A THESIS

entitled

LIFE HISTORY OF THE WHITE WHALE, <u>DELPHINAPTERUS LEUCAS</u> (PALLAS),

IN THE WATERS OF BAFFIN ISLAND, CANADA

by

Paul Frederick Brodie, B.Sc., M.Sc.

Submitted in partial fulfillment of the requirements
for the
Degree of Doctor of Philosophy
at
Dalhousie University, March 1970.

Department of Biology,
Dalhousie University,
Halifax, Nova Scotia.

TABLE OF CONTENTS

ABSTRACT

The beluga or white whale, <u>Delphinapterus leucas</u> (Pallas), was studied in Cumberland Sound, Baffin Island.

Tooth and mandible layers were used for age determination. Sexual maturity is attained after four years in females and after seven years in males at 85% and 90% of physically mature lengths, respectively, with an estimated 2:1 ratio of sexually mature females to males. Whitening occurs after six years with the life-span estimated to be 30 years.

Multiple ovulations and accessory corpora are typical of beluga. The breeding season is in May followed by a gestation period lasting 14-14½ months. Single births occur in late July and August, with a mean calf length of 159.6 cm and mean weight of 79 kg. Lactation lasts about two years resulting in a three year reproductive cycle. Tooth eruption begins late in the second year with partial eruption by the third and fourth years.

Feeding is not intensive during July and August, though a broad food web is suggested. This population is considered to have been over-exploited by commercial hunting. Productivity estimates of this species are 40% of those suggested by Soviet researchers.

ACKNOWLEDGMENTS

INTRODUCTION

The white whale or beluga, _Delphinapterus leucas_
(Pallas 1776) is as the genus name implies, a dolphin with-
out a dorsal fin, which inhabits the arctic and subarctic.
It is of the suborder Odontoceti, family Delphinidae, sub-
family Delphinapterinae (Kleinenberg _et al._, 1964). Lengths
range between 3-7 meters among adults of various populations.
Colour ranges from dark gray in the calf, through shades of
gray to white in the near physically mature adult. Sixteen
to twenty pairs of teeth are present in the adult jaws.
Though it does not have a dorsal fin, a back ridge is
present.

The most comprehensive studies to date have been by
Vladykov (1944), Tomilin (1957) and Kleinenberg _et al._ (1964).
There is considerable disagreement over basic features of
the life history of _D. leucas_ among these and other authors.
This thesis is an attempt to account for the discrepancies,
and to draw together a more consistent life history.

These Cetacea are exploited commercially for hides, oil
and meat. (Sergeant (1962a) estimates the total annual
commercial kill to be approximately 5000 animals and cautions
that local populations may be depleted by large fisheries.
This thesis attempts to provide a more rational basis for
exploitation and proper herd management.

Material for reproductive analysis in this study came
from the beluga population of Cumberland Sound, Baffin

Island (see Figs. 1 and 2). The animals were either hunted from a canoe or captured in specially made nets. All measurements and dissections were made by the author to maintain consistency of sampling methods. All animals were utilized by the local people as food, oil, or traded hides.

Migratory studies were carried out jointly with Dr. D.E. Sergeant in Hudson Bay, the MacKenzie River Delta and Cumberland Sound, using a harpoon tagging technique.

Figure 1 is a map of the major portion of
the Eastern Canadian Arctic. The area of
field work, Clearwater Fiord is encircled
at the head of Cumberland Sound.

FIGURE 2

Figure 2 is a series of aerial photographs showing the
upper half of Clearwater Fiord. Most of the studies and
sampling were carried out in this fiord. The amount of
freshwater influx and turbulence due to this, plus tidal
action is well illustrated by muddy water pouring into
the river estuary.

Of the .... nets. The re........... .... Among the hun........... .... toward younge........... .... most of the .... "muktuk", consid........... .... also easier to hunt........... .... hors are commercial fisheries, ... animals, payment being by l........... ....69a).

Nets used for capture were .... 18 to 20 inch extended mesh measure, ... The foot line was lead-weighted and t........... floated. Due to the extremely violent tidal currents, shore ties at both ends were preferable to anchored nets, for example by setting nets between the shore and a nearby rock or island. The main lines used for tying to shore were at first 3500 pound test nylon, which proved to be sufficient to withstand the tidal strain coupled with that strain of captured animals. Later, natural fibre rope of one inch diameter was used with some breakage.

Usually two nets were sewn together to form a 300 foot net. Triple and single nets were used to a lesser extent. Some nets were also set using anchors, but this involved a great deal of effort and was not practical due to the strong

10 KM

6

METHODS OF CAPTURE

Of the 124 animals sampled, 107 (86%) were captured in nets. The remaining 17 were taken with rifle and harpoon. Among the hunted animals, there would tend to be a bias toward younger animals or females accompanying calves since most of the Eskimo hunters were after the edible skin or "muktuk", considered superior in younger animals, which are also easier to hunt. In areas such as Hudson Bay where there are commercial fisheries, hunting bias is toward the larger animals, payment being by length (Sergeant and Brodie, 1969a).

Nets used for capture were 150 feet long, nylon, of 18 to 20 inch extended mesh measure, 40 to 50 meshes deep. The foot line was lead-weighted and the head line cork-floated. Due to the extremely violent tidal currents, shore ties at both ends were preferable to anchored nets, for example by setting nets between the shore and a nearby rock or island. The main lines used for tying to shore were at first 3500 pound test nylon, which proved to be sufficient to withstand the tidal strain coupled with that strain of captured animals. Later, natural fibre rope of one inch diameter was used with some breakage.

Usually two nets were sewn together to form a 300 foot net. Triple and single nets were used to a lesser extent. Some nets were also set using anchors, but this involved a great deal of effort and was not practical due to the strong

tidal currents and poor anchorage on the soft bottom, even when two and three anchors were used on each end.

The 25-30 foot tides were a major problem since nets had to be set well off shore to function at all tidal levels. Nets drawn tight at high tide were slack at low tide and prone to damage by captive animals. Even with the lead-weighted foot line the entire net would lie on the surface during the more turbulent periods of the outgoing and incoming tide, reducing its effectiveness by 2-3 hours per tide. To overcome this, rocks were tied on the foot line as additional weights, helping to keep the net below the surface.

The 1966 sample was taken mainly from the catch of an experimental net fishery, nets being set along the shore and in the more shallow areas of the central part of the fiord. A cross section (in sex ratio and age distribution) of the population was captured. In 1967, however, there was a deliberate bias toward the capture of younger animals and sexually mature females. This study is, of necessity, qualitative rather than quantitative since I attempted to obtain as much useful reproductive information as possible from the smallest sample. Males are of little value for the study of reproductive rates, and emphasis was therefore placed on capture of females, making use of as many as possible of those taken by the local inhabitants. All animals taken were either eaten as food, or skinned for hides, with the fat rendered for oil. Some of the meat was used for dog food in the village of Pangnirtung.

It is interesting to note that no animals were seen to strike the net, an indication that they become enmeshed during the darker periods of the arctic summer night, suggesting that vision plays a role in some aspects of beluga navigation.

Figures 3 and 4 are length-frequency histograms for the total sample and separate sexes, respectively.

TOTAL SAMPLE

FREQUENCY

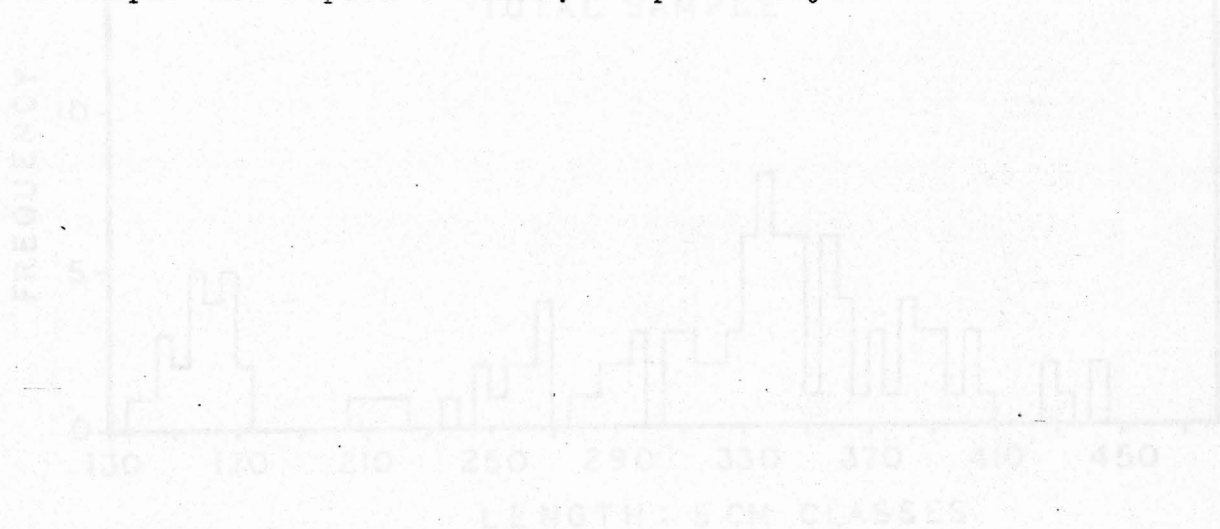LENGTH: 5 CM CLASSES

Figure 3 is a histogram of length frequencies in
5 cm classes for the total sample of 124 beluga.
The high number of newborn animals is due to
sampling bias.
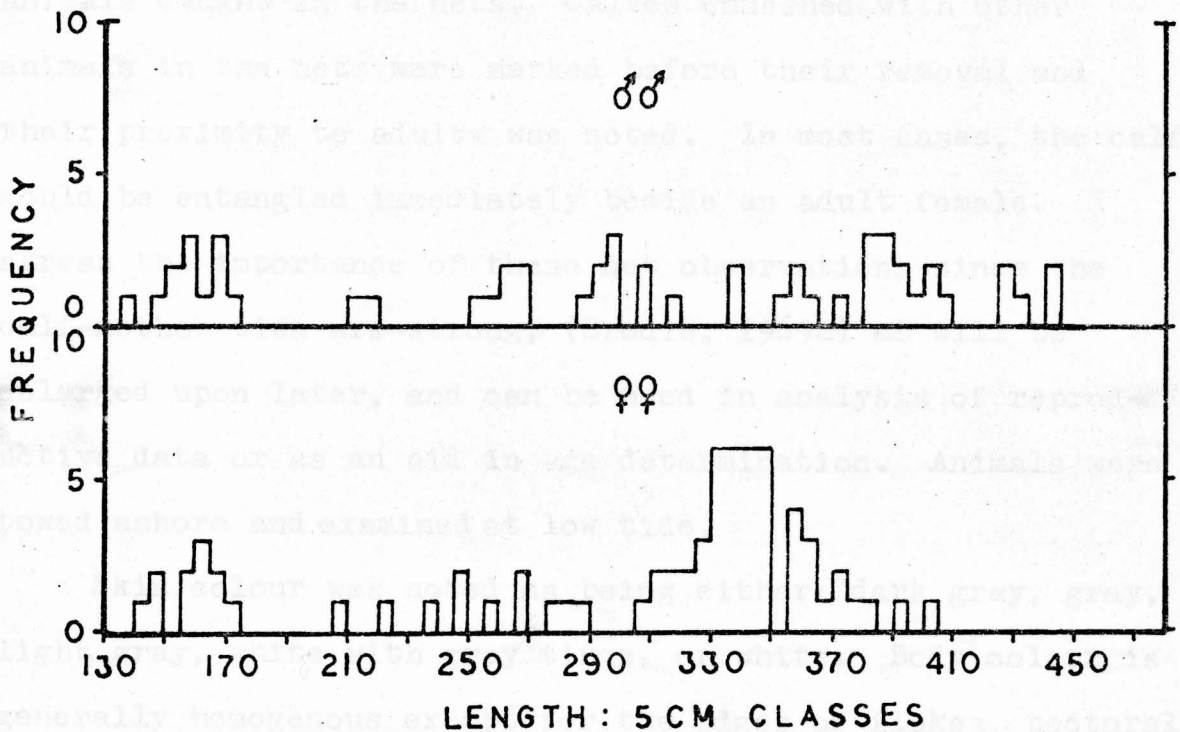
Figure 4 shows two histograms of length frequencies
for the total sample in 5 cm classes. Sexes are
separated to indicate the bias toward adult females
and newborns of both sexes. The male adult peak is
virtually absent.

Particular attention was paid to the association of animals caught in the nets. Calves enmeshed with other animals in the nets were marked before their removal and their proximity to adults was noted. In most cases, the calf would be entangled immediately beside an adult female. I stress the importance of these net observations since the calf-mother ties are strong, (Brodie, 1969a) as will be enlarged upon later, and can be used in analysis of reproductive data or as an aid in age determination. Animals were towed ashore and examined at low tide.

Skin colour was noted as being either: dark gray, gray, light gray, white with gray tinge, or white. Body colour is generally homogenous except for the edges of flukes, pectoral fins and dorsal ridge, which remain darkly pigmented throughout life. There may be some mottling of yearling calves (see Fig. 21).

All superficial markings were noted, measured or photographed, particular attention being paid to large scars and fresh wounds. Skin was examined for ectoparasites and commensals. Since the animals were either skinned for food or for hides, all areas of the body were well examined during this process.

Total length was measured in a straight line from the tip of the upper lip to the base of the tail notch. In no case did the frontal bulge or "melon" protrude beyond the

11

upper lip when the animal was in a level position. When the tail was cut off for easier removal from the nets, it was labeled, saved and held in position for length measurements. Maximum girths were measured at the full girth on small animals that could be easily moved and as half the girth of larger animals. Measuring full girth of large specimens tends to be inaccurate since the tape is usually bent or slack due to the difficulties of positioning the tape at maximum girth and in a right angle plane to the body axis. By measuring half the girth from the extreme anterior extension of the dorsal ridge to the mid-ventral line the tape can be drawn tight and the measurement taken with little difficulty.

Weights were taken of the smaller animals by using a 230 kg spring scale suspended by a pulley system from a metal tripod. Animals in excess of 230 kg were cut into sections and weighed.

Fat thickness was measured dorsally, laterally and ventrally in the transverse plane of maximum girth. Tooth protrusion and number of teeth were noted in all young animals.

For age determination the distal half of one mandible was taken using a hacksaw. The proximal part is extremely brittle and prone to shatter if broken with any force and must be sawed. Teeth were later extracted from this jaw section.

The mandible was not collected for thin sectioning from the first 70 animals, however, all later specimens were sampled.

When examining the male beluga the testes were removed, measured in three axes and in most cases weighed. In the later field work only one testis per individual was measured, there being little variation in size; however both were checked for anomolous structures which were noted when found. A median section having a depth of 10 mm was collected from each testis and epididymis and preserved in either aqueous Bouin's fluid or 10% formalin.

Females were checked for obvious milk secretion, length, width and depth of mammary tissue being measured later during the skinning operation. Mammary ducts were examined for the presence of milk. A central section of tissue was preserved in 10% formalin. Before the reproductive tract was removed, one ovary was severed from the uterine hilus. The right ovary was severed with several centimeters of uterine hilus attached, for the purpose of identification as to left or right. One ovary was always left attached during removal of the complete reproductive tract. This avoided confusion in orientation of the tract after removal since such disorientation can easily occur when working in adverse field conditions.

The uterus was examined for signs of pregnancy, indicated by the ovarian corpora lutea (the glands which support the embryo) or by the size of the uterine horns or

cornua (see Fig. 13).

Foetuses were measured for length and their sex noted. Small foetuses were preserved in Bouin's fluid or 10% formalin. Large foetuses were weighed and a mandible collected.

Internal collapsed diameters were taken at the mid-point of each cornu. The complete tract was opened and examined.

Both ovaries were examined in the field, and large externally visible corpora or follicles were roughly measured. Noting the position and approximate size of large corpora and follicles was a further measure to avoid confusion between the two ovaries during laboratory analysis.

The stomach was opened and checked for amount of food, milk in the case of younger calves. An estimate of the contents in eighths of main stomach volume was made when sufficient quantities of food were present. Samples of stomach contents were preserved in 10% formalin. The stomach wall was examined for macro-parasites and specimens were collected and preserved. When time permitted, middle ear sinuses, lungs, liver and kidney were examined for macro-parasites.

All ageing and reproductive material was labeled and preserved in the same container to avoid mixing field samples.

Problems and Methods.

To avoid repeating much of this well documented subject I refer to Klevezal and Kleinenberg (1967), Jonsgard (1969) as the latest surveys of marine mammal age determination.

The use of skin colour phases of beluga has been used as a method of determining the age (Kleinenberg et al. (1964); however this is a crude index. Ovarian analysis with respect to number of corpora albicantia and its application to age determination has been used for several species (Laws, 1961) though I dispute its usefulness in the study of beluga (p. 49).

One of the major problems in the field of cetology has always been a lack of an accurate method of age determination. Concerning the odontocetes, laminations in the skeletal parts and teeth can be correlated with known age of smaller, captive, aquarium specimens; however difficulties arise when attempting to correlate laminations with the growth and behaviour of wild specimens. Movements and behaviour of most non-commercial species are usually known for only part of the year. This is certainly true of arctic beluga populations when there are only several weeks each year to gather material. The alternative is to glean as much information as possible from costly aerial and ship surveys during the remainder of the year.

In this present study, emphasis has been placed on

15

tooth and mandibular laminations correlated with field observations i.e., association of animals during capture, injuries sustained, reproductive condition and body size.

Description of Teeth.

Delphinapterus leucas exhibits a secondary homodont condition indicated by the similar conical structure in younger animals and the peg-like similarity of all the teeth as adults (see Fig. 7). Teeth are not shed but remain for the life of the animal, the only loss being due to abrasion. Longitudinal growth is a result of dentine addition from the pulp cavity and width is from additions of cement (see Fig. 5, p. 17). Teeth grow continuously, though at varying rates, according to age and sex. Figure 8 shows the thickness of dentine layers in microns plotted against increase of layer numbers. Growth rates of teeth in males are significantly greater than in females (P between 0.01-0.001).

Since it is considered that laminations are correlated with changes in nutrition (Laws, 1953), the obscurity of the first two to four layers in many of the teeth may be due to the nursing period, when food and mineral supply are more constant than during any other portion of the animal's life. Figure 6[8] shows a tooth considered to have four layers, and these are quite apparent. If these laminae are not considered individual layers, then the first layer would be

16
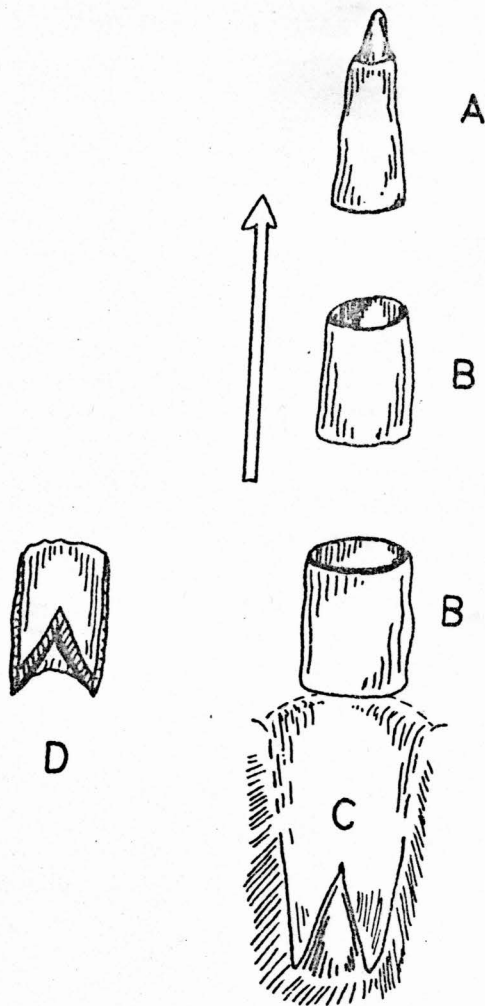
Figure 5 is a highly schematic illustration of the origin of tooth laminations in beluga.

(A) is the prenatal tooth with its surrounding cement cylinder.

(B) is a hollow cylinder of cement with a conical bottom composed of dentine.

(C) is the tooth socket with the conical pulp papilla producing dentine while cement is formed at the socket wall or aveolar surface.

(D) is a cross-section of the tooth increment. In reality, growth is continuous, with mineralization the variable, or increment.

FIGURE 6

Figure 6 shows prenatal teeth with increasing additions of dentine and cement increments.

(A) is a 15 mm tooth of a 220 cm calf considered to be a yearling. Two narrow layers can be seen between the white prenatal tooth and the pulp cavity.

(B) is a 17 mm tooth of a 250 cm calf considered to be two years old. Four narrow dentine layers can be seen. The prenatal tooth and pulp cavity are outlined.

(C) illustrates the gradual erosion of the prenatal teeth, shown outlined along with the pulp cavities. Tooth lengths are 31 mm and 25 mm respectively.

A
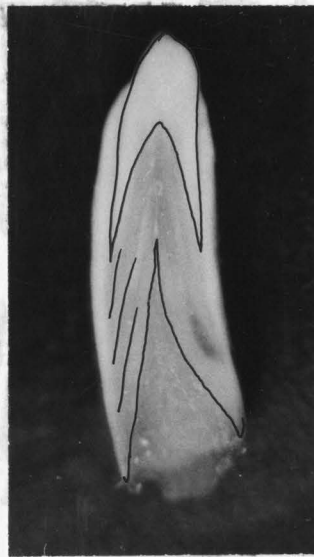
B
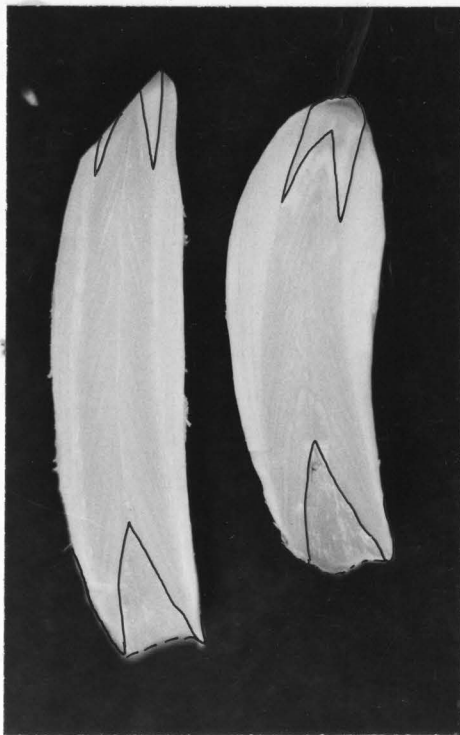
C

FIGURE 7

Figure 7 illustrates tooth-wear of adult beluga.

(A) shows the anterior portion of a single mandible. Teeth
are well worn showing the dentine core surrounded by the
thick cylinder of cement laminations.

(B) is a longitudinal half-section of a well worn tooth.
The prenatal tooth and many succeeding layers have obviously
been worn away. The pulp cavity is almost absent (shown
outlined). Length of tooth 39 mm.
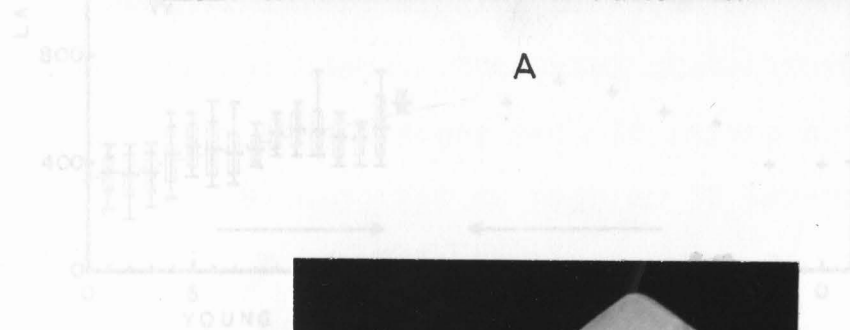
A

B

Figure 8 shows width of tooth layers in micra (measured at 250 magnification) related to increase in number of layers. Sexes are separated. Arrows indicate the direction of measurement for younger animals with prenatal teeth still present and for older animals with prenatal teeth plus many succeeding layers eroded. A single, older, female is shown plotted. Growth rates of teeth in males are significantly greater than in females.

Range and mean are indicated with single standard deviation represented by rectangles.

22

the combined width of at least two laminae resulting in a layer width inconsistent with the trend indicated by the fitted lines of Fig. 8.

As is indicated in Fig. 8, the limit is 15 layers for most teeth containing the foetal tooth at the tip. To measure layer thickness of the oldest animals, the succession of layers was measured from the pulp cavity upwards. Figures 7 and 8 illustrate that layer thickness appears to attain a maximum thickness after 15 layers are deposited, then begins a gradual decline during deposition of the last 20. The number of layers missing between the two series of measurements is not known. The total number formed must be at least the sum of the young and old layers shown here, since Sergeant (1959) observed as high as 50 layers retained in Hudson Bay animals while 41 layers were recorded in Cumberland Sound animals (Brodie, 1969b).

(a) Tooth mineralization.

Macroscopic observations (using reflected light) of longitudinal half-sections, display light and dark dentine laminations, the wider laminations being light (see Fig. 9). On microscopic inspection (Fig. 9), again using reflected light, the light laminae are penetrated with tubules (sometimes referred to as Tomes' fibres or protoplasmic extensions of the odontoblast). The dark, narrow laminae are void of such tubules which, in the wider layers, radiate at right angles from the conical pulp cavity, with smaller branches stemming from the main tubule. In unstained material the

23

whiteness of the laminae under reflected light is due to the
refraction of light at the tubule-ground substance interface.
Laws (1962) refers to "vacuolar dentine" in reference to
small vacuoles which appear in the ground substance void of
tubules, in the teeth of certain seals. These vacuoles app-
ear white for the same reasons as the tubules in the beluga
teeth. The ground substance of beluga is similar in its
transparency throughout the dentine, any differences in
transparency dependent on the presence of tubules.

(b) Test for Mineralization.

To test for collagen, the matrix within which mineral-
ization occurs, thin sections were stained with Light Green.
As Fig. 9^c indicates, only the area between the tubule axes
shows presence of collagen, the ground substance void of
tubules, showed no collagen was present. To test for the
presence of mineralization, inorganic phosphates were con-
verted to cobalt sulphide, appearing black (after Pritchard
and Ruzicka, 1950). Thin sections were placed for five min-
utes in 2% cobalt nitrate solution, washed in distilled wat-
er and placed in dilute ammonium sulphide. As Fig. 9^D shows,
only the surface of the odontoblast process appears stained,
an indication that inorganic phosphates are in the immediate
vicinity of the tubule. The collagen is more widespread
than the actual mineralization, i.e., mineralization con-
sists of a sheath around the odontoblast tubule (see Miles
1967). The finer laminations in the ground-substance are
all the same width, indicating a rather constant rate of

24

FIGURE 9

Photomicrographs of 75μ tooth sections. Individual layers
are $600-700\mu$ in width.

(A) Tooth layers shown under reflected light. Pulp cavity
is in the vicinity of the lower, right corner.

(B) Tooth layers under reflected light and at greater
magnification. The individual odontoblast processes (Tomes'
fibres) can be seen. Note the abrupt cessation of tubules
forming the well demarcated layers.

(C) Light Green test for collagen as seen by transmitted
light. The ground substance between the tubules has taken
up the stain while the area between the layers, void of
tubules, is unstained.

(D) Test for inorganic phosphates, seen by transmitted
light. Phosphates were converted to cobalt sulphide shown
here as black sheaths around the odontoblast tubules. Note
also the horizontal laminations of ground substance within
the larger layers which are being constantly secreted from
the pulp cavity.

deposition. In other words, teeth growth is constant

A

B

ated from the mainbody it is carried away from the pulp by
the constant deposition of ground substance. Another layer
of tubules forms shortly after this separation resulting in
the cyclic appearance of the tubule bands or layers.

Similar to the homeostatic
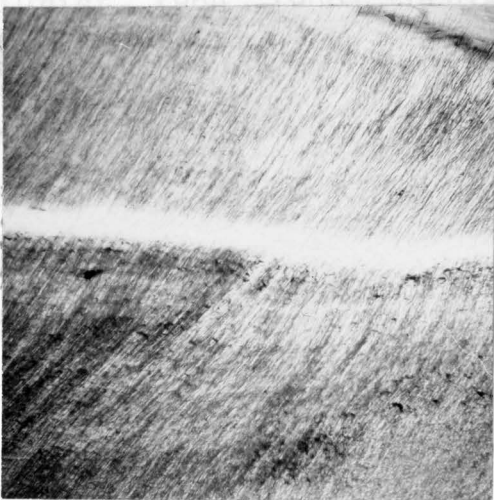
C

D

body scars, all these animals were greatly injured. There
appears to be a correlation between severe injury and cell
differentiation, upsetting patterns of mineralization in
tooth forming epithelium. This requires further research.

deposition. In other words, tooth growth is constant
(Brodie, 1969b) with mineralization the variable. There
is a cyclic occurrence of odontoblast tubules and resulting
mineralization. This may coincide with periods of increased
feeding and nutrient availability (Laws, 1953; Scheffer and
Peterson, 1967).

Since the cessation of tubule extensions are well
demarcated (see Fig. 9), the odontoblast mainbodies in the
pulp must pinch off the tubule, or cease to support it, in
an extremely coordinated manner. When the tubule is separ-
ated from the mainbody it is carried away from the pulp by
the constant deposition of ground substance. Another layer
of tubules forms shortly after this separation resulting in
the cyclic appearance of the tubule bands or layers.

Similar to the homeostatic system of bone, body fluid
(Urist, 1964, 1966) tubule formation seems to be controlled
by the availability of minerals in the blood stream. Urist
also states that there is little resorption of dentine once
deposited, which if true of beluga would mean that the teeth
of beluga are a permanent record of mineral availability with
the only loss being due to tip wear. There were several
instances where tooth remodelling or irregular growth
occurred in the sample from Cumberland Sound. Judging from
body scars, all these animals were greatly injured. There
appears to be a correlation between severe injury and cell
differentiation, upsetting patterns of mineralization in
tooth forming epithelium. This requires further research.

Correlation of Tooth and Skeletal Laminae.

There is disagreement over the number of skeletal and tooth layers representing an annual increment. Studies of Physeter catodon (Nishiwaki et al.1961) indicated that mandibular periosteal layers are equal in number to tooth layers. Gambell and Grzegorzewska (1967) have concluded that two tooth layers are deposited annually in P. catodon. Studies by Kleinenberg and Klevezal (1962) on Delphinus delphis indicate that two tooth layers and one mandibular layer are deposited annually. Sergeant (1959) suggested that two layers were deposited annually in D. leucas while Khuzin (1961) supported the theory that single tooth layers were deposited annually for the same species. This deserves some attention since calculations of productivity based on age could be overestimated or underestimated by as much as 100%.

In a recent paper (Brodie, 1969b)the mandibles of beluga were examined. Material was taken from the Cumberland Sound population. Longitudinal half-sections of teeth were cut, polished and examined under reflected light for numbers of dentine and cement layers. Mandible samples were cut in the region of the posterior mental foramina using a diamond-grit circular saw. Sections were 75-100 microns thick, requiring no polishing after the sawing process (Fig. 10).

These were mounted on slides, stained with aniline blue-acid fuchsin and examined under a microscope using transmitted light. Mandibular periosteal layers were present and increased in number with the increasing length of the animals.

FIGURE 10

Figure 10 illustrates preparation and sectioning of mandibles.

(A) shows three mandible sections imbedded in a bioplastic block, attached to a perspex cutting template. A thin section has already been cut from all three.

(B) shows a prepared thin section of mandible with a portion of tooth section included. Several periosteal layers can be seen on the right side of the mandible. Total length of section shown here, 42 mm.

(C) shows mandibular periosteal layering on the lateral exterior. Total width of layers 1.25 mm with mean number of tooth layers 13.5.

A
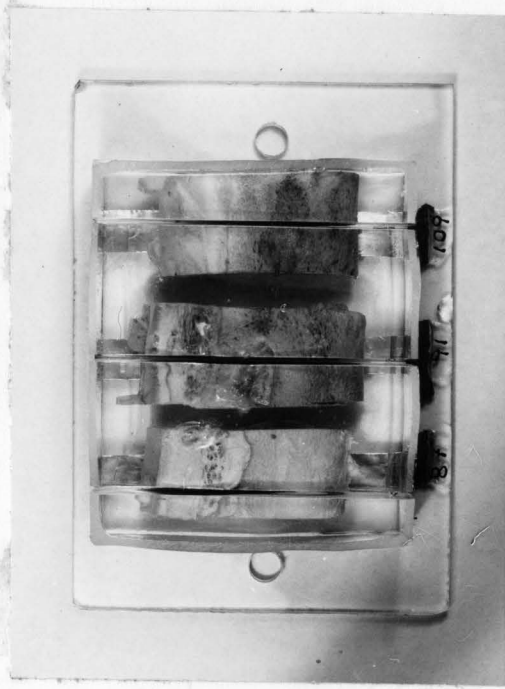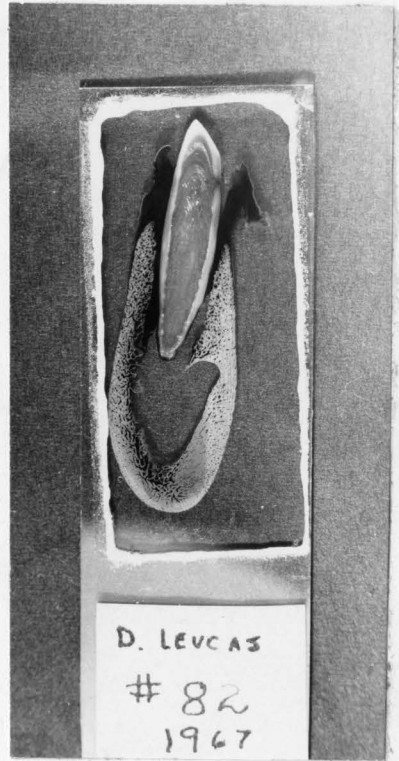
D. LEUCAS
#82
1967

B
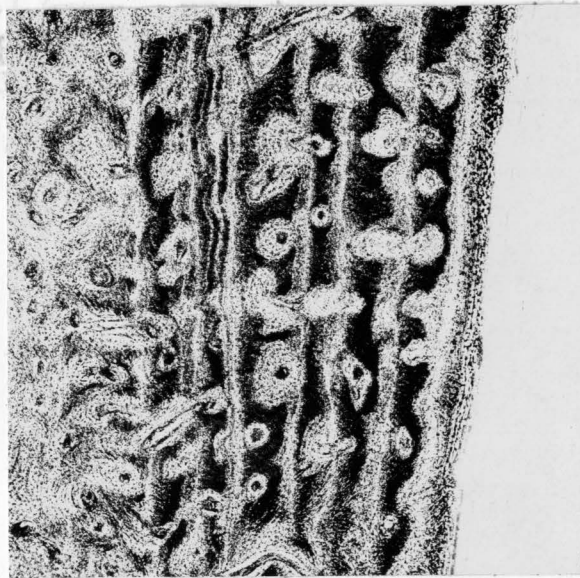
C
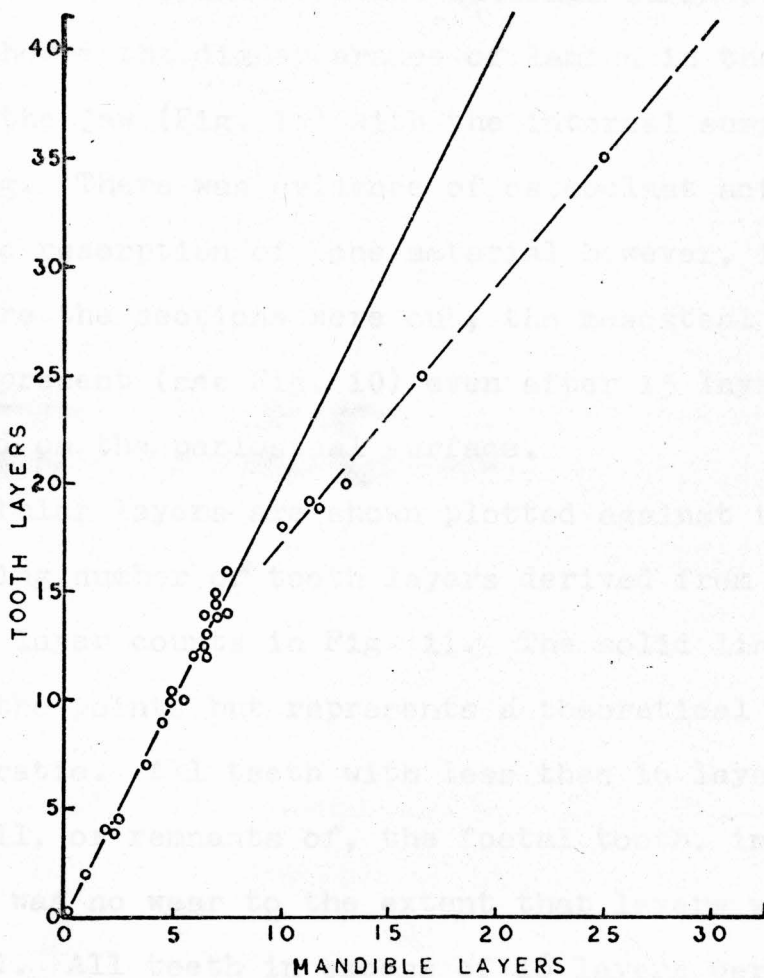
Figure 11 is a plot of tooth layers
present against mandibular layers of
the same individual. The solid line
represents a 2:1 tooth-jaw layer
ratio. The broken line is fitted to
the six divergent points representing
animals with well worn teeth. The
area between the two lines is
considered the zone of tooth wear.

31

In all cases the layers were thickest on the exterior
lateral surface. Several sections showed the layers to be
continuous over the internal and external surface. The
majority showed the dissapearance of lamina in the ventral
region of the jaw (Fig. 10) with the internal surface void
of layering. There was evidence of osteoclast activity
causing the resorption of bone material however, in the
region where the sections were cut, the mesosteal portion
was still present (see Fig. 10) even after 15 layers had
been formed on the periosteal surface.

Mandibular layers are shown plotted against their
corresponding number of tooth layers derived from dentine
and cement layer counts in Fig. 11. The solid line is not
fitted to the points but represents a theoretical 2:1 tooth-
jaw layer ratio. All teeth with less than 16 layers still
retained all, or remnants of, the foetal tooth, indicating
that there was no wear to the extent that layers were mis-
represented. All teeth in excess of 16 layers were worn
(see Fig. 7) yet were obviously depositing layers at a rate
greater than the rate of erosion.

Studies of teeth show that about four layers are added
to the tooth before it erupts through the gum and becomes
exposed to wear. Eleven or twelve layers are added to these
before the prenatal tooth is eroded beyond recognition and
tooth layers are misrepresented. The area between the 2:1
line and a line fitted through the six divergent points can
be considered the zone of tooth wear. Since the tooth is

pointed and erosion is more rapid due to the smaller surface area, initial tooth wear is probably non-linear.

The highest number of tooth layers recorded from the Cumberland Sound sample is 41 (the jaw from this specimen was not collected). Using Fig. 11 an abscissa from 41 will intersect the line through the six divergent points at 30 on the X or mandible axis. The implication here is that, considering tooth wear, the ratio may still be maintained and that probably 19 layers were eroded from this tooth.

The question now arises, which series of laminae represent annual increments? If the tooth layers are annual then some explanation must be found for the formation of mandibular layers on alternate years. This does not seem practical since beluga must be regulated to a great extent by harsh arctic seasonality. The alternative would be to consider the mandibular layers as annual increments, then attempt to justify the presence of two tooth layers per year.

Studies of the fur seal Callorhinus ursinus (Scheffer and Peterson, 1967) show that tooth growth-rate of young seals is fairly constant, with layering being caused by changes in nutrition. The mother is at sea for a mean of 9.4 days and returns to nurse the pup for a mean of 2.0 days, over a four month period consisting of mean 10.9 cycles. The layering is sensitive enough to be correlated with these periods of nursing. Laws (1953, 1962) correlates laminations with feeding-fasting behaviour of the elephant

seal, _Mirounga leonina_. Felts and Spurrell (1966) discuss the variations in density of radii of _D. leucas_;however they draw no definite conclusions other than suggesting possible changes in body and environmental temperature as the cause.

Considering the above findings, it is quite possible that beluga form more than one tooth layer per year. During mid-July to mid-September, Cumberland Sound beluga appear to feed lightly. Their teeth indicate that deposition of a mineralized layer has already been completed and a transparent non-mineralized ground-substance is being extruded from the pulp papilla (Brodie, 1969b). A migration or period of low intensity feeding during mid-January to mid-March could account for another spatially consistent layer. Movements of this population during these months are obscure. As discussed on p. 66 the breeding season is in May, seeming too late a period to cause a check mark in the dentine and maintain spatial constancy of laminae. Migration to the breeding area could be the cause, though this is speculative. Kleinenberg et al. (1964) mention the sudden appearance of beluga herds in various parts of the Soviet North during the months of December to February. Sergeant (personal communication) suggested a change in diet rather than low feeding rate as a possible cause of low mineral availability.

If the tooth layers of _D. leucas_ were annual, the ratio of 2:1 would require mandibular layers to be formed on alternate years, highly improbable for an animal so regulated

by harsh arctic seasonality.

Though further research will be carried out on this, conclusions at present are that two tooth layers and one mandibular layer are formed annually. The difference may be sensitivity of teeth to condition, or that skeletal structures have priority over teeth for available minerals.

Physical Maturity and Attainment of White Colouration.

Figure 12 shows the total sample of animals of which age in tooth layers is known. Due to tooth wear, all tooth layer counts over 16 are underestimates, the discrepancy increasing with increase in number of layers.

The mean lengths of males with more than 20 tooth layers present is 427 cm and for females 362 cm. These lengths may approximate those of physical maturity.

Whitening of female beluga occurs between 12 and 17 tooth layers, the male turning white between 15 to 17 tooth layers.

The white colour can be used in the field to establish at least a minimum age and to indicate that the animal is near physically mature size (see also Sergeant and Brodie, 1969a).

Length of Life.

Khuzin (1961) concludes that 40 years is the maximum lifespan for beluga. Kleinenberg et al. (1964) review the works of several authors where conclusions range between

35

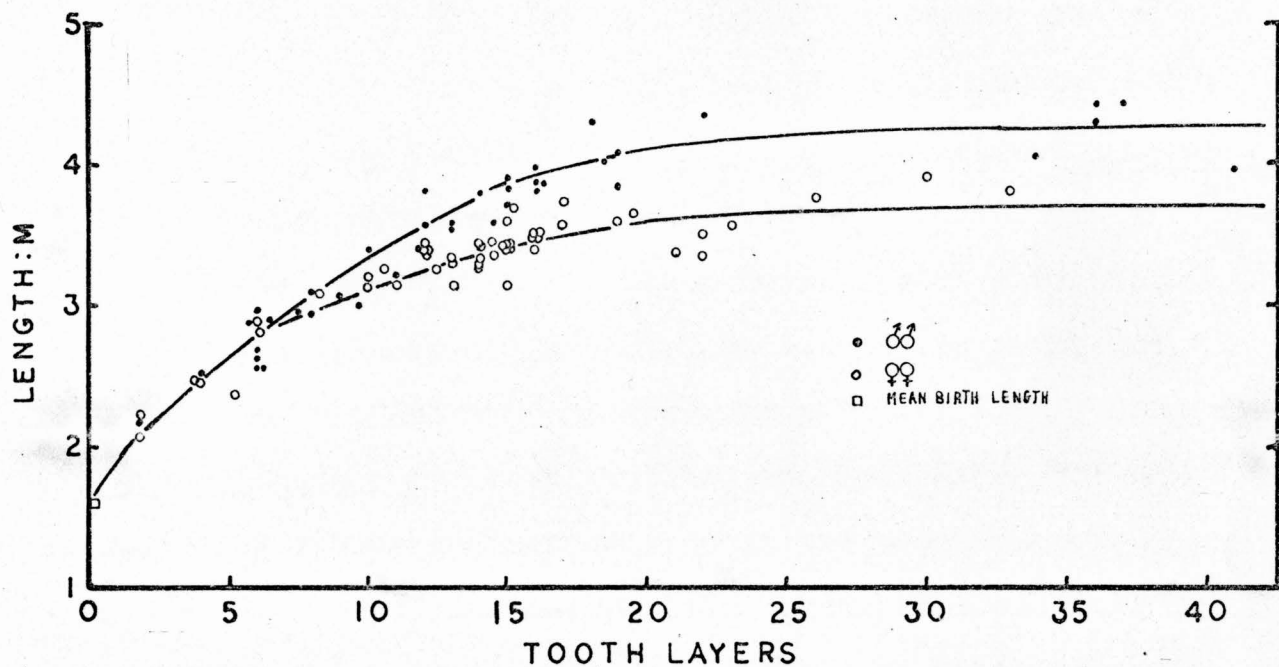Figure 12 is a plot of length in meters against age in tooth layers. All ages greater than 15 tooth layers are under-estimates due to tooth wear, the discrepancy increasing with age. Mean length of 23 newborns is shown plotted as a single point. Curves are fitted by eye.

20 to 32 years. Brodie (1969b) has suggested that the
maximum lifespan is about 30 years, based on tooth and
mandible layers.

General Considerations.

Beluga, like all Cetacea, have a bicornuate uterus.
Both ovaries are functional, multiple births being uncommon
(Vladykov, 1944; Kleinenberg et al., 1964). Figure 13 shows
the upper reproductive tract of a recently parturient beluga.

Cetacea are unusual in that their corpora albicantia
usually remain as distinguishable bodies in the ovary for
the life of the animal. Dempsey and Wislocki (1941) studied
Megaptera nodosa and have provided an explanation for this,
suggesting the large initial size of the cetacean corpus
luteum poses physiological problems or mechanical limitat-
ions on the vascular supply, which fails to reach the cent-
ral portion of the body. The central cavity becomes filled
with hyalin and fibrous tissue, these tissues persisting as
the main core of the regressed albicans. If vascular pene-
tration from the periphery into the spherical corpus luteum
is limited, one would expect less penetration in larger
species with larger corpora, the consequent hyalization re-
sulting in greater retention of corpora. Sergeant (1962b)
has concluded that all corpora albicantia gravidans of
Globicephala melaena are retained and about 50% of corpora
of ovulation remain as detectable bodies after regression
is complete.

Laws (1961) divided the regression of corpora into
three stages. stage #1 or "young" corpora having undergone

least regression and are usually apparent externally on the ovary. Luteal tissue has begun to degenerate due to reduction in vascular supply, and connective tissue is more conspicuous than in the corpus luteum. Stage #2 or "medium" corpora, which in beluga are not as easily discernible on the surface of the ovary, have thick-walled blood vessels on the periphery and a more obvious fibrous structure due to the loss of luteal tissue and the continued shrinkage of the corpus. The blood vessels cause the tissue to appear yellow-brown in colour. Stage #3 or "old" corpora is the final state of regression where connective tissue is the most obvious structure outlined by a thin margin of orange-brown pigmented cells.

These stages, described by Laws in greater detail and as outlined above, have since been used by many authors in describing regression of cetacean corpora. Since the time of sampling beluga coincided with the birth period there were corpora lutea and albicantia macroscopically indistinquishable from each other, the categories separated only by hours or days before or after birth. To reduce the temporal span between these stages, I will expand the stages into early stage #1, Late stage #1, early stage #2, late stage #2, in addition to the third main stage of each. Due to the very rapid regression of the corpus after birth, the subdivision of stage #1 is considered valid, subdivision of stage #2 may be less accurate and more subjective (see

Figs. 13 and 14). I stress the importance of having noted the association of animals captured in passive nets since calf age can be used with some confidence in interpreting corpora, especially when the calf is newborn. Extent of uterine distortion is obvious evidence along with state of lactation and fat thickness. The fact that the nets were passive and that usually only one to three animals were enmeshed at one time, added even greater significance to animal associations.

Because of the small number of sexually mature females (45 animals with a total corpora number of 181), the bias toward females with newborn calves and the small number of older females, classification of corpora by size alone has little significance. Only where the amount of data permit, can any statistical tests be applied.

FIGURE 13

(A) shows the upper part of the female reproductive tract. The bicornuate uterus is much enlarged due to a very recent birth (see the newborn, Fig. 21 (A). The ovaries are shown outlined at the ends of the cornua. Tape is extended 20 cm.

(B) shows the ovaries of a female in full-term pregnancy. Two corpora lutea (accessory corpora) are shown on the left ovary. The stigma can be seen on the surface of the upper corpus. See Fig. 18 for cross-sectional view of same.

(C) shows the ovaries of a female in full-term pregnancy. A single corpus luteum is seen on the left ovary. A corpus albicans can be detected at the base of the right ovary.
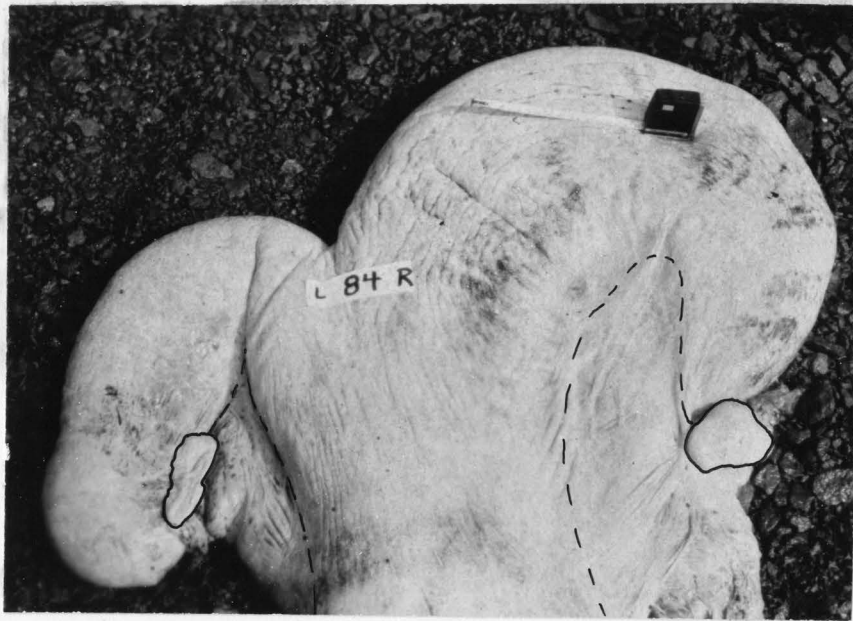
A
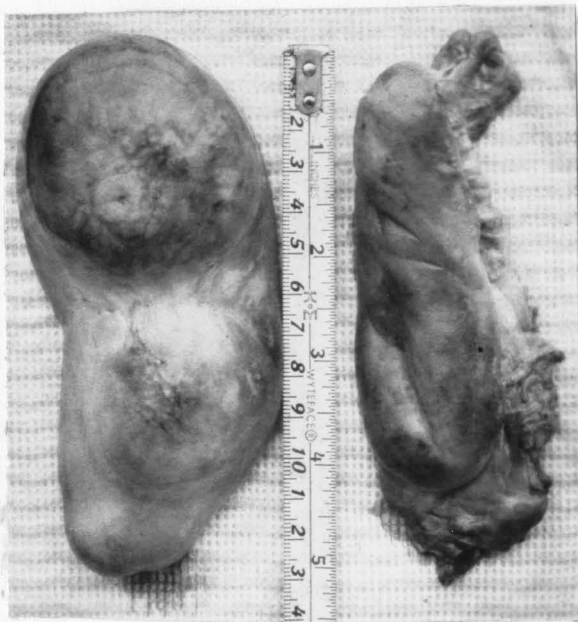
B
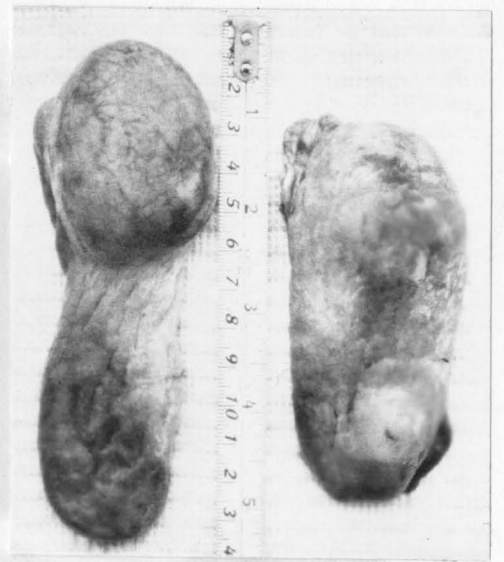
C

FIGURE 14

Figure 14 illustrates cross-sections of corpora in stages of regression.

(A) shows a 47 mm corpus luteum of a female with a 290 mm foetus. The luteal tissue is highly convuluted and is not "typical" of beluga.

(B) shows a 39 mm corpus albicans in early stage #1 regression. This female had undergone recent parturition. A small amount of fibrous tissue is seen at the top of the corpus.

(C) shows a 19 mm corpus albicans in early regression stage #2. The fibrous tissue is more obvious.

(D) shows an 8 mm corpus albicans in regression stage #3. The fibrous center is the most obvious structure with orange-brown lipid at the periphery.

A

B

C

D

Sexual Maturity.

Presence of corpora is considered to be the best criterion of maturity. The significance of the presence of foetuses is obvious. Figures 16 and 17 show corpora numbers against age and length respectively. The animal which appears to have matured earliest had two corpora at an age of 10 tooth layers. This animal (enmeshed beside a 139 cm calf) had recently given birth and had one 25 mm corpus albicans in early stage #1 and one 7 mm corpus in stage #2, probably from an unsuccessful ovulation immediately before impregnation on the second ovulation (now the larger corpus). The 14 month gestation period (see p. 63) would place the animal at 8 tooth layers on its first ovulation.

By excluding one atypical animal, immature at 15 layers, and back-calculating to account for gestation periods of nine animals with low corpora counts, the age of sexual maturity ranges between 9 and 11 tooth layers with a mean of 10 (SD = 1.00). Considering that two tooth layers are deposited annually (Brodie, 1969b) sexual maturity is attained on the average at five years and at about 85% of physically mature length (see p. 35).

Due to the great discrepancies in body size among various beluga populations in the arctic and sub-arctic (Sergeant and Brodie, 1969a) size at sexual maturity must also vary considerably. Vladykov (1944) using colour phases for age determination, concludes that sexual maturity

is attained usually in the third year. Examining the body lengths he gave and considering that beluga of the St. Lawrence population are of the same size as those of Cumberland Sound (Sergeant and Brodie, 1969a) these would conform in length to animals four and five years old by tooth layer counts (8 to 10 tooth layers).

Doan and Douglas (1953) state that beluga in Hudson Bay become sexually mature as early as their third summer (reworded in their summary as three years old), based on length frequencies. On examining their data I suggest that they have grouped two age-classes together, probably the newborns and the yearlings since the range of lengths is greater (relative to their length) than for older animals (see "Early Development", p. 77).

Kleinenberg et al. (1964) used length frequencies and have attributed prodigious growth rates to beluga by combining newborn, yearling, two and probably three year old animals in the newborn to several-months-old age category. Their length range ran from 150 to 290 cm. These authors agreed with Khuzin (1961) that sexual maturity was common after six years; however Khuzin considered that single tooth layers were produced annually. Such females would be three years old at two layers per year (Sergeant, 1959; Brodie, 1969b). Also, Khuzin may have included the first two or three thin layers of dentine as one layer (see Fig. 22 showing increase of layer thickness with age, and p. 16). There is obvious confusion here, but the point to be stressed is

46

that there is an extreme overlap of colour phases and length frequency modes, resulting in clumping of one or more age classes. This has the obvious effect on estimation of growth and maturity rates (see also p. 45).

Ovarian Analysis.

(a) Retention of Corpora Albicantia.

Figure 15 shows sizes of corpora albicantia ranked according to total number present.

The retention of corpora albicantia can be studied from their size distribution. Since sampling was carried out during the calving period there were animals with large, fresh albicantia. These corpora are not representative as they are just beginning the period of rapid regression and greatly distort any plot of size. Such fresh corpora have been eliminated from Fig. 15, reducing the number of corpora in most animals by one (two, where accessory corpora were present) and eliminating animals with a single fresh corpus.

Laws (1961) and Best (1967) applied tests similar to that of Fig. 15 to fin and sperm whales. A continued downward trend in size would indicate a cessation of size reduction. Higher corpora numbers among older animals suggest but do not prove that the downward trend does not continue (Fig.15) since also a levelling off or rise possibly could be the result of a sudden loss of corpora either by resorption or by exclusion during examination. It is doubtful however, that there is a rapid increase in resorption at this

47

20

15   7   8   6   8   2   2   1   2   1

CORPORA DIAMETER MM.

10

5

0

0   2   4   6   8   10   12   14   16
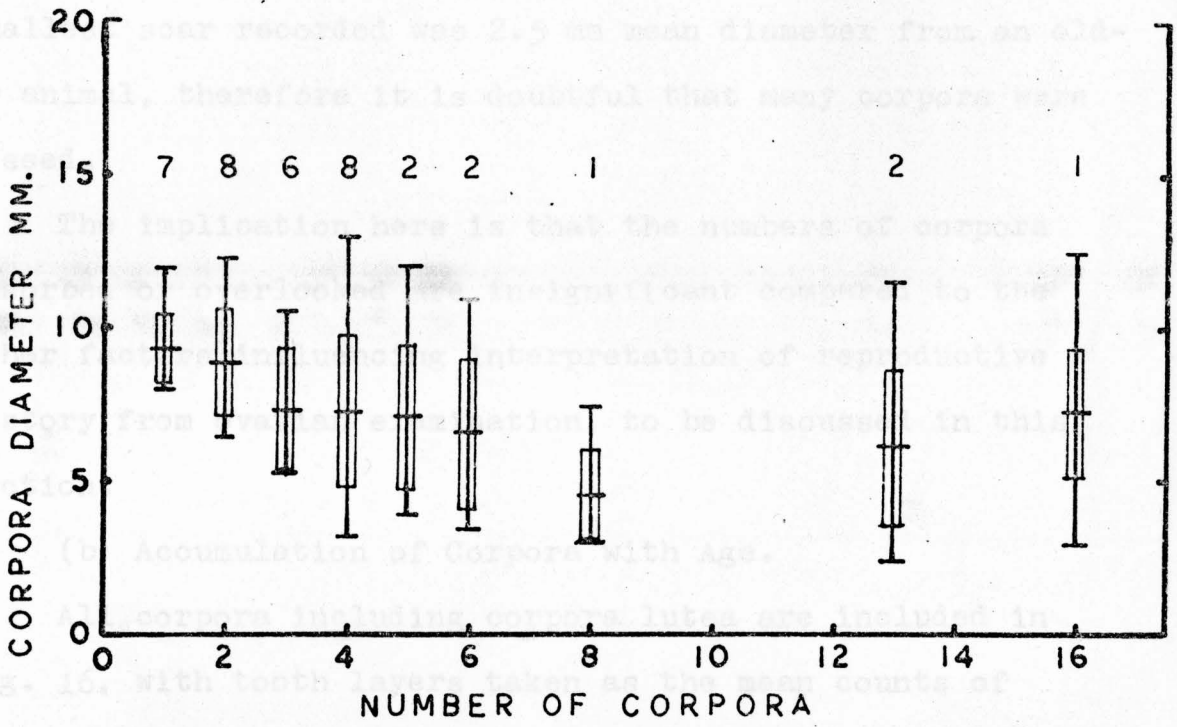
NUMBER OF CORPORA

Figure 15 illustrates the reduction of mean corpora
diameter with increase in accumulated corpora.
Large, unregressed corpora are not included here.
Number of females within each group is indicated
immediately above.

Range and mean are indicated with single standard
deviation represented by rectangles.

48

stage since these corpora are composed mainly of fibrous tissue, not easily destroyed by phagocytic activity. The small number of ovaries examined permitted rather careful scrutiny of sections, two to three mm in thickness for all but the youngest animals (about 3 mm in thickness). The smallest scar recorded was 2.5 mm mean diameter from an older animal, therefore it is doubtful that many corpora were missed.

The implication here is that the numbers of corpora resorbed or overlooked are insignificant compared to the other factors influencing interpretation of reproductive history from ovarian examination, to be discussed in this section.

(b) Accumulation of Corpora with Age.

All corpora including corpora lutea are included in Fig. 16, with tooth layers taken as the mean counts of dentine and cement layers. Tooth wear has not been considered in this illustration (Brodie 1969b) therefore all ages beyond 16 are underestimates, the discrepancy increasing with age. The scarcity of older animals and loss of their tooth layers discourages any attempt to calculate corpora accumulation rates by regression analysis. Far more revealing is the variation in numbers of corpora accumulated by younger animals of similar ages.

The abrupt increase in corpora over a short range of body length (Fig.17) is to be expected since sexual maturity

49

Figure 16 is a plot of total corpora per female against
tooth layers. The peripheral animals have been
arbitrarily grouped into:

(A) young animals with few corpora,

(B) young animals with many corpora,

(C) older animals with few corpora,

(D) older animals with many corpora.
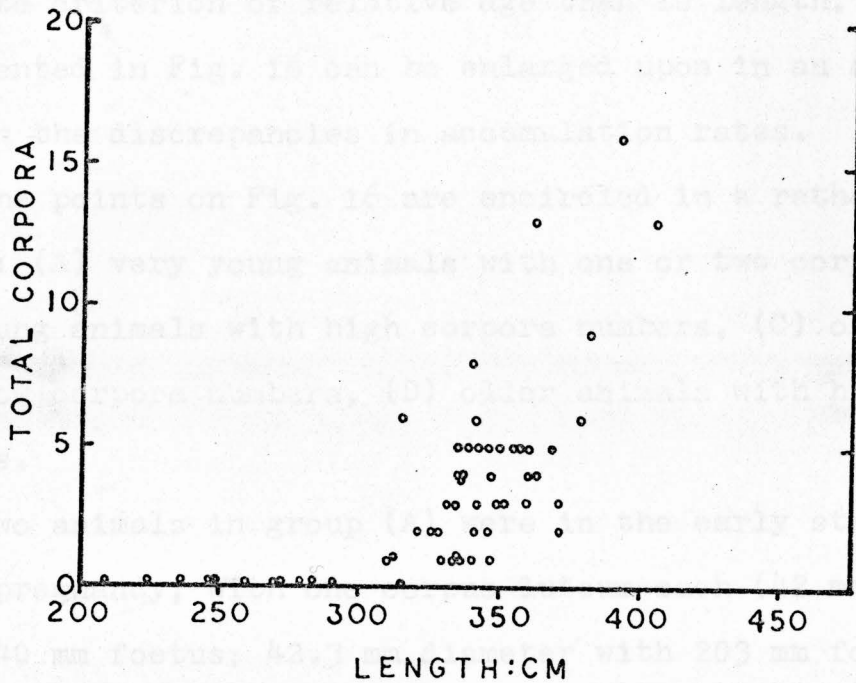
Figure 17 is a plot of total corpora per female against body length. The sudden presence of corpora after 310 cm body length indicates the onset of sexual maturity. The abrupt increase of corpora within a short length range is a result of sexual maturity being near the physically mature body length.

is attained near physical maturity (see p. 45), males showing a similar increase with respect to testes size (see p. 88). Since layers in unworn teeth (less than 16 layers) are a more accurate criterion of relative age than is length, animals represented in Fig. 16 can be enlarged upon in an attempt to explain the discrepancies in accumulation rates.

The points on Fig. 16 are encircled in a rather arbitrary manner: (A) very young animals with one or two corpora, (B) young animals with high corpora numbers, (C) older animals with low corpora numbers, (D) older animals with high corpora numbers.

Two animals in group (A) were in the early stages of first pregnancy, with one corpus luteum each (42 mm diameter with 240 mm foetus; 42.3 mm diameter with 203 mm foetus). Their mammary tissue averaged 21 mm deep and neither was lactating (see Fig. 20). Four animals exhibited, had recently given birth and three of these were lactating and contained single corpora albicantia in early stage #1 (21, 28, 37.7 mm diameter). The fourth animal possessed two corpora, a fresh 25 mm albicans in early stage #1 and a 7 mm albicans in early stage #2. The smaller corpus is considered to be the result of an ovulation immediately before impregnation on the second ovulation, during the same estrus cycle. The smaller corpus could not have been from a prior reproductive cycle since this animal was much too young to have gone through almost three years of gestation and lactation (see p. 75 concerning the "Reproductive Cycle"). Being in early stage #2,

52

it is doubtful that the corpus could have been the result of an aborted pregnancy or stillbirth prior to successful impregnation, since it would have shown greater regression.

The seventh animal in this group possessed one corpus; however there are insufficient data to draw any conclusions about its origin. In summary, group (A) is composed of animals successfully impregnated on their first ovulation and in one instance, on the second ovulation of the same estrus period. Formation of more corpora was inhibited by the period of gestation and the greater portion of the lactation period, maintaining these low corpora numbers.

Group (B) is composed of two animals with 12 tooth layers and five or six corpora. The female with 5 corpora had just given birth and possessed twin or accessory corpora (see p. 56), in early stage #1 (21.7 and 15 mm in diameter) one 7.7 mm stage #2, and two in stage #3 (5.3 mm and 4.3 mm in diameter). This animal is too young to have gone through a complete reproductive cycle of almost three years and then through a 14 month gestation period just ended. To account for the other corpora it would appear reasonable to assume that the animal was unsuccessful on its first two ovulations (now represented by the two stage #3 corpora), failed to be impregnated on the first ovulation of the breeding season the year following (now the stage #2 corpus), but was impregnated on later ovulations of the same estrus period (the accessory corpus formed in addition to the larger corpus and now both in early stage #1). The animal with six corpora

in this group was lactating and from examination of the youngest corpora (7.5, 6.5, 5.5 mm all in stage #2) had given birth one or possibly two years prior to capture. Had she given birth one year prior to capture, the additional 14 months of gestation would place her at a very young age, too young to have completed a previous reproductive cycle. The remaining three corpora (5, 5, 3.5 mm all in stage #3) were probably the remnants of an unsuccessful multiple ovulation during its first estrus period. The following breeding season she was impregnated on the last of three ovulations (probably represented by the largest of the three stage #2 corpora).

Summarizing group (B), both animals were too young to have gone through more than one complete reproductive cycle, and the high corpora numbers are attributed to unsuccessful multiple ovulations and in one case to accessory corpora of pregnancy. Foetal abortion during an earlier pregnancy cannot be excluded; however any such pregnancy must have been short-lived.

Group (C) is composed of animals with between 13 and 14.5 tooth layers with one or no corpora present. Of these, two animals had recently given birth and were lactating with single early stage #1 corpora (36.6, 25.3 mm). Sexual maturity and successful ovulation must have been attained approximately 14 months prior to capture (11 and 13 layers). Two animals were lactating with no sign of recent birth, single corpora 12 mm and 10.2 mm in early stage #2. These

54

females had calved the year previous and therefore became
sexually mature 26 months (12 + 14 months) prior to capture,
or at 10 to 11 tooth layers. One sexually immature animal
is included in this group (15 tooth layers, no corpora but
many follicles less than 4 mm diameter). This animals was
found enmeshed beside an adult female and her newborn calf.
More will be said about these associations later (see p. 100).
Summarizing group (C), their reproductive history can be
accounted for either by late maturity and recent parturition
or by sexual maturity at the usual age with parturition a
year prior to capture.

Group (D) is composed of two animals with 15 tooth
layers and six to eight corpora. Both had recently calved,
one with two stage #1 corpora (27.4 and 17.7 mm, evidence of
an accessory corpus) three in mid to late stage #2 (11, 10,
9.7 mm) and three stage #3 (7.3, 4.7, 4 mm). The other animal
had one stage #1 corpus (20 mm), three stage #2 (7, 5.5, 4.5
mm) and two stage #3 (6, 4 mm). It is just possible that
both could have had a complete reproductive cycle prior to
the latest pregnancy, however it is equally likely that they
were not impregnated during the first cycle of multiple
ovulations and may have been successful in the following
year. Summarizing group (D), many unsuccessful ovulations are
evident, with at least one occurrence of accessory corpora.

Detailed case histories similar to the above exist for
all animals plotted in Fig. 16. The point to be stressed
here is that a minority of the corpora present, represents

55

successful impregnation or completed gestation. Kleinenberg
et al. (1964) attribute most corpora to pregnancies in D.
leucas. Ohsumi (1965) is criticized by Best (1967) for as-
suming that all corpora lutea represent pregnancies in P.
catodon.

A further point is that the presence of few corpora
(well spaced in regression stages) in an older animal could
mean that it has been extremely successful in reproduction
relative to animals of similar age with higher corpora numb-
ers. To indicate the area where error can occur, I quote from
Kleinenberg et al. (1964, translated edition 1969) "Most
sexually mature females captured in the far east and in the
north ... have 3-4 scars and corpora lutea in the ovaries,
i.e., they are 4-6 years old". An overall statement like
this cannot be made when Fig.16 shows the great discrepancy
in corpora number with age and their possible origins dis-
cussed in this section.

(C) Evidence For Accessory Corpora.

Four females, lactating, with distended cornua, were
captured in early August. Newborn calves were enmeshed be-
side three of them. All possessed twin corpora in very early
stages of regression (three possessing additional corpora in
more advanced regression).

Kleinenberg et al. (1964) would interpret these as one
corpus albicans (which it is) representing the recent new-
born, now being nursed. The other corpus would be consider-
ed by them, a corpus luteum of a pregnancy in early stages

56

(a result of impregnation two to four weeks after recent birth). This is the basis for their belief in annual calving by individual females.

As evidence against the above interpretation, there was no mucus plug present (its function is vague, though they state it is invariably present) in pregnant animals (see p. 67, concerning the mucus plug). The uterine cornua of recently parturient animals is thick and convuluted on its exterior surface (see Fig. 13) contrasted with the smooth, flaccid uterus of pregnant beluga, not illustrated. The calves in my estimation were born even more recently than two weeks earlier.

In addition, a pregnant animal was captured several days earlier than the above animals. She carried a male foetus 174 cm long, 94 kg in weight, in the right uterine horn. The left ovary contained two large corpora lutea (47 and 29 mm diameter; see Figs. 13 and 18). The female was obviously about to give birth within hours or days of capture. Had she been captured immediately after birth the above authors would, to be consistent, interpret the corpora as of recent parturition and of new pregnancy. Expanding their argument, this gravid female would then be good evidence for superfoetation or non-contemporary, double pregnancy (Parkes 1956). Their own argument would then be defeated by their belief in an anti-fertilization mucus plug.

FIGURE 18

Figure 18 shows cross-sections of accessory corpora lutea
of pregnancy (51 mm and 32 mm diameter) seen also in
Fig. 13 (B). The smaller corpus has a fibrous center.
The larger corpus is more typical of beluga corpora lutea
(flattened during preservation).

It is much simpler to suppose that all five animals
exhibit acc... ... ...results from
luteinization ... ...amplitude in
addition to... ...these would
probably for... ...

the corpora... ...offset
on maturation... ...1960).
At other times... ...exhibited by
a large act... ...It is
doubtful ... ...during ... ...pregnancy
is well established.

All large corpora in question were formed about 14
months prior to capture (i.e. at conception). Of 39 females,
either pregnant or recently calved and whose functional
corpora were obvious by size and appearance, five indicated
presence of contemporary corpora (12.8%). Here is primary
evidence of the inaccuracy of estimating production of young
or age by corpora counts. It can be suggested, but not
proven that accessory corpora may also result from the
effects of corpora of ovulation alone.

(d) Ovarian Activity and Symmetry.

To test for symmetry of ovarian function, only females
of which the side of origin of the ovary was known positively
were used. Corpora in all stages were totalled for 43
females, yielding 99 in the left and 73 in the right. A
Chi Square test using one degree of freedom shows the differ-
ence to be insignificant at the 1% level with probability

It is much simpler to suppose that all five animals exhibit accessory corpora of pregnancy. This results from luteinization of a second ruptured or unruptured follicle in addition to the corpus of the fertilized ovum. These would probably form during the estrus period since, of necessity, the corpora of ovulation would have a less inhibiting effect on maturation of other follicles (see also Asdell, 1965). At other times, follicle maturation would be inhibited by a large active corpus luteum gravidans, therefore it is doubtful that the accessory corpus is formed after pregnancy is well established.

All large corpora in question were formed about 14 months prior to capture (i.e. at conception). Of 39 females, either pregnant or recently calved and whose functional corpora were obvious by size and appearance, five indicated presence of contemporary corpora (12.8%). Here is primary evidence of the inaccuracy of estimating production of young, or age by corpora counts. It can be suggested, but not proven that accessory corpora may also result from the effects of corpora of ovulation alone.

(d) Ovarian Activity and Symmetry.

To test for symmetry of ovarian function, only females of which the side of origin of the ovary was known positively were used. Corpora in all stages were totalled for 43 females, yielding 99 in the left and 73 in the right. A Chi Square test using one degree of freedom shows the difference to be insignificant at the 1% level with probability

60

between 0.05 and 0.02. The same females were then randomly grouped until total corpora on either side exceeded ten. Six such groups were formed and their Chi Squares for parity summed, yielding a significant difference (P between 0.01 and 0.001). These tests indicate variability between groups resulting in non-significant differences when totalled, and it is concluded that either ovary may be dominant with respect to corpora number.

As a test for difference in time of maturity between left and right, females with low corpora numbers were used in which the smallest, most regressed corpora were obvious (the first ovulation). Of the 29 females in this category, first ovulation occurred in the left ovary of 19 and in the right of 10. A Chi Square test with one degree of freedom shows the difference from parity to be non-significant (P between 0.10 and 0.05).

To test for asymmetry of successful (fertilized) ovulations, all females with corpora lutea of pregnancy and large new corpora albicantia from a recent birth were used. Of the total number of 36 females used, 27 had the corpus of the last pregnancy in the left ovary and 9 the corpus in the right. A Chi Square test using one degree of freedom shows this to be significantly different from parity (P between 0.01 and 0.001).

Ohsumi (1964) concluded that in the beluga, 70% of corpora accumulate in the left and that the left matured earliest. He based this on the ovaries of 16 animals from

61

a Canadian population (Hudson Bay). Ohsumi also states that
differences between left and right accumulation rates are
reduced with age. His conclusions are, no doubt, a result
of multiple ovulation in young females and accessory corpora
plus the small size of his sample (see pp. 52 and 56 for
discussion).

The only conclusion of significance to be drawn from
the Cumberland Sound population is that the ova of the left
ovary are more successful in being fertilized.

(e) Post-Partum Ovulation and Pregnancy.

Kleinenberg et al. (1964) maintain that post-partum
ovulation and impregnation are natural functions of beluga.
They also state that lactation, even in the early stages
after birth, does not inhibit follicle maturation, copulation
and impregnation. Their evidence for this is the presence
of more than one large corpus (see accessory corpora, p. 56)
and that many females are lactating while in the early stages

of pregnancy (see p. 70 for "Duration of Lactation"). As
enlarged upon on p. 70, they conclude that lactation lasts
4-5 months.

There were five individuals in which follicles were
enlarged to a noticeable degree (maxima of 9.3, 10, 12, 16,
19.3 mm diameter). Two of these animals had recently given
birth (follicles 19.3, 9.3 mm), two had calved 1-2 years
prior to capture (follicles 16, 10 mm) and were lactating,
while the fifth female had not calved for at least two
years though, from the enlarged cornua and number of old

corpora, had calved at least once. She was not lactating
and had a 12 mm follicle. This was the only mature female
not in some stage of reproduction, the only evidence of
possible cessation of production in the entire sample.

The animals mentioned above are the only evidence of
follicle enlargement. If post-partum breeding was occurring
there would be a wide variation of foetal size due to May and
August breeding. Such variation does not exist except for
the one described under "Gestation", therefore it is doubt-
ful that follicles rupture in August. If ovulation does oc-
cur the chances of impregnation are reduced due to the seg-
regation of the herd within the fiord (see p.100) and the
apparent low spermatogenic activity of the males (see p. 88).

It is concluded that there is no evidence of post-
partum ovulation or pregnancy though several large follicles
were present in several mature females at varying stages of
the reproductive cycle.

Gestation.

(a) Duration of Gestation.

Although there are differences in size of adults among
populations (Kleinenberg et al., 1964; Sergeant and Brodie,
1969a) the range of length at birth is everywhere similar.
The Russian researchers have maintained that beluga have a
11.5 - 12 month gestation period, basing this on the presence
of small foetuses found during the calving period and consid-
ering that these were conceived immediately after the very

63

recent birth of a calf. The additional evidence is that these females were lactating, surmising that the nursed calf is a recent newborn. The presence of large double corpora is also used as evidence that conception immediately follows parturition (see p.56 for a discussion of this).

Foetal lengths when sampled during the early and mid-summer months from any population form two groups, one at each end of the foetal growth curve, i.e., 10-30 cm and 130-170 cm approximately. An example of such is shown for Cumberland Sound animals in Fig. 19. Lengths of newborn calves, most retaining several centimeters of umbilical epidermal sheath are also shown. Their lengths are plotted against the time of capture, or in the case of foetuses, capture of pregnant females. Lengths of the large foetuses and all calves are plotted twice (advanced 12 months to continue the foetal growth curve in proper perspective). Sergeant (1962b) applied this to the pilot whale and Best (1969) to the sperm whale. Since both these species are not arctic inhabitants, they are less subject to harsh seasonality and this may explain their greater spreads of foetal length for any time period. The contracted period of sampling beluga also reduces the range of foetal length with time. The variation in spread of beluga foetal length at any given time, between populations may reflect the degree of regulation by the local climate, selection being for animals which conformed best to the ideal calving period (a result of the time of mating, not forced foetal retention or expulsion), probably the most

64

Figure 19 is a plot of foetuses and newborns, relating body length against time of discovery or capture, respectively. Full term foetuses and newborns have been advanced 12 months to show the foetal growth curve in its proper perspective. The straight line does not take into account early embryonic growth. Estimated breeding, gestation and birth periods are indicated. Ranges of birth period and of length at birth are indicated by the broken lines.

sensitive phase in their life history (see also Sergeant and Brodie, 1969a).

A straight line method is used to calculate the gestation period (Huggett and Widdas, 1951; modified by Laws,1959). The time intercept is at 390-400 days prior to the estimated birth period of late July - early August. The straight line does not take into consideration the early growth which the originators of the method account for by multiplying this figure by 1.10 giving an estimated gestation of 14.5 months for beluga. This would place the peak of breeding in mid to late May.

Laws (1959) calculated 13-14 months for beluga using Canadian data, Sergeant (1962a) estimates 13-14 months for Hudson Bay beluga. The three estimates all fall over the 12 month period concluded by Kleinenberg et al. (1964).

The small foetuses found during the calving period and illustrated in Fig. 19,are definitely not a result of conception during this calving period. They are at least several weeks old and were conceived before beluga were able to enter the Clearwater Fiord area due to ice conditions. The smallest foetus (a female) was 155 mm in length, discovered on July 13. Kleinenberg et al. (1964) state "Increase in length is 5 cm in the first month, more than 7 cm in the second month and more than 12 cm in the third month." By their calculations conception would have been early to mid May. There is no question that the calving period in Cumberland Sound is late July - late August so that the gestation

66

period must exceed their calculations of 11.5 - 12 months.
There is therefore, little doubt that the gestation period
well exceeds 12 months and may reach 14.5 months. This
difference has very significant effects when overall
productivity of beluga is considered.

(b) Cervical Mucus Plug.

Kleinenberg et al. (1964) describe the presence of a
rubbery, semi-transparent, mucus plug in the cervix of
beluga stating that they are present only in pregnant females
regardless of the stage of foetal growth. They postulate
that it functions as an isolating mechanism, preventing
extra fertilization and that it also assists the development
of the embryo in the uterus.

Kleinenberg and co-authors cite three pregnant females
without the plug from 150 females sampled and a fourth from
previous field work, yet maintain the above statement. All
four animals showed evidence of previous pregnancy judging
from their enlarged and asymmetrical uterine horns. No plug
was present in the cervix of any of them.

Although it is possible that I overlooked such
structures, the only instance where one was quite obvious,
fitting their description, was in a non-pregnant, lactating
animal with a single corpus albicans, 12 mm in diameter. The
corpus was considered to be in early stage #2, which along
with the cornua of reduced internal width, indicated partur-
ition months prior to capture. In addition, a 214 cm calf,
judged by age determination studies and size to be a yearling

67

(see p. 78), was enmeshed beside her along with a multi-parous, lactating, non-pregnant female. A mucus plug was also noted (below the cervix) in a lactating, recently calved animal with a single late stage #1 corpus (captured with newborn).

This evidence suggest that the plug can occur in non-pregnant animals. Had the animals been in the early stages of pregnancy there would have been corpora lutea present even though the embryos could not be detected. The suggestion that the plug is necessary to prevent extra fertilization is certainly open to question, since the presence of a corpus luteam inhibits follicle maturation (Assali 1968, Asdell, 1965), especially a corpus luteum gravidans.

Birth Period, Newborn Size and Observations.

Many points have been considered in the sections on gestation and early development, however all aspects will be included here.

The birth period ranges from late July to late August with the peak of births in early to mid-August (see Fig. 19). This cannot be more positively stated since the age of the majority of newborn calves is questionable as to their being one or several days old.

Rapid post-natal growth rates and weight gains probably distort the calculations of size at birth (Bryden, 1969; Sergeant and Brodie, 1969a). The head profile of a newborn

68

is illustrated in Fig. 21. Mean length was 159.6 cm (139-175 cm, SD = 10.05), with mean girth of 108.3 cm (86-129 cm, SD = 11.39) and mean weight 78.3 kg (56-104, SD = 17.4).

The epidermis was void of any superficial markings and no macro-parasites were visible in the middle ear sinus or stomach (though found in all animals older than newborns). Teeth were well hidden beneath the gum. The brownish colour attributed to newborns (Vladykov, 1944) was not as apparent as described by the above author, when the newborn was captured and examined; however recent newborns did appear to have a reddish-brown hue when observed at a distance, swimming beside the mother (see also Kleinenberg et al., 1964).

The tail flukes were rather pliable when contrasted with those of older animals (this is of advantage for easy passage during parturition). The speed at which these newborn swim when beside their mothers must be attributed to the hydro-dynamic advantages of echelon formation (Lang, 1966) rather than calf muscle power. The ease of capture is noticeable whne the calf is separated from its mother (see also "Non-Commercial Hunting Mortality").

Several centimeters of epidermal umbilical sheath were retained by most of the calves. The breaking point of the umbilical cord was tested on the only two full-term foetuses obtained. Only relatively few pounds of force were required to pull the cord from the foetus (see also Slijper, 1962) and it literally "unplugged" from the abdomen, leaving an epidermal sheath 6-13 cm in length still attached.

Lactation.

(a) Duration of Lactation

Vladykov (1944) concludes that beluga in the St. Law-
rence River nurse their calves for approximately six months.
Kleinenberg et al. (1964) suggest a 4-5 month lactation per-
iod and have based this on the presence of milk in the anim-
als of the 280 cm range, considering these to be 4-5 months
old. Age determination and length frequencies of the Cumber-
land Sound population would place such animals at 3-4 years
of age. Sergeant (unpublished) considers the lactation per-
iod to be greater than one year and as long as two years,
based on the ratio of pregnant to lactating females studied
in Hudson Bay.

Lactating Cumberland Sound females have been captured
in nets accompanied by calves in the 209-225 cm range.
These are considered to be yearlings by dentine growth, body
scars, parasites (see p. 77) and size; therefore lactation
lasts at least one year. The breeding season is calculated
to be about mid-May (see p. 66) and since none of these fe-
males show any signs of pregnancy at time of capture in July-
August there is no reason why lactation should have ceased
at this point (if the argument that pregnancy inhibits lact-
ation is used). Kleinenberg et al. (1964) state that lact-
ation does not inhibit ovulation and pregnancy (see also
p. 62).

There are four instances where lactating, non-pregnant
animals were captured with calves considered to be two years

70

old by criteria similar to the above. This is not only evidence that lactation may last two years but also supports the theory of a long reproductive cycle (see section on "Reproductive Cycle", p. 75). Lactating animals in the early stages of pregnancy with 155 mm - 290 mm foetuses were noted so that lactation at this stage is not inhibited. All animals in this latter category possessed older regressed corpora and were of such an age that they could have completed a reproductive cycle more than one year prior to the latest pregnancy. One animal in full-term pregnancy was secreting colostrum (see p. 72) and beginning milk production. The 80 mm depth of mammary tissue is an indication that she had nursed prior to this pregnancy (see p. 73 and Fig. 20). She was old enough to have gone through several reproductive cycles and possessed four old corpora in addition to twin corpora lutea of pregnancy (accessory copora).

The argument that lactation in animals with small foetuses is due to the effect of the pregnancy does not hold true in these cases since only females capable of having had a prior pregnancy, by age and presence of additional corpora in late regression, were lactating. One female with a single corpus in its ovaries and one 203 mm foetus was not lactating. By its young age and single corpus it could not have had a prior pregnancy. Depth of mammary tissue was 20 mm.

I conclude that lactation lasts as long as two years and is not inhibited by the early stages of the following pregnancy, though it appears to cease later on so that it

71

could be slightly over 24 months. This increases my previous estimate by 2-3 months (Brodie, 1969b). Tavolga (1966) states that <u>Tursiops truncatus</u> nurses as long as 18 months in aquaria, and that the female refuses to suckle the calf if she later becomes pregnant.

(b) Evidence of Colostrum.

On July 28, 1967, two females were simultaneously enmeshed in a single net. Both had a light yellow fluid exuding from their teats (both animals were examined minutes after death). One female carried a 156 cm foetus, 64 kg (140 lb). This foetus is within range of newborn lengths and was hours or days away from birth. On sectioning the mammary tissue, similar fluid was found in the ducts.

The other female carried a 174 cm, 94 kg (207 lb) foetus and had similar fluid in the mammary ducts along with milk. This animal was probably hours away from parturition.

The fluid was tentatively identified as colostrum (see also Tomilin, 1957). Considering that Cetacea (as well as carnivores and ungulates) have a poorly fused foetal-maternal placenta and the possible correlation between passive and active antibody transfer to type of placenta, the fluid was probably colostrum (Slijper, 1962; Young, 1963; Asdell, 1965; Assali, 1968). The immunization of the calf would be active i.e., antibodies would be absorbed through the gut wall during its first nursing period. Large and precocious young are generally supported by the above mentioned type of placenta, according to the authors.

72

(c) Reproductive State and Mammary Tissue Thickness.

Figure 20 is a plot of mammary tissue depth, with groupings according to the reproductive state of the animal. It became noticeable early in the field sampling that depth shows the greatest variation of the three dimensions. Measurements were taken to the nearest 5 mm, therefore ranges have been extended by 2.5 mm at their extremes. Range and mean are indicated, with standard deviation of larger frequencies. The tissue depth of younger animals suggests that depth is not increased by the early stages of first pregnancy, relative to that of immature animals, but is increased before giving birth, at which time there is considerable variation in thickness. Multiparous females show less variation due to physical maturity and almost constant lactation, excepting the latter stages of the following pregnancy. This is demonstrated by the mammary depth of females nursing for one and two years and of multiparous animals in early pregnancy, though still nursing.

The single 362 cm, sexually mature animal, shown as the final point, is the only female with undetermined reproductive status. She was obviously multiparous, judging from the presence of 13 regressed corpora, was not lactating and had reduced uterine dimensions. One 12 mm and two 4 mm follicles were present in the ovaries, however time of capture was August and not considered a breeding period (see "Post-Partum Ovulation and Pregnancy", p. 62). This is the only female with evidence of cessation of production.

73

MAMMARY DEPTH: CM

10
9
8
7
6
5
4
3
2
1
0

19

11

1

5

4

4

2

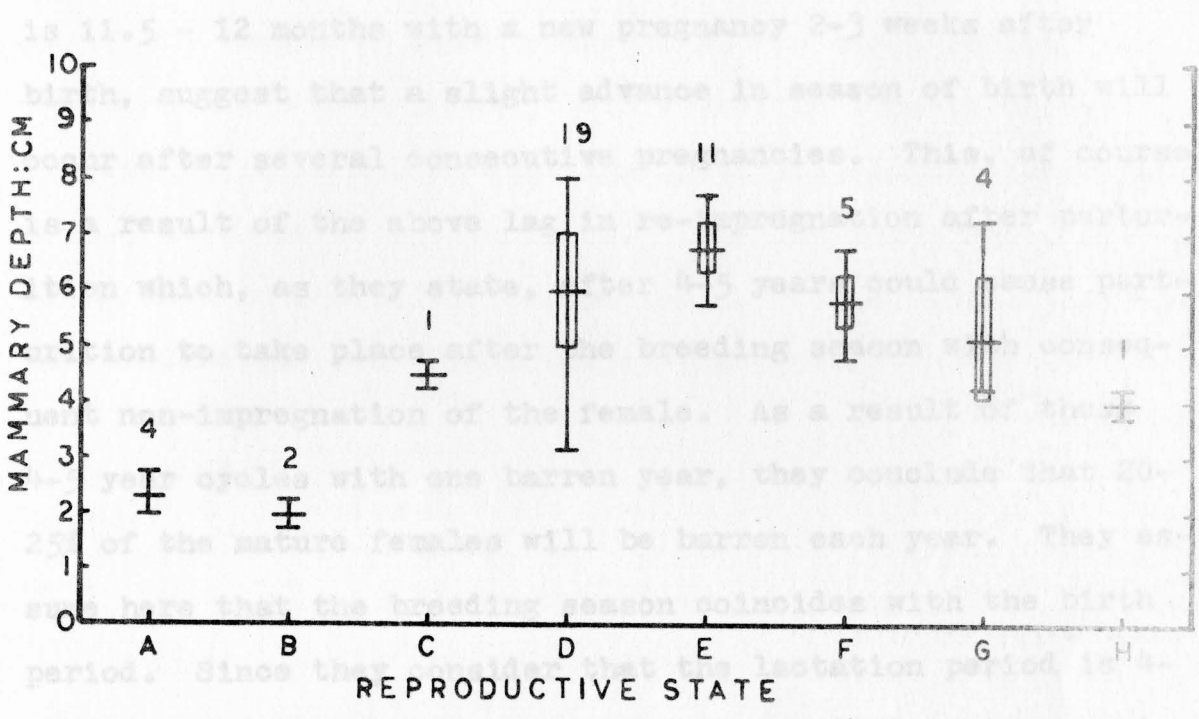A   B   C   D   E   F   G   H

REPRODUCTIVE STATE

Figure 20 illustrates change in mammary tissue depth or
thickness according to the reproductive state. Numbers
of females in each category are indicated immediately
above.

(A) immature females.

(B) animals in the early stage of first pregnancy and
not lactating.

(C) first pregnancy in full term and beginning lactation.

(D) primiparous, recent birth and lactating.

(E) multiparous, recent birth and lactating.

(F) primi and multiparous after 1-2 years lactation.

(G) multiparous in early pregnancy and lactating.

(H) multiparous, not lactating, possibly cessation of
production.

Range and mean are indicated with single standard
deviation represented by rectangles.

The Reproductive Cycle.

Kleinenberg et al. (1964), maintaining that gestation is 11.5 - 12 months with a new pregnancy 2-3 weeks after birth, suggest that a slight advance in season of birth will occur after several consecutive pregnancies. This, of course, is a result of the above lag in re-impregnation after parturition which, as they state, after 4-5 years could cause parturition to take place after the breeding season with consequent non-impregnation of the female. As a result of these 4-5 year cycles with one barren year, they conclude that 20-25% of the mature females will be barren each year. They assume here that the breeding season coincides with the birth period. Since they consider that the lactation period is 4-5 months and that it does not inhibit immediate reimpregnation, this means that lactation would be well within the gestation period and without any effect on the reproductive cycle. The cycle they propose would be of 11.5 - 12 months duration, plus 2-4 weeks due to the variation in time of impregnation. They also speak of the 4-5 year cycles made up of 4-5 one-year gestation periods; however the reproductive cycle is considered by myself to be from pregnancy to pregnancy.

There is considerable disagreement with the conclusions of Kleinenberg and co-authors in the observations of the Cumberland Sound population. The gestation period has been shown to last as long as 14.5 months (see p. 63), slightly longer than the period suggested by Sergeant and Laws (p.63). A round figure of 14 months may be suggested. Duration of

75

lactation (see p. 70) is about two years but, since at the

end of this time (late July to September, the time of sampl-

ing), the female is again pregnant with a small foetus from

the breeding season in May, this gestation time is deduced.

The result is 14 months gestation plus 21.5 months lactation;

a 35.5 month reproductive cycle. This implies a considerable

difference in individual production as well as total populat-

ion production (see "Productivity", p.118).

Calf Growth Rates.

The major reason for the vast discrepancies in published estimates of growth rates of beluga appears to be the scarcity of comprehensive data for younger animals. This is, no doubt, the period of most rapid growth, where increments of body length, weight and tooth growth are more meaningful due to the necessarily stereotyped behaviour of young animals. Lack of such information can be attributed to the usual bias toward larger animals in commercial fisheries. Where large herds are driven ashore, sometimes with full representation of all ages, a problem of processing occurs, and in the confusion, all calf-mother relationships become questionable. These conclusions are based on my experience with both methods.

Where several criteria are considered among age classes, the differences become more obvious even though the individual criteria may overlap in several aspects.

In an attempt to show that two and even three age classes have been classed as one by some authors, the body length, maximum girth, weight, teeth, body scars and parasites will be considered for the small sample of Cumberland Sound calves. Mother-calf associations are used as evidence here, though discussed more fully elsewhere (pp. 68 and 100). The calves have been tentatively divided into groups based on initial impressions in the field. It is more meaningful to

discuss their differences than to plot all the data from this small sample on a table. In the discussion that follows, ranges and standard deviations are given or ranges alone, depending on the size of the sample.

The full-term foetuses are included here for continuity. Two foetuses had a mean length of 165 cm (156 and 174 cm) and a mean weight of 79 kg (63.7 and 94 kg). No tooth layers were present on the foetal tooth.

Seventeen animals considered newborn, with pertinent data taken, are now considered. Mean length was 159.6 cm (SD = 10.05), mean maximum girth 108.3 (SD = 11.39) and mean weight 78.3 kg (SD = 17.4 kg) with no tooth layers yet deposited on the foetal tooth. No parasites were visible in the stomach or middle ear sinuses. The epidermis was smooth with no scratches or scars, to be expected of newborns. At least ten still retained several centimeters of umbilical epidermal sheath, much too delicate a tissue to remain attached for more than several days after birth. Teeth were well beneath the gum line (see head profile in Fig. 21[A], p. 80).

Three calves tentatively classed as yearlings are now considered. Mean length was 216 cm (209 - 225), mean maximum girth 148.3 cm (143 - 156) and mean weight 187.8 kg (163.8 - 232). Two narrow layers were found in the teeth of two animals, but teeth of the third were not examined. Teeth had not erupted in any of the three. It should be stated here that all animals except the foetuses and newborn

78

FIGURE 21

Figure 21 illustrates the change in head profile with age.

(A) is a newborn calf, slate gray in colour (appears lighter in this photograph). Ear opening is indicated by the arrow.

(B) is a calf considered to be a yearling. Colour is gray with the "melon" becoming apparent in the forehead. Some epidermal mottling is shown due to loss of surface lipids.

(C) is a typical adult head profile. The melon is quite apparent and body colour is completely white.
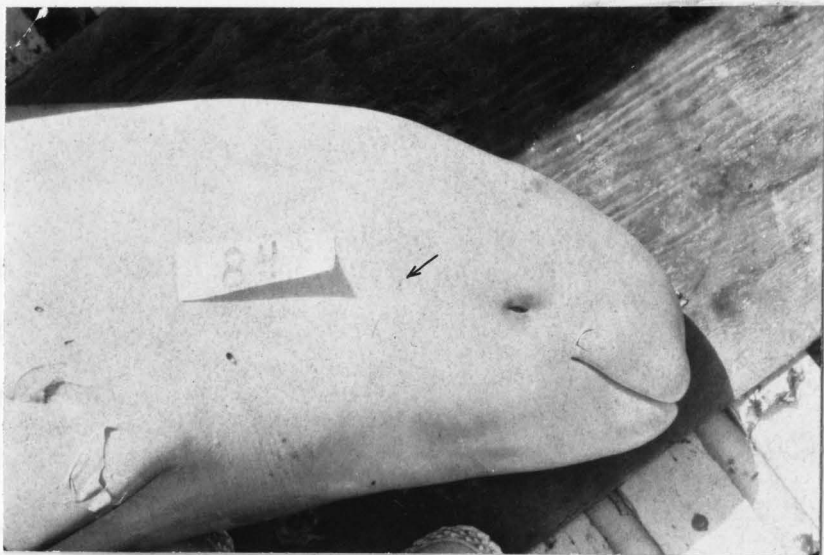
carried middle ear parasites (see p. 97), and all except foetuses and newborn had body scratches, both fresh and healed, including circular marks (see p.79 and Fig.21 for illustration of head profile). These larger calves had therefore been exposed to the environment for longer than several days. The above data are now considered critical in estimation of annual growth increments since the first year is no doubt the period of most rapid relative growth setting upper limits for following annual increments, all decreasing relatively. Though full-term foetuses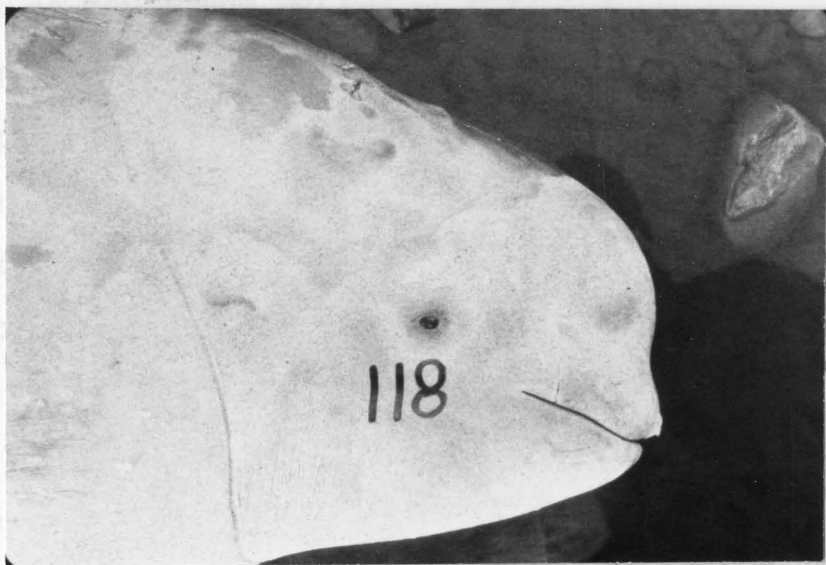 and new-born calves could be classed as one, their sizes being simi-lar, foetuses are excluded during the following comparisons.

From means of the newborn and older calves, length in-crease was 56.4 cm (35.3%), maximum girth increase was 40 cm (37%), with a weight gain of 109.5 kg (140%). These diff-erences, when coupled with the reproductive status of one accompanying adult female (see p.70 on "Lactation") and with the body scars and parasites previously mentioned, is evid-ence that the three animals described above are indeed year-lings. Since the birth period has been fixed as late July - mid August (p. 66) and sampling is carried out in this per-iod, the larger calves are doubtless 12 months old. Note also the difference in head profiles, Fig. 21A and B.

The next group considered is composed of three animals with four narrow dentine layers present (3 or 4 cement lay-ers), with a mean length of 250 cm (248 - 252 cm), mean max-imum girth of two animals of 167.5 cm (167 - 168 cm) and

weight of a single animal at 168 kg. The length and girth measurements are similar in all three, and therefore the weight is representative of all three. If these are two-year-old calves, the annual gains are 34 cm in length (15.8%), 19.2 cm in maximum girth (11.5%) and a weight gain of 79 kg (42.1%). One animal had four teeth just beginning to pierce the upper and lower gums, another had several just piercing the upper gum, while the third showed no teeth yet erupted.

The narrow range of lengths and weights for yearlings and older calves contrasts with the extreme range of lengths and weights shown for newborns. An explanation for this is that newborn calves display rapid growth immediately after birth. The increase in the subcutaneous fat layer as a thermal insulator would, no doubt, be one of the advantages of such rapid growth in a sea mammal (Bryden, 1968 and 1969; Sergeant and Brodie, 1969a). If the lengths and weights of calves captured early and late in the sampling period are compared, a difference is suggested though not a significant one due to sample size. Eleven calves captured July 28 to August 11 were of mean length 157.1 cm (SD = 7.19) and mean weight 69.5 kg (SD = 11.3), while five of those captured during August 16 to 27 were of mean length 167.8 cm (SD = 7.194) and mean weight 93.2 kg (SD = 16.00).

Another factor to be considered is that calves born early in the season may have had a shorter gestation period, yet are able to gain in length and weight so that they are similar in size to those retained as foetuses late into the

82

calving season.

It is of interest to note that newborn calves of three females identified as primiparous were of mean length 151 cm (143 - 162) and mean weight 61 kg (57 - 68.3), while newborn calves of three females considered multiparous were of mean length 160 cm (150 - 170) and mean weight 90 kg (82 - 99). The first three were captured July 28 to August 8 and the last three, August 9 to August 27.

Though speculative, it is possible that the range in body size of recently born calves decreases toward the end of the calving season in Cumberland Sound with a resultant increased uniformity of size after one year.

Differences become obscure for want of comprehensive data on 13 calves larger than those described above. Loss of ageing material from several and lack of accurate weights for all, renders conclusions difficult. In these 13 calves teeth were in the early stages of eruption with between 2-4 mm of the tip penetrating the gum and, in several instances, worn slightly. Tooth layers of nine animals ranged between 6 and 8 narrow layers. Mean length was 277.9 cm (258 - 298 cm SD = 15.16) and mean maximum girth of five animals was 179.6 cm (162 - 190, SD = 10.07). Using the formula: $[\log$ weight (kg) $= 2.605$ X $\log$ length (cm) $- 3.807]$ (see Sergeant and Brodie, 1969a), the weight range would be 298 kg to 434 kg. A weight range of 136 kg suggests that this group may be composed of more than one age class, probably two, considering the variation in numbers of tooth layers.

Kleinenberg et al. (1964) grouped all calves up to 280 cm as younger than 4-5 months old. The phenomenal weight gain implied (i.e. as high as 500%) for a small, arctic odontocete is not reasonable and would place impossible demands on the nursing mother (weighing about 650-1150 kg) when one considers the efficiency of conversion of milk. This gain would be made on milk only, since these authors assume a 4-5 month lactation period. Tomilin (1957) quotes length gains between year classes as 62-110 cm during the first year, 22-102 cm during the second and 23-103.5 cm during the third and subsequent years. Such ranges of length gains would certainly include two and even three year classes.

To illustrate the error in using colour phases, resulting in the clumping of separate year classes, I refer to Tomilin's description of the colour groupings used by various authors for beluga.

Group I includes sucklings younger than one year (140 - 280 cm) still toothless, of slate blue or dark blue colour.

Group II is composed of "gray" yearlings (250 - 390 cm), coloured pale to bluish-gray. Teeth are present yet they still follow the adult female.

Group III "blue" two year old individuals (270 - 470 cm), coloured pale-gray-bluish.

Group IV adult animals of pure white hue aged three years and older, all sexually mature (320 - 600 cm).

I agree with the length ranges shown within each colour group, but I do not consider that these groups are a valid

84

method of age classification.

I conclude that beluga under 300 cm are composed of newborns and probably four age classes.

Weaning and Tooth Eruption.

The number of teeth erupting and their increased exposure with age, is discussed under "Calf Growth Rates" (p.77). Tooth eruption begins late in the second year (three to four tooth layers), with one case recorded of eruption after three years. Teeth may erupt first in either jaw with partial eruption in both jaws by the third year.

Milk is, no doubt, the mainstay for the first year, supplemented with captured food during the second. As discussed under "Lactation" (p. 70), the calf must be completely weaned at 24-26 months since lactation appears to cease during the mid-stages of the following pregnancy. First evidence of weaning was found in the stomach of one 209 cm yearling (teeth unexposed) which had one squid beak, pieces of worm case and several 1-2 cm stones.

If the teeth function in grasping prey species the calves must compensate for lack of them during their second and third years. Suction should be considered as a possible feeding method (see also Ray, 1966). The rather indiscriminate contents of the above yearling may be a result of such a feeding method. However, fish bones, otoliths, crustacean parts and squid beaks were present in the stomachs of two and three year old calves with only a few teeth piercing the

85

gum. Along with suction as a possible method, these calves
may have been assisted by adults intentionally or unintent-
ionally killing and leaving whole or fragments of agile prey
for the calves to pick up. Kin co-operation is implied if
this behaviour were intentional (Brodie, 1969b). The nar-
whal, Monodon monoceros has a similar mouth structure with
no functional teeth through life, yet successfully feeds on
cephalopods and fish (Tomilin, 1957). This is more reason
to consider suction as a means of feeding by toothless beluga
calves.

It is of interest to note that Sergeant (1959) found
the widest layer of dentine to be deposited in the first
year of Tursiops truncatus, the bottlenose dolphin (he con-
cludes single annual layering for this species).

This is just the opposite of D. leucas where layer
width increases to middle age (see p.16 and Figs. 6 and 8).
The long pincer-like jaws of T. truncatus differ from the
blunt, thick-lipped D. leucas. As mentioned previously, the
latter species may use suction as a feeding aid while T.
truncatus requires rows of many sharp interdigitating teeth
to grasp prey. (Winge 1942; Sergeant, unpub.).

McBride and Kritzler (1951) state that teeth arise
through gum prominences of T. truncatus by the time the calf
is six weeks old. My findings are that teeth of D. leucas
do not appear until late in the second year (see also
Dergerbøl and Neilsen, 1930) and may be retarded well into
three years. Beluga tooth size at birth is a maximum of

86

14 mm, and 18 mm at one year, yet the teeth of the much
smaller dolphin (about 11.5 kg at birth contrasted with a
79 kg beluga newborn) are about 17 mm in length at six months
(Sergeant, 1959).

There is obvious advantage for the teeth of pincer-jaw
animals to be well developed before weaning. This may be
the reason for the rapid early growth contrasted with that
of belugas, if suction is considered as a possible feeding
mechanism.

Vladykov (1944) states that beluga males become sexually mature at lengths exceeding 350 cm and not before 4 years of age. Dorofeev and Klumov (1936) used colour phases and stated that maturity begins at 2-3 years at lengths 270-470 cm. Kleinenberg et al. (1964) conclude that males are sexually mature usually between 380-450 cm at an age of 2-3 years. Sergeant (1962a) considers there is little difference in age at sexual maturity of males and females; however he cautions that growth rates may be slower than those claimed by Soviet authors.

Figure 22 shows volumes of single testes plotted against body length. Volumes were estimated from measurements in three planes, at mid-length, considering the testes to be cylindrical with hemispherical ends. An abrupt increase in volume is indicated after 381 cm. This increase is not coincident with body increase, being at approximately 90% of the length at physical maturity (see p. 35). The abruptness is also demonstrated by the paucity of intermediate volumes (see also Sergeant, 1962b, and Best,1969).

Spermatozoa were not present in the testes of less than 130 cc in volume and Fig. 23 shows the immature state of the tubules. Spermatozoa were present however, in all testes examined over 360 cc in volume. Figure 23[D] shows the open lumen of such testes with some meiotic activity and spermatozoa present, though not in large numbers. Some spermat-

ozoa were present in the epididymis, although in such small quantities that the season of sampling does not appear to be a period of intensive sperm production. Best (1969) studying P. catodon, concludes that sperm density does not increase significantly during the female breeding season and suggests that increased androgen via leydig cell enlargement may produce the sexual and social changes of breeding males.

The apparent segregation of the herd within the fiord during the calving-sampling period suggest that this is not a period of sexual activity while the complete absence of any very small foetuses resulting from possible July-August matings is again further evidence that there is no productive sexual activity (see p. 62).

The youngest male to show greatly increased testes volume and spermatogenic activity had 14 dentine layers in its slightly worn teeth, indicating sexual maturity after 14 layers (assuming 2 layers per year, after seven years). With female sexual maturity after four years (p. 45) there would be approximately a two to one ratio of mature females to males, indicative of a polygynous species (see also Sergeant, 1962a; Kleinenberg et al., 1964).

The sex ratio of newborn calves does not differ significantly from parity (12 male, 11 female) but the adult sex ratio remains undetermined.
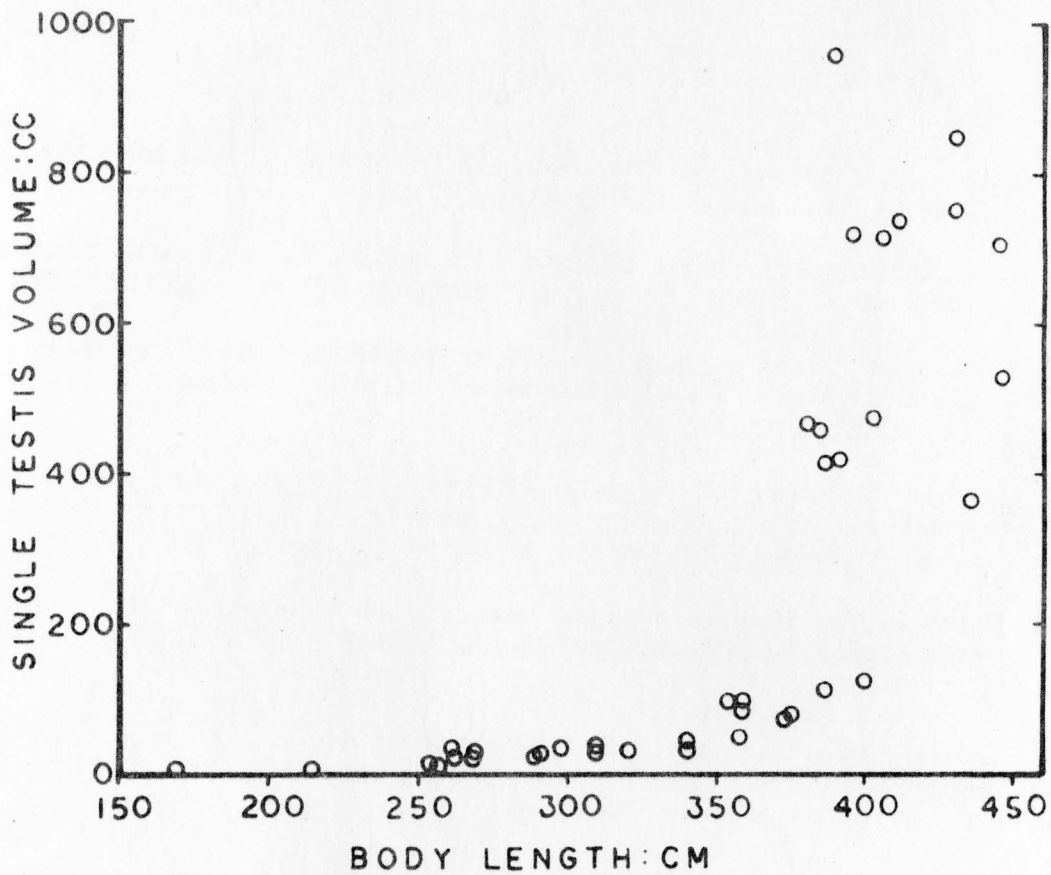
Figure 22 is a plot of calculated single testes
volume against body length. The abrupt increase
in volume indicates sexual maturity, with sperm
production found only in testes in excess of 360 cc.

FIGURE 23

Figure 23 shows photomicrographs of immature and mature testes and epididymis sections.

(A) Testis tubules of a beluga (15 tooth layers and single testis volume 149 cc) at approximately 800 magnification.

(B) A single testis tubule of the section shown in (A). Sloughed cells are shown compacted in the lumen. Magnification approximately 1600.

(C) Testis tubules of a male (21 tooth layers and single testis volume 513 cc) at approximately 200 magnification. The lumens are not compacted with cells as in the above.

(D) Lumen of a single testis tubule at approximately 1600 magnification. Spermatozoa are present among the sloughed cells.

(E) Epididymal tubule of testis shown in (C) at approximately 800 magnification. Small numbers of spermatozoa were present in some of the tubules.
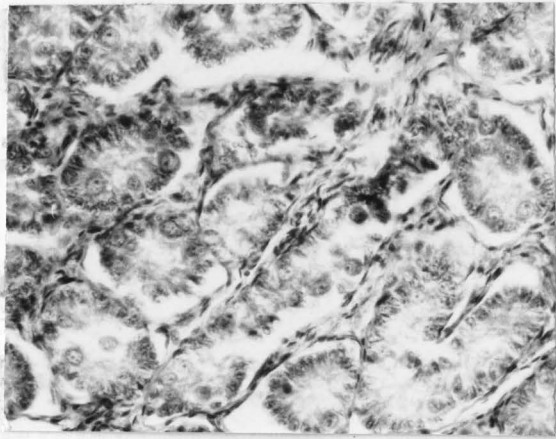
A
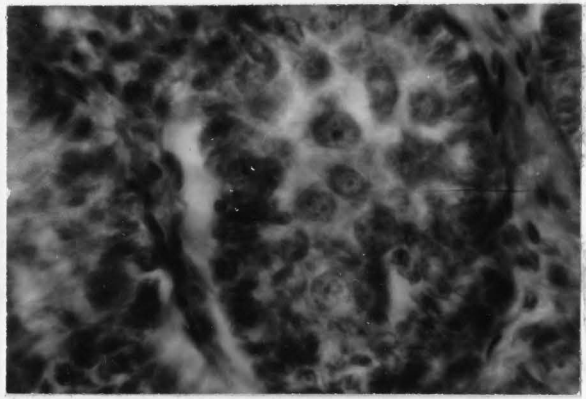
B
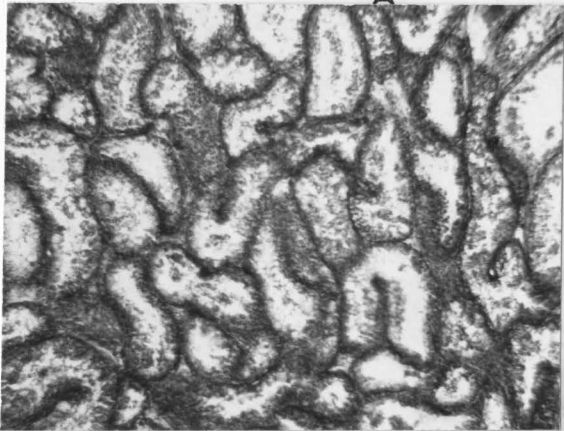
C
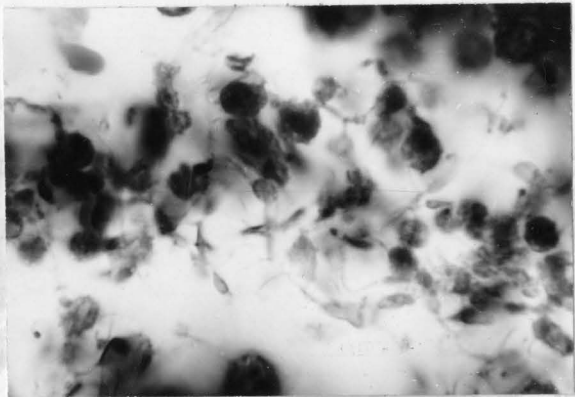
D
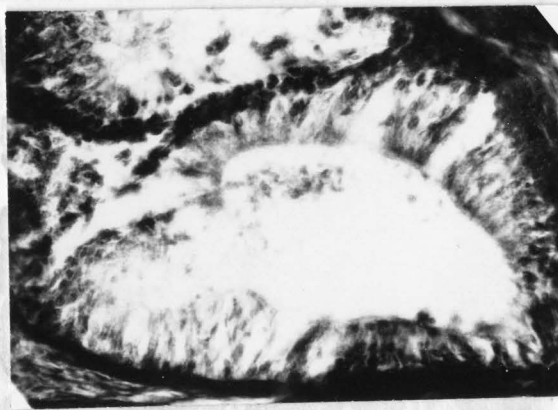
E

NUTRITION

Food and Feeding.

It became apparent early in the field work that beluga of Cumberland Sound do not feed intensively during their stay in Clearwater Fiord (see also Kumlien, 1879). Regurgitation of stomach contents during pursuit was not noted nor was it observed of live, enmeshed animals. If fright causes regurgitation (Vladykov, 1946) then the mass herding of several hundred animals during tagging programmes should have yielded, to say the least, spectacular evidence (which it did not). Moreover, the Eskimo hunters do not mention regurgitation during pursuit (probably the best evidence).

The reason for the summer presence of beluga in river estuaries is discussed by Sergeant and Brodie (1969a) and is considered more of a thermal rather than a nutritive advantage, therefore I suggest that for a major portion of the time of Vladykov's sampling, feeding may not have been intensive.

Table I shows the diversity of food species and number of times remnants were found. These apply only to the first 69 animals, whose stomach contents were preserved and later examined. The stomachs of all later specimens were examined in the field, though not preserved.

Vladykov (1946), Kleinenberg et al. (1964) provide more comprehensive analysis of stomach contents.

No quantitative analysis can be made of Cumberland Sound beluga feeding. Qualitatively, diversity of food

93

TABLE I

STOMACH CONTENTS OF 69 BELUGA

Food Species	Number of Specimens	Times in Stomach
ARTHROPODA		
Crustacea		
Decapoda		
Pagurus sp.	1	1
Sabinea septemcarinata	3	3
Sclerocrangon boreas	2	2
Spirontocaris sp.	4	2
Idoteidae (unidentified)	3	2
Anonyx nugax	150-200	4
Caprellidae (unidentified)	1	1
MOLLUSCA		
Pelecypoda		
Teleodesmacea		
Saxicava arctica	1	1
Astarte borealis	1	1
Archaeogastropoda		
Margarites sp.	8	2
Stenoglossa		
Buccinum undatum	1	1
Prionodesmacea		
Musculus sp.	2	2
Cephalopoda		
Decapoda		
Gonatus fabricii	200-300	26
(beaks only)		
ANNULATA		
Chaetopoda		
Polychaeta		
Cistenides sp.	1	1
Sabellidae (unidentified)	5	5
CHORDATA		
Ascidiacea		
Ptychobranchia		
Molgula sp.	8	5
Actinopterygii		
Teleostei		
Gadus ogac		25
Boreogadus sp.		

94

species from this sample indicates the broad food web of
D. leucas, no doubt of selective advantage, considering
productivity of arctic waters (Sergeant and Brodie, 1969a).

Fat Thickness.

The greatest variation in fat thickness of Cumberland
Sound beluga appears among the sexually mature females (see
Sergeant and Brodie, 1969a). Mature females with thin, fat
layers were found to have been nursing for one or two years,
while extremely fat animals were in full term pregnancy or
recently parturient. Males of Cumberland Sound tend to vary
little in relative fat thickness (Sergeant and Brodie, 1969a)
and we assume that the great variation in girths and weights
among separate beluga populations is due mainly to fat thick-
ness relative to their length.

Fat thickness, as insulation should decrease with in-
crease in body volume, if that is its sole function. This
is not the case, therefore this unnecessary thermal insulat-
ion may be more of a nutrient store with its variation among
populations an indication of increased selection for animals
with ability to withstand more extensive migrations or isol-
ation in a small opening of frozen sea for extended periods
(Freeman, 1968; Kleinenberg et al., 1964). The excessive
fatness of recent post-partum females could be considered as
a homeostatic mechanism for both the adult and her calf since
the calf is dependent on her for nutrition. Excessive mean-
ing thickness beyond that required as insulation and as a
food source for the calf.

Origin of Body Scratches and Large Scars.

The majority of large scars (as long as one meter) were on the back, the area exposed to the water surface during respiration. Large, fresh wounds in the same areas usually yielded fragments of bullets commonly used in the region (.222 and .243 caliber). Having hunted beluga with the local people I do not hesitate in attributing most large scars to hunting injuries. There are several that could be credited to attack by killer whales Orcinus orca; the local hunters speak of such attacks.

The long parallel scratches on the epidermis of all but newborn animals, most notably the young males, are considered by the Eskimos to be the result of polar bear attacks and clawing by seals. My first impression was that most origin-ated from intraspecific conflict, however the position of scratches on the sides and back indicate they could not have resulted from biting, therefore, explanations by the Eskimos must be considered (I have a high regard for the behavioural-anatomical knowledge of the Eskimo people). The documented occurrences of beluga trapped for several months in small open water areas of sea ice (Freeman, 1969) and reports of polar bear attacks on whales trapped in this manner (Kleinenberg et al., 1964) support Eskimo views.

The "playfulness" described by many authors in writing about odontocetes, and their curiosity, adds weight to the

possibility of scratches originating from encounters with seals. Scheffer (1969) illustrates similar scratches on the skin of the killer whale O. orca and credits these to intraspecific conflict. The majority of scratches on beluga seem most easily credited to harrassment of seals, especially by the young males.

Parasites.

No external macro-parasites or commensals were found, though all beluga other than newborns carried nematodes in middle ear sinuses and attached to the stomach wall. Small numbers of genus Anisakis were found in the stomachs. The middle ear sinus of older beluga always carried parasites of family Crassicaudidae with smaller numbers in younger animals and none visible in newborns.

Two older, sexually mature males were found to have large cysts on the end of the testes which, when sectioned, contained single female Crassicaudids approximately 10 cm in length (see Fig. 24).

Species of the family Crassicaudidae are known to be parasitic in the urogenital system of cetacea but rarely in other body systems (Yamaguti, 1961).

Kleinenberg et al. (1964) describe the parasites of D. leucas in detail (see also Skrjabin and Andreewa, 1934).

FIGURE 24

Figure 24 shows one of two cysts found in the testes of
two sexually mature males (magnification approximately
1.25). A single female Crassicauda was found within the
collapsed membranous sac depicted here as being extracted
from the cyst cavity.

As stated in ... ...urity, the herd appears to be ... ...er fiord during late July to ... ... some segregation of males ... ... Kiellen (1879) mentions that ... ... the herd to be segregated in two ... ...atang their view with no explan...

The females ab... ... ...cently calved, remain separated fr... ... ...ing close to the shore or in ass... ... ...s rather obvious judging from the animals captured and from field observations.

Reasons for segregation could be to protect the calf from physical injury within a large ... ... herd of adults, or to avoid exposing the calf to ... ... wave height and difficulties in respiration. ... ... and calf rejoin the main herd by mid-September. Temperatures in the fiord range between 5 - 9.5° C at ... ... depth with a usual reading at 7.5 - 8°C during the ... periods of the tide (August reading).

The calving area of ... River in Hudson Bay indicates ...alf-water temperatures of ... ... being consistent even during ... tides (see Sergeant and Brodie, 1969a).

Quoting from Kleinenberg et al. (1964); "....there are family groups in the herd which consist of an adult female and her young of different ages", and, "....we repeatedly

99

100

BEHAVIOUR

As stated in the section on male sexual maturity, the herd appears to be fully represented in Clearwater Fiord during late July to mid-September, yet there is some segregation of males and females within the fiord. Kumlien (1879) mentions that the Eskimo hunters believed the herd to be segregated in this same fiord, though he dismisses their view with no explanation for doing so.

The females about to calve or which have recently calved, remain separated from the main herd, and move along close to the shore or in smaller, sheltered bays. This is rather obvious judging from the animals captured and from field observations.

Reasons for segregation could be to protect the calf from physical injury within a large milling herd of adults, or to avoid exposing the calf to excessive wave height and difficulties in respiration. Both mother and calf rejoin the main herd by mid-September. Temperatures in the fiord range between 5 - 9.5° C at half-meter depth with a usual reading at 7.5 - 8°C during the calmer periods of the tide (August reading).

The calving area of Seal River in Hudson Bay indicates half-meter temperatures of 12°C, being consistent even during the tides (see Sergeant and Brodie, 1969a).

Quoting from Kleinenberg et al. (1964); "....there are family groups in the herd which consist of an adult female and her young of different ages", and, "....we repeatedly

100

observed a female with her suckling together with another

adult beluga, which was sometimes larger than the female.

As the beluga become fertilized soon after giving birth ...

it may be assumed that the other beluga was a male."

Having observed similar behaviour while studying div-

ing patterns, I agree with all but their final statement.

It is common to see a female with a newborn immediately be-

side her and with one, sometimes two, larger, non-white bel-

uga accompanying them. These larger beluga may be near the

size of the mother. This could be an extended family of

two completed reproductive cycles. Such a group may be of

selective advantage in feeding. Kin-cooperation is again

implied as it was in the chapter on "Weaning and Tooth Erupt-

ion" (see also Brodie, 1969b).

It is because Kleinenberg and his co-authors maintain

there is impregnation immediately after birth that they as-

sume a large animal accompanying a post-partum female to be

a breeding male. Also, their observations were made from a

moving aircraft while mine were made from the surrounding

cliffs. I would interpret their last observation as a rec-

ently calved female and newborn accompanied by a large im-

mature female, possibly her offspring. Considering the size

difference of male and female beluga and their age and col-

our at sexual maturity (see pp. 31 and 88) I would have ex-

pected the former authors to state that the accompanying

animal was invariably larger than the female and white in

colour: they do not.

In several instances, large immature female beluga were captured in the same nets with post-partum females. Epimeletic behaviour could be considered here along with the more acceptable theory of kin-cooperation (Hirsch, 1967; see also reviews by Caldwell and Caldwell, 1966; Evans and Bastian, 1969).

The Cumberland Sound beluga do not have a breeding period during the calving season, therefore all larger beluga observed to be accompanying nursing mothers are considered to be immature and possibly siblings.

Herding and Tagging.

In a recent paper (Sergeant and Brodie, 1969b) we describe tagging beluga in the Hudson Bay region. Over a three year period (1967-1969) approximately 1700 beluga were tagged using the dart or harpoon tag shown in Fig. 25. The Seal River, 35 miles north of Churchill, Manitoba, proved ideal for herding large numbers of beluga into shallow estuaries using as few as 5-6 canoes.

Less successful tagging programmes were attempted in the MacKenzie River Delta region and in Cumberland Sound, the difference in tagging success seemed to be related to the depth of water. The Seal River population could be driven into 2-3 meters of water where escape by diving under the canoes was reduced. The Cumberland Sound beluga when herded in Clearwater Fiord could easily dive and escape due to the depth.

In an attempt to prevent these animals from escaping, sounds of the killer whale _Orcinus_ _orca_ were transmitted underwater. Three battery powered amplifiers transmitted tape recorded sounds through submersible speakers (see Fig. 25ᴬ). The transmitters were made of relatively inexpensive components costing $75 per complete unit and weighing 7.5 kg. Four, small $7.00 transceivers (walki-talkies) were used to coordinate the herding.

The beluga did react to the sounds but whether they

103

recognized them as _Orcinus orca_ is questionable. Any under-
water noise had the same effect eg. the sound of the out-
board motors and rifles fired into the water caused a simil-
ar reaction.

Once herded into the river estuary of Clearwater Fiord
(see Fig. 2) the animals could not be forced to move up-
stream into the flood plain where they could be stranded at
low tide. This was once the practice of whalers and Eskimos
in the area.

The recent failures in attempts to force herds into this
area puzzled the Eskimos. The only conclusion I can draw is
that the flood plain has changed over the last few years
increasing the size of the silt deposit at the river mouth
(see Fig. 2) and over which the beluga will not pass.
Another reason may be change in reaction to herding. Beluga
of Cumberland Sound take advantage of the water depth and
escape by diving, a behaviour of great selective value con-
sidering the hundreds of animals once slaughtered by organ-
ized herding and stranding in this region. Kleinenberg _et al._
(1964) speak of the rapid adjustments made by beluga to hunt-
ing pressure, either by refusing to be driven or by avoiding
the area of hunting altogether.

To date, tag returns from the Seal River project have
shown the movements to be along the west coast of Hudson Bay
with indications that the small-bodied Hudson Bay animals
are an indigenous population (Sergeant and Brodie, 1969a,
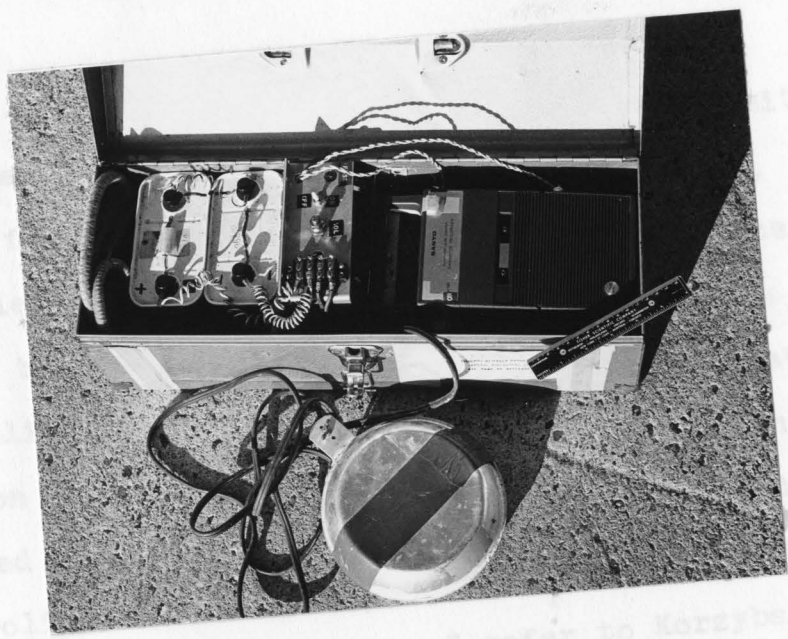1969b). Tag returns depend on the number of beluga taken

104

FIGURE 25

Figure 25 shows herding and tagging equipment.

(A) The killer whale transmitter shown with the submersible speaker which fits below the tape deck during transport. The scale is 15 cm in length.

(B) The harpoon tag (16.5 cm in total length) with labeled plastic streamer and inert metal head. Approximately 1700 of these were attached to beluga.

fishery.

(a)

A

I refer to Korzybert et al.

1964) and have a long life. (1967) for a review of the origin, nature and properties of tetracycline.

bone tracers for

1963: Linhart

During the

Bay, 93 beluga

of Tetracycline

The intention was

the range was n

smaller dosages

to having one of

animals and part

into two or mor

hydraulic pressu

not be held for the full injection. All injections were

B

106 107

commercially and this fluctuates yearly due to the sporadic
fishery.

(a) Tetracycline Injections.

Tetracycline has the property of combining with calcium
(chelate formation) when injected into organisms. Under
ultraviolet light, energy in the form of fluorescence is
released by this formation. Its other properties are that
tetracycline combines with calcium almost immediately upon
injection and that it is taken up more readily in areas of
increased bone growth activity. Most important is that
tetracyclines are readily tolerated antibiotics (Eger et al.,
1964) and have a long life. I refer to Korzybski et al.
(1967) for a review of the origin, nature and properties of
tetracycline. Tetracyclines have been used successfully as
bone tracers for age determination of carnivores (Yagi et al.,
1963; Linhart and Kennelly, 1967).

During the 1968 herding and tagging of beluga in Hudson
Bay, 93 beluga were stranded and given intramuscular injections
of Tetracycline Hcl, dosages based on body-size estimates.
The intention was to inject 25 mg per kg body weight; however
the range was no doubt 15-25 mg per kg body weight. The
smaller dosages were injected in the larger animals due partly
to having one of two syringes broken during capture of the
animals and partly the fact that large dosages must be injected
into two or more points on the back muscle to reduce the
hydraulic pressure of the injection. Larger animals could
not be held for the full injection. All injections were

intramuscular rather than intravenous, the former considered less dangerous to the animal. Injections were in the least mobile part of the body in a highly muscularized region, in this case, the back muscle dorsal to the flippers. This was done since the injections can be extremely painful in a flexible region.

To date, no injected animals have been returned by hunters.

Population Estimates Based on Aerial Survey.

Judging from the reports of Eskimo hunters and from my four years of travel in Cumberland Sound, all or almost all beluga occur in Clearwater Fiord during late July to mid-September. Both sexes and all age groups are represented.

Prior to the aerial count, observations on diving behaviour were made from the surrounding cliffs. Single and grouped animals were watched with binoculars and their diving patterns timed with a stop watch. An average diving sequence consisted of 5.5 shallow dives during which time the animals were constantly visible from the air. The shallow dives were followed by a single dive of greater duration and depth, when the animals were invisible. The mean duration of the whole sequence was 122 seconds, during 87 of which the whale was visible.

A light aircraft was chartered from Frobisher Bay on August 30, 1967 and a count of Clearwater Fiord beluga yielded 476 and 455 animals on two consecutive counts. Two adjustments must be made to the mean figure of 465.

(1) Animals below visible range, are previously calculated relative to visible numbers as 35/87 or .40, thus: 465 + (465 X .40) = 652.

(2) Due to the small size and dark colouration of the newborn and year old calves, it is assumed that the majority of these were excluded, only the larger and lighter coloured

animals being included. Using 10% as the number of newborns present and (considering first year mortality) 8% as the number of yearlings present: 652 + (652 X .18) = 769, the population in late August, 1967.

The diving pattern used to calculate the number invisible was derived from a population that was not considered to be feeding intensively, and was milling about in random fashion. It is questionable whether this correction factor could be applied to a migratory herd.

A surface count would have a majority of animals invisible since respiration and back exposure time is approximately 3 seconds in duration.

Non-Commercial Hunting Mortality.

The number of beluga killed by Eskimo hunters in the more remote camps of Cumberland Sound is not definite. Having lived in several of these camps during the migration of beluga past them, I estimate several animals are taken by each camp of hunters each season. Camps closer to the calving area at the head of the Sound would probably take more animals, since beluga remain there for 8-10 weeks. Approximately ten camps existed in Cumberland Sound, seven of these near the migratory path of beluga. In the camps, any large hunted beluga are obvious on the beach or moored to a rock in the tidal zone. On occasion, hunted newborn beluga had been noticed in the bottom of freighter canoes or whaleboats, or dragged up on the beach. These calves are not large

110

enough to be conspicuous and may represent a rather signif-
icant factor of calf mortality. For example, three newborn
beluga were found in one whaleboat and were taken by a hunt-
er with a rifle while proceeding up Clearwater Fiord (prob-
ably 1-2 hours duration). The taking of newborns is made
easy once the calf is separated from its mother, losing the
apparent assistance of echelon swimming formation, and be-
coming disoriented.

In addition to the sporadic commercial hunting of beluga,
this annual killing by hunters should be considered. A very
conservative estimate would be forty adults and calves taken
in this manner. The camps are now being abandoned with con-
sequent reduction of this mortality, quite significant when
considering the small size of the population.

Estimation of Earlier Population Size.

The calculations resulting from the aerial census ind-
icate that the population must have been greatly reduced in
recent years, when it is considered that, until the early
1960s, this population was exploited commercially.

Sergeant (1962a) tabulated the annual catches for the
commercial fishery in Cumberland Sound, calculating the
number of individuals captured, from the oil yield (using the
Churchill, Manitoba, plant mean yield of 30 gallons per
beluga). Because of the larger size of Cumberland Sound
beluga (Sergeant and Brodie, 1969a), 40 gallons may be a
closer estimate of mean yield. This would reduce Sergeant's

111

estimated mean annual catch between years 1948 to 1960 from
163 to 134 animals. To this figure must be added the conser-
vative estimate of 40 animals taken non-commercially (see
p. 110). If all natural mortality is considered (no doubt
being greatest in calves) an annual herd production of 8%
can be used as an estimate to back-calculate earlier populat-
ion size from the 1967 census (see Table II, p. 113). The
population estimated to exist in 1960, after the summer's
calculated catch of 194 animals is about 700 beluga. This
was the year of the cessation of commercial hunting. Follow-
ing this procedure to 1948 (the first year of recorded oil
yield, Sergeant, 1962a), it is calculated that, prior to the
summer's catch, the population must have been of the order
of 1750 animals. The estimated mean kill of 174 animals
(see also Doan and Douglas, 1953) from commercial and non-
commercial hunting was apparently greater than the annual
herd production between 1948 and 1960. The hunting pressure
would have an increasing effect as herd size diminished. It
is also assumed here that the herd remained intact, that is,
that all remaining animals returned to Clearwater Fiord each
year.

There are admittedly, many assumptions in the above
calculations. However these are justified, in part, by
Soper (1928) who writes of the commercial hunting in upper
Cumberland Sound (Issortukdjuak Fiord, now called Clearwater
Fiord). In 1923, about 600 were killed by herding and
stranding. In early July, 1924, about 800 were killed by

112

TABLE II

Back-calculation to estimate earlier population size.
The population censused in 1967 is shown in brackets.
The arrow indicates the direction of back-calculation.

Year	Before Kill Plus Births	Commercial Kill	Non-Commercial Kill	Fall Population
1947	-	-	-	1617
1948	1746	80	40	1626
1949	1756	128	40	1588
1950	1715	65	40	1610
1951	1739	219	40	1480
1952	1598	156	40	1402
1953	1515	160	40	1315
1954	1420	140	40	1240
1955	1339	194	40	1105
1956	1193	125	40	1028
1957	1111	104	40	967
1958	1044	63	40	941
1959	1016	153	40	823
1960	889	155	40	694
1961	750	-	40	709
1962	766	-	40	726
1963	784	-	40	744
1964	804	-	40	764
1965	825	-	40	785
1966	848	-	80 ←	768
1967	829 ←	-	60 ←	(769)

113

the same method. On July 29, 1924, "large numbers" of
beluga were observed in Clearwater Fiord and in the summer
of 1925, "large numbers" of white whales were killed for
commercial use. If his kill estimates are accurate, the
population must have been quite large to have 800 and 600
taken in two summers, plus a large (but unknown) kill two
years later. It must also be assumed that there was a non-
commercial kill by the many active camps of that period.

The conclusions here are that the initially large bel-
uga population of the early 1920s was rapidly reduced by mass
strandings, remnants of this herd being more slowly reduced
by the smaller commercial fishery of the 1940s and 1950s
(hunting pressure in the 1930s is unknown). By the 1960s,
the herd had been reduced to such a size that non-commercial
hunting and natural mortality have accounted for much of the
herd increase. This also indicates that production is not
high (see p.118 for further discussion).

DISCUSSION

Comparison of Studies.

Many points have been covered in this thesis, no doubt some of academic interest, rather than of practical value. These can be omitted here and left to the summary.

The object of this study has been to carry out a rather intensive analysis of a small sample in order to find those aspects where variability and misinterpretation can lead to gross error when making generalizations. Though I consider the observations documented by Kleinenberg et al. (1964) as accurate, I disagree with many of their interpretations. Most of my findings have been contrasted to those of the above authors, since theirs are the most comprehensive studies published on the species Delphinapterus leucas and the only ones which come to decided conclusions.

Some disagreement is no doubt the result of size variations between populations (Sergeant and Brodie, 1969a), while another source may be temporal differences of activities among populations due to variations in climate and ice conditions in the circumpolar regions of the arctic (i.e: breeding and calving periods).

The disagreement about reproductive potential is due to differences in interpretation and it would seem more practical to list the more critical aspects covered by the Soviet authors while referring to my own findings:

(1) They have grouped three and possibly four separate year classes along with the newborns. This has the obvious effects of underestimating ages of adults and of implying prodigious growth rates of calves (see "Early Development", p. 77).

(2) They considered large corpora as representing previous pregnancies. No consideration was given of multiple ovulation or accessory corpora as additional sources (see pp. 49 and 56).

(3) When accessory corpora were found, they interpreted them as representing a corpus from a very recent birth plus a corpus of an early pregnancy. This conclusion supports their theory of 11.5 - 12 months gestation, and annual reproductive cycles. I found that these double corpora were from one pregnancy only, with no evidence of post-partum pregnancies (p. 62).

(4) They argue that "the sharp decrease in the numbers of females with five or more scars apparently indicates intensive elimination of the older age groups". While accounting for corpora number variation among animals of similar ages, I found that few represented pregnancies, most resulting from unfertilized ovulations and accessory corpora. My conclusion is that corpora scars are no real indication of production and that an older animal with several well spaced (temporally) scars could have been much more productive than a younger animal with many corpora (most being of ovulation only). There is some stability of the reproductive cycle

116

among older females, such as better coordination of ovulations with mating activity and possibly a selection for larger, older females by the males. This results in increased rate of pregnancy per ovulation.

(5) They interpret observations of larger beluga accompanying post-partum females as evidence of post-partum breeding, correlating this with the accessory corpus. I interpret these groups as consisting of a post-partum beluga adult accompanied by an older calf, possibly a sibling of the newborn.

(6) Having found milk present in the stomachs of beluga calves of 280 cm, they conclude that these are 4-5 months old, since they believe lactation only lasts 4-5 months. These calves are approximately 3 years old (see p.83).

(7) To account for the non-pregnant, sexually mature females they postulate a 4-5 year series of annual pregnancies, gradually going out of phase with their proposed post-partum breeding season (since they consider there is a 2-4 week lag in impregnation after birth). There is then a one year "resting period" since they missed being impregnated.

I would interpret these non-pregnant animals as ones which have calved 1-2 years previously, and are nursing an older calf.

Their arguments become circular since they have based all their analyses on the false premise that the reproductive cycle is annual. A three year reproductive cycle such

as assumed in this thesis, explains the facts much more economically, and without contradictions.

Productivity.

Kleinenberg et al. (1964) are rather vague in their estimations of the age at female sexual maturity, their more consistent reference being that females over three years old are sexually mature, rarely at two years. They consider that births are annual over 4-5 year cycles with a one year break in production (see p. 75).

My conclusions are that the majority of females are sexually mature at five years and as early as four. The reproductive cycle is considered to be one calf every three years (see p. 75).

A simple comparison of potential rate of increase can be made if no mortality or density dependence is assumed. Multiple births are extremely rare, Kleinenberg et al. (1964).

Using the equation given by Cole (1954) and applied to pinnipeds by McLaren (1967):

$$1 = e^{-r} + b e^{-ra} - b e^{-r(m+1)}$$

Where: r = instantaneous coefficient of potential rate of increase.

a = mean age of females producing their first young (increased here by one year to allow for gestation) i.e. 4 and 6 years.

b = potential annual birth rate of female young. From my calculations 0.125, considering births every 3 years and 0.40 for Soviet researchers, considering 4 births every 5 years.

$$m = \text{potential mean age of females}$$
producing their last young,
considered here to be 20 years
(though an arbitrary figure).

This procedure of estimating r is approximate, but adequate for the purpose. Estimates arrived at are: r = 0.056 based on my conclusions and r = 0.143 based on the conclusions of Kleinenberg et al. (1964), the latter 2.5 times the former (at an arbitrary 20 year lifespan). This difference deserves resolution if intensive commercial exploitation is planned in future.

CONCLUSIONS

(1) The total sample of 124 beluga, <u>Delphinapterus</u> <u>leucas</u>, was collected in Cumberland Sound, Baffin Island. Particular attention was paid to the associations of captured animals. A sampling bias existed toward sexually mature females and newborn calves.

(2) Tooth mineralization is regulated by the presence of the odontoblast processes, in turn probably being controlled by the availability of body minerals. Two tooth layers and one mandibular layer are considered to be annual increments.

(3) Whitening of the females occurs after 12 tooth layers, 15 layers in the male. Physical maturity is attained at approximately 362 cm in females and at 427 cm in males. Life-span is considered to be about 30 years.

(4) Females attain sexual maturity after four years at approximately 85% of their physically mature length. Multiple ovulations during the single annual estrus period are typical and along with accessory corpora account for the majority of ovarian scars. The variability in numbers of corpora accumulated by beluga females renders age determination and production estimates from corpora numbers inaccurate.

(5) The breeding season is in May with a gestation period as long as 14.5 months. Single births occur in late July and early August followed by two years of nursing. Reimpregnation occurs in the latter months of the second year

120

of nursing. The reproductive cycle is considered to be 35.5 months.

(6) Calves are a mean length of 159.6 cm at birth and mean weight of 79 kg, increasing length and weight during the first year by 35.3% and 140% respectively. Length and weight gains during the second year are 15.8% and 42.1% respectively.

(7) Weaning and tooth eruption begin during the second year; however, teeth do not protrude in any numbers until well into the third and fourth years. Suction and kin-cooperation are suggested as aids in feeding of the toothless calves.

(8) Sexual maturity of males occurs after seven years at approximately 90% of physically mature length. An abrupt increase in testes volume coincides with production of spermatozoa. There is an approximate 2:1 ratio of sexually mature females to males if survival of both sexes is similar.

(9) Very little feeding takes place during the migration into Clearwater Fiord though the small amounts of food present in the stomachs suggest a very broad food spectrum. The reason for the presence of beluga in this fiord is considered to be more of a thermal advantage rather than nutritive.

(10) Fat thickness variation is greatest among the sexually mature females due to the long lactation period.

(11) Large wounds are attributed mainly to bullet injuries while the long scratches are most readily attributed to the harassment of seals, especially by the younger animals.

(12) Large numbers of nematodes, Crassicauda sp. were found in the middle ear sinuses of all but newborn animals. Small numbers of Anisakis were present in the stomachs. Two males were found to have testes cysts containing single Crassicauda sp.

(13) There was full representation of the herd in Clearwater Fiord; however, there was segregation within females and newborns remaining close to shore and away from the main herd. Adult females may be accompanied by one or more of her previous offspring in addition to a newborn.

(14) During migration studies 1700 beluga were tagged in Hudson Bay, 93 of these injected with tetracycline.

(15) An aerial survey of Clearwater Fiord indicated the beluga population in 1967 to be an estimated 769 animals. By considering commercial and non-commercial mortality over the last 20 years it was concluded that this population was exploited far beyond their reproductive capacity.

(16) Considerable disagreement exists between these findings and those of other authors. The increase in age of female sexual maturity and increase of gestation and lactation periods, results in a productive capacity approximately 40% of that calculated by Soviet authors.

REFERENCES

ASDELL, S.A. 1965. Reproduction and development. 1-41. In W.V. Mayer and R.G. van Gelder (eds) Physiological Mammalogy 2, Academic Press. 326 p.

ASSALI, N.S. 1968 (ed). Biology of Gestation. 2 vol. Academic Press. 507, 405 p.

BEST, P.B. 1967. The sperm whale (Physeter catodon) off the west coast of South Africa. 1. Ovarian changes and their significance. S. Africa Div. Sea. Fish., Invest. Rep., No. 61. 27 p.

1969. 3. Reproduction in the male. ibid No. 72. 20 p.

BRODIE, P.F. 1969a. Duration of lactation in Cetacea: An indicator of required learning? Am. Mid. Nat., 82: (1) 312-314.

1969b. Mandibular layering in Delphinapterus leucas and age determination. Nature 221: (5184) 956-958.

BRYDEN, M.M. 1968. Growth and function of the subcutaneous fat of the elephant seal. Nature 220: 597-599.

1969. Relative growth of the major body components of the southern elephant seal (Mirounga leonina). Aust. Jour. Zool. 17:(1) 153-177.

CALDWELL, D.P., CALDWELL, M.C. 1967. Dolphins, porpoises and behavior. Underwater Natur., 4:(2) 14-24.

COLE, L.C. 1954. The population consequences of life history phenomena. Quart. Rev. Biol. 29: 103-137.

DEMPSEY, E.W., WISLOCKI, G.B. 1941. The structure of the ovary of the humpback whale (Megaptera nodosa). Anat. Rec. 80: 243-257.

DERGERBØL, M., NIELSEN, N.L. 1930. Biologiske Tagttagelser over og mallinger av Hvidhvalen. Medd. om grønland. 77, 119 p. (partial translation by D.E. Sergeant).

DOAN, K.H., DOUGLAS, C.W. 1953. Beluga of the Churchill region of Hudson Bay. Bull. Fish. Res. Bd. Can. 98: 27 p.

DOROFEEV, S.V., KLUMOV, S.K. 1936. On the economic important migrations of the white whale in the region of Sakhalin Island. Trudy VNIRO 3: 7-23.

EGER, W., KAMMERER, H., TRAPP, L., 1964. Simultaneous
flourescence and polarization microscopic
investigations on undecalcified thin sections of
bone tissue. Zeiss Information 1964, 64.-68.

EVANS, W.E., BASTIAN, J. 1969. Marine mammal communcication:
social and ecological factors, 425-475. In H.T.
Andersen (ed) The Biology of Marine Mammals.
Academic Press, 511 p.

FELTS, W.J.L., SPURRELL, F.A. 1966. Some structural and
developmental characteristics of Cetacean (Odontocete)
radii. A study of adaptive osteogenesis. Am. Jour.
Anat. 118 (1) 103-134.

FREEMAN, M.M.R. 1968. Winter observations on beluga
(Delphinapterus leucas) in Jones Sound, N.W.T.
Can. Field-Nat. 82: (4) 276-286.

GAMBELL, R., GRZEGORZEWSKA, C. 1967. The rate of lamina
formation in sperm whale teeth. Norsk Hvalfangst-
Tidende 6: 117-121.

HIRSCH, J. 1969. Behaviour-Genetic Analysis. McGraw-Hill
Book Co. 522 p.

HUGGETT, A. St.G., WIDDAS, W.F. 1951. The relationship
between mammalian foetal weight and conception age.
J. Physiol. 114: (3) 306-317.

JONSGARD, A. 1969. Age determination of marine mammals,
1-30. In H.T. Andersen (ed) The Biology of Marine
Mammals. Academic Press. 511 p.

KHUZIN, R. Sh. 1961. Methods of age determination and
material on reproduction of beluga. Nauchno-
Tekhnicheskii Bull. PINRO 1: (15) 58-60.

KLEINENBERG, S.E., KLEVEZAL, G.A. 1962. Contributions to
the method of age determination of toothed whales.
Dokl. Akad. Nauk SSSR, 145: 460.

KLEINENBERG S.E., YABLOKOV, A.V., BEL'KOVICH, B.M., TARASEVICH,
M.N. 1964. Beluga (Delphinapterus leucas)
Investigation of the Species. Translated into English
1969 by Israel Program for Scientific Translations Ltd.
376 p.

KLEVEZAL, G.A. KLEINENBERG, S.E. 1967. Age determination
of mammals by layered structure in teeth and bone.
F.R.B.C. translation series No. 1024, 1969. 142 142 p.

KORZYBSKI, T., KOWSZYK-GINDIFER, Z., WŁODZIMIERZ, K. 1967. Antibiotics: Origin, Nature and Properties 1. Pergamon Press.

KUMLIEN, L. 1879. Natural History of Arctic America. Bull. U.S. Nat. Museum 15. Dept. Interior. 179 p.

LANG, T.G. 1966. Hydrodynamic analysis of cetacean performance 410-432. In K.S. Norris (ed) Whales, Dolphins and Porpoises. Univ. Calif. Press. 789 p.

LAWS, R.M. 1953. A new method of age determination for mammals with special reference to the elephant seal, Mirounga leonina L. Sci. Rep. Falkland Is. Dep. Surv. 2: 1-11.
1959. The foetal growth rates of whales with special reference to the fin whale Balaenoptera physalus L. Discovery Repts. 29: 281-308.

1961. Reproduction, growth and age of southern fin whales. Discovery Repts. 31: 327-486.

1962. Age determination of pinnipeds with special reference to growth layers in the teeth. Zeitschrift fur Saugetierkunde 27: 129-146.

LINHART, S.B. KENNELLY, J.J. 1967. Fluorescent bone labeling of coyotes with Demethylchlortetracycline. Jour. Wldlf. Mgm't. 31: (2) 317-321.

McBRIDE, A.F., KRITZLER, H. 1951. Observations of pregnancy, parturition and postnatal behaviour in the bottlenose dolphin. Jour. Mamm. 32 (3) 251-266.

McLAREN, I.A. 1967. Seals and group selection. Ecology 48: (1) 104-110.

MILES, A.E.W. (ed) 1967. Structural and Chemical Organization of Teeth. 2 vols. Academic Press. 525, 289 pp.

NISHIWAKI, S., OHSUMI, S., KASUYA, T. 1961. Age characteristics in the sperm whale mandible. Norsk Hvalfangst-Tidende 12: 499-506.

OHSUMI, S. 1964. Rate of accumulation of corpora on right and left ovaries of cetaceans. Inst. Whale Res., Tokyo, 18.

1965. Reproduction of the sperm whale in the Northwest Pacific. ibid. 19:1-35.

PARKES, A.S. (ed) 1956. Marshall's Physiology of Reproduction. 3. Longmans. 1168 p.

PRITCHARD, J.J., RUZICKA, A.J. 1950. Comparison of fracture repair in the frog, lizard and rat. Jour. Anat. (Lond) 84: 236-261.

RAY, C. 1966. Discussion in K.S. Norris (ed) Whales, Dolphins and Porpoises. Univ. Calif. Press, 789 p.

SCHEFFER, V.B. 1969. Marks on the skin of the killer whale. J. Mamm. 50: 151.

SCHEFFER, V.B., PETERSON, R.S. 1967. Growth layers in teeth of suckling fur seals. Growth, 31: 35-38.

SERGEANT, D.E. 1959. Age determination in Odontocete whales from dentinal growth layers. Norsk Hvalfangst-Tidende 6: 273-288.

1962a. The biology and hunting of beluga or white whales in the Canadian arctic. F.R.B.C. circular 8, 15 p.

1962b. The biology of the pilot or pothead whale Globicephala melaena (Traill) in Newfoundland waters. F.R.B.C. Bull. 132, 84 p.

SERGEANT, D.E., BRODIE, P.F. 1969a. Body size in white whales, Delphinapterus leucas. Jour. F.R.B.C. 26: 2561-2580.

1969b. Tagging white whales in the Canadian arctic. Jour. F.R.B.C. 25: 2201-2205.

SKRJABIN, K.I., ANDREEWA, N.K. 1934. A new nematode: Crassicauda giliakiana n.sp. found in the kidneys of Delphinapterus leucas. Ann. de Parasit. 12: 15-28.

SLIJPER, E.J. 1962. Whales. Hutchinson (Lond) 475 p.

SOPER, J.D. 1928. A faunal investigation of southern Baffin Island. Nat. Mus. Can. Bull. 53 (15) 143 p.

TAVOLGA, M.C. 1966. Behavior of the bottlenose dolphin (Tursiops truncatus): Social interactions in a captive colony, 718-730 in K.S. Norris (ed) Whales, Dolphins and Porpoises. Univ. Calif. Press. 789 p.

TOMILIN, A.G. 1957. Mammals of the U.S.S.R. and adjacent countries. Vol.9 (Cetacea). Translated into English 1967, Israel program for scientific translations, Jerusalem 717 p.

URIST, M.R.   1964.   The origin of bone.   Discovery 21: (8).

   1964.   Further observations bearing on the bone-
   body fluid continuum.   151-179 in H.M. Frost (ed)
   Bone Biodynamics.   Little, Brown Co. Inc.

   1966.   Origins of Current Ideas about Calcification.
   Clinical Orthopaedics 44.

VLADYKOV, V.D.   1944.   Chasse, biologie et valeur economique
   du Marsouin Blanc ou Beluga (Delphinapterus leucas)
   du fleuve et du Golfe St. Laurent.   Dept. des
   Pecheries, Quebec.   194 p.

   1946.   Nourriture du Marsouin Blanc ou Beluga
   (D. leucas) du Fleuve St. Laurent.   Dept. des
   Pecheries, Quebec.   129 p.

WINGE, H.   1942.   Review of the interrelationships of the
   whales (Cetacea), translated by G.S. Miller Jr.
   In: Winge, The interrelationships of the mammalian
   genera, 3:   222-302.   Copenhagen.

YAGI, T., NISHIWAKI, M., NAKAJIMA, M.   1963.   A preliminary
   study on the method of time marking with lead salt
   and tetracycline on the teeth of fur seal.
   Inst. Whales. Res. Tokyo.   117.   191-195.

YAMAGUTI, S.   1961.   Systema Helminthum 1:   Digenetic
   Trematodes (1).   Interscience Pub.   N.Y., Lond.
   848 p.

YOUNG, J.Z.   1963.   The Life of Mammals. (2nd Ed.) Oxford.
   820 p.