of relative age. Later, when more specimens and comparative data had been accumulated, the latter relationship was re-examined. The results, outlined below (p.124), indicate that the number of cementum layers is a relatively precise indication of age in males.

Another method briefly investigated was suggested by Plehanov's (1933) report of annuli in the claws of harp seals (Phoca groenlandica). Walrus claws, however, are comparatively fragile, and though layering was found to be prominent, no more than three annuli were ever found in one claw.

Counts of corpora lutea and corpora albicantia in the ovaries were tried in view of their usefulness for interpreting ages of cetaceans (Wheeler, 1930; Laurie, 1937) and their probable value in ageing pinnipeds (Bertram, 1940). The conditions for success in using this technique depend

upon the reproductive cycles of the animal; a monoestrous annual breeder which retains all corpora permanently is most ideal. The irregular ovulations of walruses, coupled with bi- and triennial conceptions, render interpretation difficult, and the writer's first trial was unsuccessful due to smallness of sample and what appeared to be a total lack of correlation between corpus numbers and body measurements. It was not until more specimens had been acquired that the design of ovulation became evident, and the results finally obtained were of considerable value in the construction of an age classification for females (see below). At best, however, corpus counts are probably very crude indices of age.

Indirect methods.--Since the bulk of the calves are born within one month in spring, it would be expected that at a given instant all individuals of the same age would have approximately the same body dimensions. The frequency diagram of a given measurement from all the animals in a population sample would, then, be expected to have a poly-modal form, each mode representing a separate, normally distributed age class. Using this technique, age criteria have been independently derived for the Pacific walrus by Belopolsky (1939), Brooks (1954), Freimann (1940), and the writer, but each analysis differs slightly from the others. The reasons behind this disagreement seem to be that first, Belopolsky had too few data, and he did not consider sexual

dimorphism. Second, Freimann apparently overlooked the fact that the sample should be recruited within a short space of time, for growth can obliterate instantaneous modes within a few months (his collecting period covered about four months). Partly because of this, he also failed to recognize that the tusks grow throughout the lifetime at a relatively greater rate than body length and are therefore a better measure of age. Third, Brooks was a victim of limited time and inadequate library facilities, for he had potentially at his disposal the same data utilized in the following pages. To the extent that he was able to pursue the problem, his conclusions nearly coincide with those which were tentatively reached by the writer at an equivalent stage in the analysis.

The data utilized below were from specimens taken between April 20 and mid-June at Gambell, Savoonga, Wales, and Little Diomed Island. The majority was recruited during the last half of this period. It was not possible to obtain body measurements in sufficient quantity for analysis as Freimann had done, so the most available features, the tusks, were used instead. Tusks from freshly killed animals were measured to the nearest 1/8-inch along the anterior surface from the gum line to the distal tip. This measurement was recorded as Observed External Length or "OEL" to distinguish it from other tusk lineaments under consideration. Accompanying circumferences at the gum line were measured to the nearest millimeter or sixteenth of an inch.

Histograms of OEL frequencies are shown by sexes in Figure 14. Males will be considered first:

(1) The male OEL's exhibit a series of reasonably prominent modes which are apparent both in spring and summer samples. If these are significant trends, it should be expected that the Eskimos, who are most familiar with the animals, would have some knowledge of at least the most obvious ones, i.e. those at the lower end of the age scale. Indeed, the Gambell men readily classify specimens up to four years of age on the basis of OEL, and their concepts of these are approximately as indicated in Figure 14. Corresponding body lengths also agree with Freimann's (1940, Fig. 1) body length-age class modes; hence it is highly probable that these represent true age classes. Beyond the fourth OEL mode there are three others well defined which probably represent ages 5, 6, and 7, respectively, but before their validity can be judged, some other tusk lineaments must be considered. These are shown in Figure 15.

(2) The tusk can be grossly divided into three basic parts, (a) the Root Length, "RL", which is enclosed in the alveolus, (b) the Observed External Length, "OEL", which has already been considered above, and (c) the part, "W", which has been Worn or broken from the distal tip mostly as a result of the feeding process. Together, these constitute the Absolute Total Length or "ATL." In the field, the first two are readily measured when the tusks have been re-

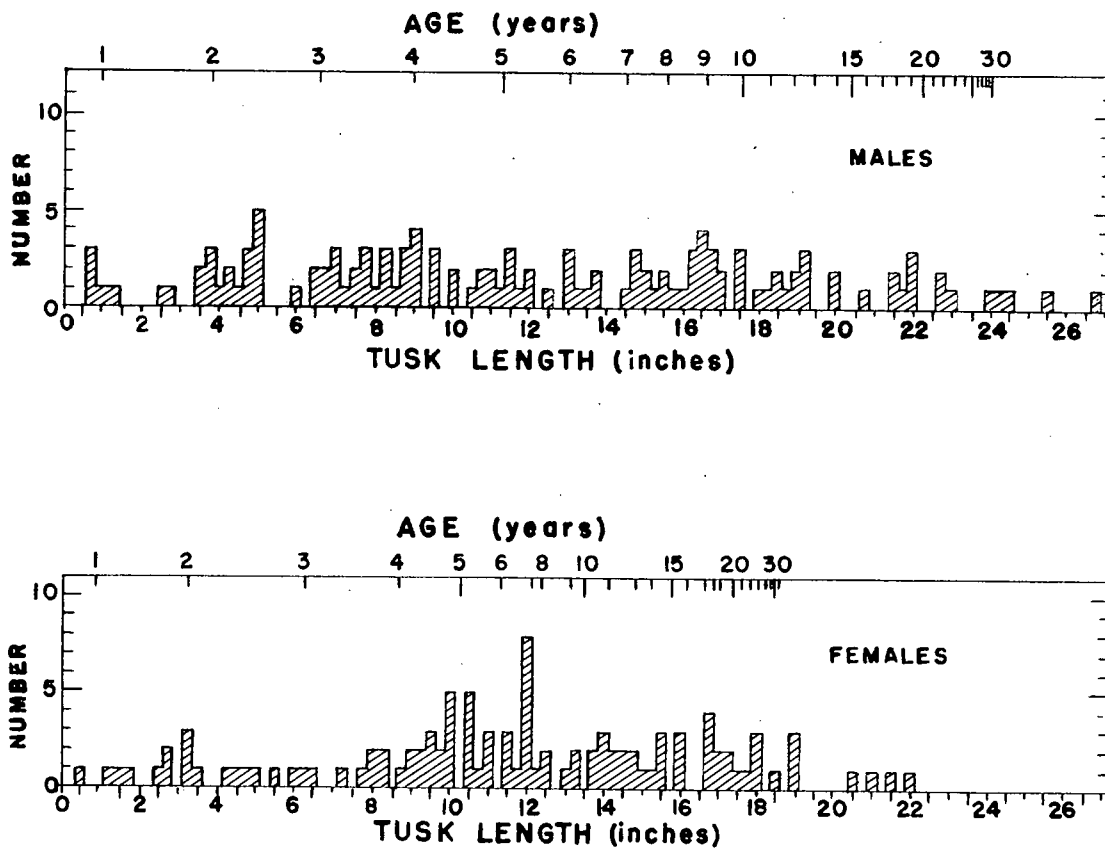


Fig. 14.--Frequency histograms of Observed External Lengths (OEL's) of male and female tusks measured in late April, May, and early June. Age scales are from data in Appendix IIA,B.

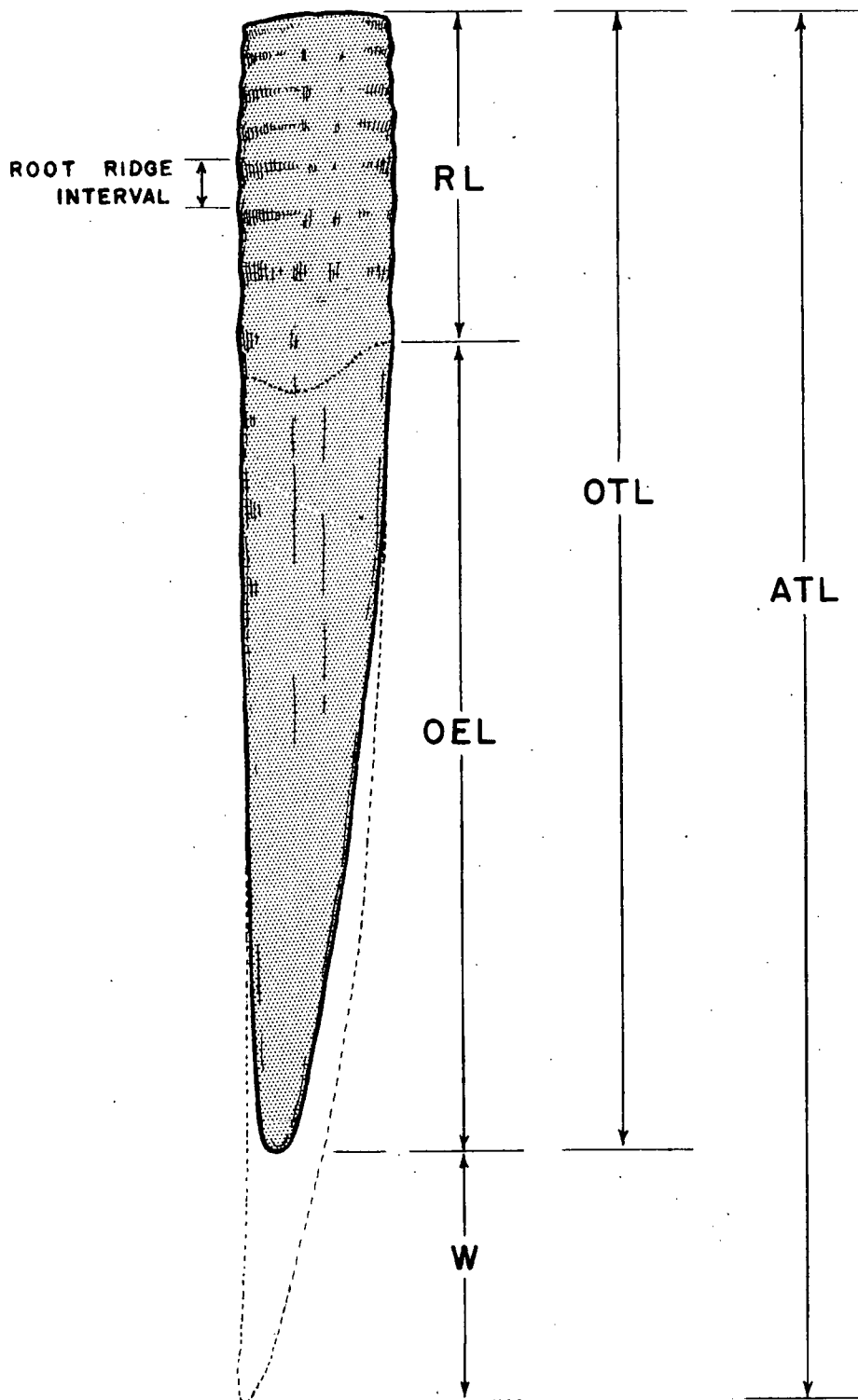


Fig. 15.--Tusk lineaments utilized in age and growth analyses: RL - root length; OEL - observed external length; W - linear or distal wear; OTL - observed total length; ATL - absolute total length.

moved from the skull, but the third is most difficult to evaluate unless a large series of tusks of various ages is available for visual and metric comparison. At St. Lawrence Island the writer was able to obtain the first two paired measurements (RL and OEL) from sixty-two individual animals. Together, these were designated as Observed Total Lengths ("OTL"), and a frequency histogram of their values revealed a series of modes equivalent to those in the OEL frequency. That is, modal values of the OTL classes, less the average root lengths (RL's) per class, were equal to the apparent OEL modes up to 5 years, beyond which the sample was too small to be of value. Since OTL is a better measure of tusk growth than OEL (i.e., it is closer to the true value, ATL), the OTL modes should be more reliable as indices of age classes. Consequently the OEL modes must also be reasonably valid representations of age classes 1 to 5.

(3) With the above data, the regressions RL and OTL on age were plotted, and both were tentatively projected to 7 years by visual estimate and the use of OEL modes 6 and 7 plus projected RL values. Using a series of seventeen male tusks of various ages from birth to 6 years (by OEL), the linear wear, W, was estimated for each age class. This, when added to the respective OTL values, yielded a possible curve of Absolute Total Length-growth ($OTL + W = ATL$) up to 6 years which could be projected with reasonable accuracy to 9 years.

(4) If the root ridges are annual formations, the interval between any two succeeding ridges must be equal to the linear increment of ATL growth for one year. Assuming this to be true, the root ridge intervals on tusks from twenty-three individual animals were measured. These tusks ranged in size from 19 1/2 to 38 inches, OTL, the youngest being six years old (by OEL) and the oldest near maximum old age (by Eskimo standards). These were tabulated and their position in the table carefully adjusted such that the values of each incremental series were of comparable magnitude to the next (Table 11). The resulting mean increments were then smoothed graphically and the ultimate ATL-growth curve plotted as a projection of that which was derived in step 3 above. The two curves coincided in the region of overlap (5-9 years).

(5) In order to test the accuracy with which root ridge intervals had been matched in Table 11, the empirically defined (root ridges) portion of each specimen's ATL growth-history was plotted graphically. This gave a series of short curves (Fig. 16) which, by visual matching and combination of slopes, yielded a second possible ATL-growth curve. The form of the latter was nearly identical to that obtained in step 4, the only difference being a slight divergence at the extreme upper end of the age scale. It was concluded that the combined ATL/age curves of steps 3, 4, and 5 are probably close to the true curve of average linear tusk

TABLE 11

ROOT RIDGE INTERVALS (inches) ON MALE TUSK ROOTS

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TABLE 11--Continued

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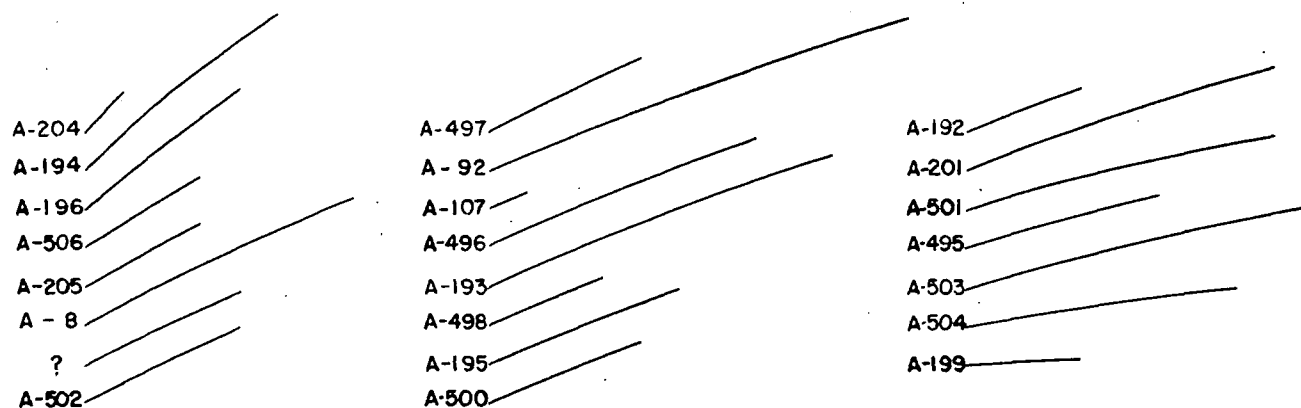
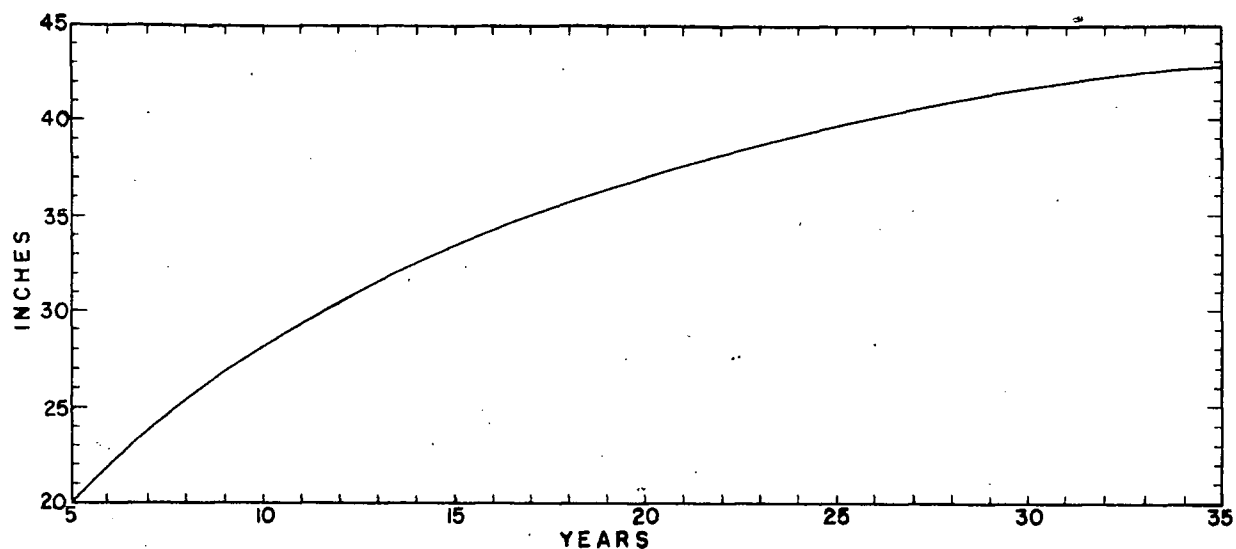


Fig. 16.--Tusk root ridge curves (lower). Each curve is a graphic representation of Absolute Total Length growth as depicted by root ridge intervals (Table 11) of individual specimens. By matching shapes and superimposing the equivalent ones, a complete ATL growth curve (upper) was derived.

growth up to 30 years. The latter is near the expected maximum longevity (p.143).

(6) Assuming that the tusks used in the root ridge analysis were of ages corresponding to their position (by slope comparison) on the ATL-growth curve, their OTL/age and RL/age values were plotted. With the aid of these points, the RL curve of step 3 was projected to 30 years and an approximate projection of the OTL curve to 30 was sketched in.

(7) As noted above (step 3), the rate of wear from 0 to 6 years was known. Beyond 6 it could be estimated from the difference between ATL and the OTL sketch curve. By making slight adjustments (smoothing) in the resulting "negative increment" values, a final OTL curve was constructed which fitted the observed data well. A table of tusk lineaments in which

$$(ATL - W = OTL) - RL = OEL$$

is given in Appendix IIA, and a graphic representation is shown in Figure 17.

It is fairly evident that the above technique has some weaknesses and that the final synthesis has necessarily been rather subjective. Nevertheless, having checked, cross-checked, calculated and re-calculated the same data by several other methods too numerous and confusing to mention here, the writer has concluded that the result shown in Figure 17 is a true and accurate representation of aver-

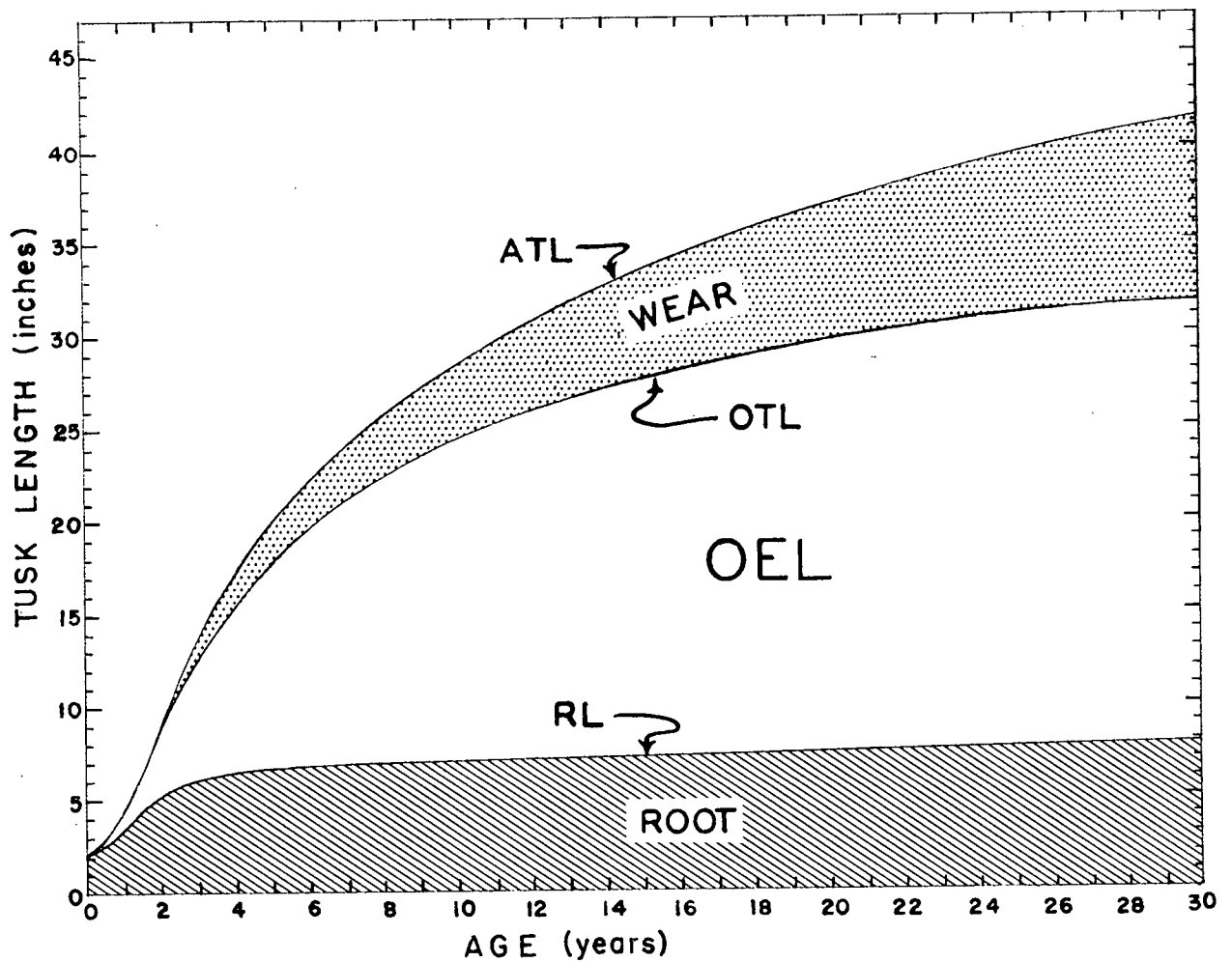


Fig. 17.--Average linear growth and wear of male Pacific walrus tusks, based upon Appendix IIA.

age male tusk growth.

The pattern of female tusk growth was more difficult to interpret, for the OEL distribution (Fig. 14) has no modal regularity comparable to the males', and there were few complementary measurements of other physical features which could be utilized for evaluating the possible modes. A reasonable plan has, however, been deduced as follows:

(1) In general, the teeth of female pinnipeds are slightly smaller than the males'. This is probably a function of relative growth in most instances, though it is even evident in some species which do not display prominent sexual dimorphism of body size (e.g. Phoca hispida). The molariform teeth of female walruses are only about three-fourths the size of the males', the tusk circumferences for equal lengths about 75-85 per cent, and the OEL maxima recorded by various investigators, 75-85 per cent. Thus it was expected that the female ATL-growth curve would have the same or similar slope as the male's, but that its asymptote would be a somewhat smaller value. In view of the smaller cross-sectional area, it was also expected that the wear rate would be greater and, as a result, the OTL values proportionately smaller. This should become more pronounced with advancing age, though the relative difference between male and female wear rates should diminish due to changes in size and shape (p. 130) of the surface being abraded.

(2) The St. Lawrence Island men recognize females

up to at least 4 years of age on the basis of general morphology, including tusk OEL. Their concepts of the latter agreed with the writer's field conclusions and were similar to the males' (Fig. 14), for although the OTL's were actually smaller, the root lengths were also smaller. Body lengths of these presumed age classes agreed closely with those depicted by Freimann's (1940, Fig. 1) large sample.

(3) Beyond 4 years, separation of age classes was less certain, but the ovaries contributed supporting evidence to some probabilities of the OEL frequency. According to the Gambell men, animals experiencing their first oestrus would be mostly 4-year-olds -- an idea upheld by the OEL range and median for such specimens (Fig. 18 and Table 12). On this basis, the next reproductive class (Parturition I) should be mostly 5-year-olds, the third (Conception II) mostly 6-year-olds, etc. Since medians of first parturients, second conceptions, and second parturients (Table 12) correspond to possible OEL frequency modes at $10 \frac{1}{4}$, $11 \frac{1}{4}$, and 12 inches, respectively, the latter have been regarded as the most probable OEL modes for ages 5, 6, and 7.

(4) The ranges and medians of tusks from animals in later pregnancies did not follow any regular progression (Table 12). This apparent non-conformity could be due to smallness of sample, but another factor, namely variations in wear rates, could also have had considerable effect. Experiments with rats and farm animals have demonstrated

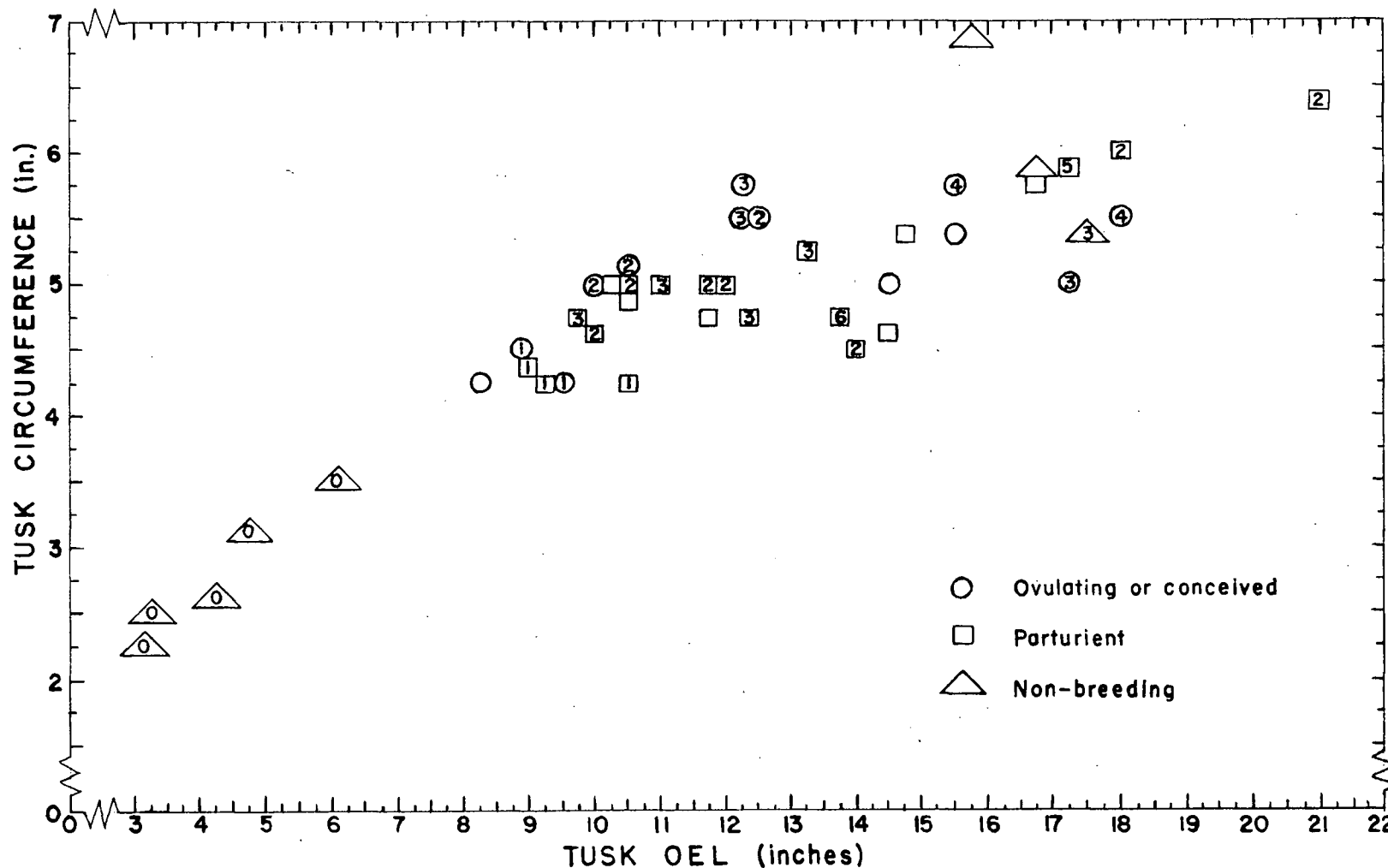


Fig. 18.--Relationship between female tusk size and reproductive history. Numbers within the symbols represent total pregnancies, including current conceptions and ovulations, experienced by each individual. Symbols without numbers are from Brooks (1954, Table 6, and in litt.) or specimens from which only one ovary was secured.

TABLE 12
FEMALE TUSK LENGTHS AT SUCCESSIVE STAGES IN REPRODUCTION

Reproductive Class	No. of Specimens	Tusk Length (OEL) in Inches		Expected Mean Age (years)
		Range	Median	
Conception I	3	8 1/4 - 9 1/2	8 7/8	4
Parturition I	3	9 - 10 1/2	9 3/4	5
Conception II	3	10 - 12 1/2	11 1/4	6
Parturition II	5	10 - 14	12	7
Conception III	2	12 1/8 - 12 1/4	12 1/4	8
Parturition III	3*	11 - 13 1/4	12 1/8	9

*Excluding the specimen in Fig. 18 with 9 3/4" OEL, whose tusks had been broken.

that the food intake during pregnancy is slightly higher than usual and that "lactating animals...consume two to three times as much food as non-lactating animals" (Brody, 1945, p. 821). Assuming this to be basically true of all mammals, it would be expected that walrus tusk wear would increase proportionately during pregnancy and lactation, since it is largely an effect of feeding. Also, it follows that, taking any two females of like age, the more productive one would have the shortest tusks.

In Brooks' and the writers field data there are numerous evidences which uphold these hypotheses. In Figure 18, for example, the animal with the longest tusks (21 inches) had experienced only two pregnancies, while the specimen with the most pregnancies (six) had very short tusks (13 3/4 inches). The difference between these two is partly a result of breakage, but breakage is also a result of wear which tends to weaken as well as shorten the tusk (p. 130). Individual differences in tusk shape and circumference also appear to be important factors in this process.

Consider an animal which has experienced three pregnancies in biennial succession with 18-20-month lactations following each one. The resulting overlap of pregnancies and lactations should affect a wear rate at least double that of an equivalent aged female who had one or no pregnancies during the same period. Since the former

appears to be the mode in early years of maturity, a random sample of OEL's from the female population should reveal a major peak of overlapping age classes between 4 and 10 years.

Following the third (or second) pregnancy there is a period of "reproductive quiescence" resulting either from missed pregnancies, a reduced ovulation rate, or both (p. During this period the wear rate should be lower than previously, and the OEL's should therefore increase at a relatively greater rate. In the OEL frequency, this period should be represented by a slight trough.

Finally, with further intermittent pregnancies and a gradual reduction in tusk growth rate there should be a less prominent but broader peak of OEL's extending from the trough above to the asymptote of average OEL "growth."

Each of these major peaks and troughs does exist (cf. Figs. 14, 18; Freimann, 1940, Table 1); thus it is apparent that the average curve of OTL (hence OEL) growth cannot be a smooth progression but must be punctuated at intervals by minor undulations, each the result of increased wear during a pregnancy-lactation period.

(5) Using the data derived in steps 2, 3, and 4, preliminary OTL/age and RL/age curves were plotted to 9 years. Wear estimates for the first five years were obtained by visual comparisons of tusks in the same manner as was done for the males. With the aid of these, an approximate ATL-growth curve was derived and tentatively extended to

7 years. Since there are no definite root ridges on female tusks, it was not possible to project the ATL curve further by that technique, but knowing the approximate value for its upper end (i.e., at 25-30 years) from specimen measurements and wear estimates, a probable approach to the asymptote was plotted. This was accomplished by using a slope equivalent to the males'. From the same specimens upon which the upper ATL limits were based, average OTL and RL values at 25-30 years were also established.

(6) An adjusted table of hypothetical tusk growth was then constructed (Appendix IIB), using values of the above ATL curve as the bases and derived OTL values to 9 years as the most probable ones for the lower end of the OTL curve. Again this was constructed by the method

$$(ATL - W = OTL) - RL = OEL.$$

Allowance was made for three consecutive biennial pregnancies, beginning with the first oestrus at age 4, and three additional pregnancies in later life -- a total of six, the maximum observed. The latter three were spaced, temporally, according to the relationship observed in Figure 18.

The final synthesis (Fig. 19 and Appendix IIB) satisfies every requirement for average female growth and reproductive history; indeed there seems to be no alternative solution. Its goodness of fit to the observed conditions of OEL frequency was tested by sampling a theoretical population having tusk lengths normally distributed about the

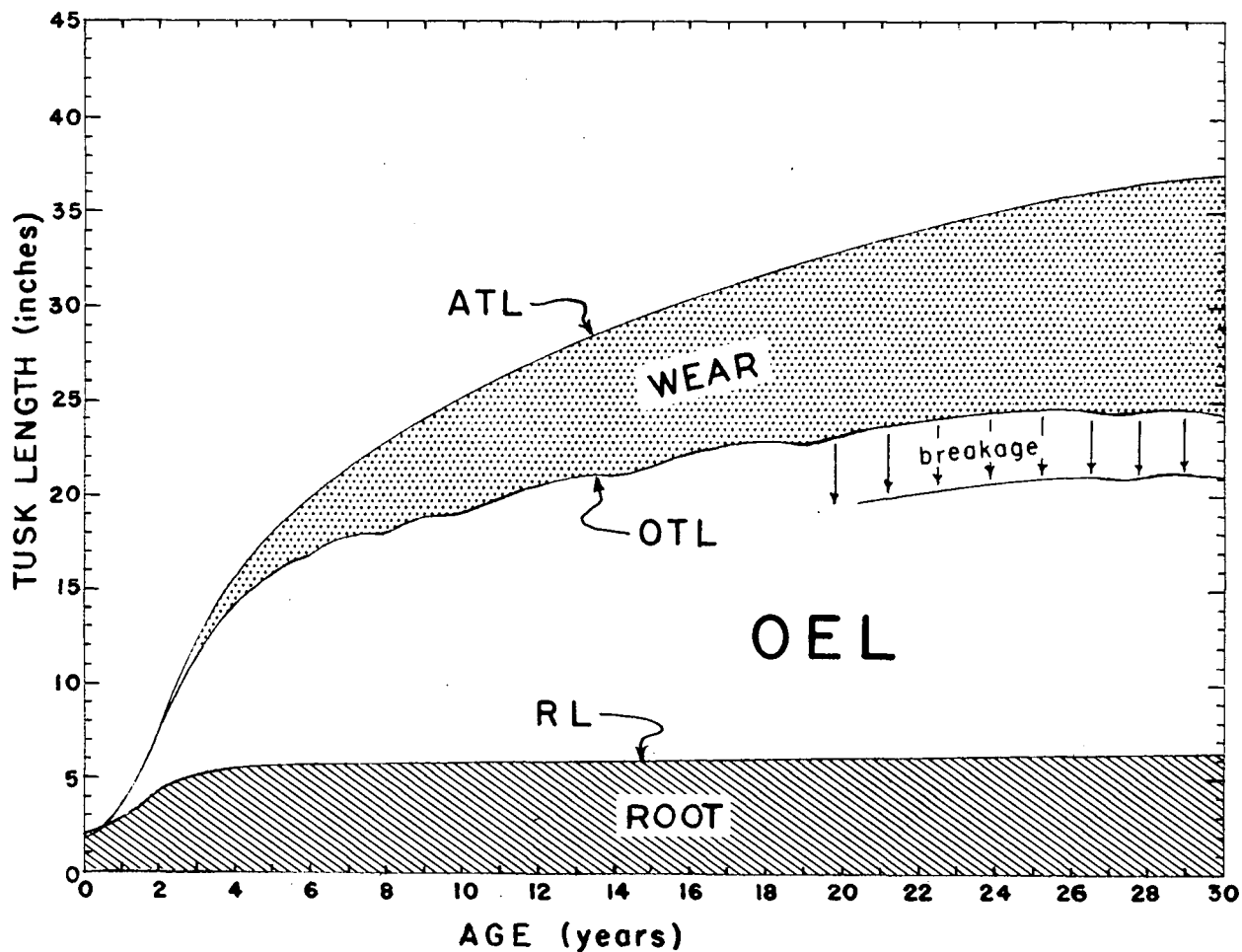


Fig. 19.--Average linear growth and wear of female tusks, based upon Appendix IIB. Irregularities in the OTL-growth curve are due to increased wear rates during pregnancy and lactation.

hypothetical OEL/age means of Appendix IIB. The male "catch-curve" (p. 145) was used as a model for size and age distribution of the sample. This yielded an OEL frequency whose major peaks and troughs were statistically identical to Figure 14 and Freimann's (1940) data.

It must be stressed once more that this plan of tusk growth is designed to fit average conditions. For this reason it has a major weakness in that it cannot be applied directly to animals having more or fewer pregnancies per unit of time than have been allowed for. Such deviates, however, can usually be diagnosed individually when tusk morphology and reproductive history are known.

Age designations for specimens of both sexes utilized throughout the present study have been primarily based upon the above hypothetical tusk growth patterns. When no tusk measurements were available, ages were approximated for females from evidence (ovaries) of their reproductive history and for males by the number of cementum layers in their teeth. The latter technique is discussed below (p. 124).

Body Growth

In the fall of 1951 two young walruses were acquired by North American zoological parks, and by request, serial body weights were recorded during their brief life spans. The writer is indebted to Dr. Robert McClung, of the New York Zoological Society, and to Mrs. Belle J. Benchley and

Dr. Glen G. Crosbie, of the Zoological Society of San Diego, for their kind assistance in collecting these data, shown in Figure 20. Some presented by Mohr (1952, p. 246) have been included for comparison. All are Atlantic walruses, but their weights do not differ from Pacific specimens of equivalent age recorded by Brooks (1954). Thus, it is assumed that the young of both populations have similar growth histories in the first two years of life.

There are two features of particular interest illustrated by Figure 20. The first is that, although each animal's growth during the first year was rather different from the others, all tended to approach the same value and slope in the second year. Prior to their arrival at the zoos, growth had been retarded (probably due to inadequate nutrition), but upon receiving a regular nutritive diet, each compensated for its losses until the intrinsic growth rate (Brody, 1945, p. 544) was attained. Teeth and tusks from two of these specimens ("Bosco" and "Herbert") were examined by the writer, and it was found that there had been no compensatory accretion there. The second feature to be noted is a unanimous, though slight, indication of seasonal growth rhythm, with maximum increases from late spring to early winter and minimums in late winter and early spring. As would be expected, the maxima and minima of this rhythm antecede the periodic increases and decreases of blubber thickness reported by many Eskimo and White observers, including Brooks (1954) and Vibe (1950).

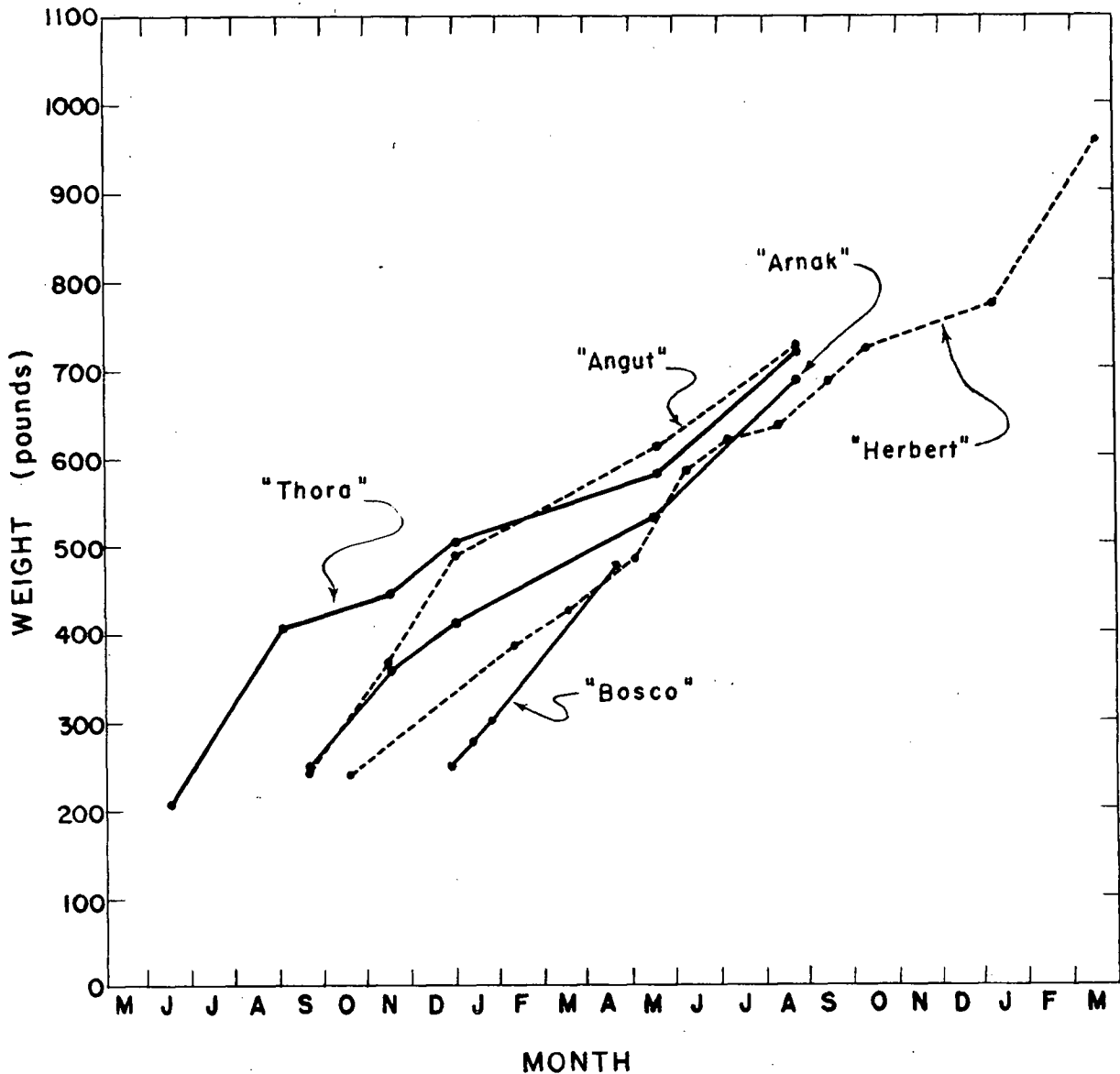


Fig. 20.--Body weight growth of five young Atlantic walruses in captivity. Initial weights were presumably recorded when the animals first arrived at the zoos, except for "Bosco" who was received two months earlier. Each was under one year of age when captured.

The animals are fattest in fall and winter, thinnest in spring and summer.

Generalized body length, weight, and hind foot length-growth of the Pacific walrus from birth to old age are shown in Figures 21, 22, and 23, as derived from the records of Brooks (1954), Nikulin (1940), Perfilyevsky (in Nikulin, op. cit.), and the writer. As was noted earlier (Table 5, p. 48) the degree of sexual dimorphism is not excessive and is by no means comparable to the differences recorded for harem breeders. Males of the latter (Otaria: Hamilton, 1934; Callorhinus: Scheffer and Wilke, 1953; Mirounga: Laws, 1953) exhibit a sort of "double" sigmoid growth pattern (Fig. 24) in which the added sigmoid curve is apparently a secondary sex characteristic associated with dominance order. It is initiated prior to puberty and culminated at "sociological maturity" (Scheffer and Wilke, 1953, p. 131) when the animals have reached a sufficiently large size for effective competition with older harem masters. Adaptive double-sigmoid growth is probably in the genetic potential of all pinnipeds, but the mechanisms for its selection are not generally activated except when the conditions for harem maintenance are particularly suitable. As might be expected, the males of wholly promiscuous species (Phoca vitulina and P. groenlandica: H.D. Fisher, in litt.; Leptonychotes Weddelli: Bertram, 1940) appear to reach full adult size in a single geometrically-decelerating curve

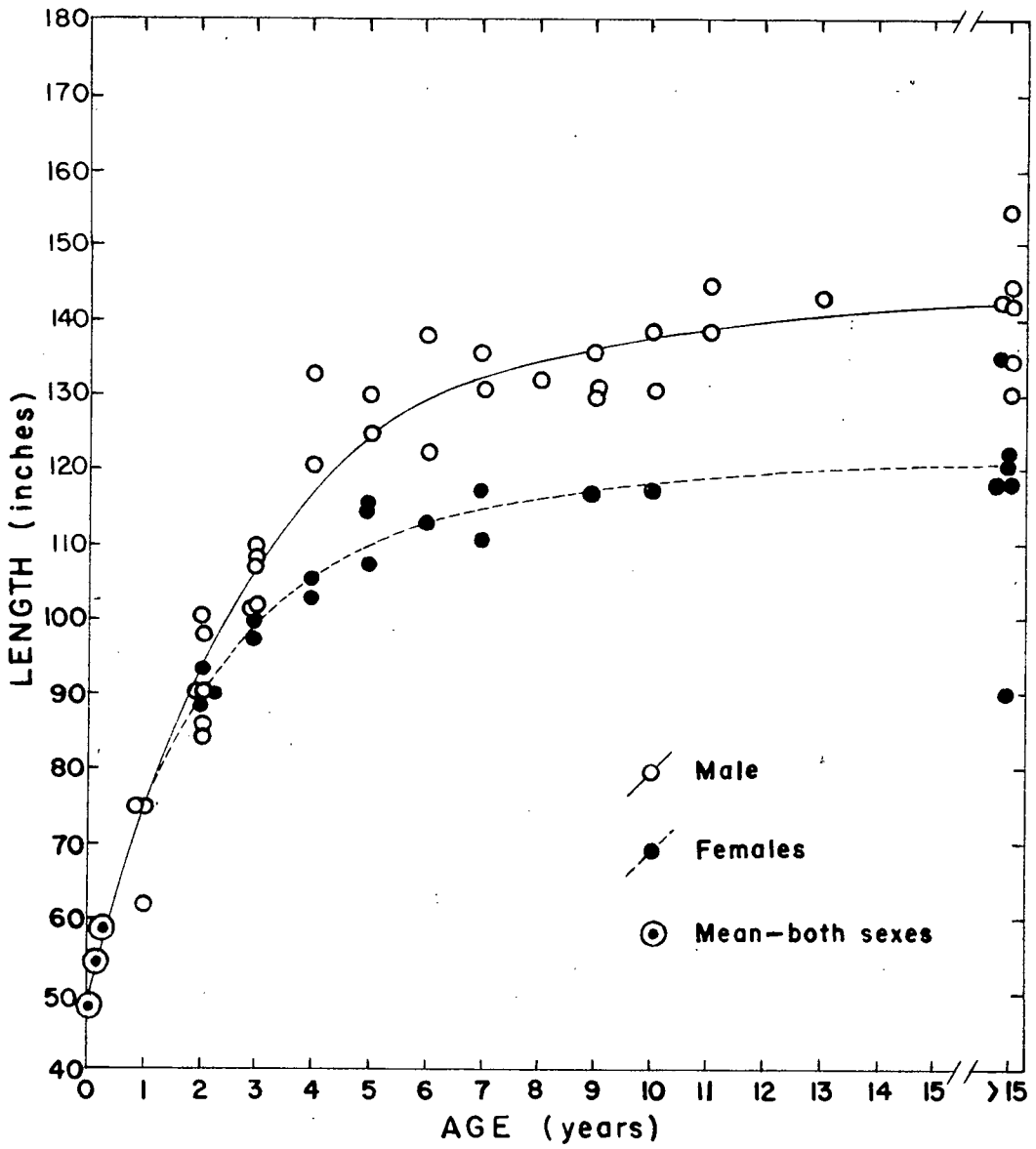


Fig. 21.--Average body length (nose-tail) growth of Pacific walruses.

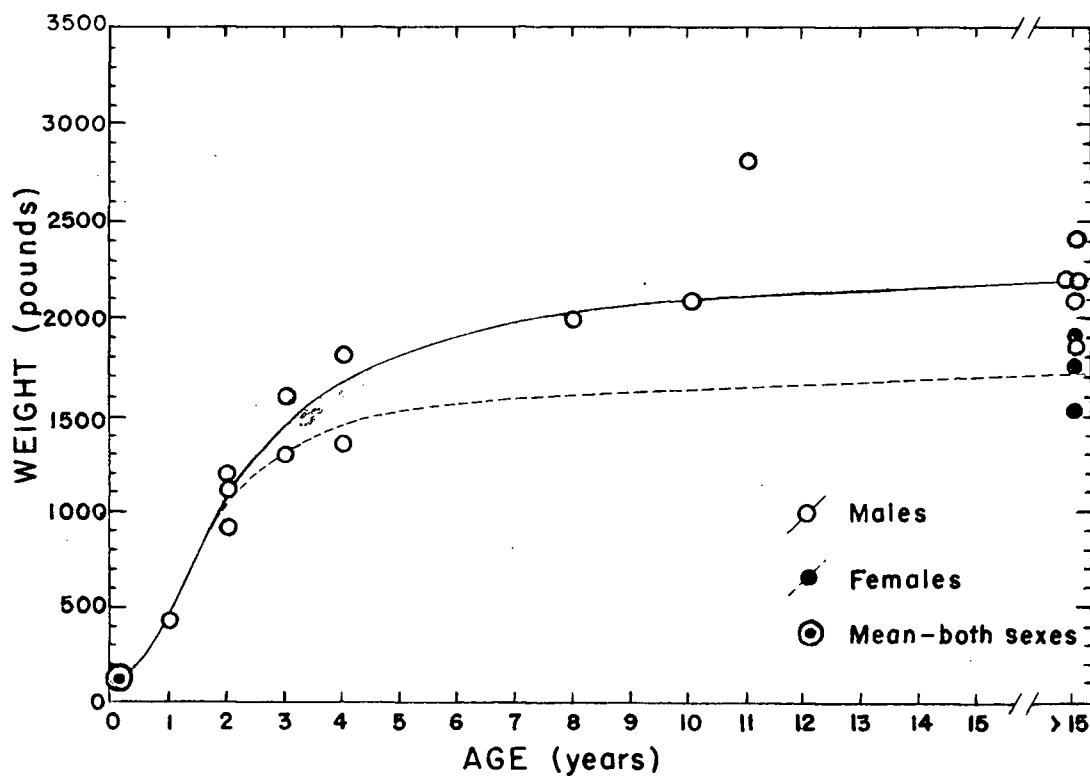


Fig. 22.--Approximate average body weight growth of Pacific walruses.

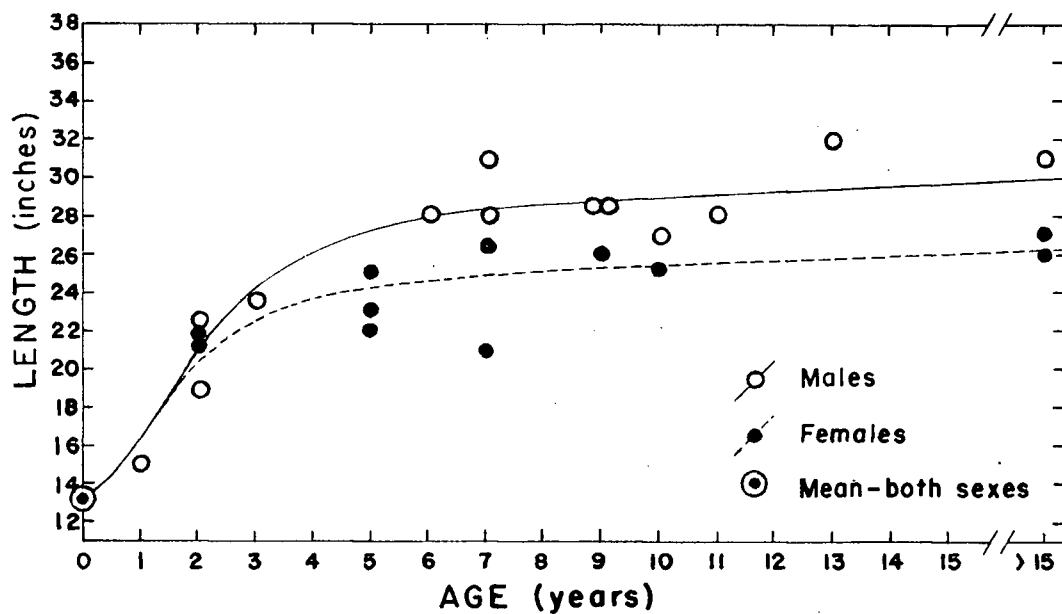


Fig. 23.--Average hind foot length (heel to tip of longest toe) growth of Pacific walruses.

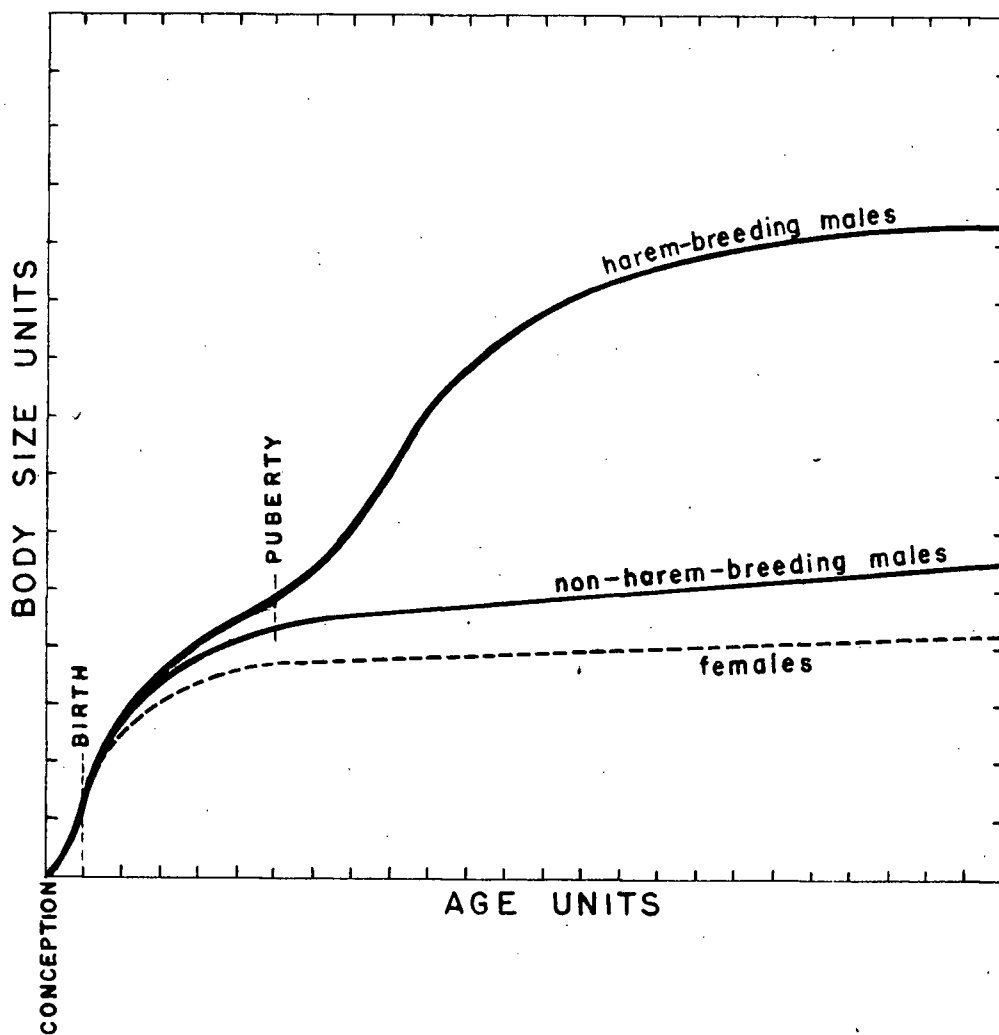


Fig. 24.--Relative pinniped body growth, illustrating the "double sigmoid" curve of harem breeders.

similar or identical to the females'. There are a few species such as walruses and gray seals, Halichoerus grypus, which appear to be intermediate in their breeding behaviour and would be expected to have correspondingly intermediate growth patterns. Neither Figure 21 nor 22, however, yields any definite indication of it for the Pacific walrus.

Baculum Growth

Baculum size is a crude guide to age, since length and weight increase rapidly during the first five or six years. The approximate average growth history of this bone is shown in Figures 25 and 26. At birth it is about 20 per cent of adult length and 0.5 per cent of adult weight. Thereafter its growth is strongly sigmoid, with weight increases lagging slightly behind length. The bone, itself, is generally S-shaped (Fig. 27), though as Murie (1936) observed, the form may be rather variable. Sagittal sections have revealed layering in the internal structure, but it does not appear to be of any value for ageing.

A peculiar phenomenon associated with this structure is the occasional breakage which occurs under natural conditions. Murie (1936) illustrates several specimens of this kind and states that fifteen out of twenty-five sent to him from St. Lawrence Island by Otto Geist had healed fractures. This proportion, however, does not appear to be the usual one, for Gambell natives consider broken bones to be rather uncommon. In the writer's sample of 217 specimens, only

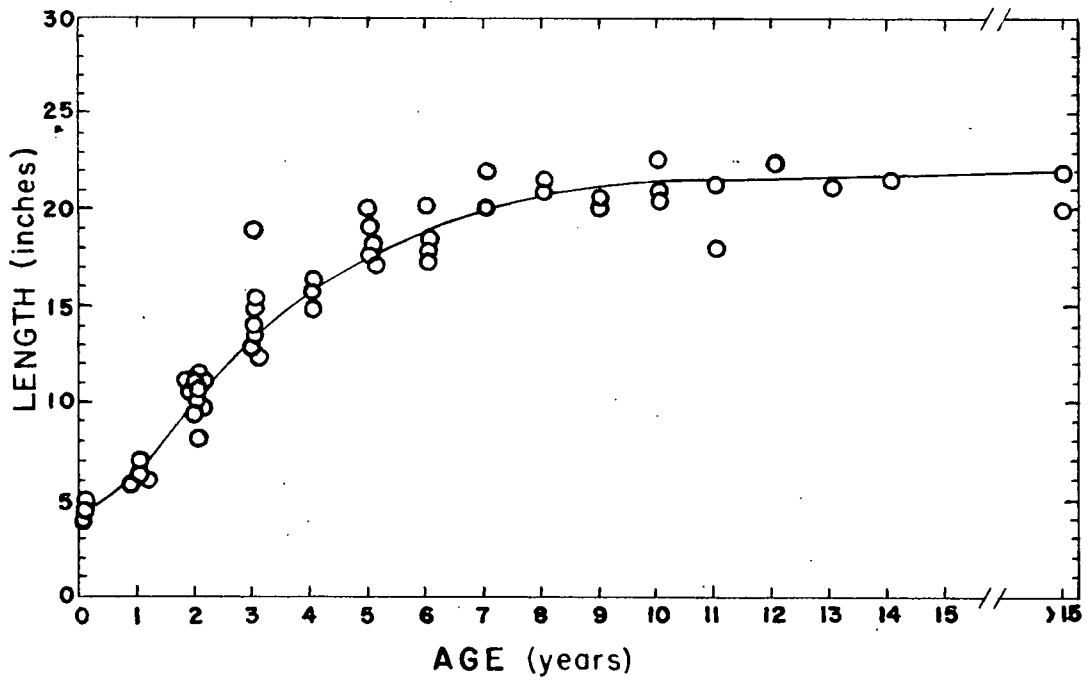


Fig. 25.--Average baculum length growth of Pacific walruses.

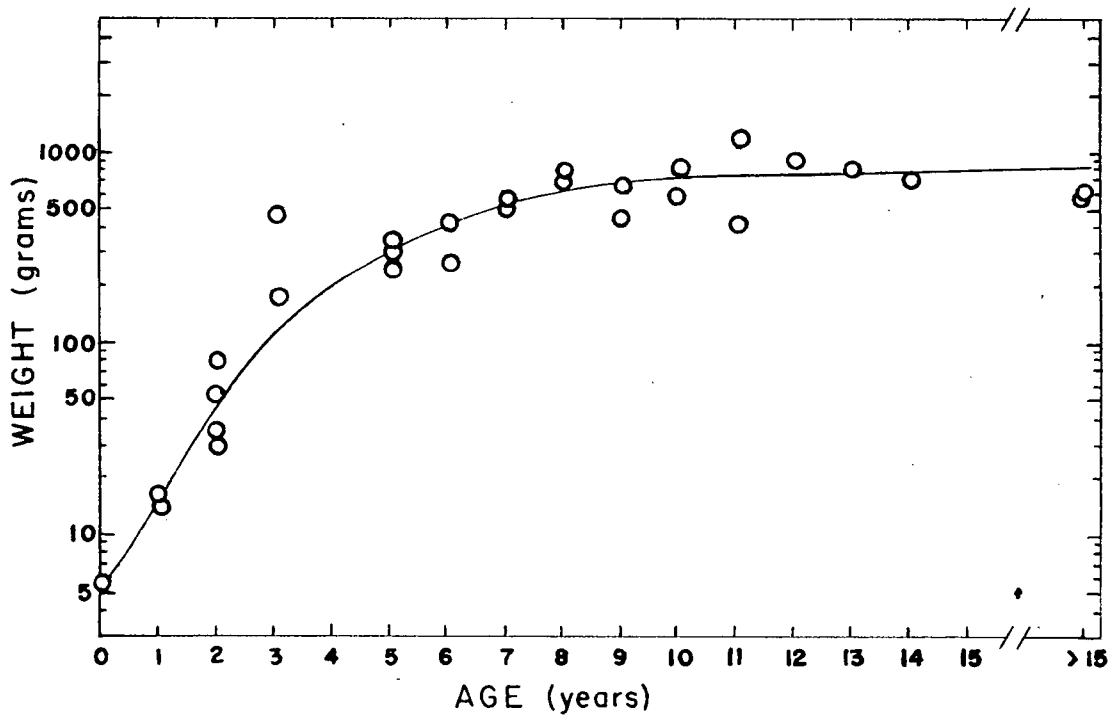


Fig. 26.--Average baculum weight growth of Pacific walruses. Arith-log scale.



Fig. 27.--Comparison of calf and adult bacula, the latter showing typical s-shape.

three had obviously been broken, and three others displayed slight irregularities which might have been sites of earlier injuries. Two of the broken bones, one a new fracture and the other partially healed, were from calves. The third was a fully healed young adult baculum. It is difficult to imagine how these loosely-supported structures could be broken, especially in the calves, though Murie (1936) considers that, due to the great bulk of the adults, such minor injuries might easily result from mishaps which occur while climbing about on uneven ice floes.

A female counterpart of the baculum, the os clitoridis, was found in most specimens examined by the writer (Table 13). The proportion of non-osseous structures in the oldest animals was significantly higher than that of the calves, suggesting that ossification decreases with age. In walruses these bones are generally somewhat question-mark shaped, though a few exhibit a totally unrelated form.

Skin and Pelage

Chapsky (1936) gives the following for skin thickness of Kara Sea walruses: young 8 mm.; yearlings 13.5 mm.; sub-adults 20 mm.; adult males 26 mm.; and adult females 22 mm. These agree closely with Brooks' (1954) data, and he notes that the bulls' neck skin may be as much as 7 cm. thick. Nikulin (1940) reports 3-4 cm. as an average for Pacifics. It was believed by several earlier writers (e.g. Brown, 1868; Brehm, 1926) that the characteristically

TABLE 13
OS CLITORIDIS WEIGHTS

Age (years)	Number of Specimens	Weight (grams)	
		Range	Mean \pm S.E.
0	7	cartilage
0	34	0.026 - 0.242	0.1182 \pm .0005
1 - 2	4	0.049 - 0.237	0.1397 \pm .0426
6 - 9	4	0.023 - 0.202	0.0827 \pm .0402
>20	3	cartilage
>20	1	0.028

thick, scarred skin of adult bulls was the result of tusk wounds received during breeding season forays, for at that time walruses were thought to be aggressive harem masters. This theory of origin has been rejected by Brooks (1954), Chapsky (1936), Freimann (1940), and Nikulin (1940), and the writer's experience upholds their views. Thick, lumpy skin on the neck and shoulders is merely a secondary male sexual character, and its surface scars seem to be mostly the result of injuries caused by sharp-edged ice on the projecting tubercles, though a few are undoubtedly tusk-inflicted wounds. Freimann (op. cit., Tables 4 and 5) has demonstrated that this characteristic tuberculation appears at about age 6 to 8 in most bulls.

General changes in blubber thickness and pelage color with age have been adequately discussed by Brooks (1954) and others. The question of pelage molts has not as yet been fully answered, largely, it seems, because it has not been fully investigated. Seals in general display three stages of hair covering: foetal or lanugo, juvenile, and adult (Mohr, 1952). The lanugo may be molted in utero or at some time within three or four weeks post-partum, depending upon the species; the juvenile-adult molt usually occurs in the succeeding autumn. Information concerning an equivalent lanugo stage in walruses is not complete, but apparently the slate colored natal coat is shed one or two months after birth (Nikulin, 1940). A molt (juvenile to adult?) in the

first autumn seems to be well established by the report of Sokolovsky (Mohr, 1952) and corroborating observations by R. McClung (in litt.) of another young captive. These began shedding between October and December, and the new hair was fully grown by spring.

Mohr (1952) presents convincing evidence of an annual adult molt which occurs between May and July in Atlantic walruses, both wild and captive. This corresponds to the general seasonal rhythm of other pinnipeds described by her. Gambell natives have not recognized such a phenomenon in their locality, and it was never noticed by the writer, but herds of females photographed near Point Hope in late May (Ryder, 1954) show a patchy coat which is suggestive of the irregular sheetmolt pattern displayed by some other pinnipeds (cf. Laws, 1953, pl. Vb).

It has been noted (Mohr, 1952) that the whiskers or vibrissae are shed annually and are not, as Allen (1880), Brooks (1954), and others have suggested, permanent fixtures which grow continually throughout life. This may account for some of the wide variety of measurements recorded in the literature, since they must be very short (worn) just prior to molting and very long when fully grown anew. The maximum lengths reported are 10 1/2 inches for Atlantics (Mohr, op. cit.) and 10 inches for Pacifics (Nikulin, 1940) -- the shortest, about 1/8-inch. Replacement seems to be intermittent over a period of several months in summer and fall and all of the vibrissae may not be shed each year

(Mohr, op. cit.). Possibly there is a regular increase in the basal diameters of these structures with advancing age.

Skull Growth

General skull growth is depicted in Figures 28 and 29, in which a few of the primary measurements have been plotted by age. These were extracted from the work of Allen (1880), from specimens collected by the writer, and from those in various North American Museums. The writer is indebted to J.W. Brooks, University of Alaska; C.O. Handley, Jr., U.S. National Museum; Barbara Lawrence, Museum of Comparative Zoology; and W.C. Pelzer, Milwaukee Public Museum, for the latter.

It is apparent that adult skull dimensions are attained at about five years of age by both sexes, but that slow growth persists throughout the life span, especially in the rostral and mastoid regions. The latter is most evident in males and is believed to be directly correlated with tusk development. Lacking other means, good criteria for identifying the sexes of adult Pacific walrus skulls are the rostral and mastoid breadths, those of the males being characteristically larger than the females', as indicated.

Dentition

Succession.--Typically, pinnipeds are born with their adult dentition preformed, though it may not erupt for several days or weeks thereafter. A minute, non-functional set of milk teeth is resorbed either in utero (phocids) or shortly

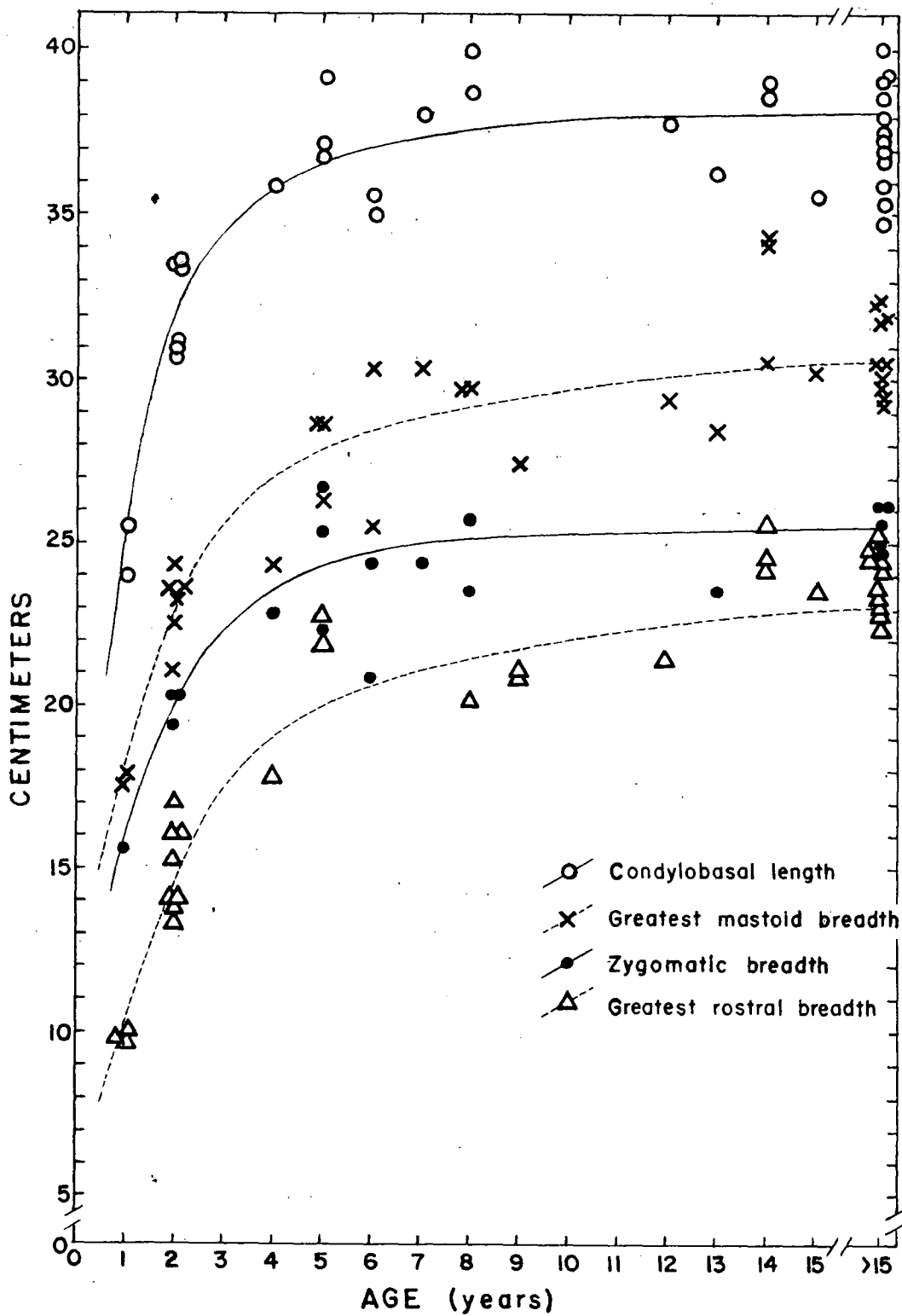


Fig. 28.--Age-relative increase of male Pacific walrus skull dimensions.

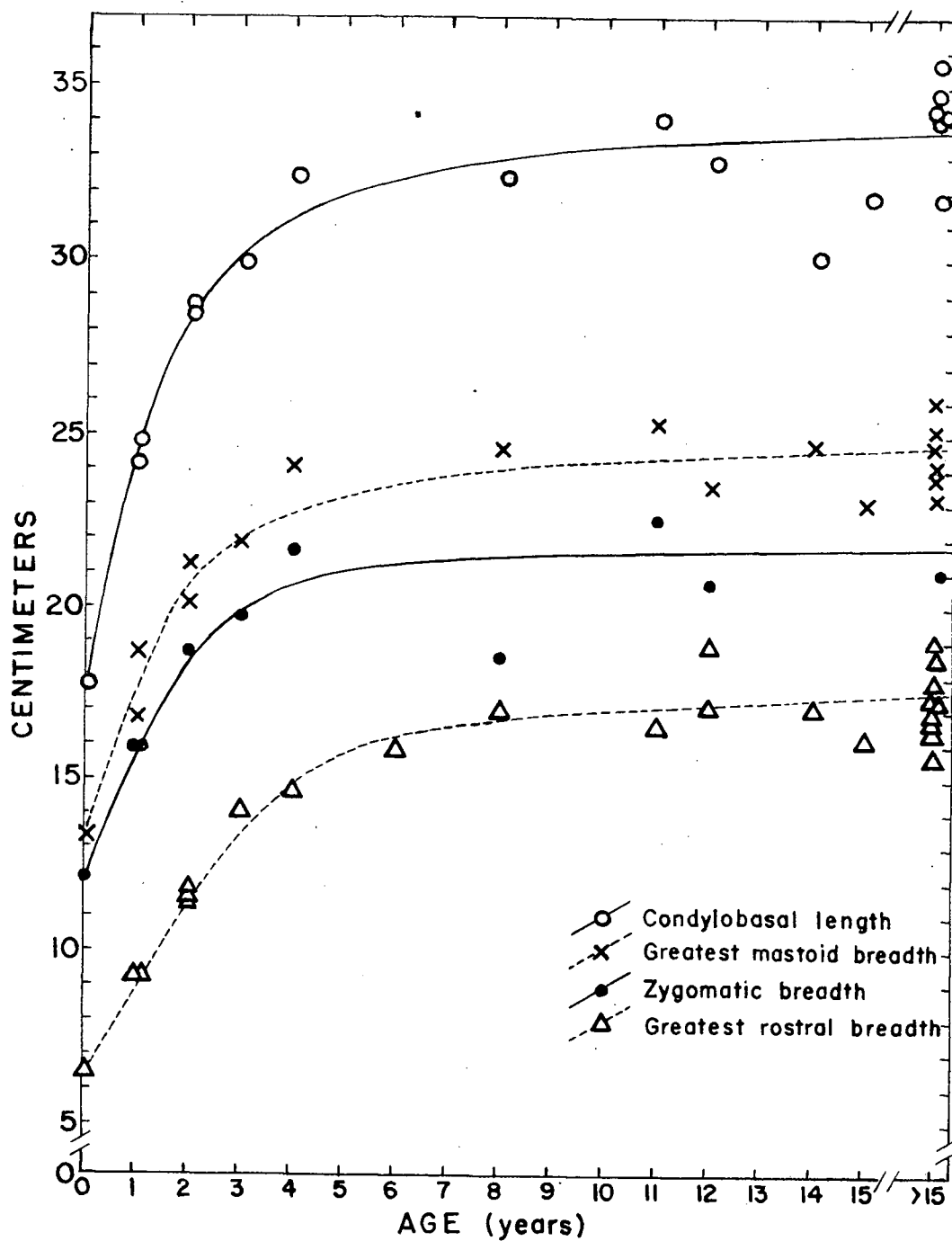


Fig. 29.--Age-relative increase of female Pacific walrus skull dimensions.

after birth (otariids). The progressive stages of walrus dental development are most closely allied to the otariids, but they have some peculiarities which distinguish them from both of the other pinniped groups.

The full deciduous dentition of walruses had not yet been investigated, since it apparently is present only during some prenatal stage. It is presumed to be

$$I \frac{123}{123} \quad C \frac{1}{1} \quad P \frac{234}{123} = 28$$

but the maximum observed formula at birth seldom exceeds

$$I \frac{23}{123} \quad C \frac{1}{1} \quad P \frac{23}{123} = 18$$

due to prenatal resorption. Upper milk premolar no. 4 has been found in only one natal skull, a specimen collected at Gambell. Contrary to Cobb's (1933) conclusions, it seems very improbable that any of the milk set is actually shed or retained to adulthood. Instead, the entire battery seems to be resorbed before one year of age without ever breaking the surface of the gums. In twenty-one calves and fetuses examined at Gambell, only one had an erupted milk tooth, and resorption of the remaining few in Cobb's and the writer's natal skulls was already well under way.

The full set of successional teeth is present at birth, but except for an occasional lower canine, none is erupted. The maximum observed formula is

$$I \frac{23}{23} \quad C \frac{1}{1} \quad P \frac{1234}{123} \quad M \frac{1}{12} = 32$$

though, again, it is seldom realized, for $I \frac{2}{23}$, $P \frac{4}{4}$, and $M \frac{1}{2}$

are vestigial and are often absent, especially after adulthood is reached.

Structure and growth of the cheek teeth.--Cobb (1933) has given a detailed account of dental development as he saw it in a series of museum skulls, but due to the limitations of his specimen material and information on natural history, there are some features which he seems to have evaluated incorrectly or not at all. Since these may be relatively important as a background for future investigations, they are treated briefly below.

The hollow, conical natal tooth is composed of dense primary dentin with a thin cap of enamel (Fig. 30a), and by one year of age, more dentin has been added internally and a single layer of cementum externally. Dentin deposition ceases after the third or fourth year. In succeeding years only cementum is added, "sealing off" the dentinal portion and gradually increasing the cross-sectional area (Fig. 30d,e). Each tooth is continually erupted as its exposed surfaces are worn away, and the lingual and buccal surfaces remain about level with the gum line at the gingival-dental junction at all times (Fig. 30d,e).

Within the dentin some more or less prominent laminations occur, the most constant and sharply defined of which is marked by the "neonatal line" (Massler, et al, 1941) between foetal and post-natal dentin (Fig. 30b). In human teeth the major incremental lines result from "constitutional adjustments such as birth,...weaning,...dietary disturbances,

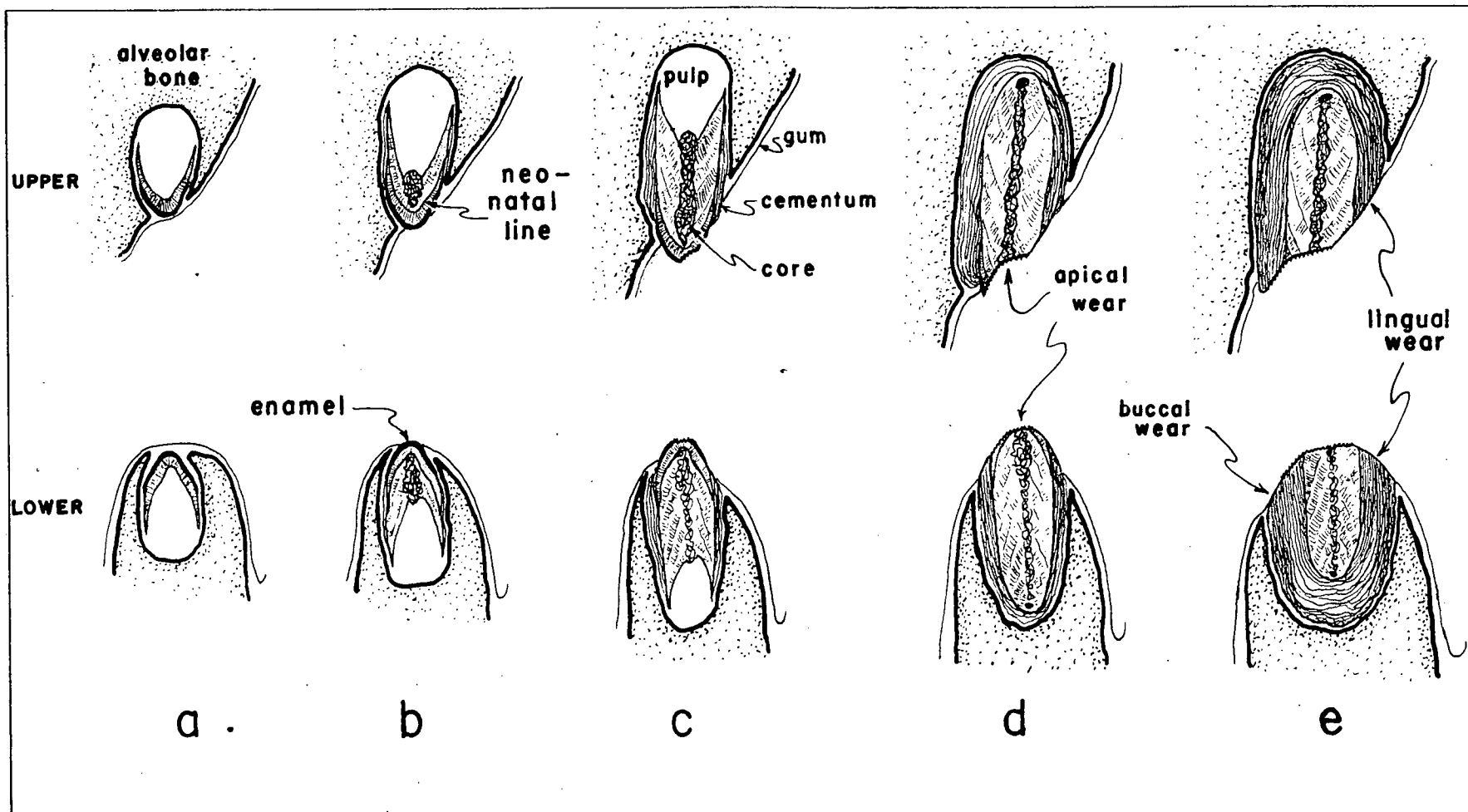


Fig. 30.--Sagittal sections of the second upper and lower premolars in situ showing structural growth: a - newborn; b - yearling; c - two years; d - four or five years; e - about ten years. Scale about three-fourths actual size. Detail slightly exaggerated.

...[and] diseases that affect calcium metabolism directly..." (Noyes, et al, 1938, p. 125), and in teeth of the elephant seal Laws (1952) notes that they are a result of regular fasts during breeding and molting periods. Externally, canines of the latter and of the Alaska fur seal (Scheffer, 1950) reveal prominent annular ridges, each of which marks the end of one year's growth. Some Pacific walrus molariforms display similar laminae and ridges, but for reasons not yet understood neither of these phenomena appears to have any definite annual rhythm, individuals of the same age (by OEL) often having different patterns of lamination. Possibly this is due to the fact that the dentinal portion of the tooth is formed entirely before puberty, and during that time there are no regular, sharply defined physiological adjustments excepting birth. Definite annular ridges on the tusk roots do not form until after puberty.

In the center of each tooth there is generally a slender core of translucent material which is most prominent in males. This is not dentin, as usually defined, but consists instead of a mass of imperfectly calcified "pulp stones" or "denticles" (Kronfeld, 1937, p. 59) partially fused together and usually with numerous interglobular "spaces" filled with organic material. This core is a distinctive characteristic of walrus dentition (Cammann, 1954; Penniman, 1952) and is particularly well developed in the tusks (p. 129).¹²⁹

The degree of hypercementosis displayed by walruses

appears to be unexcelled among mammalia, except perhaps for the hooded seal, Cystophora cristata. Cobb (1933) considers this to be a result of stresses involved in crushing clam shells -- a logical conclusion under the circumstances but one which the writer believes to be incorrect. Almost without exception, the stomach contents of walruses examined by the writer and reported in the literature were composed of non-masticated pelecypod feet and siphons which, in life, are expressed beyond the margins of the shells and cannot be withdrawn between the valves. As seen in the walrus stomachs they appeared to have been bitten or squeezed off at their bases by pressure exerted either with the muscular lips or the toothless incisive portion of the jaws -- probably the former. Occasional marginal fragments of the shells also attest to this process. If, on the other hand, the shells had first been crushed in the mouth and the soft parts later extracted by tongue and lip action, we should expect to find at least some of the feet and siphons masticated and a larger proportion of mantles, gills, visceral masses, and shells present in the stomach. There would appear to be no advantage gained by crushing the shells if only the exposed tissues are eaten.

A second point of disagreement with Cobb's conclusion was found in the teeth, themselves. Histological examinations of occluded, non-occluded, and non-erupted teeth from two 2-year-old specimens revealed that every tooth from a given animal has the same proportion of cementum, regardless of

its functional status. This suggests that cementogenesis is governed by overall physiological controls which may not be related to the feeding process at all. Indeed, it appears to be correlated with tusk growth (see p. 128).

This also negates Cobb's theories of tooth wear, for if shells are not taken into the mouth, they cannot be responsible for the pattern observed. Wear occurs on three planes: lingual, apical, and buccal. The first usually results in a highly polished, convex surface, the second a rough, concave surface, and the third mostly a polished, convex surface (Fig. 30d,e). Occlusal abrasion accounts for all apical and part of the buccal wear, and from its characteristics it is evident that particles of a harder substance than either dentin or cementum are partly involved -- probably sand and/or gravel. Gravel is a common part of the stomach contents, as might be expected, and in winter it is frequently observed about walrus breathing holes where it has been spewed out upon the ice in large quantities. Clam shells, mostly unbroken, are occasionally found with it or near it. Thus it is believed that lingual wear, both upper and lower, is due to tongue action plus abrasion by accidentally mouthed sand and gravel, while the smooth portion of buccal wear is also due to sand and gravel plus friction of the gingival tissue below the opposing tooth (Fig. 30e).

Since cementum layering in human teeth follows no seasonal rhythm, the number of layers is only a crude in-

indicator of relative age (Noyes, et al, 1938). But in the teeth of hooded and elephant seals examined by Laws (1952) they appeared to be deposited in an annual cycle similar to the dentinal laminae, and the number of layers was therefore equal to the individual's age. Pacific walruses also have an annual rhythm of cementogenesis, though it did not become apparent until the problems of tusk growth had first been solved, for the rate of deposition is irregular in the first 6 to 7 years. It was suspected earlier that in adulthood one cementum layer was deposited per year, for those which are formed at that time are much more clearly defined than the pubertal and prepubertal lamina, and in the tusks there is one layer per root ridge. This relationship was tested by (1) plotting the regression OEL on number of cementum layers, (2) constructing a y-axis age scale on the basis of Appendix IIA and an x-axis age scale on the above assumption, and (3) drawing a sketch curve which satisfied both the empirical data and the hypothetical age scales. The result (Fig. 31) is a satisfactory demonstration that cementum layers are as good indices of age as tusk lengths; in fact, they are probably better in the later years.

The only specimen for which tooth, OEL, and root ridge data were available was used as a partial test of conformity amongst the three ageing methods. The values obtained were 21, 20, and 22 years, respectively. This could be mere coincidence, of course, for it is evident that the OEL range per layer number is rather wide. Insufficient

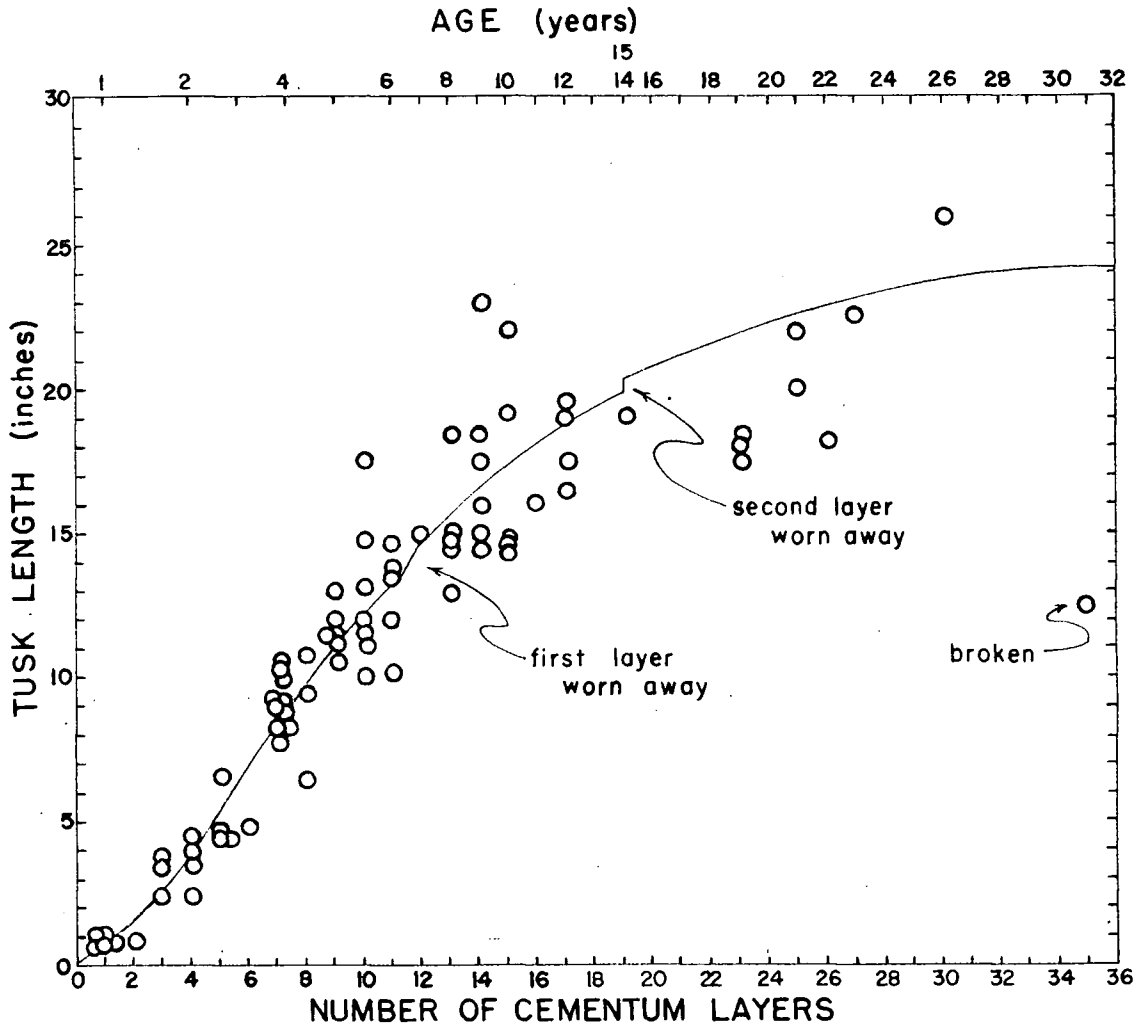


Fig. 31.--Relationship between tusk OEL and number of cementum layers in the cheek teeth of male Pacific walruses. The sketch curve is based upon OEL age classes (Appendix IIA) and the x-axis age scale, which assumes that one layer is added per year after the first seven years.

data are available for the females, but preliminarily their OEL/cementum layer relationship appears to be radically different from the males' and may have little or no practical application.

Structure and growth of the tusks.--At birth the upper canines are completely enclosed in the alveoli and do not erupt until four to six months later (Chapsky, 1936; Nikulin, 1940). Judging from records of captive specimens, this may be delayed still further by nutritional deficiencies, some appearing as late as December (B. Benchley, in litt.; R. McClung, in litt.). The natal canine has the same general structure as a molariform tooth (viz. a delicate, hollow cone of primary dentin capped with enamel), and, similarly, by one year of age more dentin has been added internally and one layer of cementum externally (Fig. 32a,b). Unlike the molariforms, dentinogenesis continues thereafter at a relatively high rate throughout the entire life span. Thus the canine becomes a tusk, for as dentin is added to the root, the distal portion is expressed further from the alveolus. The structural pattern involved may be likened to a series of hollow cones, each nesting within the one below and one or more being added at the top (root apex) each year. As new ones are added, the older ones are pushed farther away from their point of origin. Histologically, this results in a series of diagonal contours in a sagittal section (Fig. 32d), and concentric rings in a transverse

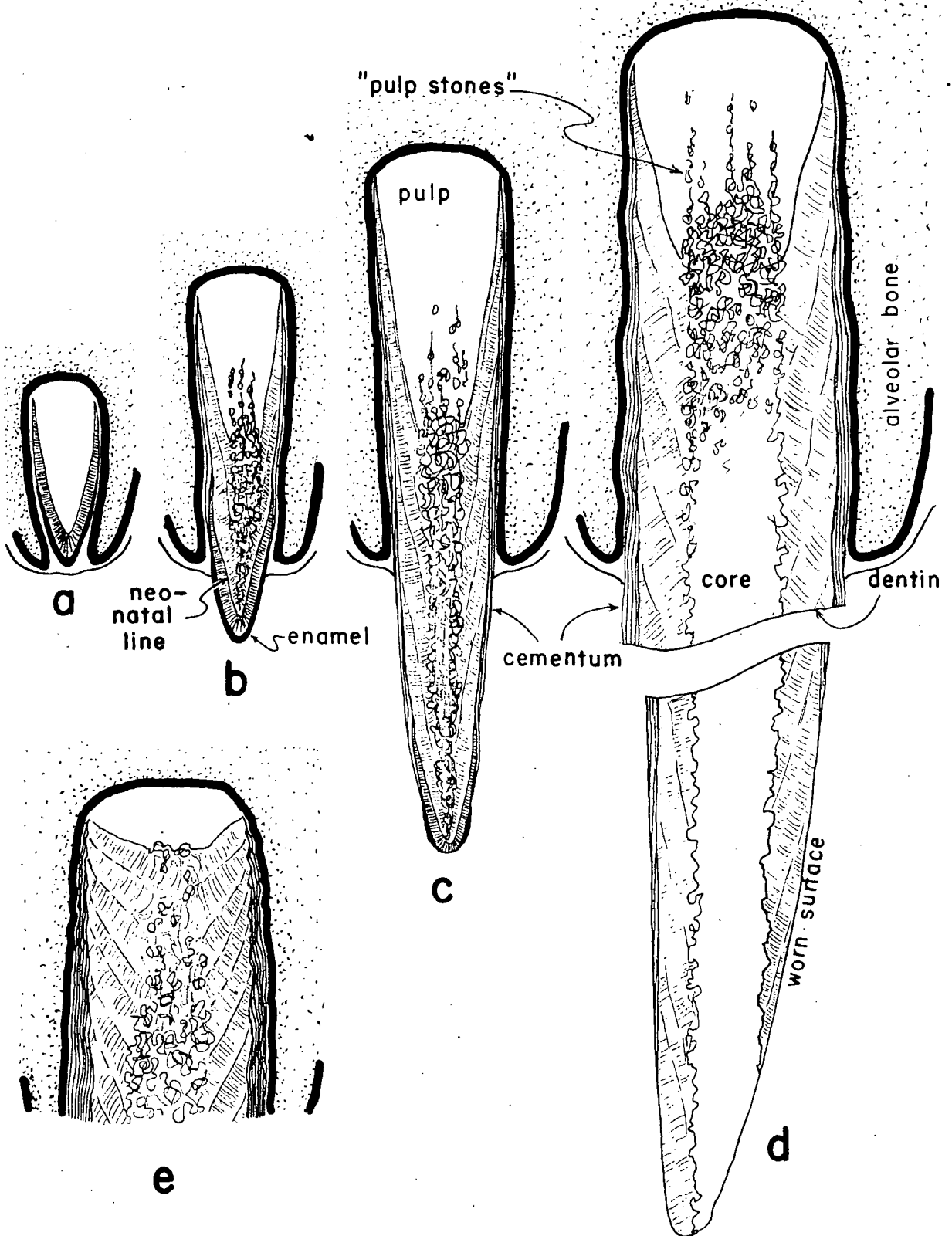


Fig. 32.--Sagittal sections of male tusks in situ, showing structural growth: a - newborn; b - yearling; c - two years; d - about ten years; e - "very old." Scale about one-half actual size. Detail slightly exaggerated.

section (see Penniman, 1952, pl. VIII). The significance of the indistinct contours formed in the early years of life is unknown (except for the neonatal line), animals of the same apparent age having different patterns and some having none whatever. Sometime after sexual maturity is attained the laminations become very regular and pronounced, the upper extremity of each lamina being visible externally as a "root ridge" (p. 80). These ridges and contours, as noted above, appear to be formed during late winter and early spring and are believed to be the result of poor nutrition or reproductive cycles (or both). They may be present though less distinct in female tusks.

Cementum layers are added to the root surface in the same chronological order as was observed in the molariforms, each of the 1, 2, and 3-year-old animals examined having the same number in both cheek teeth and tusks. Though their relationship to cheek tooth function seems dubious, they have a definite functional relation to tusk growth. Cementum acts primarily as a place of attachment for fibers of the periodontal membrane, a connective tissue occupying the space between tooth root and alveolar bone (Kronfeld, 1937). This serves to hold the tooth in place and to cushion it when in use. As dentin is added within the pulp cavity, the whole tusk must move downward in order to make room for the new material, and when this happens, the periodontal fibers are broken from their point of attachment in the

cementum. They must then be anchored into a new cementum matrix at the new point of contact. This process is probably a gradual one, though the cementum laminae suggest that it occurs spasmodically. Obviously, when the tusks are extruded most rapidly, more cementum layers must be added per unit time; hence the rate of deposition would be greatest in the early years of life. Later, when root ridges begin to form, only one layer per ridge is added in male tusks. It has been concluded that the rate of cementogenesis is probably governed by tusk growth rate and that it is expressed in all of the other teeth at the same time by a universal physiological mechanism. Quantitatively, cementum comprises about the same proportion of tooth bulk in females as in the males, but there seems to be no definite pattern of lamination.

In the center of each tusk is a thick core of "pulp stones" fused into a matrix of irregular dentin (Fig. 32, and see Penniman, 1952, pl. VIII). This structure is relatively larger in male tusks, comprising one-third to one-half their bulk, while in female tusks it generally constitutes less than one-fourth. As in the molariforms, formation commences sometime shortly after birth, but in the tusks it continues thereafter to old age, when it finally ceases. The core is then sealed over by dentin (Fig. 32e).

In transverse section the tusks of both sexes have the form of a slightly flattened ellipse. This shape is most

elongate in young tusks (Fig. 33), becoming gradually rounder with age as circumference increases (Fig. 34). The ratio of root-apex-circumference:gum-line-circumference is generally a positive value to about 7 or 8 years, after which it generally becomes negative. This is primarily due to reduced linear increments in late years and consequent greater bulk of overlapping cementum layers at the gum line (Fig. 32d,e).

As a general rule, male tusks are parallel or slightly divergent (see Brooks, 1954, Fig. 1), while females' range from nearly parallel to strongly convergent. The former is mainly due to postero-laterad curvature and a twist (clockwise, right; counterclockwise, left) of about one-fourth turn per 35 inches. Some male tusks, however, have neither curve nor twist. All female tusks observed by the writer had postero-mediad curvature, and twist seldom exceeded one-eighth turn per 35 inches.

Tusk wear may be divided into three types: antero-lateral, distal, and medial. The first is apparently caused by grubbing for mollusks on the sea bottom, and its location suggests that it is brought about by a side-to-side sweeping motion. The loss of tusk material in this manner is far greater than either of the other two, and in old animals it often exposes the core for two-thirds the OEL (Fig. 32d). By making the tusk more slender, it also increases the potentiality for distal wear, the second type being considered. The latter includes breakage and has already been quantita-

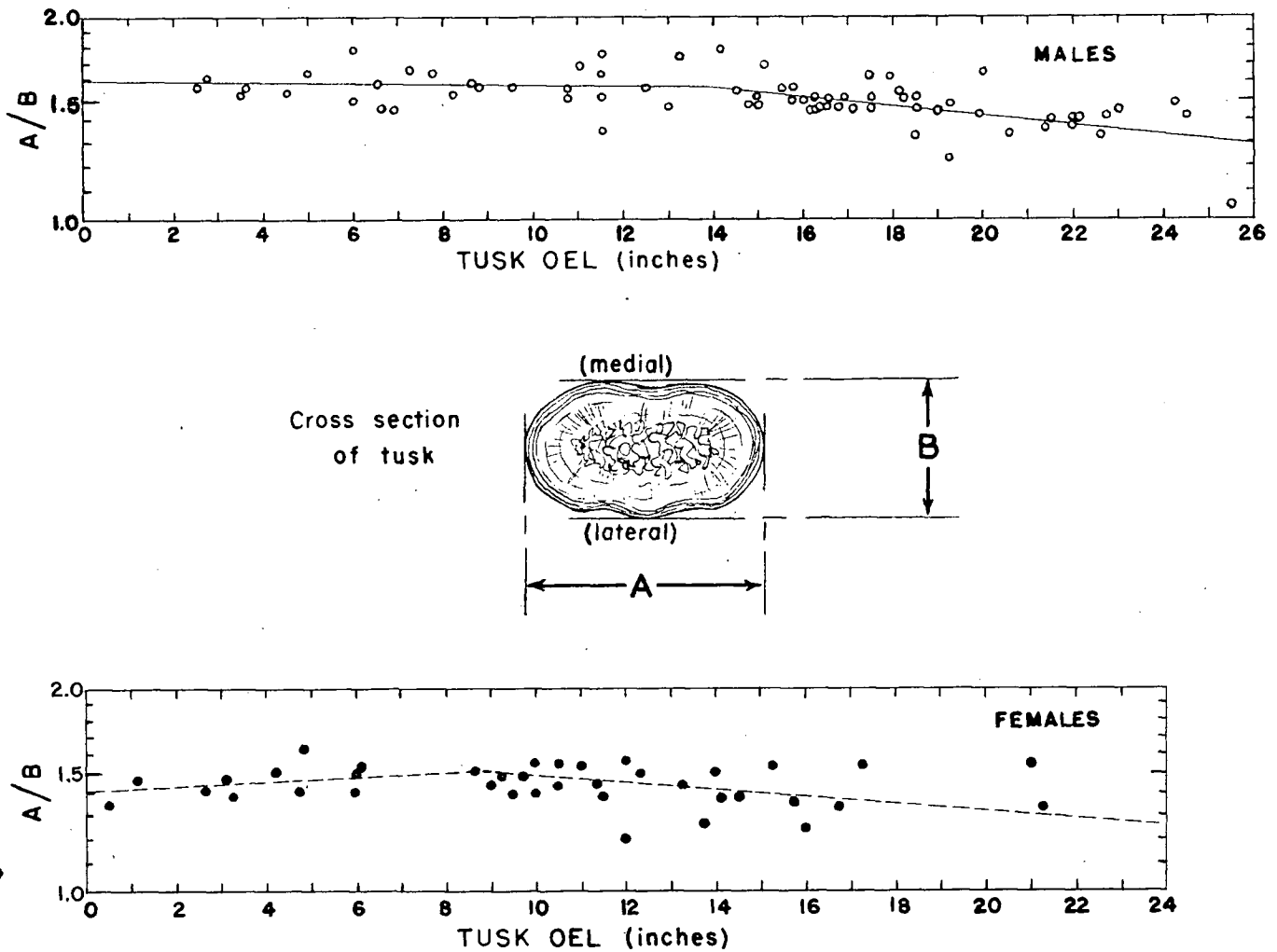


Fig. 33.--Relationship between tusk length (OEL) and cross-sectional shape at the gum line. (Arith-log scale)

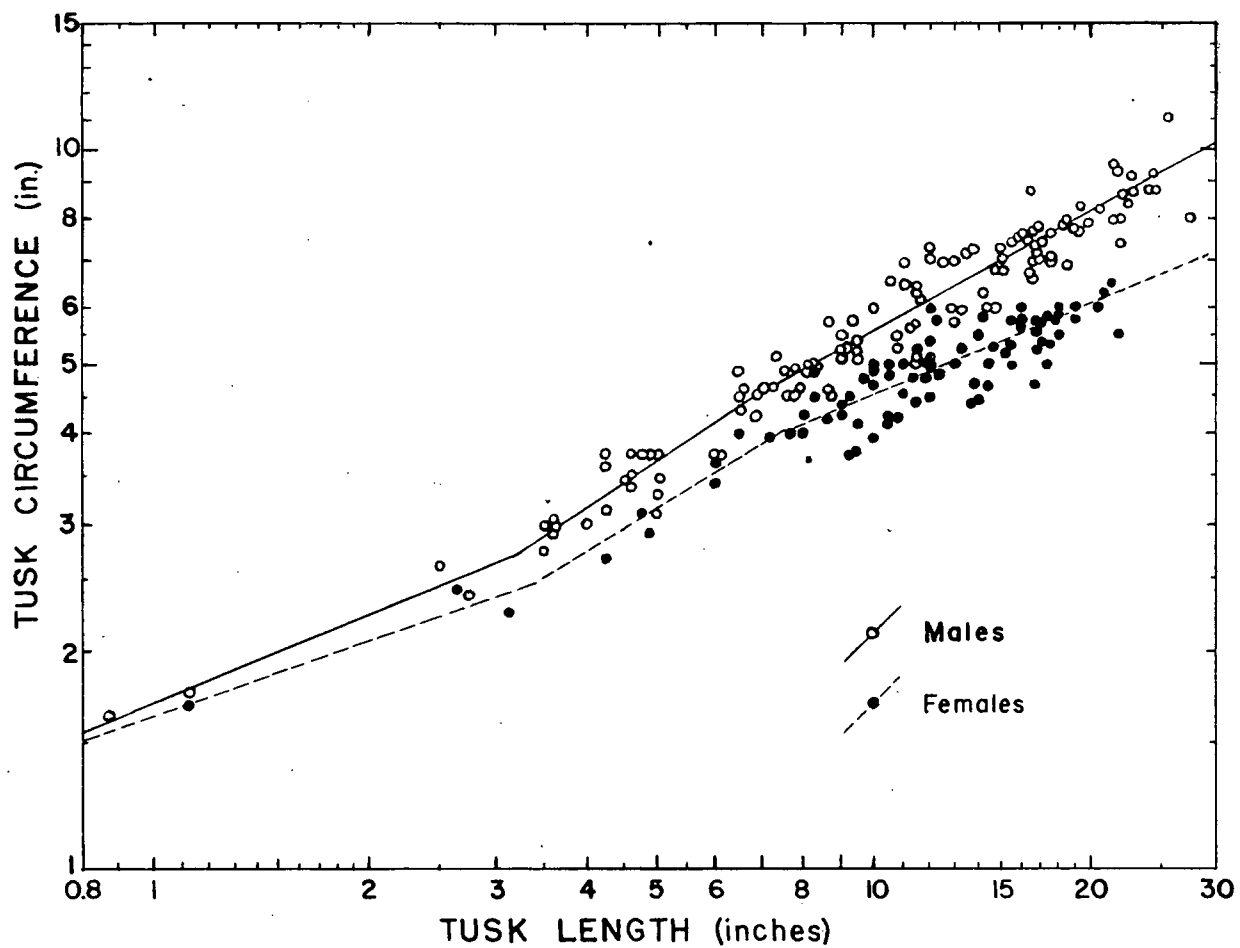


Fig. 34.--Relationship between observed external length (OEL) and circumference (at gum line) of the tusks. (Log-log scale)

tively discussed above (p. 85 et seq.) in connection with linear tusk growth. The third type, medial wear, occurs immediately below the gum line, creating a series of shallow depressions which are scarcely visible except when sighting along the medial surface. On male tusks the distances between troughs appear to be equal to equivalent root ridge intervals, and on old tusks which have practically ceased growing, a broad, relatively deep trough occurs near the gum line. In addition to the usual shallow ones, middle-aged and elderly females often display a series of the deeper troughs widely spaced along the medial surface (Fig. 35).

Because of the initial location next to the gum, the causal factor of medial tusk wear is unquestionably associated with some activity of the mouth, probably while feeding. It appears to be a result of either lower jaw action (with sand and gravel between it and the tusk) or forcible expulsion of materials from the mouth. Eskimo theories favor the latter. Its appearance as serial depressions seems to be an effect of varying tusk growth rates (seasonally) and a more or less constant rate of feeding; that is, when tusk growth is slowest (winter and spring), wear is concentrated over a relatively smaller area per unit time than when growth is rapid (summer and fall). This is verified by young, rapidly-growing tusks on which wear extends evenly over the whole medial surface and there are no noticeable depressions. The deep troughs (Fig. 35) hold greater



Fig. 35.--Posterior view of old female (upper) and old male (lower) tusks showing heavy medial wear. The "deep" trough on the male tusk is immediately below the gum line; on the female tusk several are visible along the medial surface.

significance, for they must be caused by either (a) drastic reduction in tusk growth rate or (b) an enormous increase in feeding activity. The first applies to old animals, specifically, and to occasional aberrants whose growth rates have been reduced by disease or injury. Several of the latter were examined by the writer. The second applies generally to females, and the increased food intake is believed to be associated with pregnancy and lactation (p. 97), for the depressions usually occur in pairs, the first more shallow than the second. The distance between the deepest troughs is comparable to the total ATL increments between pregnancies postulated in Appendix IIB. Expected and observed data are shown in Table 14. Again, the probable explanation for their absence or shallowness on tusks of young parturients is that tusk growth is more rapid then, and wear is therefore distributed over a wider area. On this premise it would be expected that the latest formed depressions on old tusks would be the deepest (tusk growth decreases with age), which is definitely true. The possibilities of applying this information as a field technique for evaluating recent reproductive history is self-evident.

DEATH

To the natural historian, one of the most elusive features of wild populations is length of life. Whole generations are born and die, leaving scarcely a trace of the

TABLE 14
INTERVALS BETWEEN MAJOR MEDIAL
WEAR LOCI ON FEMALE TUSKS

Parturitions	ATL Increment (inches)			
	Expected*	Observed		
		A-139	A-79	A-198
3rd to 4th	4	5 1/2	-----	-----
4th to 5th	3 3/4	-----	2 3/4	3 3/8
5th to 6th	4 1/8	-----	5 1/4	3 1/4

*Values extracted from Appendix IIB.

time, place, and manner in which they ceased to exist. Among the least understood are the marine mammals, since they are seldom observed for more than an instant, and their dead are often lost to the sea. Much of the information on walrus mortality has been gained from the dramatic accounts of Eskimos, sea captains, and explorers, to whom objective and quantitative interpretations were unknown. To evaluate these in terms of their relative importance is practically impossible, but a brief discussion of the various categories is presented below for the sake of completeness. This is followed by a crude evaluation of mortality rates and longevity.

Density Independent Factors

Weather.--As noted above (p. 52), some calves are born very early in the spring (March-April) when air temperatures are still rather low ($0^{\circ} \pm 10^{\circ} \text{F}$). According to the writer's and Belopolsky's (1939) Eskimo informants, these occasionally freeze to death shortly after birth. While this may be possible, it seems more likely that freezing is a post-mortem effect, for dead calves are about as frequently observed in May. No detailed autopsies have been performed on any of these young animals.

Winter storms may be a fairly frequent cause of juvenile and some adult mortality. About St. Matthew Island, Hanna (1920) observed carcasses of five young animals which had apparently been crushed by shifting ice, and a dead juvenile was also reported from there in 1954 by R. Rausch

(in litt.). Numerous others (mostly sub-adults) have been seen at various times about Nunivak Island (R.B. Gibson, in litt.), the Pribilofs (Preble, 1923; E.B. Elliot, voc. com.; V.B. Scheffer, voc. com.), and the Commander Islands (Barabash-Nikiforov, 1938). These records are sufficiently abundant and consistent to indicate a significant juvenile mortality along the edge of the winter pack, and it is possible that the cause of death is, as Hanna has suggested, accidental crushing between ice cakes during severe storms. Again, however, this could be post-mortem effect, and until autopsies can be performed on the fresh specimens, no definite conclusions can be reached.

Stillbirths and orphans.--Stillbirths and miscarriages had been observed infrequently by the Gambell men. One of the former was reported in 1954, and another potential one was observed by the writer in 1952. The latter specimen's amnionic sac was filled with semi-putrid blood from a recent hemorrhage, and it would undoubtedly have been born dead. Since the calf harvest at Gambell from 1952 to 54 was about 175-200 animals, these records suggest that about 1 per cent of the calves are dead at birth.

One emaciated orphan was observed near Gambell in 1954 by W. Caldwell (voc. com.), but, generally, separation of mother and offspring probably does not happen very often except as a result of human interference. At Little Diomedé and King Island large numbers of adult females are killed

annually for ivory, and their calves are set free. Unless these young are adopted by foster mothers, there is little likelihood that they survive, for they appear to be unable to feed themselves. Natives believe that most of these are adopted by other cows (Brooks, 1954) -- perhaps those which have lost their own young by stillbirth or accident. One female taken at Gambell in 1953 had borne a calf one or two days previous to being captured, yet she was accompanied by a 2-month-old calf which could not have been her own.

Orphaned yearlings may be able to sustain themselves in most instances, judging from Brooks' (1954) and Heinrich's (1947) observations, though the writer's specimen (p. 68) indicates that their survival is not assured. It probably depends upon the amount of bottom feeding experience acquired prior to separation.

Parasites and diseases.--The literature and the writer's observations indicate that parasites and diseases play a very insignificant role in Pacific walrus mortality. Ectoparasites are common but appear to be only irritants; endoparasites are rare, and no pathological effects have been observed. Except for Heinrich's (1947) report of a tuberculosis-like infection in one specimen, no major disease symptoms have been recorded. Occasional uterine tumors (= "cysts" of Brooks, 1954, p. 62) seemed to have had no ill effects upon the bearers, and animals with gangrenous tusk roots were otherwise in good health, judging by gross

appearance. The latter is probably the cause of occasional one-tusked and tuskless individuals, but tusk loss seems to have no serious consequences.

It is conceivable that in a more dense population disease would be relatively more common, but there are no indications that it ever has been.

Non-human predation.--From the literature and native reports it is clear that killer whales (Grampus rectipinna) prey upon walruses, but it seems probable that they account for only a very small fraction of the annual mortality, for they do not usually frequent the pack ice region. At present they are uncommon in the Bering Sea (Kenyon, et al, 1954).

Polar bears (Thalarctos maritimus) have often been cited as possible walrus predators, but judging from Brooks' (1954), Nikulin's (1940), and Sverdrup's (Mohr, 1952) conclusions, they probably do not have much effect upon the walrus population. Their predation appears to be limited mainly to play (Brooks, 1954) and to situations in which no regular foods (i.e. seals) are available.

Human predation.--Unquestionably, human predation has been the primary factor controlling walrus numbers within the past 150 years in both eastern and western hemispheres. Its effect has been a marked reduction in population size and maintenance of low densities thereafter. White hunters in quest of oil and ivory were responsible for the major decimation of Pacific walruses prior to 1930, but Natives armed

with high-powered repeating rifles have played an important part in keeping the herds in check since then. The latter has been due partly to modern demands for ivory and partly to poor techniques for securing dead and wounded animals.

So far as the writer is aware, intensive ivory hunting is practiced only in Alaska at present and in only two localities there -- Little Diomedé and King Island. It accounts for at least one-third of the total annual kill in Alaskan waters.

The problem of securing the animals after they have been shot is a universal one, for in the seasons when they are most vulnerable to hunting, they are also most likely to sink when killed in the water. In Alaska about 50 per cent of the dead and wounded are lost, and it is estimated that at least half of these eventually die. There are no data available on Soviet losses, but they are probably not as great, for ivory hunting is not practiced there, and the entire carcasses are utilized. At Gambell, where the same policies apply, losses are 30-40 per cent.

The average annual harvest in Alaskan waters is currently about 1200 per year (Appendix IIIA) -- the actual kill about 17-1800. Judging by earlier reports (Brooks, 1954; Nikulin, 1940; Taracouzio, 1938), the annual Siberian kill is between 2-3000.

Density Dependent Factors

Under primitive conditions, walrus populations were

unquestionably much larger than they are at present, and factors other than human predation must have controlled population size. What these factors may have been can only be reasoned from present conditions and the few bits of information written by early explorers. Two possibilities are suggested below.

Food.--Pelecypods are very abundant in certain northern localities, and the extensive shallows of the Bering and Chukchee Seas provide broad expanses of potential habitat. But walruses consume enormous numbers of these animals (e.g. Zalkin, 1937, found more than 2000 feet and siphons in one bull's stomach), and it is conceivable that a very dense walrus population could effectively control the pelecypod population, hence control itself. Possibly this was one of the causes for broader range of walruses in early times, for they would be expected to disperse more widely in search of better feeding grounds.

Social aggregates.--An exotic factor intrinsic of the social behaviour is death by crushing and suffocation. When large herds haul out on land, a few individuals on the bottom of the pile succumb from the tremendous weight of their companions on top. In a dense population there would be relatively more large herds (i.e., the chances of individuals meeting other individuals would be greater) and death by crushing should, therefore, be relatively more frequent. Extensive deposits of "beach ivory" at many old

and new hauling grounds (cf. Wilke, 1942) are probably a result of this phenomenon.

Calves and juveniles are occasionally crushed in this manner, but in general they tend to stay on top of the "pile." One crushed calf was taken at Gambell in 1954.

The Effect

Maximum longevity.--Tooth and tusk analyses above indicate that walruses have a potential physiological longevity of about thirty years. This agrees with the general "rule" that the life span of mammals is roughly five times the period of growth (Brody, 1945, p. 681). Similar figures have been reported for some other pinnipeds (e.g. Phoca groenlandica-28 yrs; Fisher, 1952; Halichoerus-26 and 42 yrs; Matheson, 1950), but the majority range about twenty years.

Ecological longevity.--"Ecological longevity is the empirical average longevity of the individuals of a population under given conditions" (Bodenheimer, 1938, p. 19). This statistic can be readily calculated from the age structure of the population, but age structure in itself is more useful than the average figure, for it can be used as a basis for calculations of mortality rates, survivorship, and productivity. The relative abundance of age classes in the present Pacific walrus population has been approximated as follows:

(1) In the spring of 1953, one tooth was collected from each of 155 bulls (exclusive of calves) killed at Gambell and Savoonga. Using cementum layers as indices of age, a "catch curve" of these specimens was plotted and smoothed with a running average of five. The result (Fig. 36) bears a close resemblance to some presented by Ricker (1948) for fish populations, and it illustrates the St. Lawrence Island policy of selecting adult animals.

(2) For purposes of discussion, Ricker (op. cit.) divides catch curves into three parts: (a) the ascending left limb, which is a result of incomplete sampling of the youngest age classes, (b) the dome-shaped middle portion, and (c) the descending right limb. The latter, in the fish populations considered, is a random sample of the older age classes and can, therefore, be used as a measure of survivorship and mortality rates within that portion of the population. The above walrus catch curve is believed to be a random sample of the male population over 7 or 8 years of age, for selection is inoperative beyond that point. Though there are many irregularities, probably due to random error of sampling, the right limb from about 8 years on can be considered as a straight line with a slope of about 0.12 ($= \underline{i}$, the instantaneous mortality rate).

(3) Several estimates of proportions of the population represented by younger age classes (under 8 years) have been obtained by other methods. First, it was observed above

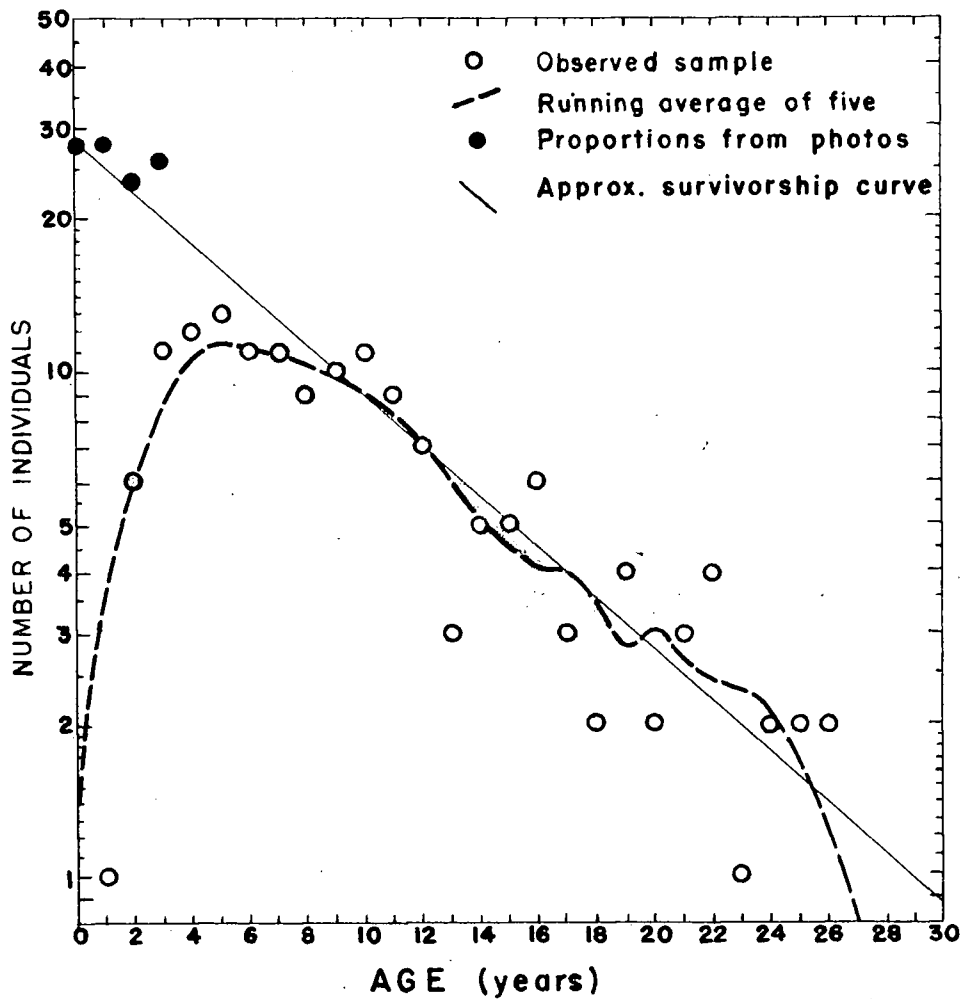


Fig. 36.--Catch curve of male walruses taken at Gambell and Savoonga in the spring of 1953 (arith-log scale). Approximate age structure and survivorship of the male population are indicated by the right limb of the curve plus relative proportions of young and juveniles, derived from photo analyses. See text (p. 144 et seq.) for explanation of techniques.

that the crude birth rate is about 0.39 calves per adult cow (over 3 years of age) per year. Assuming that the populations of both sexes are approximately equal, the proportion of male calves per bull over 3 years of age should be about 0.20:1. Applying this to the catch curve sample (137 animals over 3 years), a value very close to the y-intercept of the adult survivorship curve (step 2, above) was obtained.

(4) Several recent photographs of large herds were supplied by the U.S. Navy (U.S.S. Burton Island) in conjunction with Ryder's (1953a; 1954) reports on walrus observations. In these photos it was possible to distinguish animals of ages 1 to 3, inclusive, by means of general morphology and tusk size. With the exception of yearlings, only those animals whose tusks were visible were counted. These yielded ratios (number of males in age class t to total males 4 and over) of 0.20:1 for yearlings, 0.17:1 for 2-year-olds, and 0.19:1 for 3-year-olds. Applying these to the catch curve sample as in step 2, three additional points very close to the adult survivorship curve were obtained (Fig. 36).

Since all of the data utilized above represent rather small samples, only the broadest generalities can be concluded from them. As a whole, the age structure (of males, at least) indicates a stable, highly productive population in which the birth rate and death rate are approximately uniform and are of about equal magnitude. The total annual

mortality (crude death-rate) is about 12 per cent of the population, most of which is due to human predation. This is roughly comparable to Brooks' (1954) productivity estimate (13 per cent per year) and to Chapsky's (1936) conclusion that the stable Kara Sea population has a 10-15 per cent annual turnover.

Ecological longevity at present is approximately nine years, according to the above calculations. This checks favorably with an estimate derived from "corpus counts" in the ovaries of forty-two adults. The average number of pregnancies per female, 4 years and over, was 2.4, which is equivalent to a longevity of about eight or nine years.

PART III
THE POPULATION

The problem is not entirely solved, but the solution is near at hand. Within the limited time that it has been pursued, a number of significant facts and hypotheses have been derived, and these, with some further exploration, should yield all of the necessary biological bases for sound population management. Tentatively, a few conclusions can be reached regarding the present population's numerical status and its probable past and future trends.

From the harvest figures (Appendix IIIA) it is apparent that there has been a slight decrease in the number taken in Alaskan waters over the past fifteen years. This applies specifically to the coastal points, some of which have dropped more than 50 per cent. According to Brooks (1954), R.F. Gray (in litt.), and personal interviews, the change has been a result of reduced hunting effort as well as a notable scarcity of walruses in some localities. The latter is also indicated by other data (see below) and has probably resulted in an equivalent decrease in current Siberian harvests. Very roughly, the total annual kill (Alaskan-Siberian) in the late 30's must have been about 5,000, while at present it is approximately 4,500 (Table 15).

Since human predation appears to be responsible for the bulk (more than three-fourths) of annual mortality, and the death rate is roughly 12 per cent per year, it follows that the total population is probably upwards of 40,000

TABLE 15
ESTIMATED ANNUAL PACIFIC WALRUS MORTALITY
FROM HUMAN PREDATION

Late 1930's

Location	Harvest Per Year ^a	Losses ^b	Total Kill Per Year
Alaska	1300	650	1950
Siberia	2300	800	3100
Totals...	3600	1450	5050

Early 1950's

Alaska	1170	590	1760
Siberia	2070 ^c	720	2790
Totals...	3240	1310	4550

^aSee Appendix IIIA

^bAlaskan - 50 per cent; Siberian - about
35 per cent

^cAssuming a decrease equivalent to the
Alaskan (10 per cent)

individuals. This figure compares favorably with Brooks' (1954) conclusion that 15,000 migrants passing through the eastern half of Bering Strait represented less than 50 per cent of the population. It also agrees, roughly, with another estimate derived from Ryder's (1954) data, which were utilized in a crude census of the migrant population (Appendix IIIB). The resulting figure (38,000 animals) approaches the others in magnitude.

Overall hunting pressure seems to have remained fairly constant except at the most northerly Alaskan villages, many inhabitants of which emigrated to Barrow in recent years for employment at the Naval Petroleum Reserve. In view of this, the Alaskan harvest data indicate a slight decline in the walrus population since the late 30's -- probably less than 10 per cent. This amount would be imperceptibly small to the average observer except over a period of several decades, for the number of animals encountered near any Alaskan village fluctuates widely from year to year, and local opinions of population status vary directly with these fluctuations. If opinions were recorded over a long enough duration, however, some definite trend should be evident. Table 16 presents a compilation of these as extracted from various sources. Unfortunately they are not of equal weight, for some represent reports from individuals, and others are averages from several, but in both groups of data there is a consistent trend pointing toward a slight

TABLE 16
NUMBER OF REPORTS ON POPULATION TRENDS

Years	Population Status*		
	Increasing	Stable	Decreasing
1939-45	1	3	3
1951-54	2	4	4

*Based upon Collins (1940), Brooks (1953, 1954), personal questionnaire replies, and various reports in U.S. Fish and Wildlife Service files.

population decline.

Another comparison of the population of the 30's with the present one was accomplished by matching Freimann's (1940, Fig. 2 and Table 1) data against Brooks' (1954, Fig. 6) and writer's (Fig. 14). Freimann's tusk OEL frequencies (both sexes) exhibit a higher proportion of old adults than the recent ones do, suggesting a difference in age structure corresponding to a declining population (cf. Allee, et al, 1949 p. 281).

There is no apparent danger of extinction under present conditions; indeed, a state of semi-equilibrium has been or is being achieved. Nonetheless, in terms of maximum benefits for all, the population should be permitted to increase, for the current harvest rate per native village is too erratic. The people of Gambell, for example, need at least 200 walruses per year to satisfy their maintenance requirements (exclusive of ivory), yet their harvests from 1952 to 1955 ranged between 70 and 275 (Appendix IIIA). This variation was independent of hunting effort (average 1 hunting day per 2.4 calendar days each spring). It appeared to be entirely a result of ice conditions which were, in turn, a product of the weather. Should walruses become more abundant, the chances of these variations occurring would be very much reduced by reason of the greater density of animals per unit area. Should the population remain unchanged or become less abundant, the few villages dependent upon it must either diminish in size or

become burdens to the Government.

The remedy is simple: eliminate ivory hunting and hunting losses. These wasteful practices can be tolerated no longer, for they serve no social or economic purpose, and at present they are responsible for more than one-fourth of the total annual mortality. Admittedly, unless every animal is harpooned before being shot (which is feasible but not necessary), there will continue to be losses from wounding and sinking, but a planned, long-term educational program could easily reduce losses by one-half. The consequent decrease in mortality (losses halved and ivory hunting eliminated) would permit the walrus population to double in less than thirty years.

Application of the remedy would be fairly complex, for as Brooks (1954) and Scott (1951) have noted, there are many socio-economic problems involved. Since these have already been adequately dealt with by the above authors, no further comment is necessary, except to say that they could be solved within a few years and the time to begin is now. Biological investigations should be continued, and, ultimately, international (Soviet-U.S.) cooperation must be achieved.

APPENDICES

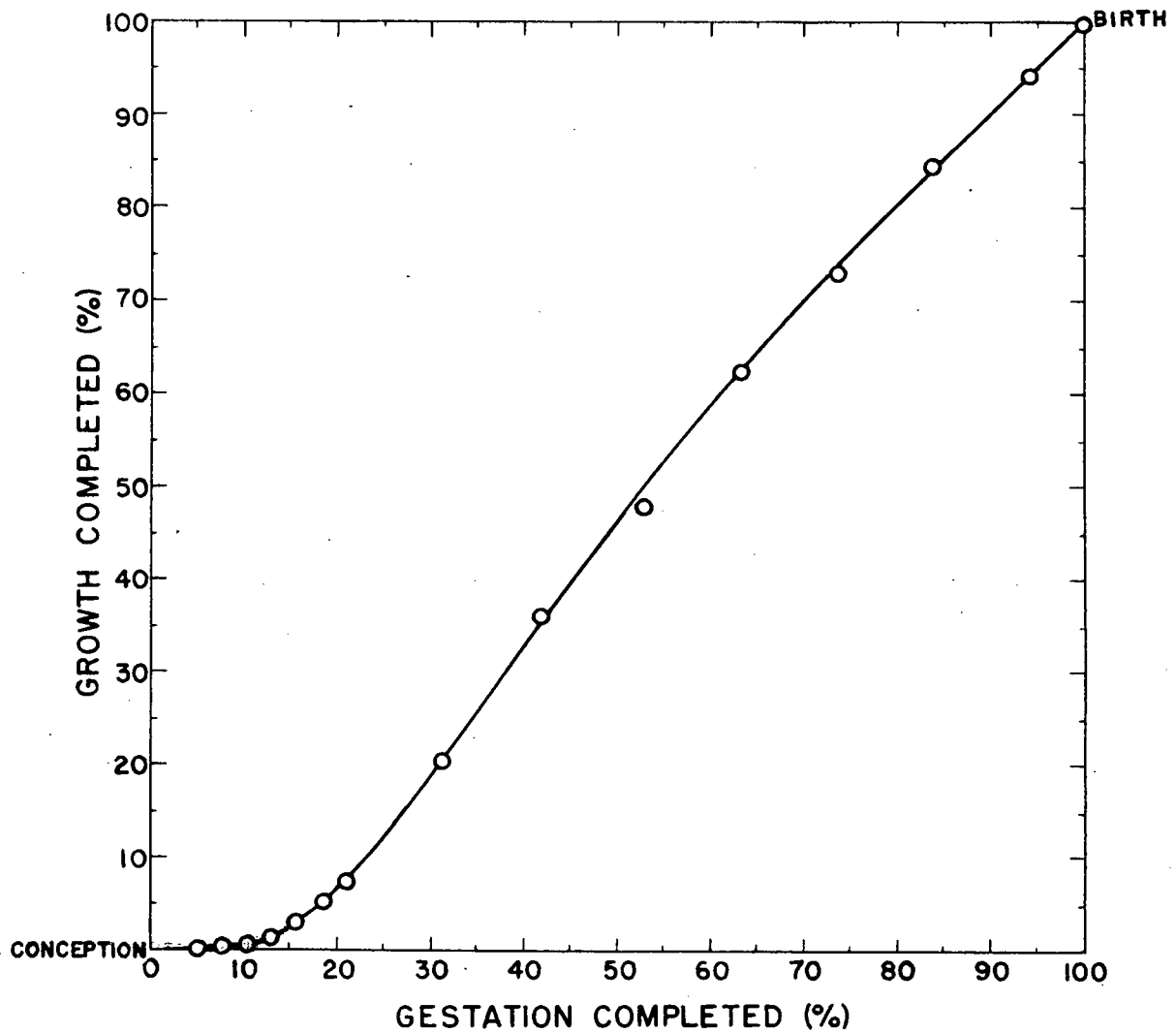
APPENDIX I

PRENATAL CROWN-RUMP LENGTH GROWTH OF HUMANS*

No. of Days Since Conception	Per cent of Total Gestation	Crown-rump Length (mm.)	Per cent of Natal C-R Length Achieved
14	5.2	0.1	0.30
21	7.8	1.5	0.45
28	10.4	2.5	0.74
35	13.1	5.5	1.64
42	15.7	11	3.27
49	18.3	17	5.06
56	20.9	25	7.44
84	31.3	68	20.2
112	41.8	121	36.0
140	52.3	167	47.9
168	62.7	210	62.5
196	73.2	245	72.9
224	83.6	284	84.5
252	94.0	316	94.1
268 (Birth)	100.0	336	100.0

*Data from Noyes et al (1938, p. 52).

APPENDIX I--Continued



Curve of equivalent foetal crown-rump length growth, based upon Noyes, et al's (1938) data for humans.

APPENDIX IIA

LINEAR GROWTH, WEAR, AND OBSERVED
LENGTHS OF MALE TUSKS IN INCHES

Age	ATL		Wear		OTL	RL	OEL
	Increment	Total	Rate	Total			
0	2 1/8	2 1/8	0	0	2 1/8	2 1/8	0
1	2 3/8	4 1/2	0	0	4 1/2	3 1/2	1
2	4 7/8	9 3/8	3/8	3/8	9	5 1/4	3 3/4
3	4 3/8	13 3/4	1/2	7/8	12 7/8	6 1/4	6 5/8
4	3 1/4	17	5/8	1 1/2	15 1/2	6 5/8	8 7/8
5	3	20	1/2	2	18	6 3/4	11 1/4
6	2 1/4	22 1/4	3/8	2 3/8	19 7/8	6 3/4	13 1/8
7	1 7/8	24 1/8	1/2	2 7/8	21 1/4	6 7/8	14 3/8
8	1 5/8	25 3/4	3/8	3 1/4	22 1/2	6 7/8	15 5/8
9	1 1/2	27 1/4	3/8	3 5/8	23 5/8	7	16 5/8
10	1 3/8	28 5/8	1/2	4 1/8	24 1/2	7	17 1/2
11	1 1/8	29 3/4	3/8	4 1/2	25 1/4	7 1/8	18 1/8
12	1 1/8	30 7/8	3/8	4 7/8	26	7 1/8	18 7/8
13	1	31 7/8	3/8	5 1/4	26 5/8	7 1/4	19 3/8
14	7/8	32 3/4	3/8	5 5/8	27 1/8	7 1/4	19 7/8
15	7/8	33 5/8	3/8	6	27 5/8	7 1/4	20 3/8
16	3/4	34 3/8	3/8	6 3/8	28 1/8	7 3/8	20 3/4
17	3/4	35 1/8	1/4	6 5/8	28 1/2	7 3/8	21 1/8
18	3/4	35 7/8	3/8	7	28 7/8	7 3/8	21 1/2

APPENDIX IIA--Continued

Age	ATL		Wear		OTL	RL	OEL
	Increment	Total	Rate	Total			
19	5/8	36 1/2	1/4	7 1/4	29 1/4	7 1/2	21 3/4
20	5/8	37 1/8	1/4	7 1/2	29 5/8	7 1/2	22 1/8
21	5/8	37 3/4	1/4	7 3/4	30	7 1/2	22 1/2
22	1/2	38 1/4	1/4	8	30 1/4	7 1/2	22 3/4
23	1/2	38 3/4	1/4	8 1/4	30 1/2	7 1/2	23
24	1/2	39 1/4	1/4	8 1/2	30 3/4	7 1/2	23 1/4
25	1/2	39 3/4	1/4	8 3/4	31	7 1/2	23 1/2
26	3/8	40 1/4	1/4	9	31 1/4	7 1/2	23 3/4
27	3/8	40 5/8	1/4	9 1/4	31 3/8	7 5/8	23 3/4
28	3/8	41	1/4	9 1/2	31 1/2	7 5/8	23 7/8
29	1/4	41 3/8	1/4	9 3/4	31 5/8	7 5/8	24
30	1/4	41 5/8	1/4	10	31 5/8	7 5/8	24
31	1/8	41 7/8	1/4	10 1/4	31 5/8	7 5/8	24
32		42		10 1/2	31 1/2	7 3/4	23 3/4

ATL = Absolute Total Length

OTL = Observed Total Length or ATL-Total wear

RL = Root Length

OEL = Observed External Length or OTL-RL

APPENDIX IIB

LINEAR GROWTH, WEAR, AND OBSERVED LENGTHS
OF FEMALE TUSKS IN INCHES

Age	ATL		Wear		OTL	RL	OEL
	Increment	Total	Rate	Total			
0	1 3/4	1 3/4	0	0	1 3/4	2	0
1	1 7/8	3 5/8	0	0	3 5/8	2 3/4	7/8
2	4 1/8	7 3/4	3/8	3/8	7 3/8	4 1/8	3 1/4
3	4 5/8	12 3/8	5/8	1	11 3/8	5 1/8	6 1/4
4 ^o	3 1/4	15 5/8	1/2	1 1/2	14 1/8	5 1/2	8 5/8
5 ^p	2 3/8	18	5/8	2 1/8	15 7/8	5 5/8	10 1/4
6 ^o	1 7/8	19 7/8	7/8	3	16 7/8	5 5/8	11 1/4
7 ^p	1 1/2	21 3/8	5/8	3 5/8	17 3/4	5 5/8	12 1/8
8 ^o	1 3/8	22 3/4	1	4 5/8	18 1/8	5 3/4	12 3/8
9 ^p	1 1/4	24	1/2	5 1/8	18 7/8	5 3/4	13 1/8
10	1 1/8	25 1/8	3/4	5 7/8	19 1/4	5 3/4	13 1/2
11	1	26 1/8	3/8	6 1/4	19 7/8	5 3/4	14 1/8
12 ^o	1	27 1/8	3/8	6 5/8	20 1/2	5 3/4	14 3/4
13 ^p	7/8	28	3/8	7	21	5 7/8	15 1/8
14	7/8	28 7/8	3/4	7 3/4	21 1/8	5 7/8	15 1/4
15	3/4	29 5/8	1/4	8	21 5/8	5 7/8	15 3/4
16	3/4	30 3/8	1/4	8 1/4	22 1/8	6	16 1/8
17 ^o	3/4	31 1/8	1/4	8 1/2	22 5/8	6	16 5/8
18 ^p	5/8	31 3/4	3/8	8 7/8	22 7/8	6	16 7/8

APPENDIX IIB--Continued

Age	ATL		Wear		OTL	RL	OEL
	Increment	Total	Rate	Total			
19	5/8	32 3/8	1/2	9 3/8	23	6	17
20	5/8	33	1/4	9 5/8	23 3/8	6	17 3/8
21	1/2	33 1/2	1/4	9 7/8	23 5/8	6	17 5/8
22	1/2	34	1/4	10 1/8	23 7/8	6 1/8	17 3/4
23	1/2	34 1/2	1/4	10 3/8	24 1/8	6 1/8	18
24	1/2	35	1/4	10 5/8	24 3/8	6 1/8	18 1/4
25 ^o	1/2	35 1/2	1/4	10 7/8	24 5/8	6 1/8	18 1/2
26 ^p	3/8	35 7/8	3/8	11 1/4	24 5/8	6 1/4	18 3/8
27	3/8	36 1/4	1/2	11 3/4	24 1/2	6 1/4	18 1/4
28	3/8	36 5/8	1/4	12	24 5/8	6 1/4	18 3/8
29	1/4	36 7/8	1/4	12 1/4	24 5/8	6 1/4	18 3/8
30	1/8	37	1/4	12 1/2	24 1/2	6 1/4	18 1/4
31	1/8	37 1/8	1/4	12 3/4	24 3/8	6 3/8	18
32	1/8	37 1/4	1/4	13	24 1/4	6 3/8	17 7/8

ATL = Absolute Total Length

OTL = Observed Total Length or ATL-Total wear

RL = Root Length

OEL = Observed External Length or OTL-RL

^oOestrus

^pParturition

APPENDIX IIIA
THE ALASKAN WALRUS HARVEST*

Location	Harvest Per Year												
	Average: Late 1930's	1939	1940	1944	1945	1947	1950	1951	1952	1953	1954	1955	Average 1945-55
Barrow	75	---	---	---	---	---	---	0	105	4	1 ⁺	---	35
Diomedes	250	---	---	---	400 ⁺	---	---	---	350	507	120	---	350
Gambell	200	313	---	---	---	---	---	---	275	200	70	120	170
Hooper Bay	25	---	---	---	---	---	---	---	---	---	---	---	25
King I.	300	147	---	---	---	---	---	---	---	300	50	---	250
Kipnuk	---	---	---	---	---	---	4	---	---	---	---	---	5
Mekoryuk	25	---	20	---	---	---	---	---	---	20	5	---	15
Nome	25	---	---	---	---	---	---	---	---	12	---	---	10
Pt. Hope	75	---	---	---	---	---	---	---	5	---	---	---	5
Pt. Lay	75	---	---	---	---	---	16	2 ⁺	---	0	---	---	5
Savoonga	100	---	---	---	---	---	---	---	---	175	120	---	150
Shaktoolik	---	---	---	---	---	19	---	---	0	---	---	---	5
St. Michael	---	---	---	---	---	---	---	---	11	---	---	---	5
Tananuk	---	---	---	---	---	---	---	---	6	---	---	---	5
Togiak	---	---	---	---	---	---	---	---	75	---	---	---	75
Unalakleet	---	---	---	---	---	---	---	---	10	---	---	---	5
Wainwright	100	---	---	76	---	---	---	0	4	---	---	---	5
Wales	50	---	---	---	---	---	---	---	42	70	---	---	55
Totals	1300	---	---	---	---	---	---	---	---	---	---	---	1175

*Data and averages from: Brooks (1954), Collins (1940), Hughes (1953), Lantis (1946), "Mukluk Telegraph" (Dec. 1951), W. Caldwell (in litt.), R.B. Gibson (in litt.), C.K. Ray (voc. com.), U.S. Fish and Wildlife Service files, questionnaire replies, and personal observation.

APPENDIX IIIA--Continued

THE SIBERIAN WALRUS HARVEST

Taracouzio (1938) gives the following figures for walrus harvests of the early 1930's in Siberian waters:

Year	Total Harvest by Hunting Vessels
1930	1560
1931	3244
1932	1428
1933	2728
Average...	2240

Nikulin's (1940) data, while less specific or complete, suggests that the harvests from 1935-38 were about the same as those above and that less than 200 additional animals were taken annually at coastal native villages. Hence a conservative estimate of the average late 30's harvest is about 23-2400.

APPENDIX IIIB

CALCULATION OF TOTAL POPULATION
BY THE STRIP SAMPLING METHOD

1. Ryder's (1954) data consist of 57 separate observations within the spring pack of the North Bering Sea and Chukchee Sea between latitudes 61°N and 72°N in May, 1954.

2. These can be divided into four "strips," two one-way trips from the region of St. Lawrence Island to Point Barrow, and two return trips between the same points.

3. The approximate linear miles traveled in each strip were measured and multiplied by 3, the estimated strip width in miles. Serious error could be involved here, since Ryder states (in litt.) that strip width varied widely and at times was nil, due to fog and darkness. The proposed 3-mile width is an attempt to average these conditions.

4. The mean number of walruses per square mile thus derived was applied to the probable total walrus-occupied area shown in Figure 4 (p. 9) -- about 130,000 square miles. The results are tabulated below.

APPENDIX IIIB--Continued

Strip No.	Direction Traveled	Linear Miles Traveled	Square Miles Censused	Walruses Seen	Walruses Per Square Mile
I	North	770	2310	841 ⁺	0.36
II	South	575	1725	81	0.05
III	North	580	1740	1297 ⁺	0.75
IV	South	630	1890	35	0.02
Totals...		2555	7665	2254 ⁺	----
Averages...		639	1916	563 ⁺	0.29

Total population = (total area) x (avg. walruses per sq. mile)

$$130,000 \times 0.29 = 38,000^+ \text{ animals}$$

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