The Life History of the Narwhal (*Monodon monoceros* L.) in the Eastern Canadian Arctic

by

Keith Alexander Hay
Institute of Oceanography
McGill University, Montreal

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ABSTRACT

The life history of the narwhal Monodon monoceros was studied utilizing animals captured by the Inuit in northern Baffin Island. Segregation by age and sex within this population is evident, with summering groups consisting of mature females with calves, immature and maturing males, and large mature males. The diet consists of arctic cod, shrimp, and squid during June and July, but feeding activity declines markedly during the open-water months of August and September. Growth layers in the unerupted teeth and periosteal zone of the mandible were found to be related to age but absolute rates of accumulation of these layers are uncertain. The maximum life span is estimated to be 40 to 50 years. Male narwhals, which mature sexually at lengths exceeding 390 cm and at 16-17 growth layers, display protracted maturation and a possible annual cycle of spermatogenesis. Females, which mature sexually at lengths exceeding 340 cm and at 12 growth layers, are seasonally polyoestrous, experiencing up to four consecutive ovulations during the breeding season. The gestation period is estimated to be 15.3 months. The season of conceptions is March to May and calving occurs during July and August. Since the lactation period exceeds 12 months, the interval between successive conceptions is usually three years, but about 20% of females conceive at the first breeding season following birth of their calves. The annual population birth rate is calculated to be about 0.07. The basic life history features of the narwhal are similar to those of other medium-sized toothed whales.

RÉSUMÉ

Une étude du cycle vital du narval Monodon monoceros a été menée à partir de spécimens obtenus durant la chasse conduite par les Inuit de la partie septentrionale de l'Ile de Baffin. Il existe une ségrégation évidente entre les groupes d'âge et entre les sexes dans cette population durant la période estivale; certains groupes sont constitués de femelles matures et leur baleineaux, d'autres d'animaux immatures et de jeunes mâles en période de maturation, enfin d'autres de gros mâles matures. La diète est constituée de saidas (morues arctiques), de crevettes, et de calmars (encornets) durant les mois de juin et juillet, mais l'activité alimentaire diminue de façon marquée durant la période d' eau libre de glace en août et septembre. Les couches de croissance observées sur la dent enfouie (qui ne perce pas) et sur le périoste de la mandibule sont associées à l'âge mais les fréquences absolues de dépôt de ces zones n'ont pu être déterminées avec certitude. La longévité maximale est estimée entre 40 et 50 ans. Les mâles, qui atteignent la maturité sexuelle à des longueurs dépassant 390 cm et à 16-17 couches de croissance, ont une maturation progressive qui se prolonge sur une longue période de temps et ont possiblement un cycle annuel de spermatogénèse. Les femelles, qui atteignent la maturité sexuelle à des longueurs excédant 340 cm et à 12 zones de croissance, sont polyoestres sur une base saisonnière ayant jusqu'à 4 ovulations consécutives pendant la saison d' accouplement. La période de gestation est estimée à 15.3 mois. La saison de fécondation s'étend de mars à mai et les mise bas ont lieu en juillet et août. Etant donné que la lactation dure plus de 12 mois, l'intervalle entre deux fécondations successives est généralement de 3 ans, mais 20% des femelles sont fécondées dès la première saison d' accouplement suivant la naissance d'un baleineau. Le taux annuel de natalité pour l'ensemble de la population a été calculé comme étant environ 0.07. Les caractéristiques de base du cycle vital du narval sont semblables à celles d'autres odontocètes de taille moyenne.

DEDICATION

This thesis is dedicated to the memory of Professor Fritz Müller, who introduced me to the Arctic and led me to learn to understand and appreciate its strange beauty and essence.

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INTRODUCTION

The narwhal Monodon monoceros L. has traditionally been hunted and utilized by the Inuit (Eskimo) of the eastern Canadian arctic and Greenland. It is still hunted today by the Inuit of northern Baffin Island, primarily for its muktuk (the edible skin) and the valuable ivory tusk.

The substantial annual catch of narwhals by the Inuit of the northern Baffin region allowed the opportunity to collect biological materials and data which were used to study the biology and life history of the population in eastern Canadian arctic waters. These data and specimens were collected from narwhals taken by Inuit hunters during 1974-76 and captured by a scientific netting operation during 1963-65. It was necessary to develop a method of age determination so that life history parameters could be deduced from samples of animals of known age. The study of the reproductive organs of both male and female narwhals allowed the elucidation of certain features of the reproductive biology and the estimation of life history parameters, especially the age at the attainment of sexual maturity, the birth rate, and the durations of the various stages of the reproductive cycle. Determination of these basic features of the life history may be helpful in providing a rational basis for management of the narwhal population in the eastern Canadian arctic.

During the last 15-20 years numerous studies of the life history of the smaller odontocetes have been carried out. In spite of many controversial points regarding age determination (see Perrin and Myrick 1980) and the estimation of life history parameters, several general features of the life histories of odontocetes are beginning to emerge. This study attempts not only to describe the life history of the narwhal but also to place the results in the framework of the general patterns of odontocete life history.

This thesis represents the first comprehensive quantitative study of the basic biology and life history of the narwhal. This study was initiated by Dr. Arthur Mansfield, Director of the Arctic Biological Station, Ste Anne de Bellevue, Quebec; a preliminary report on his earlier studies has been published (Mansfield, Smith and Beck 1975). Most previous accounts on the narwhal deal with such qualitative aspects as morphology and anatomy, distribution, migration, feeding, and exploitation. Some general literature reviews are available, among the best of which are Tomilin (1957), Reeves and Tracey (1980), and Arvy (1978). Bruemmer (1966, 1969) has written excellent general accounts as well.

STUDY AREA

The study area comprises the coastal waters of northern Baffin Island, especially Admiralty Inlet, Pond Inlet, Navy Board Inlet, and Eclipse Sound. These localities are frequented in summer by large numbers of narwhals which are hunted by the Inuit of Arctic Bay and Pond Inlet. The hunt occurs at the floe edge in June and July, and in shallow coastal waters in summer. A map of the general study area is presented in Figure 1. The Inuit communities of Arctic Bay and Pond Inlet, and the locations of the main summer whaling camps (Kakiak Point and Kaunak), are indicated on this map.

For useful socio-economic and other background information the reader is referred to the Area Economic Survey of Bissett (1970) and an historical account by Brody (1976). Published accounts of wildlife surveys in the region include those by Ellis (1957) and Miller (1955) on the mammals. Tuck (1957) reported on seabirds and marine mammals at Cape Hay, northwest Bylot Island. Degerbøl and Freuchen (1935) reported on the wildlife observed in the Pond Inlet region during the Fifth Thule Expedition, and reference to this same material is made by Freuchen and Salomonsen (1958). General knowledge of marine mammal distributions in the area has expanded recently, with the reports of Greendale and Brousseau-Greendale (1976), Webb (1976), Johnson, Renaud, Davis and Richardson (1976), and Renewable Resources Consulting Services Ltd. (1977). Several government expeditions, notably those reported upon by Low (1906) and Anderson (1934), took note of the marine mammals encountered in the study area. Wilkinson (1955) and Scherman (1956) wrote good popular accounts based on their personal expeditions to the area.

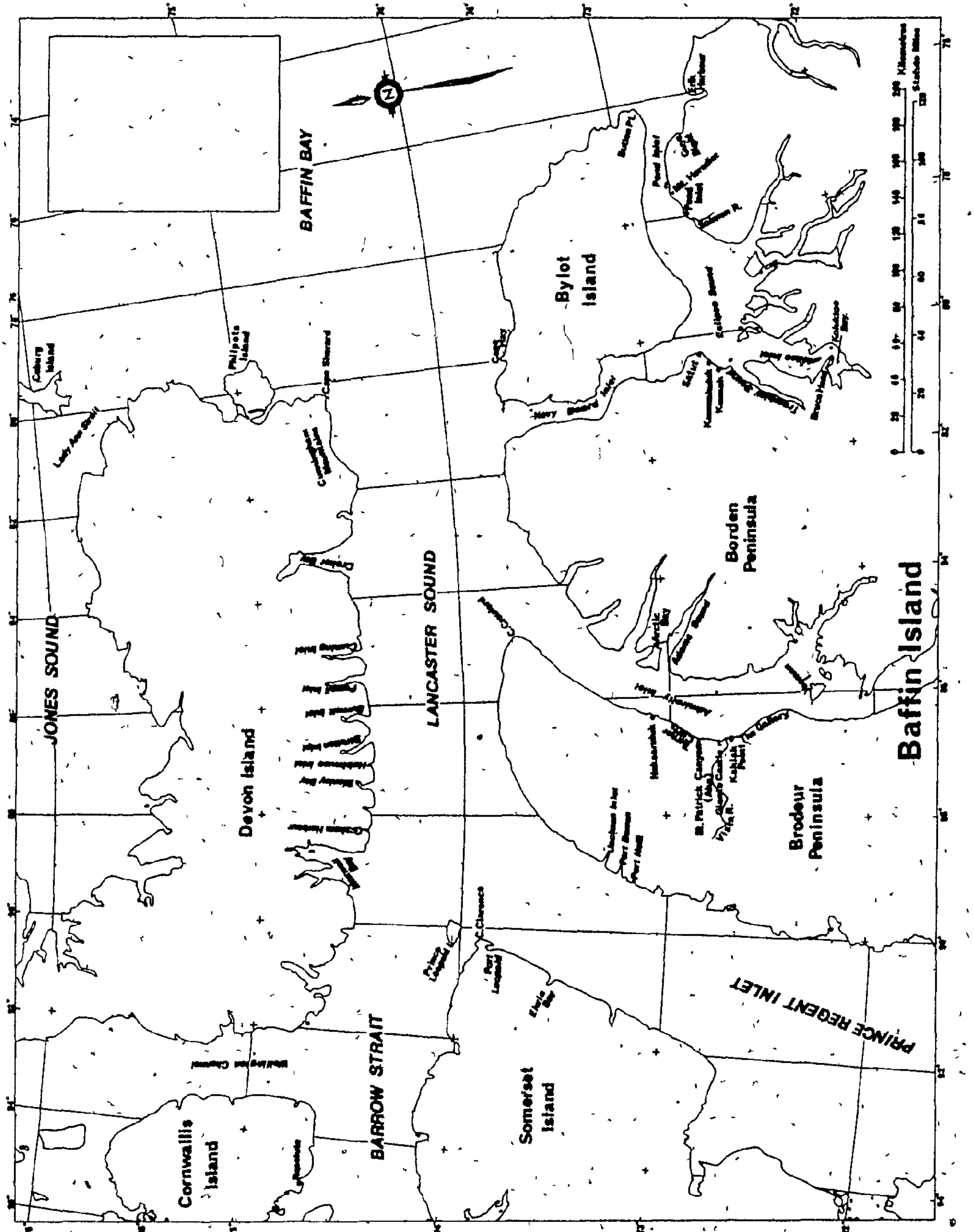

Figure 1. Map of the study area.

MATERIALS AND METHODS

Data Collection

The interpretation of the life history of the narwhal was based upon study of specimens collected from narwhals netted at Koluktoo Bay (1963-65) or killed by Inuit hunters of Arctic Bay and Pond Inlet (1974-76). Sixty-two narwhals were netted during the summers of 1963-65, using double nylon nets 91.4 m long and of 36 or 46 cm stretched mesh (Mansfield et al. 1975). These nets were 25 or 50 meshes deep and were set in deep water from points of land; Bruce Head was the best netting locality (Fig. 1). Drifting ice in the bay was often a problem and caused some damage to the nets. A canoe was often used to tow ice away from the nets, but more often the nets were lifted whenever ice menaced nearby.

During the summers of 1974-76, 131 narwhals taken by the Inuit of Arctic Bay and Pond Inlet were sampled. Most of these were killed near the summer camps at Kakiak Point and Kaunak but, in 1976, 43 were taken at the floe edge near Guys Bight. Table 1 presents the distribution of narwhal samples by year and locality. A total of 194 narwhals was sampled in this study.

The narwhals were hauled onto the beach or ice by manpower or occasionally by block-and-tackle. Each whale was assigned a serial number; the sex of the whale, location and date of kill, weather, sea and ice conditions, and the time after death were recorded. Before flensing and dissection, the following measurements were taken:

1. Body length from tip of upper jaw to notch of tail flukes, measured in a straight line, to the nearest cm.
2. Girth or circumference, measured to the nearest cm, at the axilla (just posterior to the pectoral flipper), umbilicus, and anus. Because of the difficulty in handling larger whales, measurements were usually made from the dorsal ridge to the mid-ventral line on one side and multiplied by two to obtain the girth.

Table 1. Number of narwhals sampled during this study, based on locality, method of capture, and year.

		Location					
Year	Method of capture	Koluktoo Bay	Kakiak Point	Kaunak	Pond Inlet Floe Edge	Cumberland Sound[a]	Total
1963-65	net	62					62
1967	net					1	1
1974	hunt			13			13
1975	hunt		25	40[b]			65
1976	hunt		7	3	43		53
Total		62	32	56	43	1	194

[a] One female narwhal was netted during a study of white whales at Cumberland Sound, near Pangnirtung, N.W.T. The data for this specimen were provided by Dr. P. F. Brodie.

[b] Three of these specimens were captured near the settlement of Pond Inlet.

3. Lateral spread of the tail flukes from tip to tip in a straight line, measured to the nearest cm.
4. External tusk length to the nearest cm, and cross-sectional basal diameter to 0.1 cm.

Also prior to flensing, colour patterns, scars, and other markings were noted and occasionally photographed. The thickness of the blubber was measured to the nearest 0.1 cm in three locations: mid-dorsal, mid-lateral, and mid-ventral.

After flensing (removal of skin and blubber), the carcass was available to the field technicians for dissection. The abdominal wall was opened and the viscera were exposed. The contents of the forestomach (storage compartment) were removed and preserved in 70% ethyl alcohol. The ovaries of females were removed and preserved in 10% formalin. Right and left ovaries were distinguished and the presence of a corpus luteum was recorded. The length of a foetus was measured to 0.1 cm in its natural position within the uterus, and its sex and the uterine cornu (left or right) in which it occurred were also recorded. The weight of a foetus was measured with a spring balance, and foetuses were preserved in 10% formalin. The internal diameter of each uterine cornu was measured to 0.1 cm at the mid-point of its anterior arch. The mammary glands were exposed and sectioned, and the thickness of each gland was measured to 0.1 cm just anterior to the mammary slit. The nature of any fluid seen in the mammary ducts or seen exuding from the nipples was noted; this was usually the turbid green milk of lactating females or the translucent oily fluids of postlactation females.

The testes were removed from male narwhals. As there seemed to be no consistent difference in size between the two, that of the right side was selected for measurement and study. The length, width, and depth of the testis was measured to 0.1 cm; weight was determined with a spring balance, and volume was measured by water displacement. The epididymis was cut and examined for the presence or absence of a white, viscous fluid. A 1 cm thick transverse section of the testis and epididymis was removed at the mid-length of the organ and preserved in Bouin's preservative for 48 hours. These samples were then placed in 70% ethyl alcohol with daily changes for three to four days.

As time permitted, ecto- and endoparasites were examined and preserved in 95% ethyl alcohol or 10% formalin. Nematodes were preserved in 10% glycerine-alcohol (10 ml of 100% glycerine in 90 ml of 70% ethanol).

After the head of the narwhal was cut off an unerupted tooth was removed. This smaller tooth or tugarrusirq (the Inuit name for "small tusk") is hidden in the maxilla from which it is extracted by using a hatchet. Females have two unerupted teeth, one embedded in each maxilla, while males have one unerupted tooth in the right maxilla and an erupted tooth in the left maxilla which develops into an elongated tusk. Only the right tooth was removed from most animals. In addition, the distal 15-20 cm of the left mandible was removed and cleaned of fat and muscle tissue. Both the tooth and the mandible were collected for purposes of age determination.

Of the 62 narwhals netted at Koluktoo Bay during 1963-65, 41 (21 females and 20 males) were weighed in pieces using a tripod and spring balance. The weight of each animal was obtained in this way, as well as the weight of integument, meat, skull, skeleton, and individual visceral organs. Estimates of the weight of skin and blubber were derived from weighed subsamples of each and the measured total weight of the integument (skin and blubber).

Associations between the whales captured by the nets were noted. This was especially valuable in interpretation of female reproductive data, since several females were netted with calves of various likely ages (neonates, one- and two-year-olds).

Narrative of Field Work

Sampling of netted narwhals in Koluktoo Bay was carried out from 5 August to 2 September, 1963 by D. Robb, B. Beck, and A.W. Mansfield; from 9-26 August, 1964 by D. Robb, B. Beck and A.W. Mansfield; and from 13-25 August, 1965 by D. Robb, B. Beck,

F. Bruemmer, C. Ray and A.W. Mansfield. From 22-29 August, 1974 R. McClung and I sampled 13 narwhals at the Kaunak hunting camp on the western shore of Eclipse Sound. In 1975, W. Doidge and R. Adams sampled 25 narwhals at Kakiak Point from 23 July to 28 August, while D. Stendahl, P. Brodie and I sampled 37 narwhals near Kaunak from 26 July to 1 September. Seeana Attagootak of Pond Inlet sampled three male narwhals at Pond Inlet on 22 September, 1975. Thus, a total of 40 narwhals were sampled near Pond Inlet in 1975 (shown under Kaunak in Table 1).

From 15 July to 1 August, 1976, H. Silverman and I sampled 12 male and 31 female narwhals taken at the floe edge near Guys Bight. We preferentially sampled non-tusked whales (females) on a random basis. Due to heavy ice conditions, we did not reach the summer camp at Kaunak until 25 August. Here we sampled one male and two females. We spent the period 2-6 September, 1976 near the head of Tremblay Sound, where narwhal observations were made and physical oceanographic data were collected to a depth of about 90 m. From 12-17 August, 1976 seven narwhals were sampled near Kakiak Point by W. Doidge and R. Greendale.

During August 1976, 20 narwhals, 16 at Kakiak Point and four at Kaunak, were tagged with small numbered monel metal darts with orange plastic-coated metal streamers about 15 cm long, thrust into the animal's blubber by hand harpoon. This is the same type of tag as was used successfully on white whales in Hudson Bay by Sergeant and Brodie (1969). Narwhals were driven close to shore by one or two canoes to facilitate the tagging, which ~~must~~ be done at close range.

Laboratory Analysis

Age determination - The unerupted (embedded) teeth were cut in half longitudinally using a jeweller's circular saw of carbon steel (0.635 mm x 12.7 cm), rotated at 1725 revolutions per minute by a 0.25 horsepower motor. Care was taken in positioning the tooth to ensure a median longitudinal (mid-sagittal) cut from tip to root. The cut surfaces were then ground with medium and 120 grade sandpaper to remove the saw marks; they were then polished with 220 and 320 grade waterproof sandpaper until perfectly smooth, and preserved in a mixture of equal parts of water, absolute alcohol, and glycerin. Examination of the teeth and counts of growth layers were carried out using an illuminated lens of low magnification. In selected teeth the thicknesses of successive dentinal layers were measured using vernier calipers, and the nature of the most recent dentinal zone, adjacent to the pulp cavity, was noted.

The mandible was also used for determining age in the narwhal. Transverse sections about one cm thick were cut from the anterior part of the mandible between the mental foramina. These sections were embedded in acrylic resin (Ward's bioplastic) and cut perpendicular to the mandibular axis using a Gillings-Hamco dental sectioning machine to obtain sections of 75-125 μ in thickness (Plate IV, a). These sections were stored in 70% ethyl alcohol and examined microscopically with a Leitz Wetzlar model 1XQ2 trichinoscope in order to count and measure the periosteal growth layers. The scale on the projection screen of the trichinoscope was calculated from the magnification, which could be set at 50 or 80 diameters. For the mandibles of selected whales, thicknesses of successive growth layers and the thickness of the periosteal bone were measured directly on the screen. In addition, a few thin sections of unerupted teeth were obtained and studied in this fashion. Also, bioplastic-embedded longitudinal thin sections of an unerupted tooth, the polished cut surfaces of a longitudinally-bisected unerupted tooth, and thin mandibular sections were stained with silver nitrate by the modified von Kossa method (Drury and Wallington 1967) to demonstrate the distribution of calcium salts in these tissues and to ascertain the physiological basis of hard tissue layering (i.e. differential mineralization). This method stains calcified tissues black.

Male reproduction - Initial examination of histological materials from all 27 males captured during 1963-65 indicated that post-mortem degeneration of the seminiferous and epididymal epithelia was substantial after four hours post-mortem, and in the 1974-76 sample only males that were examined within four hours of death were selected for histological study. Only 13 males in this sample satisfied this criterion, giving a total sample of 40.

The testes and epididymes collected in the field were processed by Bio-Research Laboratories Ltd., Senneville, Quebec. The tissues were embedded in wax, and thin sections were cut with a microtome and stained with haematoxylin and eosin. The mounted sections were examined with a Leitz Wetzlar Orthoplan Universal widefield microscope, and photographs of seminiferous and epididymal tubules were taken with a Leitz Wetzlar Orthomat-W automatic microscope camera, at magnifications of 125, 500, and 1250 diameters. The diameters of ten seminiferous tubules and ten epididymal tubules per male, chosen at random, were measured with a calibrated eyepiece micrometer. In addition, the relative diameter of the lumen of the seminiferous tubules, development of interstitial tissue between the tubules, and amount of spermatozoa and cellular detritus in the lumen were estimated. The extent of folding of the epididymal epithelium and the relative amounts of spermatozoa and detritus in the lumina were also estimated.

Female reproduction - All 108 pairs of ovaries were sectioned at approximately 3 mm intervals with a scalpel and examined under an illuminated lens at low magnification. The diameter of the largest follicle in each ovary was measured to 0.1 mm using vernier calipers. All corpora lutea, corpora albicantia, corpora atretica and luteinized follicles were identified and measured. Descriptions, drawings, and photographs were made of these various ovarian structures.

Sections of representative ovarian structures, fixed in formalin, were sent to Bio-Research Laboratories Ltd. for histological preparation. These tissues included two sections of ovarian cortex for the study of follicular growth and atresia, a section of a follicle that appeared to have recently ovulated, two sections of corpora lutea of pregnancy, five sections of luteinized follicles in various stages of atresia, four sections of corpora albicantia in different stages of regression, and one corpus atreticum. Mounted sections were examined and studied microscopically and photographed.

Stomach contents - Items in the preserved stomach contents were sorted in the laboratory. Representative specimens were examined and identified by other investigators, usually to species.

GENERAL BIOLOGY OF THE NARWHAL

Identity, Nomenclature, and Evolution

The narwhal belongs to the suborder Odontoceti, family Monodontidae, and superfamily Monodontoidea (Tomilin 1957). The scientific name is Monodon monoceros Linnaeus, 1758 and the type locality is Arctic Seas (Linnaeus) (Tomilin 1957).

The etymology of the name narwhal is Scandinavian, "nar" meaning "corpse". Thus narhval means "corpse whale" which refers to the presumed likeness of its mottled skin to that of a drowned man (Mansfield et al. 1975).

Winge (1921) outlined the evolution and taxonomic characters of the Monodontidae, the most primitive of the Delphinid line. The evolution of the family is further discussed by Kulu (1972), who pointed out that the monodontid stock apparently arose from a primitive, blunt-snouted, lower Miocene extinct delphinid (Eurhinodelphis). The white whale Delphinapterus leucas appeared in upper Miocene while the narwhal appeared later, in the Pliocene, from which period narwhal fossils have been recorded (Kellogg 1928). The similarity of the narwhal karyotype to those of other species of whales (Andrews, Dill, Masui and Fisher 1973) adds support to the contention that the cetaceans are monophyletic in origin.

Morphology

Appearance and colouration - Newborn calves (Plate I, a) are uniformly grey or brownish-grey, while young suckling animals (Plate I, b) are uniformly dark grey or black. White patches first appear around the genitals, anus, and umbilicus,and gradually extend to the rest of the ventral side and then up the flanks to the back (Plate I, e). The back, head, neck, and edges of flippers and flukes of the adult usually remain black while the ventral side retains a few faint smudges of grey and a thin dark discontinuous mid-ventral line. A mottled effect is seen on the lateral surface (dark spots on a white background) while the back may be almost solid black. The surfaces of the flippers and flukes are white with some dark smudges.

and striations. Males tend to become whiter in old age than do the females. In older animals, especially males, the tips of the pectoral flippers are often curved upwards and the flukes may overlap in the region of the tail notch. The adult colouration is demonstrated in Plate I., e and f. Post-natal animals are hairless (Eales 1950).

Dimensions - The mean length at birth is 161 cm. Adult males achieve a length of 470 cm and a weight of about 1600 kg; adult females, 415 cm and 900 kg. The tusk may be up to 210 cm in external length with a basal cross-sectional diameter of 8 cm. All these values refer to narwhals sampled at Pond Inlet and Arctic Bay in this study. According to Tomilin (1957), males may reach 600 cm in length and females, 500 cm; he also stated that tusks can be up to 300 cm long of which 30-35 cm is socketed, with a basal diameter of 10 cm. Tusks of northwest Greenland narwhals reach a length of 315 cm or 10 ft (Bruemmer 1971). Tusk weight may exceed 10 kg (Bruemmer 1971) or it may achieve values of 12-14 kg (Ivashin, Popov and Tsapko 1972). One of the biggest narwhal tusks that was examined in this study weighed 8.2 kg.

Anatomy

Tusks and teeth - The dentition of the narwhal has received considerable attention in most published accounts dealing with this species. The presence of a remarkable tusk that may exceed a length of 3 m has undoubtedly contributed to much of the public and scientific interest in this species. The narwhal is related to and likely responsible for the myth of the unicorn (Bruemmer 1969). Bonner (1951) has given a good historical account of the unicorn's horn.

The development of the narwhal's dentition has been described by several authors. In very early foetuses, six pairs of dental papillae are present in the maxillae (Eales 1950). Only the first two pairs of dental papillae develop and persist, the last four pairs remaining rudimentary and eventually disappearing. Two pairs of tooth germs are also found in the mandibles of embryos but these too fail to develop (Eales 1950). However, Mitchell and Kemper (1980) reported the presence of a small curved erupted tusk from the right mandible of an adult male narwhal. Further study of foetal dentition in the narwhal (Turner 1872, 1873, 1876, 1912; Fraser 1938; Gervais 1873; Eales 1950) indicates that the anterior pair of dental papillae forms the tusks while the posterior teeth remain small and vestigial and may eventually be resorbed in the adult. The full-term foetus and early neonate have two pairs of maxillary teeth: the anterior teeth, which are elongate (up to 10 cm in length), cone-shaped, and filled with dental pulp, and the posterior teeth, which are small and occluded.

The left tooth usually erupts as a tusk only in males. Most authors recognize that it is a canine tooth since its socket is in the maxilla (Turner 1873; Tomilin 1957). The pulp cavity is broad and conical near the base, 10-20 cm from which it narrows to a canal of 0.5 cm diameter that passes nearly to the tip of the tusk (Tomilin 1957; Owen 1868; Home 1813). In very old males, the tip and root of the tusk are solid and its pulp canal is nearly filled (Porsild 1922; Home 1813). The cellular structure of the pulp tissue of the tusk has recently been studied by Dow and Hollenberg (1977).

Although the narwhal displays a pronounced sexual dimorphism with regard to the presence of an erupted tusk, tuskless males, females with one tusk, and narwhals with two tusks (male and female) have been reported (Pedersen 1931; Clark 1871; Scoresby 1820, 1823; Fraser 1938; Eales 1950; Porsild 1922; Degerbøl and Freuchen 1935). The right tusk of two-tusked whales is nearly always shorter and less robust than the left (Porsild 1922; Fraser 1938), and the tusks of females are shorter and narrower than those of males (Clark 1871; Pedersen 1931). In the present study, two young tuskless males (336 cm and 338 cm) were captured. Embedded in the maxillae of each young male were the two teeth characteristic of females. A young male of length 372 cm had two erupted tusks (external lengths of 85 cm on the left and 53 cm on the right). Also, three females with one tusk emergent from the left maxilla were taken: a pregnant female, 372 cm body length, tusk 118 cm; one of body length 370 cm, tusk 100 cm; and a 390 cm female in late pregnancy, tusk length 141 cm. At Kakiak Point in 1975, Inuit took a two-tusked narwhal which they claimed was a female. The field technicians saw only the skull, however, and they measured the external tusk lengths as 135 cm and 147 cm for the left and right tusks, respectively.

On the basis of the occurrence of these dental conditions in the sample from 1963-76, it is estimated that the frequency of whales with two tusks is 1.03%, that the frequency of tuskless males is 2.47%, and that the frequency of tusked females is 2.65% or 3.51% (excluding and including the two-tusked whale (claimed to be a female) from Kakiak Point, respectively). Also, 1.23% of the males had two tusks.

The surface of the tusk is marked with a series of spiral grooves which turn clockwise from the basal end when the tusk is viewed from its tip. This sinistral spiral is evident on both tusks of two-tusked specimens (Gervais 1873; Clark 1871), in apparent violation of the laws of bilateral symmetry. Thompson (1952) attempted to explain the origin of the spiral markings of the tusk by assuming that there exists a rotatory component of each beat of the tail during locomotion, and that the skull and especially the tusk respond to this component with a "torque of inertia". This effectively results in the rotation of the tusk within its socket as it grows longitudinally, and the spiral pattern is supposed to be impressed onto the tusk by a spiral set of ridges on the wall of the alveolus. No evidence for a rotatory movement of the tail of whales exists, and it is likely that the spiral pattern is the result of a specific genetic growth function.

The structure and development of the embedded teeth have received less attention than the tusk. The males usually have one of these teeth embedded horizontally in the right maxilla while females have one embedded horizontally in each maxilla. These teeth stop growing relatively early in postnatal life, achieving a maximum length of about 29 cm in males and 23 cm in females. The left tooth of females is longer than the right and is closer to the tip of the rostrum (Fraser 1938). A spiral pattern of ridges and grooves is present on the surface of some embedded teeth, as was noted also by Home (1813) and Brown (1868).

Skull and skeleton - Eales (1950) has described the anatomy of the skull of the early foetal narwhal. The mandibles of small foetuses contain seven pairs of hair germs, but postnatal narwhals are hairless. Fraser (1951) also described foetal skull anatomy and dentition.

The skull of the narwhal displays a marked asymmetry, manifested by the greater development of the maxillaries and premaxillaries on the left and of the brain case on the right (Tomilin 1957). Ness (1967) found that the relative asymmetry of the narwhal skull increases with skull length but is equally developed in both sexes. The mid-line of the nasal bones was displaced an average of 33 mm to the left of the mid-dorsal skull axis. Due to twisting of these bones, the left naris is smaller than the right (Ness 1967). Apparently, the number and position of the erupted tusks do not influence the skull's asymmetry (Ness 1967; Clark 1871).

Scoresby (1820) realized that the cervical vertebrae of the narwhal are unfused, one of the distinguishing characteristics of the Monodontidae. His dissection of the vertebral column revealed the presence of 7 cervical, 12 dorsal, 23 lumbar and 12 caudal vertebrae, for a total of 54 vertebrae. Turner (1912) gave the number of vertebrae as 50, the formula being 7-11-6-26 for the respective vertebrae.

Tomilin (1957) made some remarks on other aspects of the narwhal's skeleton: the number of phalanges decreases with age; the sternum is segmented; the pelvic bones are rudimentary and asymmetrical in size, and are located below the last lumbar and the first two caudal vertebrae. Eales (1954) has studied the anatomy and arrangement of the bones of the narwhal's manus.

Internal anatomy - Published accounts of the internal anatomy of the narwhal include detailed studies of the muscles (Howell 1930), the larynx and urogenital and digestive systems (Hein 1914, 1915), the digestive system (Turner 1889; Woodhead and Gray 1889, 1890), and the thoracic retia mirabilia (Wilson 1879; Vogl and Fisher 1976). Turner (1876) dissected and studied the placenta of a female with a 165 cm foetus. Eales (1950) examined the brain of foetal narwhals and concluded that olfactory lobes and nerves were absent.

Anatomical studies have also been made of the eyelid (Huber 1934), eye (Jamieson and Fisher 1972), ear (Huber 1934; Fraser and Purves 1960; Kellogg 1928) and the facial musculature and nasal passages (Huber 1934; Mead 1975; Raven and Gregory 1933).

The average brain weight of three large adult males captured at Koluktoo Bay, northern Baffin Island, was 2.99 kg, representing 0.19% of the mean body weight. Brain weights are proportionately larger in younger animals, reaching a value of 0.58% of body weight of a 290 cm female.

Distribution and Migrations

Range - The general range of the narwhal in Canada has been summarized by Mansfield et al. (1975). Narwhals occur regularly in Lancaster Sound, Baffin Bay, Davis Strait, northern Hudson Bay, Foxe Basin, Jones Sound, and Prince Regent Inlet. They have also been observed in Peel Sound and Franklin Strait (Manning and MacPherson 1961), in Hudson Strait (Low 1906), along the east coast of Baffin Island (Degerbøl and Freuchen 1935; Webb 1976), and in Smith Sound and Kane Basin (Vibe 1950). Finley, Davis and Richardson (1974) have documented the spring and summer distribution of the narwhal in Barrow Strait, Wellington Channel, Peel Sound, and McDougal Sound. Narwhals also frequent Creswell Bay, southeastern Somerset Island, and Bellot Strait (Finley et al. 1974; Davis, Finley, Bradstreet, Holdsworth and McLaren 1975).

Recent observations of the occurrence of narwhals at the extremities of their range in Canada include those of Mercer (1973), who documented the stranding of a 486 cm male narwhal with a 216 cm tusk at Bell Island, Newfoundland (50°40'N, 55°30'W) on 12 June 1969; Merdsoy, Lien and Storey (1979), who recorded a young male narwhal trapped by ice in Hall's Bay, Newfoundland (49°30'N, 56°00'W), during March 1978; Smith (1977) who discovered a skull with tusk on a beach along the western coast of Victoria Island; and Roe and Stephen (1977), who observed 10 narwhals in Maclean Strait (77°20'N, 103°20'W) on 6 September 1976. More recently, an adult male narwhal became entangled and drowned in a net set for seals on 19 December 1979, near the settlement of Westport, White Bay, Newfoundland (49°47'N, 56°38'W). The body length of this narwhal was 453 cm and the exposed portion of the tusk was 192 cm long (unpublished data). The narwhal also occurs infrequently in the coastal waters of Alaska (Geist, Buckley and Manville 1960; Huey 1952).

The distribution of the narwhal in the Soviet arctic has been outlined by Tomilin (1957). It occurs in the Barents, White, Kara, Laptev, East Siberian, and Chukchi Seas, usually well offshore (Fig. 2). It is rare in the waters of the Siberian arctic and the Beaufort Sea (Scammon 1874; Tomilin 1957). Narwhals also occur occasionally in the Bering Sea (Johnson, Fiscus, Ostenson and Barbour 1966; Tomilin 1957); the southernmost Soviet record is from Bering Island (Tomilin 1957).

The narwhal occurs regularly in the waters of west Greenland (Vibe 1950) and east Greenland (Gray 1887, 1889; Boyd 1932). The narwhal is known to penetrate to high latitudes in summer, at least up to 85°N in the Eurasian arctic (Nansen 1897; Chapskii 1946; Rutilevskii 1958; Herbert 1969).

The narwhal occurs rarely in European waters. Fraser (1949) documented five narwhal strandings in the British Isles since 1588 and commented upon their occasional occurrence in the North Sea, while Fleming (1811) documented a stranding at the Shetland Islands in 1808. The stranding of a two-tusked pregnant female narwhal in the Elbe River in 1736 was noted by Johansen (1912) and Eales (1950). Schultz (1970) presented eight records of the narwhal in the North

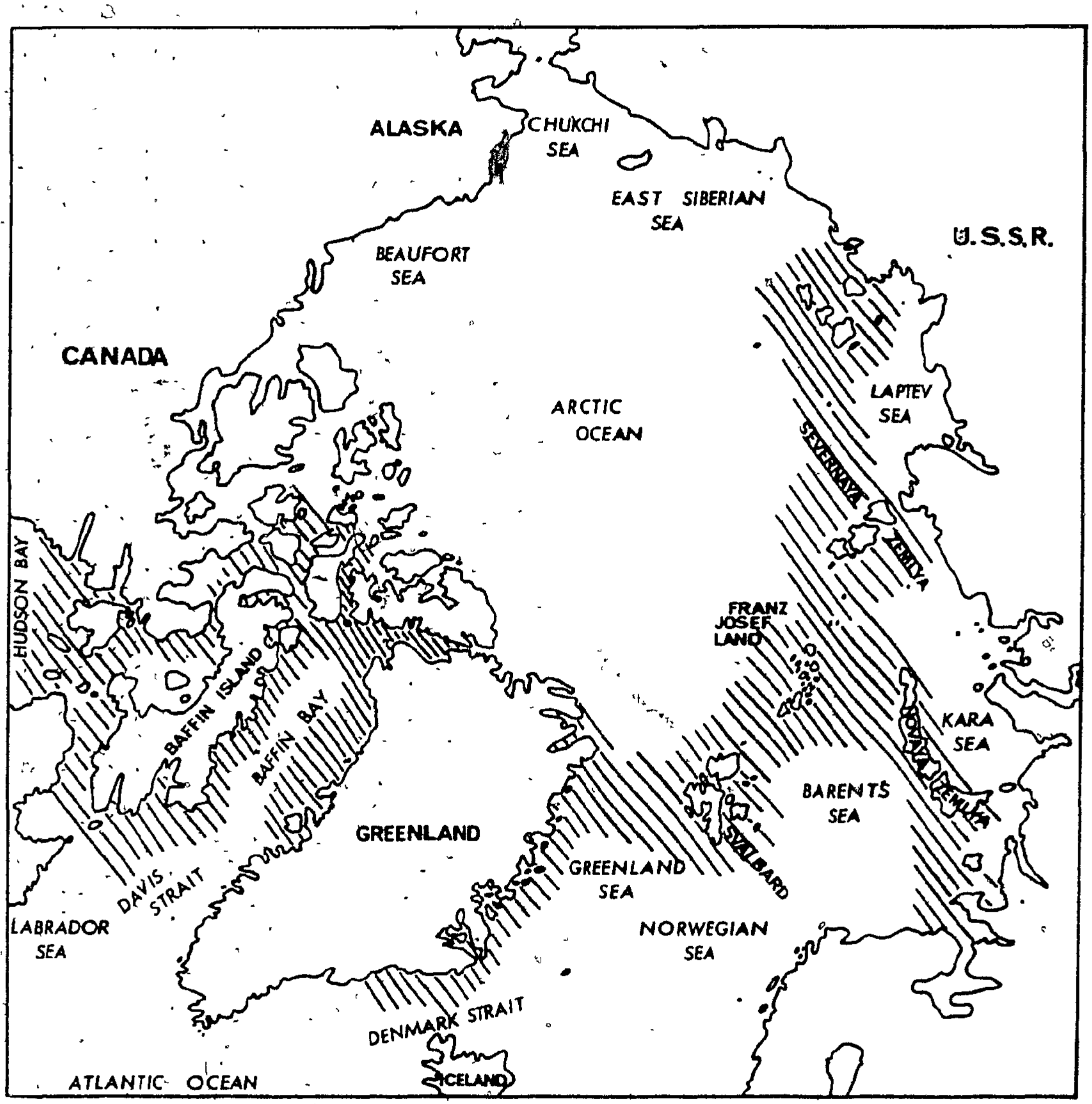

Figure 2. Summer distribution of the narwhal.

Sea and Baltic Sea, the earliest from Norfolk, England in 1588 and the most recent from Essex, England in 1949.

Few winter records of narwhals exist. Vibe (1950) and Freuchen and Salomonsen (1958) stated that narwhals spend the winter in the "North Water" (an area of light ice coverage or open water in northern Baffin Bay and Smith Sound), Davis Strait, Baffin Bay, and Lancaster Sound. Winter sightings in the Canadian arctic have been recorded by Davis (1876), whose men, while drifting southwards on pack ice in Baffin Bay, observed narwhals during February-March 1873 at 63°47'N and 68°50'N, near the coast of Baffin Island. Webb (1976), considering the fall migration of narwhals south along the Baffin Island coast, suggested that narwhals may winter off Cape Dyer within the pack ice, while Renewable Resources Consulting Services Ltd. (1977), considering satellite imagery, suggested that a small proportion of the population wintered in the North Water while most individuals wintered in Davis Strait (in the vicinity of Disko Island). Turl (1977) has recently observed narwhals in the pack ice of Davis Strait during winter.

Vibe's (1950) observation of white whales on 6 February 1923 near Cape Parry, northwest Greenland suggests that some narwhals may also spend the winter in the North Water. Observations by Degerbøl and Freuchen (1935) of narwhals at the Admiralty Inlet floe edge and Cape York, Lancaster Sound, in April 1924, and by Renewable Resources Consulting Services Ltd. (1977), of narwhals in the Devon Island flaw lead in April 1976, suggest that some narwhals spend the winter in the North Water. On the basis of aerial surveys of the North Water in March-April 1978 and March 1979, Finley and Renaud (1980) suggest that this area has extemely limited potential for supporting marine mammals during winter. They saw only 12 narwhals during their surveys of the North Water and suggest that most high arctic narwhals must winter in regions with less severe ice conditions. Some narwhals also overwinter in northern Hudson Bay and Foxe Basin (A.W. Mansfield, pers. comm.) and in the mouth of Hudson Strait and in the offshore waters of southeast Baffin Island (MacLaren Marex Inc. 1979).

The question of the wintering range of narwhals which summer in the eastern Canadian Arctic and at northwest Greenland has recently been resolved by McLaren and Davis (1982, 1983). Their extensive aerial surveys during March of 1981 and 1982 showed that the great majority of narwhals overwinter throughout the heavy pack ice of northern Davis Strait and southern Baffin Bay, while few narwhals overwinter in the loose pack ice off West Greenland and none, in the open water.

The wintering region of narwhals in Eurasian waters is not well-known, although Gray (1931) suggested Denmark Strait as a likely place. They most probably overwinter in the pack ice of the Greenland and northern Barents Seas.

Migrations - Lancaster Sound is the main route by which marine mammals enter the Canadian arctic archipelago from Baffin Bay. Tuck (1957) estimated that 6,000 narwhals passed Cape Hay, northwest Bylot Island, from 3-19 July 1957, while Greendale and Brousseau-Greendale (1976) recorded 6,145 at the same location during June and July 1976. Prior to this movement past Cape Hay, large numbers of narwhals pass Button Point, southeast Bylot Island, in June and July (Freuchen and Salomonsen 1958; Anderson 1934).

The westward movement of narwhals through Lancaster Sound during 1976 has been investigated by Johnson et al. (1976), whose aerial surveys on seabirds provided incidental but excellent information on migrating marine mammals in the eastern part of the sound. During May and June, they saw a few narwhals along the fast ice edges of southern Lancaster Sound, but in late June the migration intensified, and the maximum number of narwhals was recorded on 4- 5 July. The migration at Cape Hay peaked on 15 July after a gradual increase in the number of narwhals which were migrating (Greendale and Brousseau-Greendale 1976). According to Johnson et al. (1976), 67.4% of the narwhals which they observed were near the coast, but the total number migrating in offshore waters was calculated to be considerably greater than the number migrating near the coast. Migrating narwhals were seen to occur predominantly near fast ice edges (Johnson et al. 1976). On the westward migration, approximately equal numbers were observed migrating along the south and north shores of Lancaster Sound (38.3% and 33.8% respectively), while 27.9% were seen in offshore waters. Large concentrations of migrating narwhals were observed along the ice edge at Navy Board Inlet and near southeastern Devon Island (especially Dundas Harbour). Very few whales were encountered further west along the Devon Island coast, implying that many narwhals must cross Lancaster Sound from Devon Island. After 4-5 July, the migration in Lancaster Sound decreased in intensity as narwhals began to enter the fiords of northern Baffin Island (Navy Board Inlet and Admiralty Inlet).

Observations by Renewable Resources Consulting Services Ltd. (1977) confirmed this main migration during July; in addition, this group saw a small number of narwhals on the south side of Lancaster Sound during May and June 1976. They also observed narwhals in the Devon Island flaw lead during April 1976.

Narwhals enter the fiords and bays of northern Baffin Island during the break-up of coastal fast ice in the spring (Wilkinson 1955; Degerbøl and Freuchen 1935). Large numbers enter Navy Board Inlet (Tuck 1957) and Admiralty Inlet (Johnson et al. 1976) after passing Cape Hay. Relatively few narwhals migrate further west, into Barrow Strait, Prince Regent Inlet, and Peel Sound (Finley 1976). When ice conditions permit, narwhals migrate to the heads of certain fiords, such as Tay Sound, Milne Inlet, Koluktoo Bay, Tremblay Sound, and Admiralty Inlet (Bissett 1970). Ellis (1957) found that narwhals enter Eclipse Sound from Pond Inlet during July, when the Inuit catch consists mostly of cows and their young. According to Miller (1955), the range in date of arrival of narwhals is 18 July to 1 August in the company of bearded seals Erignathus barbatus, while break-up of the ice (defined as the first day that a canoe can safely cross Eclipse Sound) can vary by 25 days (17 July to 11 August).

The observations of this study tend to confirm most of those cited above. During early June 1975 small numbers of narwhals were observed at the floe edges of Admiralty, Navy Board, and Prince Regent Inlets and eastern Barrow Strait. In May and June 1976, there were small numbers of narwhals at the Pond Inlet floe edge, and during July many whales were moving through the breaking ice of Pond Inlet and eastern Eclipse Sound; these whales were migrating to the heads of the fiords where they spend the summer.

According to Bissett (1970), narwhals begin to move from the fiords of northern Baffin Island to Lancaster Sound and Baffin Bay in September. Johnson et al. (1976) observed several hundred narwhals swimming north along the western shore of Admiralty Inlet on 19 September 1976. They also reported that many narwhals were moving eastwards or northeastwards through Lancaster Sound during late September. Of the total number observed at this time, 33% were migrating along the south shore of the sound, 50% offshore, and 17% along the north shore. The observations of Renewable Resources Consulting Services Ltd. (1977) also confirm this fall migration of the narwhal.

Webb (1976) has shed additional light on the autumn movements. He documented the distribution of the narwhal in Pond Inlet and Eclipse Sound during late September 1976 and documented a movement (during September and October) southwards along the Baffin Island coast as far as Broughton Island, where narwhals are usually hunted from mid-October to mid-November. There may also be a return spring migration along the same coast. Webb (1976) also noted the autumnal eastward migration of narwhals along the southern Devon Island and northern Bylot Island coasts.

Migratory routes of the narwhal in Hudson Bay and Foxe Basin are not known. Degerbøl and Freuchen (1935) stated that narwhals are only seasonal visitors to Hudson Bay and Foxe Basin, implying that they utilize Hudson Strait as a migratory route.

Narwhal migrations along the west coast of Greenland have been summarized by Vibe (1950). Apparently they move northward during

March and April in the offshore waters of Davis Strait following the retreating edge of the ice (Freuchen and Salomonsen 1958; Raven 1927). During June narwhals migrate northwards along the ice edge of Melville Bay (see Meldgaard and Kapel 1981) en route to Inglefield Bay, where 1,000 to 2,000 narwhals spend the summer (Vibe 1950; Bruemmer 1971). Some whales may continue as far as Smith Sound and occasionally into Kane Basin and Hall Basin (Vibe 1950).

Narwhals leave Inglefield Bay and the Thule area of northwest Greenland in mid-September to late October (Vibe 1950; Bruemmer 1971). They are sometimes hunted in Melville Bay while on their southward migrations during November (Freuchen and Salomonsen 1958). According to Tomilin (1957), narwhals reach Umanak by November and Disko Island by December.

The narwhal catch statistics tabulated by Kapel (1977) provide a general indication of the migration pattern of narwhals along the west coast of Greenland, showing that narwhals occur in the Disko Bay area from January to May, in the Umanak area in April-May (northward migration) and October-January (southward migration), and in May-November in the Upernavik region. They may be seen in the Thule region from June to September. Therefore it can readily be seen that the narwhal migration occurs over a protracted period along the west coast of Greenland, and they may be found in certain localities throughout the year (e.g. Upernavik).

Vibe (1967) discussed the effects of recent climatic warming in the arctic on the migrations of the narwhal and white whale, showing that the distributions of these whales have shifted towards the north and that the timing of the migrations changed; narwhals departed for the north earlier and returned south later than they did prior to the period of climatic warming.

The migrations of the narwhal in the seas east of Greenland are not well-known. The whaling captain R. Gray (1931) described their migration patterns in the Greenland Sea. Narwhals migrate southwards during autumn to the Denmark Strait, between Iceland and Greenland, where they are believed to spend the winter. In spring, narwhals migrate north into the ice fields of the Greenland Sea. Apparently males head these migrations with the females and young following (Greendale and Brousseau-Greendale (1976) observed a similar pattern at Cape Hay, Bylot Island). They head north or northeast into the pack ice searching for food, particularly squid (Gray 1931). Some whales migrate eastwards from the Greenland Sea to the north and east of Franz Josef Land (where Nansen (1897) also observed eastward migrating narwhals). Some narwhals may even reach the New Siberian Islands on this migration. In addition, many narwhals migrate northwestwards in spring from the Greenland Sea, visiting the fiords of east Greenland in summer (Pedersen 1931). They reappear in the northern Greenland Sea in autumn (Gray 1931).

Savssats - Savssat is the Greenlandic word for an aggregation of animals at an opening or polynya in the sea ice (Porsild 1918). The occurrence and origin of savssats consisting of white whales and/or narwhals in Disko Bay, west Greenland, have been described by Porsild (1918). Savssats are formed when whales become trapped within the new ice near the head of a bay during a sudden cold spell in calm weather, and the whales are forced to maintain breathing holes at which they may come into close contact as they compete for breathing space.

Savssats occur fairly often in certain fiords and bays along the coast of West Greenland, such as Disko Bay (Porsild 1918). They occur rarely in the Thule region of northwest Greenland (Bruemmer 1971; Vibe 1950), and occasionally in Melville Bay (Vibe 1950). In April 1860, hundreds of narwhals and white whales were found at such a breathing hole near Christianshaab (Brown 1868). Porsild (1918) described several savssats which were found in Disko Bay during the very cold winter of 1914-15, and he mentioned one instance where 1,000 narwhals were shot and harpooned by the Inuit, although many narwhals were killed but not retrieved. Kapel (1977) documented several savssats which have occurred more recently along the west coast of Greenland.

Savssats in the Canadian eastern arctic are recorded infrequently. Degerbøl and Freuchen (1935) recorded savssats at Lyon Inlet, Foxe Basin in 1916 and at Moffet Inlet, a fiord of southern Admiralty Inlet, in April 1924. This latter savssat initially comprised 600 narwhals utilizing a breathing hole the size of "two tents", but a tide crack allowed many to escape. They reported that the Inuit secured 203 narwhals with tusks and an equal number of tuskless whales, while many other narwhals drowned. Two narwhals were seen in a tide-produced hole in the sea ice at the mouth of Pangnirtung Fiord on 24 December 1925 (Anderson 1934). R. Harrington (in litt. 27 September 1962) documented the occurrence of narwhals in a small, regularly-occurring polynya, four miles north of Cape Coulman (in Peel Sound, near Stanwell-Fletcher Lake, Somerset Island), during December 1961. The most recent savssat in the Canadian arctic, comprising about 115 narwhals (mostly females with newborn), occurred on about 9 October 1979 at Agu Bay, Gulf of Boothia, at 70°18'N, 86°30'W (Mitchell 1981). Almost all of these narwhals were secured by Inuit hunters.

The importance of savssats as a source of natural mortality in narwhal populations is difficult to assess, but it could be significant in very cold years in regions where large numbers of narwhals spend the winter (e.g. Disko Bay area).

Food and Feeding

Previous studies - The feeding habits of the narwhal are fairly well-known for those seasons during which investigators have had access to this species (i.e spring to fall). The prey species eaten by narwhals during winter are not as well-known, but the winter diet is presumed to be mainly oceanic cephalopods.

Tomilin (1957) outlined the general feeding habits of the narwhal, which he classifies as a "teuthophage" or squid eater. The reduction in teeth, wide rostrum, coarse palatal surfaces, and deep diving ability exhibited by the narwhal are all adaptations for feeding on squid (Tomilin 1957). Tomilin (1957), citing others, stated that the narwhal feeds on squid Gonatus fabricii (Lichtenstein 1818), cod, flounder, skate Raja batis, halibut, salmon and herring.

The food of the narwhal in the Thule area of northwestern Greenland includes mainly arctic cod Boreogadus saida (Lepechin) and in addition shrimps and Greenland halibut Reinhardtius hippoglossoides (Walbaum) (Vibe 1950; Bruemmer 1971). The arctic cod becomes accessible to the whales when the ice breaks up (Vibe 1950).

At Scoresby Sound, east Greenland, narwhals feed on arctic cod (Pedersen 1931) and squids (Scoresby 1820). Gray (1887, 1889) has examined the stomach contents of narwhals which were harpooned in the Greenland Sea during July and August of 1886 and 1888. He found that remains of Gonatus fabricii were predominant, while the pelagic shrimp Pasiphaea tarda Krøyer and the surface-dwelling crustacean Hymourdora glacialis Buchholz occurred in several stomachs. Clarke (1966) stated that narwhals feed on Gonatus fabricii in the Norwegian Sea.

The stomach contents of narwhals in the Canadian arctic have been recorded by Degerbøl and Freuchen (1935), who reported that narwhals feed on small "tomcod" (arctic cod?) and shrimp during June and July in Eclipse Sound. They saw groups of up to nine narwhals in a line chasing "tomcod". However, the stomachs of 24 narwhals killed near Button Point on 5 July 1924 were empty. Degerbøl and Freuchen (1935) stated that narwhals feed on "salmon trout" (arctic char Salvelinus alpinus?) and Greenland halibut in Eclipse Sound in the autumn. Brown (1868) reported on the stomach contents of a female narwhal taken at Pond's Bay (Pond Inlet) in August 1861. Crustacea, fish bones, squid beaks (from Sepia loligo) and polychaetes were found in this stomach. At Wager Bay (western Hudson Bay) narwhals fed upon "salmon" (arctic char?) and sea scorpions (sculpins) (Degerbøl and Freuchen 1935).

Analysis of stomach contents - The 62 narwhals netted at Koluktoo Bay during 1963-65 had mostly empty stomachs, although a small number of otoliths (from arctic cod) and squid beaks (from Gonatus fabricii) were found in ten stomachs and small amounts of unidentified fish remains, in another three stomachs. In addition, two specimens contained remains of the decapod Sabinea septemcarinata (Sabine 1824). No remains of arctic char Salvelinus alpinus (L.) were found in the stomachs of these netted narwhals, in spite of extensive runs of char from the Robertson River into Koluktoo Bay (Mansfield et al., 1975).

The stomachs of narwhals taken in open water during August and September of 1974-76 were also empty, except for small numbers of otoliths of arctic cod and squid beaks (Gonatus fabricii) and sometimes fish bones or partly-digested fish. Finley and Gibb (1982) found that most narwhals taken during the open water seasons of 1978-79 at Pond Inlet had empty or nearly-empty stomachs. Vibe (1950) observed that the stomachs of narwhals killed in summer in northwestern Greenland were often empty, but he implied that this was due to regurgitation of the food during the stressful pursuit of the hunt.

Narwhals were feeding heavily as they migrated through the breaking fast ice in Pond Inlet during July 1976. The stomachs were usually full of undigested or partly-digested food; the most important items were arctic cod Boregadus saida, the pelagic shrimp Pasiphaea tarda Krøyer, and the squid Gonatus fabricii. Small numbers of the decapod Eualus gaimardi belcheri (Bell, 1855) were found in one specimen and, in addition, the mysid Boreomysis nobilis G.O. Sars was recorded in several stomachs. Only one intact specimen of Gonatus was recovered; this species was generally represented in the stomachs by large numbers of beaks, eye lenses, and some semi-digested tissues. Beaks were identified as belonging to the family Gonatidae, while the intact specimen was referable to Gonatus. Consideration of the geographical distribution of Gonatus led to the conclusion that these specimens were Gonatus fabricii (Dr. C.C. Lu., in litt. 7 January 1977). Arctic cod specimens were nearly intact or partly- digested, while the crustaceans were often intact or in various stages of digestion. Vibe (1950) and Bruemmer (1971) also observed full stomachs of narwhals which were taken at the floe edge of Inglefield Bay, northwest Greenland. During the open water (summer) season, narwhals evidently feed lightly, and the few otoliths and squid beaks observed may have been retained in their stomachs since their last main feeding in the spring. Finley and Gibb (1982) suggest that squid beaks may be retained in the stomach for a long period after ingestion.

No remains of Greenland halibut were detected in any of the narwhal stomachs examined, but at the floe edge of Pond Inlet on 28 May 1976, Inuit hunters shot a male hooded seal Cystophora cristata, the stomach of which contained six large Greenland halibut. It is possible that at the floe edge, prior to break-up of the ice, narwhals feed on Greenland halibut and squid, for which they must probably dive to a considerable depth; during the break-up period narwhals move through the ice field and feed pelagically, mainly on arctic cod and Pasiphaea, and perhaps the occasional squid. The majority of squid beaks in their stomachs at this time have probably been retained since feeding at the floe edge or in Baffin Bay while on northward migration.

Finley and Gibb (1982) reported on studies of feeding habits of narwhals taken in the Pond Inlet area during 1978 and 1979. They found that the diet consisted of fish (93%) and Gonatus fabricii (7%), with negligible quantities of decapods and mysids. Arctic cod was a major food item of narwhals taken at the ice edge, while polar cod (Arctogadus glacialis) was important for whales taken in the ice cracks. Greenland halibut was important at ice edges and in cracks and occurred predominantly in adult males. Gonatus fabricii was found in the stomach contents of narwhals taken at the ice edge and in ice cracks (Finley and Gibb 1982).

There is apparently no information on the distribution and abundance of these prey species in the Lancaster Sound-Baffin Bay area. Squires (1957) stated that Pasiphaea tarda is a bathypelagic (800-1200 m) species that occurs in regions influenced by water of Atlantic origin. The distribution and depths of occurrence of this species in Pond Inlet and Eclipse Sound are not known. On the other hand, Boreogadus saida is pelagic (underneath the ice) while Greenland halibut is demersal (at depths of 200-600 m) and typical of Atlantic- influenced subarctic seas (Andriyashev 1954). Gonatus fabricii is eurybathic, occurring from near the surface to deeper than 4000 m (Akimushkin 1963); adult squids occur at greater depths than larval or juvenile squids, which are found near the surface (Akimushkin 1963; Clarke 1966). Probably the feeding behaviour of the narwhal during spring is a combination of pelagic and deep-water feeding. More work on the spatial and depth distribution of prey species in relation to narwhal feeding habits will help to resolve this problem.

Behaviour

Many accounts of the narwhal deal with the behaviour of this species, but the majority of the descriptions are anecdotal in nature and of little scientific value. An investigation of the social behaviour of the narwhal has recently been completed by Silverman (1979), who studied in great depth most of the topics reviewed here.

Group structure and size - Narwhals usually occur in groups of three or four, occasionally up to 10 (Tomilin 1957). Sexual segregation in the narwhal has been observed by Scoresby (1823), who recorded schools of 15 to 20 males "fencing" with their tusks and other groups of up to six individuals; all of one sex. Pedersen (1931), on the other hand, described mixed schools of 50 individuals headed by old males. Sexual segregation is also evident in herds of migrating narwhals. Large groups of males head the migration, followed by the females and young (Greendale and Brousseau-Greendale 1976). On the other hand, migratory schools may consist of 6 to 10 animals of all age/sex classes (Degerbøl and Freuchen 1935); 3 to 10 animals in large herds (Bruemmer 1971); 10 to 20 animals of all age/sex classes (Vibe 1950); or up to 15 to 20 narwhals (Pedersen 1931). Foraging narwhals are found in groups of up to nine animals (Degerbøl and Freuchen 1935).

Summering groups of narwhals may also be segregated by age and sex. Vibe (1950) stated that females and calves are usually found in summer at the head of Inglefield Bay in the Thule region, while males occupy the outlying regions. Gray (1887) also noted that male narwhals segregate from the females and calves in east Greenland waters during July.

Tables 2 and 3 present the composition of groups from the netted sample (1963-65) and the hunted sample (1974-76), respectively. The floe edge catch of 1976 was not analysed in this way since, at this hunt, usually only one animal is removed from each group and females were sampled selectively. This analysis was carried out with the assumption that the near-simultaneous capture of several whales of the same age or sex in the same net or in the same hunting area would reflect the occurrence of groups of narwhals of different age and sex structure. Table 2, which is based on the netted sample, strongly suggests the existence of segregation by age and sex within the summering narwhal population. These groups include immature and maturing males, mature females with young, and adult males (Table 2). Evidence for segregation from the composition of the hunted sample is less convincing, since daily catches here are often selective and tend to consist of a mixture of males and females in various stages of maturity (Table 3). These daily catches probably consist of individuals from several different pods, while nets are more likely to capture several individuals from the same pod. Hence the non-selective netted sample provides better evidence for segregation than the hunted sample. Appendix 3 provides statistical evidence for segregation in the summering population.

Vibe (1950) and Mansfield *et al.* (1975) found that mature female narwhals tend to segregate from the herd, selecting the heads of the fiords as summering places. Sexual segregation similar to that observed in the narwhal has also been noted in the pilot whale *Globicephala melaena* (Sergeant 1962), the sperm whale *Physeter catodon* (Ohsumi 1966; Best 1979), and dolphins of the genus *Stenella* (Kasuya 1976).

Table 2. Age and sex composition of narwhals captured in each net set in Koluktoo Bay, 1963-65.[a]

	Number of males				Number of females			Total
Date	Calves	Immature	Maturing[b]	Mature	Calves	Immature	Mature	Captured
Aug. 9/63		2				1		3
Aug. 10/63		1	2	1				4
Aug. 13/63					1	1	1	3
Aug. 16/63					2		2	4
Aug. 19/63		2						2
Aug. 9/64	1						1	2
Aug. 10/64					1		1	2
Aug. 12/64	1				1		3	5
Aug. 25/64	1	1						2
Aug. 13/65		1	1					2
Aug. 14/65				4				4
Aug. 19/65		1			1		1	3
Aug. 19/65							4	4

[a] excluding net sets capturing only one individual.

[b] defined in section "Reproduction in the Male".

Table 3. Age and sex composition of narwhals captured by Inuit hunters on a single day and in a particular area, 1974-76.[a]

Date	Number of males				Number of females			Total
	Calves	Immature	Maturing[b]	Mature	Calves	Immature	Mature	Captured
				Pond Inlet				
Aug. 27/74		6		1			1	8
Aug. 27/74						1	3	4
Aug. 03/75		2						2
Aug. 04/75						1	2	3
Aug. 04/75		1			1	1	2	5
Aug. 14/75		1	1			2		4
Aug. 20/75	1						3	4
Aug. 27/75		1		1				2
Aug. 29/75	1	2					3	6
Sept. 01/75		2	1	1		1	2	7
Sept. 22/75			1	2				3
Aug. 28/76					1		1	2
				Arctic Bay				
July 27/75				3				3
Aug. 02/75						2		2
Aug. 11/75		1					6	7
Aug. 15/75	1					2		3
Aug. 12/76			2				1	3
Aug. 16/76			1			1		2

[a] excluding hunts capturing only one individual.

[b] defined in section "Reproduction in the Male".

Diving and swimming - Vibe (1950) recorded that narwhals may dive for up to 15 minutes or about 100 m between successive surfacings while on migration. Rutilevskii (1958) gave the diving time as 7-8 minutes and occasionally up to 20 minutes; he also claimed that narwhals can swim for 2 km under the ice. Scoresby (1820) noted that harpooned narwhals could dive to a depth of 200 fathoms (366 m).

Many observers have noted "sleeping" behaviour in the narwhal (Gray 1889; Degerbøl and Freuchen 1935; Miller 1955). This often occurs when a group of whales surfaces at a hole in the sea ice or near the floe edge. The narwhals remain at rest for up to 10 minutes, with only part of the back above water; this position is resumed after a brief respiratory period. Occasionally, the tusk may be raised above the water. A group of whales will dive in unison after such a resting period. In rough seas, narwhals rest at some depth and only come to the surface for respiration (Gray 1889).

Bruemmer (1971) has related narwhal swimming behaviour to different activities. During feeding, narwhals move erratically and spend little time near the surface; during migration, swimming is rapid, directional, and near the surface. Narwhal hunting is most successful when the whales are moving slowly or milling around, spending up to one-third of their time at the surface.

Uses of the tusk - The tusk of the narwhal has captured the imagination of many naturalists and numerous suggestions have been put forth as to how it is employed. Tomilin (1957) suggested that it may be used in fighting or for defense against sharks, but Degerbøl and Freuchen (1935) and Porsild (1922) pointed out that a tusk composed of such brittle material as narwhal ivory would not likely be used in this way. The possible role of the tusk in feeding has been discussed by many observers. Tomilin (1957) thought that the tusk may have been used early in the narwhal's evolutionary history for feeding, but that it now serves as a weapon. Degerbøl and Freuchen (1935) and Winge (1921) suggested that the tusk is used to scour the bottom for benthic food organisms, as evidenced by the fact that the tip is always worn smooth and flattened ventrally. In addition, Porsild (1922) found that 34% of a large sample of tusks were broken but that the fracture was invariably worn smooth and polished, while Degerbøl and Freuchen (1935) noted that the cavity at the fracture site was often plugged with sand or other bottom material. These observations suggest that the tusk may be used in foraging near the bottom, although Mansfield et al. (1975) pointed out that, since the tusk points slightly downward, wear at the tip and occasional breakage could be caused by the tusk accidentally scraping the bottom as the narwhal pursues Greenland halibut or bottom shrimps. Jardine (1837) and others speculated that the narwhal may spear prey with its tusk, but this has never been observed. The role of the tusk in feeding must be quite minor for, as Scoresby (1820) pointed out, female narwhals, segregated from males for a considerable part of the year, get along without tusks quite well.

In order to explain tusk wear, Scoresby (1820) and Tomilin (1957) suggested that it was used to break thin ice. This is unlikely for, as Degerbøl and Freuchen (1935) have stated, the tusk is extremely brittle, and observations on savssats (Porsild 1918) show that narwhals use the head or back to break thin ice, manipulating their tusks very carefully.

Possibly the tusk is used in aggressive male display (Mansfield et al. 1975) since the narwhal is probably polygamous, as evidenced by the male's larger size and later attainment of sexual maturity compared to females (see section on "Reproduction in the Male"). Possible evidence of this usage is indicated by the occurrence of numerous scars, believed to be made by the tusk, on the melon, head, and flanks of some males. These are thought to result from accidental physical encounters as adult males display to each other. Silverman (1979) has studied this problem in detail, and her findings concur with this hypothesis.

Porsild (1922) and Knudsen (1958) have documented the unusual occurrence of the tip of a tusk inserted into the fractured tip of a large broken tusk. There have been speculations as to how this might happen, but a simple explanation could be that one tusk is occasionally rammed by another, if head-to-head aggressive display is practiced by adult males. Dow and Hollenberg (1977) have incorrectly attributed these plugs in fractured tusks to the deposition of new dentine.

Recently, Silverman and Dunbar (1980) presented convincing evidence that the tusk is used in aggressive encounters between adult male narwhals, especially during the breeding season. Best (1981), utilizing observations from the literature including those of the above authors, concluded that the tusk functions as a secondary sexual character for non-aggressive assessment of hierarchical status among males.

Acoustic behaviour - The narwhal does not seem to be as vocal as its relative the white whale, but its limited repertoire does include various communicative whistles and shrieks and the "rusty hinge" sounds used in echolocation. The reader is referred to Watkins, Schevill and Ray (1971) and Ford and Fisher (1978) who have recorded and analyzed the sounds of free-ranging narwhals. Robisch, Malins, Best and Varanasi (1972) have investigated the biochemical nature of the lipids that may be involved with sound reception through the mandible of the narwhal.

Behaviour at mating and birth - The only published observation of copulation by narwhals is that of Vibe (1950), who recorded that a Polar Eskimo observed narwhals copulating vertically, belly to belly; the location was Melville Bay, but the season was not stated. Pedersen (1931), probably on the basis of Eskimo lore, claimed that narwhals are born tail-first and that birth lasts several weeks.

Predators

Other than man, the main predator of the narwhal is probably the killer whale Orcinus orca. According to Brody (1976), the Inuit of Baffin Island believe that narwhals are anxious to enter the ice-covered fiords in spring because killer whales are lurking offshore in the open water of Baffin Bay. Because of the high dorsal fin, killer whales are not adapted to living within the pack ice. They are present in small numbers in the eastern Canadian arctic in summer, but the magnitude of their predation on narwhals has not been assessed. According to Inuit informants killer whales occasionally drive narwhals into very shallow water where they strand, becoming easy victims for hunters. Degerbøl and Freuchen (1935) documented several instances of narwhals driven inshore by killer whales in Eclipse Sound, northern Baffin Island, and, in addition, Royal Canadian Mounted Police game reports make occasional reference to this phenomenon. Polar bears occasionally attempt to catch narwhals, since specimens have been seen with characteristic claw marks on the head (personal observation and H.D. Fisher, in litt.). Inuit hunters reported that a polar bear caught a narwhal from a hole in the sea ice near Pond Inlet during spring 1976. According to Gray (1931) walruses infrequently attack and kill sleeping narwhals.

The Greenland shark Somniosus microcephalus is not an active predator of the narwhal, as some authors may have thought. Beck and Mansfield (1969) reported on 18 sharks captured in the same nets which were set for narwhals in Koluktoo Bay from 1963-65; some of the sharks had fed on blubber and offal from the whaling operation while others had attacked dead narwhals in the nets and torn huge chunks of skin and blubber from them. Greenland sharks are lethargic scavengers, and they frequent the edge of the ice or beach where dead narwhals are being processed.

The predation on narwhals by walruses, polar bears and killer whales probably does not comprise a significant proportion of the annual natural mortality of narwhal populations.

Parasites

The narwhal carries a substantial burden of ecto- and endoparasites. The amphipod whale lice Cyamus monodontis Lütken and C. nodosus Lütken (Leung 1967) are found in the fold of the skin at the base of the tusk and in superficial healed wounds. The internal parasites are listed in Table 4. The first four species, shown as occurring in the sinuses of the middle ear, are all synonymous. Anisakis simplex and Ascaris simplex are also synonymous, as are Terranova decipiens and Porrocaecum decipiens.

Virtually nothing is known about diseases in natural narwhal populations.

Table 4. Endoparasites of the narwhal.

Location in body	Species	Source
Middle ear sinuses[a]	*Stenurus alatus* (Leuckart, 1848)	Dailey and Brownell (1972)
	Pseudalius alatus (Leuckart)	Gray (1889)
	Torynurus alatus (Leuckart, 1848)	Tomilin (1957)
	Pharurus alatus (Leuckart, 1848)	Arnold and Gaskin (1975)[b]
Stomach	*Anisakis simplex* (Rudolphi, 1809)	Dailey and Brownell (1972)
	Ascaris simplex (Rudolphi)	Gray (1889)
Intestine	*Anisakis simplex* (Rudolphi, 1809)	Tomilin (1957)
	Terranova decipiens (Krabbe, 1878)	Tomilin (1957)
	Porrocaecum decipiens (Krabbe, 1878)	Dailey and Brownell (1972)
Lung	*Halocercus monoceris* sp. n.	Webster, Neufeld and MacNeill (1973)

[a] including eustachian tube (Gray 1889; Tomilin 1957) and veins and lungs (Tomilin 1957).

[b] identified from the cranial sinuses of narwhals captured at Koluktoo Bay, 1963-65.

AGE DETERMINATION[1]

Introduction

The use of growth layers in the teeth of pinnipeds for age determination was developed independently by Laws (1952) and Scheffer (1950), and has been extended to odontocetes. See Jonsgaard (1969) for a review of the use of the technique in sea mammals and Sergeant (1959a) for studies of age determination in odontocetes. A symposium volume on recent age determination studies in toothed whales and sirenians, including the proceedings of a workshop, has recently been published (Perrin and Myrick 1980). The embedded tooth and mandible of the narwhal contain well-defined growth layers which seem to be related to age in this species.[2]

The Embedded Tooth

The structure and development of the teeth of the narwhal have been historically reviewed in an earlier section "Anatomy". This section deals mainly with the structure of the growth layers which are observed on the cut surface of the longitudinally-bisected embedded tooth.

Description of growth and growth layers - The embedded tooth of the newborn narwhal is about 9 to 10 cm long and consists of an elongated cone of dentine, which is 2 to 3 mm thick at the apex of the tooth in a median longitudinal (mid-sagittal) section. It is covered with a very thin layer of cementum from root to tip, where there may also be some enamel tissue. In the newborn tooth (Plate II, a) a small amount of post-natal dentine may be present beyond the thin dark, often double, neonatal line, which is also distinguishable in older teeth. An external circumferential depression on the root corresponds to the intersection of the neonatal line with the surface of the tooth. The neonatal line may reflect a transient retardation of growth of the newborn narwhal for a few hours or perhaps a few days after birth. The prenatal dentine

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[1] This section has been published in modified form as Hay (1980).

[2] Bada, Mitchell and Kemper (1983) provide preliminary results on the use of the aspartic acid racemization technique for determining age of the narwhal.

is uniform in appearance (Plate II, a), translucent (Plate III, a) and highly calcified, as shown by its stainability with silver nitrate by the von Kossa method (Plate III, d). The neonatal line is poorly calcified (Plate III, d) and transparent (Plate III, a).

The tooth of the neonate subsequently elongates rapidly with deposition of the first four or five dentinal growth layers as nested elongated cones. Each growth layer consists of a broad light band and a narrow dark band, as seen in reflected light (Plate II, b to h). On closer inspection, each narrow dark band is composed of a wide bright or foamy white band bounded by a pair of narrow dark lines, as viewed in reflected light (Plate II). Examination of thin sections of dentine in transmitted light reveals that the foamy white band is extremely opaque and that the bounding narrow dark lines are translucent (Plate III, b). Silver nitrate staining of bisected teeth (Plate III, d to f) reveals that the narrow dark bands are poorly calcified compared to the wide bands. In young animals sampled during summer, such a narrow dark band occurs at the edge of the pulp cavity (Plate II, b).

Cementum is deposited around the growing tooth, but it does not seem to be useful for age determination because of its thinness (0.5 to 1.0 mm) and also because cemental layers are not uniformly represented along the length of the tooth, due to rapid elongation of the tooth during early postnatal life. In addition, cemental layers are difficult to resolve on the median longitudinal sections of the embedded teeth. Moreover, the cementum in the root portion of the tooth is irregular, forming a nodular coating 2 to 3 mm thick with a marbled non-laminated appearance. The embedded teeth cease their growth relatively early in postnatal life, owing to growth of the cementum which eventually covers the root, leading to a cessation of dentinal deposition (occlusion). This is evident in Plate III, c. Cemental layers and dentinal layers are equal in number in the teeth of very young animals.

Prominent circumferential ridges on the root of the embedded tooth which correspond to the internal narrow dark bands may also provide a means of determining age, but in older whales these ridges become obscured by cementum. Longitudinal ridges and grooves on the external surface of the tooth are also present, occasionally producing a spiralled surface pattern which also tends to obscure the ridges.

The open pulp cavities of the teeth of young animals are filled with pulp tissue. In older teeth, if deposition of dentine is still occurring, a small cone of pulp tissue remains at the proximal end of the tooth, while cementum slowly encroaches upon the dentine at the root.

Some dentinal layers contain faint zones which are considered to be accessory and are thus ignored in counts of dentinal layers. These accessory bands are variable between animals and between layers, with regard to their presence and definition, and they usually present no problems in counting the dentinal layers. However, the group which examined material from the narwhal at the Workshop on Age Determination of Odontocete Whales considered this question in detail (see Appendix 1).

The first-formed dentinal layers are deposited at an acute angle to the long axis of the rapidly elongating tooth; later-formed layers are parallel to each other and thinner. These later-formed layers form a knot of dentine at the root of the tooth; the proximal end of this knot usually curves mediad (towards the long-axis of the rostrum) from the long axis of the tooth, to which it may be almost perpendicular (Plate II). Small nodules of osteodentine occasionally form within the orthodentine of the proximal portion of the knot, but they do not interfere with counts of growth layers. Osteodentine is common in the teeth of the sperm whale Physeter catodon (Nishiwaki, Hibiya and Ohsumi 1958), the pilot whale Globicephala melaena (Sergeant 1962) and the beaked whale Berardius bairdii (Kasuya 1977).

Age determination of marine mammals based on dentinal growth layers is a difficult and controversial field of investigation. The International Whaling Commission (1969) has standardized terminology for the component zones of the dentinal growth layers which has been followed by most investigators to date. The dentine consists of alternating wide, dense, opaque bands and narrow translucent bands. The opaque bands appear light in reflected light and dark in transmitted light, while the translucent bands appear dark in reflected light and light in transmitted light (I.W.C. 1969; Sergeant 1959a). As a result of a workshop on odontocete age determination, new standardized terminology has been proposed (see Perrin and Myrick 1980).

The relative degree of mineralization of the component zones of a single growth layer is also unresolved. According to Bloom and Fawcett (1975) and Sognnaes (1960), highly calcified dentine is more transparent than poorly calcified dentine. Most investigators in this field tend to agree that the varying optical opacity of the growth zones reflects variation in mineralization or content of calcium salts, but there is considerable disagreement as to which zone of a growth layer is the more heavily calcified.

Laws (1952, 1953) examined the structure of the dentinal growth layers of the southern elephant seal Mirounga leonina. By examination of the polished cut surface of the canine tooth of this species, he found that dark, poorly-calcified "inter-globular" or "marbled" dentinal zones alternated with light, well-calcified "columnar" or dense dentinal zones. Laws (1962) added that the dense, columnar, well-calcified dentine is more optically transparent than the marbled dentine. In certain pinnipeds, such as the ringed seal Phoca hispida (McLaren 1958), a thin, poorly calcified reticulated or vacuolated dentine may be formed; this type of dentine appears foamy white in reflected light (Klevezal and Kleinenberg 1967). Brodie (1970) found that this type of dentine occurs occasionally in the teeth of the white whale Delphinapterus leucas.

The neonatal line of the narwhal is translucent and poorly calcified (Plate III, a and d). Each postnatal dentinal growth layer comprises one wide, well-calcified translucent zone and one narrow, poorly-calcified opaque zone. However, the narrow zone is foamy white in reflected light (Plate II) and appears to fit the description of marbled or interglobular dentine, which is poorly calcified but optically dense (Laws 1962). This type of dentine consists of a loose assemblage of mineralized spheres called calcospherites, between which there is much non-mineralized, organic tissue (Klevezal and Kleinenberg 1967). Possibly the high optical opacity of such poorly-mineralized dentine is due to the higher concentrations of ground substance and collagenous tissue. The prenatal dentine is more transparent and possibly more heavily calcified than the postnatal dentine (Plate III, a and d).

The neonatal line is usually the most consistently-identifiable structure visible in the teeth of odontocetes. It is transparent, narrow, and unstainable with haematoxylin in most odontocetes (Kasuya 1977; Kubota, Nagasaki, Matsumoto and Tsuboi 1961; Nishiwaki and Yagi 1953, 1954; Ohsumi, Kasuya and Nishiwaki 1963; Sergeant 1959a). Haematoxylin apparently stains well-calcified tissues after decalcification which apparently exposes the collagen matrix to the dye (Sergeant 1959a). Most investigators attribute the neonatal line to the stress of birth and associated reduced feeding (Kubota _et al._ 1961; Nishiwaki and Yagi 1953, 1954). The prenatal dentine of odontocetes is usually opaque (Ohsumi _et al._ 1963; Sergeant 1959a) and uniformly well-calcified, hence staining intensely with haematoxylin (e.g. Nishiwaki and Yagi 1953, 1954).

The degree of mineralization in relation to optical opacity of the dentine is also a controversial point. Some studies show that the transparent zones are highly calcified and poor in organic matrix; these bands therefore stain heavily with haematoxylin in decalcified sections and with silver nitrate (Klevezal and Kleinenberg 1967). The opaque dentinal bands, which contain the dentinal tubules and odontoblast processes, are poorly mineralized and stain weakly with haematoxylin (Klevezal and Kleinenberg 1967). Other studies with similar conclusions are those of Kubota _et al._ (1961) for the fur seal, Nishiwaki and Yagi (1953, 1954) for the striped dolphin _Stenella coeruleoalba_, Ohsumi _et al._ (1963) and Bow and Purday (1966) for the sperm whale, and Kasuya (1976) for dolphins of the genus Stenella. Grue Nielson (1972) has demonstrated by micro- radiographic study of the teeth of the harbour porpoise Phocoena phocoena that the narrow, optically-translucent zones are radio- opaque to X-rays and therefore have a higher content of calcium salts than the more radio-lucent broad optically-opaque zones; however, the latter zones stained better with haemalum than the narrow zones.

On the other hand, some studies show that the opaque bands are better calcified and stain well with haematoxylin (e.g. Sergeant 1959a). Treatment of sperm whale half-teeth with 5% formic acid reveals a pattern of grooves corresponding to the well-calcified opaque zones and ridges corresponding to the poorly calcified translucent bands (Gambell and Grzegorzewska 1967). This conclusion also applies to the white whale Delphinapterus leucas (Brodie 1970) and the bottlenosed dolphin Tursiops truncatus (Sergeant 1959a). Schour and Hoffman (1939) obtained similar results for a variety of vertebrates, including fish, crocodiles, various rodents, domestic animals, and man.

In addition to the main growth layers described above, supplementary or accessory translucent bands sometimes occur within the wide opaque bands and should not be counted (Klevezal and Kleinenberg 1967; Sergeant 1962). These accessory bands do not create any problems in counting the growth layers on the polished cut surface of the bisected embedded tooth of the narwhal.

It is believed that the optimal nutrition of the suckling calf may decrease the clarity of the earliest dentinal layers. For example, the first 2 to 4 dentinal layers in the teeth of the white whale may be faint (Sergeant 1973; Brodie 1970). Sergeant (1962) believed that the first opaque band in the teeth of the pilot whale Globicephala melaena represents the two year suckling period; however, he occasionally noted a faint translucent band within this first opaque band. In contrast to these results, all of the growth layers in the embedded tooth of the narwhal are conspicuous and spatially consistent, with the exception of the first layer, which is occasionally faint but usually detectable.

Each dentinal growth layer of the embedded tooth of the narwhal is composed of a multitude of fine laminae (Plate III, b). The time basis of this fine zonation is not known but could be the order of a few days. In the teeth of the beaked whale Berardius bairdii, the prenatal dentine contains 12 to 15 fine layers, each postnatal dentinal growth layer contains 22 to 31 fine layers, and cemental layers contain, on average, 12.4 fine layers (Kasuya 1977). These fine layers are also present in the teeth of the suckling Alaskan fur seal Callorhinus ursinus; each of an average of 11 nursing cycles is recorded as a narrow layer within the dentine during the four-week lactation period (Scheffer and Peterson 1967). Schour and Hoffman (1939) found that the dentine and enamel of various vertebrates from fish to man were composed of a succession of fine layers that averaged 16 μ in width. Some of these fine layers were accentuated at regular multiples of 16 μ, especially in wild as opposed to laboratory-reared animals. Schour and Hoffman (1939) maintained that this 16 μ pattern is a result of a constant physiological rhythm of calcium deposition and secretion, and that the accentuated bands (Owen's contour lines in human teeth) are caused by endocrine, nutritional, or pathological disturbances to growth and calcium metabolism.

In summary, each dentinal growth layer of the embedded tooth of the narwhal consists of a wide, translucent, well-calcified zone and a narrow, opaque, poorly calcified zone. The prenatal dentine is particularly transparent and well-calcified, as are the narrow lines (dark in reflected light) which bound the narrow opaque zones (bright or foamy white in reflected light, and similar to the marbled or interglobular dentine described by other researchers).

Occlusion and knot development - In the teeth of older animals, after the pulp cavity has disappeared, dentinal layers continue to be deposited but they comprise an enlarging knot at the root. Deposition continues until the encroaching cementum covers the entire root including its proximal end. In teeth with occluded pulp cavities, dentinal layer counts provide minimum estimates of age. The mechanics of dentinal deposition in the knot are unknown, and the reasons for the persistence of pulp tissue at the proximal end of the tooth, long after the pulp cavity has disappeared, are also unknown.

Table 5 summarizes the changes in knot development, closure of the pulp cavity, and dentinal occlusion with increasing body length and number of dentinal layers. The age (number of dentinal growth layers) at which occlusion occurs is lower than that predicted from the length-age relation (see section on Growth) because, of course, the actual age of animals whose teeth have occluded is greater than the count of dentinal layers, and it is not known how long these teeth have been occluded. The onset of formation of a knot (dentine and irregular cementum at the root) occurs, on average, at about seven layers in males and nine layers in females (Table 5). Maximum knot development in male teeth occurs at body lengths greater than 400 cm (17-18 layers); however, the teeth of a few large old males have poorly-developed knots. In males, the pulp cavity usually closes at a body length of about 330 cm (nine layers), although the pulp cavities of the teeth of a few males, with up to 15 dentinal growth layers, are still open.

The number of dentinal growth layers that are laid down prior to occlusion is quite variable, as shown in Table 5. This is also demonstrated by the observation that, although the size of the dentinal knot increases with body length in male whales with unoccluded teeth, some large male narwhals have occluded teeth and small dentinal knots, implying cessation of dentine deposition at a relatively early age, while other large male narwhals with occluded teeth have large dentinal knots, implying more recent cessation of dentinal deposition.

The dentinal knots of females develop in a manner similar to those of males, but in general they are smaller. Pulp-cavity closure occurs after nine layers have been deposited, or at a body length of about 320 cm. Table 5 demonstrates that the embedded teeth of

Table 5. Dentinal development in the embedded tooth.

	Males		Females	
	Body length (cm)	No. dentinal layers	Body length (cm)	No. dentinal layers
Sample size	75	77	94	97
Knot development				
Mean	290	7	300	9
Range	290-290	7-7	290-310	7-11
Pulp cavity closure[a]				
Mean	330	9	320	9
Range	310-390	7-15	310-330	9-9
Dentinal occlusion[b]				
Mean	400	16.0	370	13.8
Range	390-430	13-19	350-410	11-24

[a] no visibly open pulp cavity, but deposition occurring.

[b] cessation of dentinal deposition (cementum covers root).

females occlude earlier in life than those of males. However, a few larger females (380-400 cm) were still depositing dentine with 15 to 24 dentinal layers present in the embedded teeth. The incidence of dentinal occlusion increases greatly after the attainment of sexual maturity in both sexes. The average number of dentinal layers in the occluded teeth of 29 males is 16, corresponding closely to the average age at the attainment of sexual maturity by males (17 composite growth layers), while the occluded teeth of 37 females had an average of 13.8 dentinal growth layers, which is 2.0 layers greater than the average age of sexual maturity in females (see sections dealing with male and female reproduction for methods of estimating age at sexual maturity).

Thus, the embedded teeth are potentially useful for age determination to a minimum age of 11 growth layers, although most teeth are useful until sexual maturity in both sexes. Several teeth may be useful beyond this age (up to 19 layers in males and 24 layers in females), due to variability in the number of layers laid down when occlusion occurs (Table 5).

Dentinal occlusion is also a problem for determining age of many other odontocetes. The maxillary teeth of female sperm whales occlude after 30 dentinal layers have been deposited, while the maxillary teeth of males do not occlude (Nishiwaki _et al_. 1958; Best 1970). The teeth of pilot whales occlude when 12 dentinal layers, on average, have been deposited (Sergeant 1962), while teeth of _Berardius bairdii_ occlude at from 3 to 17 years of age (Kasuya 1977). The teeth of _Stenella attenuata_ occlude when 18 dentinal layers have been deposited (Perrin _et al_. 1976), while the teeth of _S. coeruleoalba_ occlude after the deposition of 14 dentinal layers, on average (Miyazaki 1977).

Growth in tooth length - The embedded tooth of the male achieves a maximum length of 17.2 to 28.7 cm after the accumulation of six dentinal layers (280-290 cm body length), while in the female the maximum tooth length of 16.3 to 22.8 cm is achieved after four or five layers (260-270 cm body length) have been deposited. In five young males whose tusk had not yet erupted or which were tuskless, the left tooth was longer than the right tooth. In 10 females, the left tooth was longer than the right in five cases; the right was longer in four cases; and in the other case they were equal in length. Seventy-one right embedded teeth of males averaged 21.67 cm, while 83 right embedded teeth of females averaged 19.24 cm in length.

Quantitative analysis of dentinal growth - Figures 3 and 4 show the increases in total apical thickness of postnatal dentine with body length and number of growth layers, respectively. These values represent, for each whale, the sum of thicknesses of all postnatal dentinal layers, measured at their apices perpendicular to the axis of dentinal layering.

In both sexes, the total thickness of dentine is proportional to body length and age (up to 15 dentinal layers); the maximum amount of dentine deposited is 39 mm in the tooth of a 340 cm male with 14 dentinal layers. The tooth of a 338 cm female with 11 layers had deposited 32.6 mm of dentine. In females there is an indication of a decreasing rate of dentinal deposition after 12 to 14 layers and 350 cm body length, but data points after these values are few owing to dentinal occlusion. The rate of dentine deposition is similar in both sexes until about 10 layers have been deposited, at a body length of about 330 cm, after which dentine deposition rate decreases in female embedded teeth while that in the male remains relatively high. However, as seen in Figures 3 and 4, the accumulation rate of dentine is highly variable amoung individuals and the rate of dentine deposition in the teeth of females is lower than that in the male.

The change in thickness of dentinal layers with age in both sexes is shown in Figure 5. The thickness of each dentinal layer varies widely among animals, but the mean layer thickness decreases as layer number increases in both males and females. In males, the mean layer thickness decreases from layer one (3.0 mm) to layer three (2.35 mm) and then increases slightly to layer six (2.88 mm). After the sixth dentinal layer, the mean value declines steadily to layer 14 (1.35 mm). The increase in layer thickness from layer four to six

Figure 3. Total thickness of postnatal dentine in the embedded tooth plotted against body length in narwhals. The linear regressions of dentinal thickness (y) on length (x) are (excluding tusks and occluded teeth):

$$y = 0.17871x - 33.98135 \text{ (males) and}$$
$$y = 0.16062x - 30.73724 \text{ (females)}$$

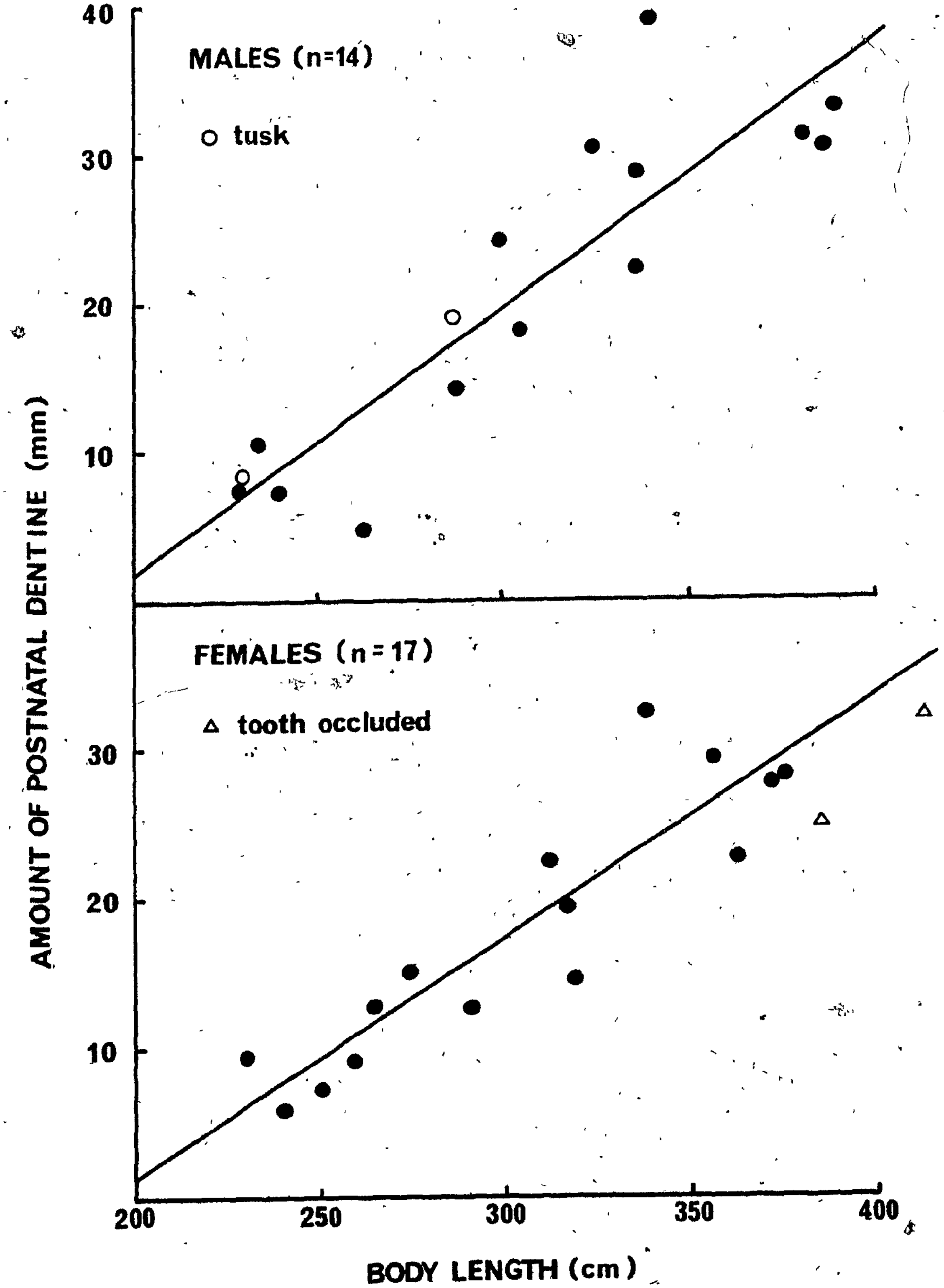

MALES (n=14)
○ tusk
FEMALES (n=17)
△ tooth occluded
AMOUNT OF POSTNATAL DENTINE (mm)
BODY LENGTH (cm)
40
30
20
10
30
20
10
200
250
300
350
400

Figure 4. Total thickness of postnatal dentine in the embedded tooth plotted against number of dentinal layers in narwhals. The linear regressions of dentinal thickness (y) on number of layers (x) are (excluding tusks and occluded teeth):

$$y = 2.35730x \text{ (males) and}$$
$$y = 2.15265x \text{ (females)}$$

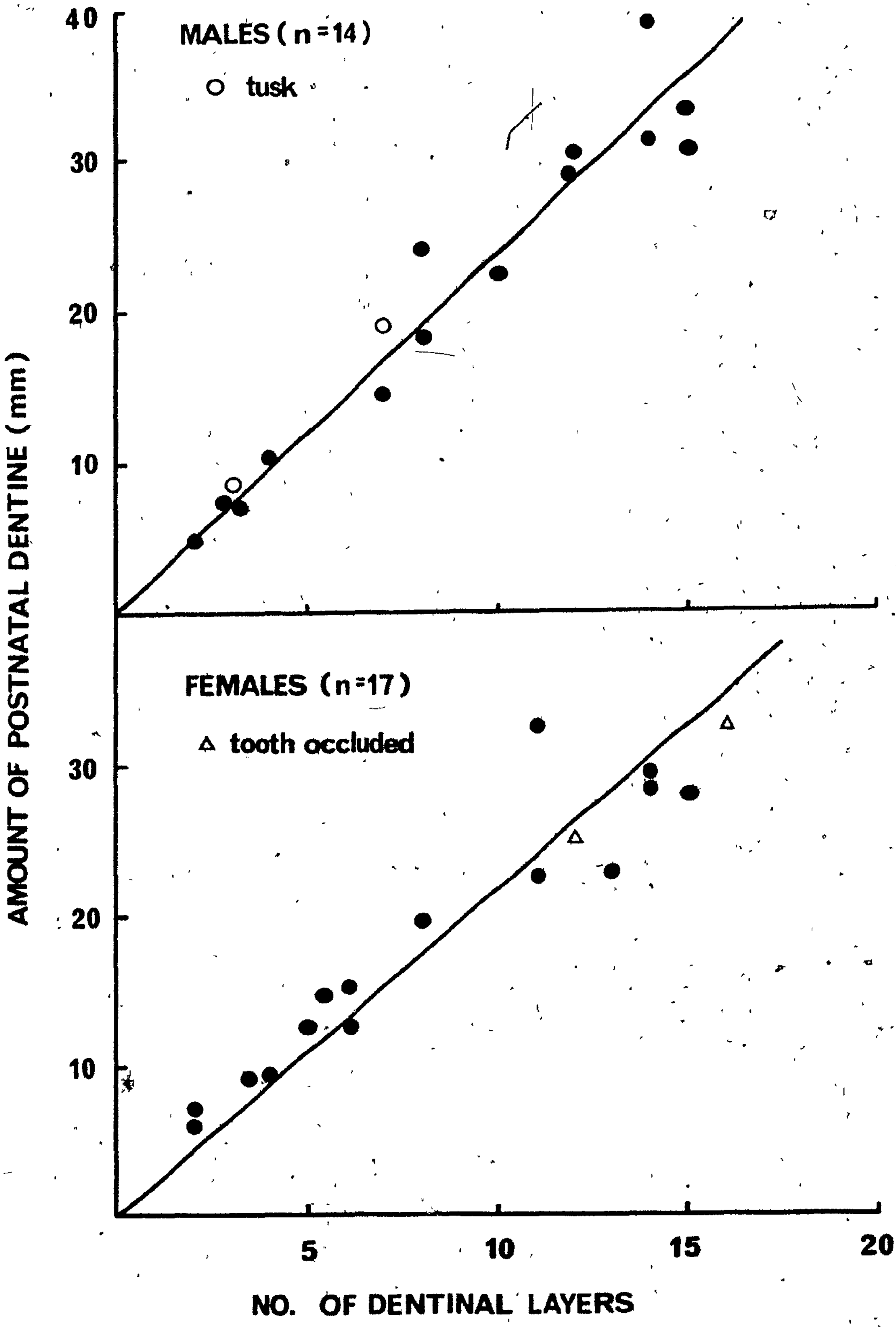
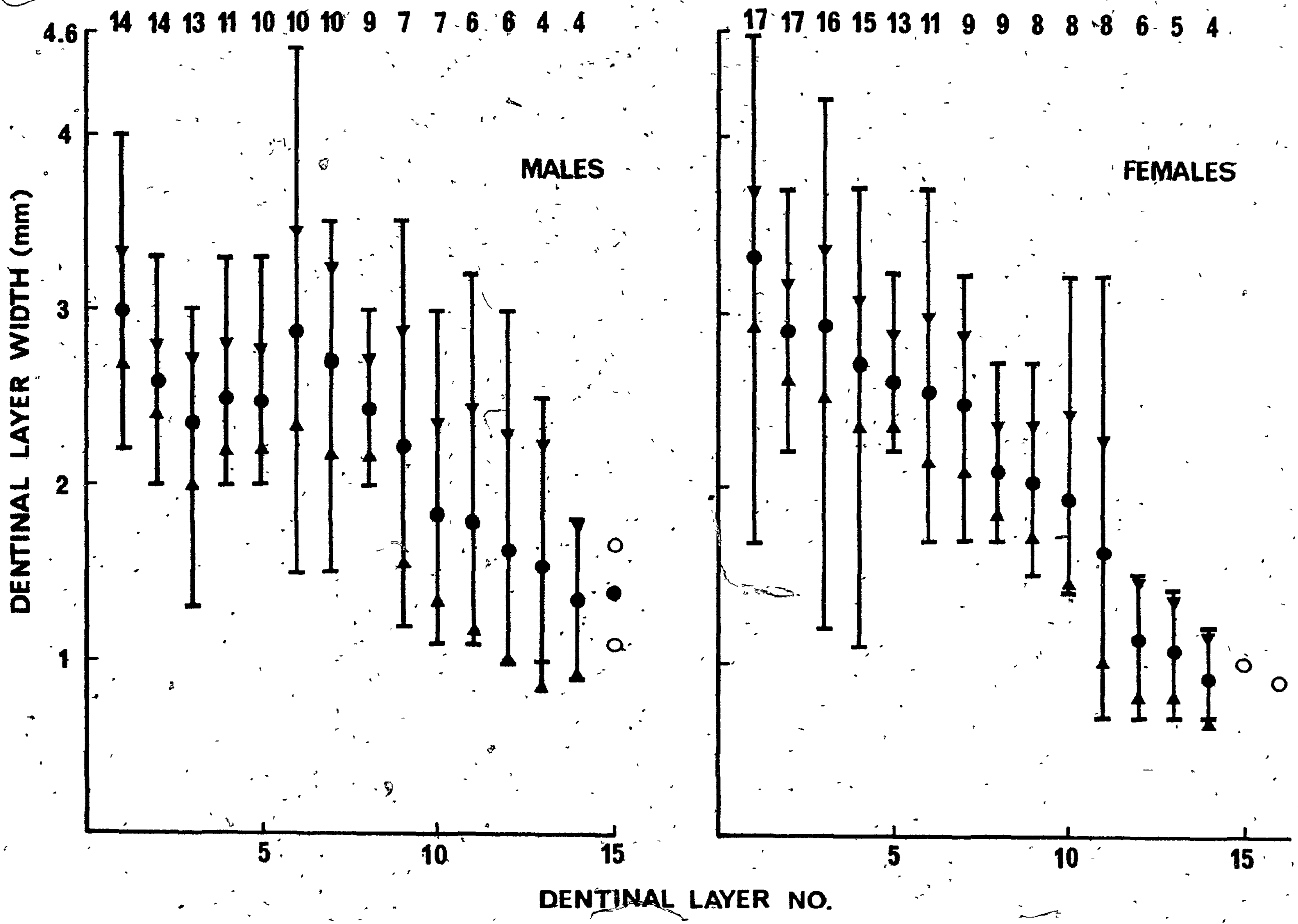

MALES (n =14)
○ tusk
FEMALES (n =17)
△ tooth occluded
AMOUNT OF POSTNATAL DENTINE (mm)
NO. OF DENTINAL LAYERS
40
30
20
10
30
20
10
5
10
15
20

Figure 5. Dentinal layer widths plotted against layer number in male and female narwhals. The mean is represented by a closed circle, triangles indicate two standard errors, horizontal lines represent the range, and open circles represent single values. Sample size is given at the top of the graph.


14 14 13 11 10 10 10 9 7 7 6 6 4 4
17 17 16 15 13 11 9 9 8 8 8 6 5 4
4.6
4
3
2
1
DENTINAL LAYER WIDTH (mm)
MALES
FEMALES
5
10
15
DENTINAL LAYER NO.

does not reflect a true increase in the growth rate but more likely a decrease, since these layers are deposited over a small surface area at the root, resulting in an increase in apical width but reduction in the volume of dentine deposited (and decrease in dentinal deposition rate). The small surface area results from a decrease in the axial growth rate of the tooth after three or four layers have been deposited, and the tooth attains its maximum length when about six dentinal layers have been deposited (see above). Klevezal and Kleinenberg (1967) have attributed this increase in thickness of later dentinal layers to a sudden reduction in axial growth rate of the tooth, and they demonstrate that layer thickness reflects actual growth rate when axial growth of the tooth finally becomes negligible.

In the embedded teeth of females, mean dentinal layer thickness declines steadily from layer one (3.1 mm) to layer nine (1.84 mm), then more rapidly to layer 14 (0.7 mm). The thickness of successive dentinal layers decreases more rapidly with age in females than in males, particularly after layer 10 (Figure 5).

Figure 6 demonstrates the increase in cumulative thickness of dentinal layers with age in both sexes. Cumulative thickness increases from layer one (3.0 mm) to layer 14 (33.0 mm) in males, with a very slight reduction in dentine deposition rate after layer 12. In females, the cumulative thickness increases from layer one (3.0 mm) to layer 14 (29.0 mm), with a pronounced reduction in dentine deposition rate after the tenth layer, up to which age the dentine deposition rate is nearly the same in males and females. It will be shown later that the age at which female dentinal growth rate is reduced corresponds closely with the age at sexual maturity (11 to 12 dentinal layers). Kleveza1 and Kleinenberg (1967) indicated that the inflections in these types of curves should occur near the age of sexual maturity.

Klevezal and Kleinenberg (1967) predicted that the ratio of the thickness of each dentinal layer to that of the previous layer should decline markedly when sexual maturity is achieved, but this was not

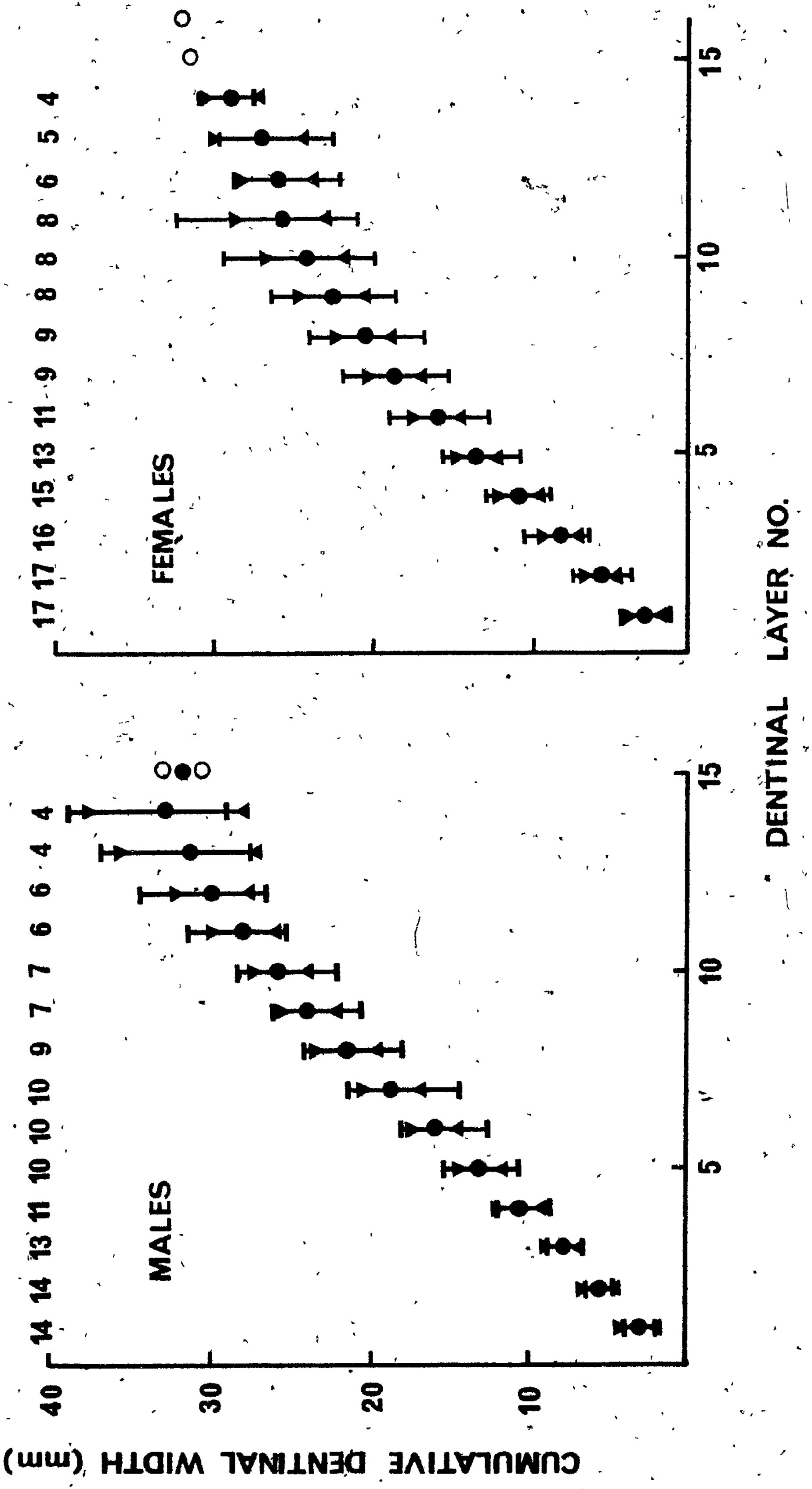


Figure 6. Cumulative dentinal width plotted against layer number in male and female narwhals. The mean is represented by a closed circle, triangles indicate two standard errors, horizontal lines represent the range, and open circles represent single values. Sample size is given at the top of the graph.

observed in the embedded tooth of the narwhal where, for the most part, the values of this ratio reflect individual layer thickness. In females, this ratio declines after layer nine to less than 0.8, while in the teeth of males this ratio is 0.9 to 1.0 until layer 14.

Sexual dimorphism in dentinal growth rate has been noted in many other odontocetes, including the sperm whale (Nishiwaki _et al_. 1958; Ohsumi _et al_. 1963) and the white whale (Brodie 1971; Sergeant 1973), in which males have greater dentinal growth rates than females, especially after the age of female sexual maturity. On the other hand, female harbour porpoises _Phocoena phocoena_ demonstrate greater dentinal growth rates than the males (Gaskin and Blair 1977). Like the narwhal, most species of odontocetes in which tooth growth has been studied quantitatively show a pattern of decreasing thickness of successive dentinal layers with increasing age. This is true of the white whale (Sergeant 1973), although in this species dentinal layer thickness increases to layer 15 and then declines gradually (Brodie 1970).

The most recent dentinal zone and season - It was possible to determine the nature of the most recent dentinal zone (narrow dark band or wide light band) in the teeth of 47 young whales (24 males and 23 females). Overall, a narrow dark band was being deposited in the teeth of 81% of these whales (92% of males; 70% of females). The teeth of young animals (300 to 340 cm males and 280 to 320 cm females) had the thickest bands at the edge of the pulp cavity (0.5 to 1.5 mm, occasionally to 2.0 mm). The teeth of four males captured during July were depositing a narrow dark band 0.5 to 1.5 mm thick, while the teeth of four females captured during July were depositing a wide light band of 0.05 to 2.0 mm thickness. In August and September, the teeth of 15 of 18 (83%) females and 18 of 20 (90%) males were depositing a narrow dark band of thickness 0.3 to 1.5 mm. There was no detectable correlation between the thickness of the most recent dentinal zone and date of capture.

For some odontocetes it has been possible to estimate the rate at which dentinal growth layers are deposited by analysing the seasonal formation of the component zones of a growth layer. Klevezal and Kleinenberg (1967), reviewing age determination studies in most orders of Mammalia, concluded that the translucent dentine is deposited during a period of reduced growth or feeding during winter and/or spring. The translucent dentinal zone in the teeth of the harbor porpoise forms during the summer (Gaskin and Blair 1977), while it forms during the winter in the bottlenose whale *Hyperoodon ampullatus* (Christensen 1973), the pilot whale (Sergeant 1962), and in dolphins of the genus *Stenella* (Kasuya 1972; Kasuya *et al*. 1974; Miyazaki 1977; Kasuya 1976). The translucent zone in the teeth of the sperm whale forms during spring (September-October) in the southern hemisphere (Best 1970) and during winter (peak in January) in the northern hemisphere (Ohsumi *et al*. 1963). Gambell and Grzegorzewska (1967) demonstrated that two translucent dentinal bands were deposited annually in the southern hemisphere sperm whale, in December-February and in June-August. More recently, Gambell (1977) has shown that the season of formation of the translucent dentinal zone varies in different age/sex groups of southern hemisphere sperm whales which he attributes to differences in their migratory behaviour.

The seasonal deposition of growth layers in the teeth of the white whale has been studied by Brodie (1970) and Sergeant (1973). Brodie (1970) noted that white whales during summer have completed a wide opaque dentinal band and are beginning to deposit a translucent band, while Sergeant (1973) noted that white whales in western Hudson Bay had completed a translucent dentinal band after an autumn migration northwards. Since it is likely that two dentinal growth layers are deposited annually in the teeth of the white whale, a second translucent zone must be laid down in mid-winter (Brodie 1970) or during a spring migration (Sergeant 1973). Both authors believed that translucent dentine is deposited when feeding activity is greatly reduced.

The evidence from dentinal structure in the narwhal suggests that a narrow dark band is deposited in August and September, when these whales are feeding lightly and depositing poorly mineralized but optically opaque dentine in their teeth (Plate II, b). Unfortunately, this analysis provides no clue to the time basis of the dentinal growth layers because of the short sampling season and the high incidence of dentinal occlusion.

Proximate factors in dentine deposition - Various hypotheses have been advanced to explain the cause of the heterogeneous, layered appearance of the teeth of marine mammals. These include seasonal variations in endocrine hormone balance (Carrick and Ingham 1962), endogenous annual rhythms (Gaskin and Blair 1977), and specific genetic growth cycles with periodic "...enhancement of some of the short cycle layers..." by environmental change or seasonality (Kasuya 1977). The most common explanation for the layered appearance of dentine and cementum relates to seasonal changes in nutritional state or feeding intensity (Laws 1953; McLaren 1958; Fisher 1954; Mansfield 1958; Scheffer 1950) but little direct evidence is available. However, Scheffer and Peterson (1967) found a direct correlation between nutrition and postnatal dentinal layering in suckling pups of the Alaskan fur seal Callorhinus ursinus. Between birth and weaning of the pup, each of an average of 11 nursing cycles (each cycle consisting of one nursing period and a period when the female goes to sea to feed) was recorded as a narrow layer within the postnatal dentine of the pup's canine tooth. Kubota et al. (1961) believed that differential calcification of the dentine in the canine tooth of the fur seal reflects alternating periods of normal and disturbed calcium metabolism, which in turn reflects the nutritional state of the animal. For example, a deficiency of vitamin C leads to a reduction in the dentinal deposition rate and subsequent pathological hypercalcification (Shaw 1955).

The deposition of well-calcified dentine in the teeth of odontocetes is generally attributed to good feeding conditions or increased feeding activity, while poorly mineralized dentine is deposited when feeding conditions are suboptimal or when feeding activity is reduced (Brodie 1970; Sergeant 1959a, 1962, 1973; Ohsumi et al. 1963). The obscurity of the first several layers in the teeth of suckling animals is considered to be evidence for the importance of optimal nutrition in building well-calcified teeth (Brodie 1970; Sergeant 1962, 1973). On the other hand, Klevezal and Kleinenberg (1967) and Kubota et al. (1961) attributed the deposition of well-calcified dentine to seasonal reductions in body growth rate (and by inference, feeding rate) and deposition rate of dentinal organic matrix, assuming that the rate of mineralization is constant.

One can only speculate on the proximate factors which are responsible for differential calcification in the dentine of the embedded tooth of the narwhal. The available evidence suggests that low feeding intensity in mid-summer is correlated with the deposition of a narrow layer of poorly-mineralized dentine; this is corroborated by the observation that the narwhals are becoming thinner at this season (see data in section on "Growth"). Reduced food intake in summer could result in a deficiency of vitamins and minerals needed for the elaboration of well-calcified dentine. These variations in mineral content are then expressed as differences in optical opacity of the dentine.

Analysis of Growth of the Tusk

Tusk length and age - In Figure 7, external tusk length is plotted against body length for 72 male and 3 female narwhals. The regression line fitted to the data for 56 unbroken tusks indicates that the tusk erupts at a body length of 264 cm. A captive male narwhal of length 277 cm had a tusk 10 cm long (Vancouver Public Aquarium Newsletter, September-October, 1970). The three tusks of females fall above the regression line. The largest tusk (210 cm) belonged to a 470 cm male. It is evident that several unbroken tusks of large males (> 410 cm) fall above the regression line, suggesting a spurt in tusk growth of sexually-mature males (see also Silverman and Dunbar 1980).

The relation between external tusk length and number of growth layers in the embedded tooth or mandible (the latter is used when the

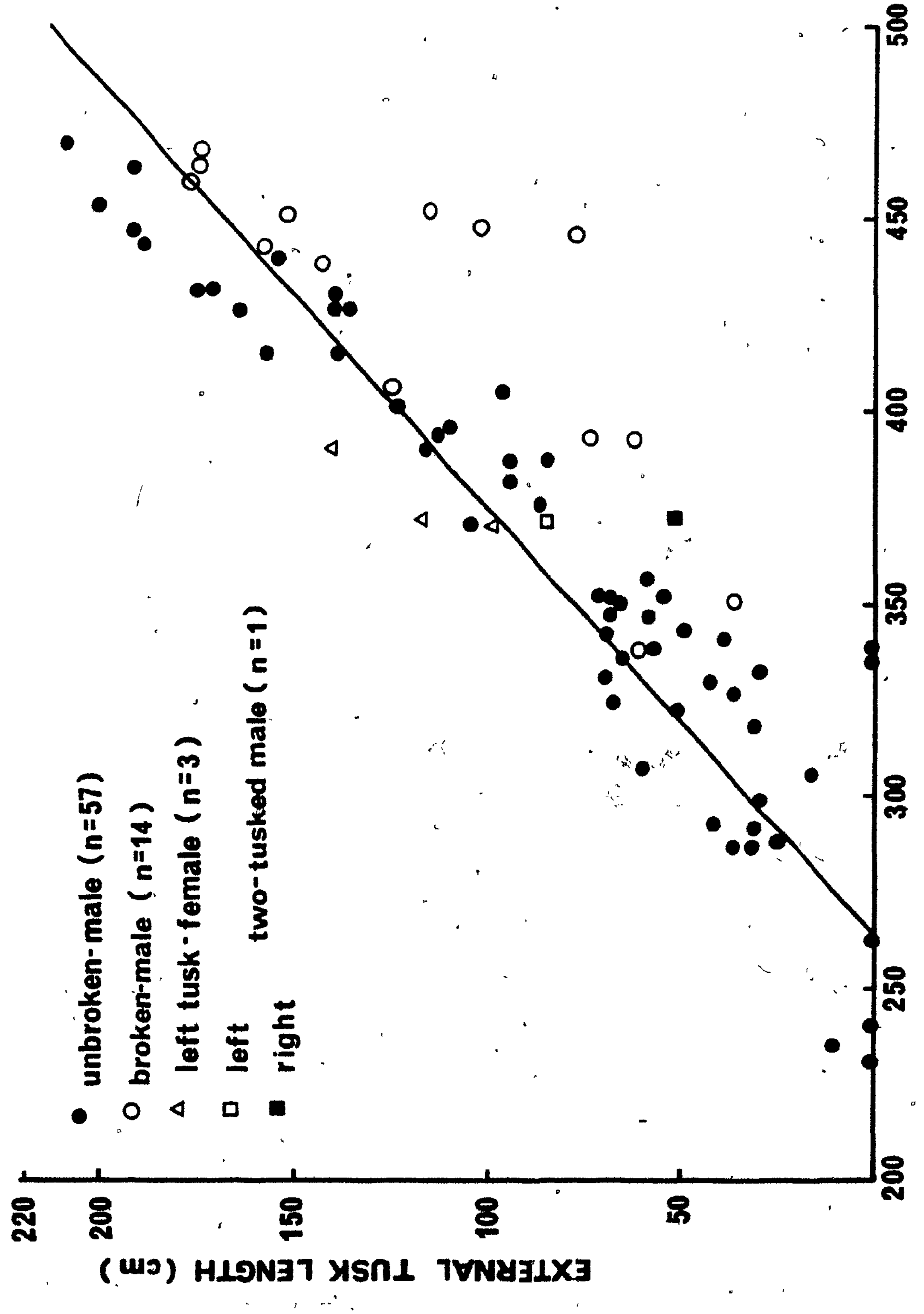


Figure 7. External tusk length plotted against body length in the narwhal. The equation for the linear regression of tusk length (y) on body length (x) for 56 left unbroken tusks of males is:

$$y = 0.91147x - 241.34613.$$

tooth is occluded) is shown in Figure 8. The curve fitted to the data by eye predicts that the tusk would erupt at about 3.5 growth layers. The tusk attains a maximum external length of about 215 cm at 50 mandibular growth layers.

Comparison with the embedded tooth - Dentinal layering in the embedded tooth was compared with that in the tusk in two young males. The first was a 230 cm animal with three growth layers in both the tusk and the embedded tooth. The tusk was 20.0 cm long and the embedded tooth, 17.1 cm. The apical thicknesses of the three layers in the tusk were slightly greater than those in the embedded tooth (3.5 vs 2.7 mm, 2.5 vs 2.5 mm, and 2.5 vs 2.0 mm for layers one to three, respectively). A 287 cm male had a tusk of 55 cm (total length) and an embedded tooth of 21.5 cm, both containing seven dentinal growth layers. The apical thicknesses of the growth layers from layer 1 to 7 (tusk followed by tooth) were as follows: 4.5, 3.0; 3.5, 2.5; 2.5, 1.3; 1.5, 2.2; 2.5, 2.2; 2.5, 1.5; 2.0, 1.8 (all in mm).

Incidence of tusk breakage - Of 73 tusks, 13 (17.8%) were assessed as broken. Considering tusks less than 60 cm in external length, one of 24 (4.2%) was broken, while 12 of 49 (24.5%) tusks longer than 60 cm were broken. Therefore, longer tusks are more prone to breakage. Silverman and Dunbar (1980) reported a higher incidence of broken tusks in adult males (61.5%) than in immature males (10.3%) with an overall incidence of tusk breakage of about 40%. Porsild (1922) found that 34% of a sample of 314 tusks were broken.

The Mandible

Description of growth and growth layers - The layered structure of bone has received far less attention in age determination than have the teeth. Laws (1960) pointed out the growth layers in the ventro-lateral area of the mandible of the sperm whale, while Nishiwaki, Oshumi and Kasuya (1961) and Brodie (1969b) examined mandibular growth layers in the sperm whale and white whale, respectively. Kleinenberg and Klevezal (1962) investigated

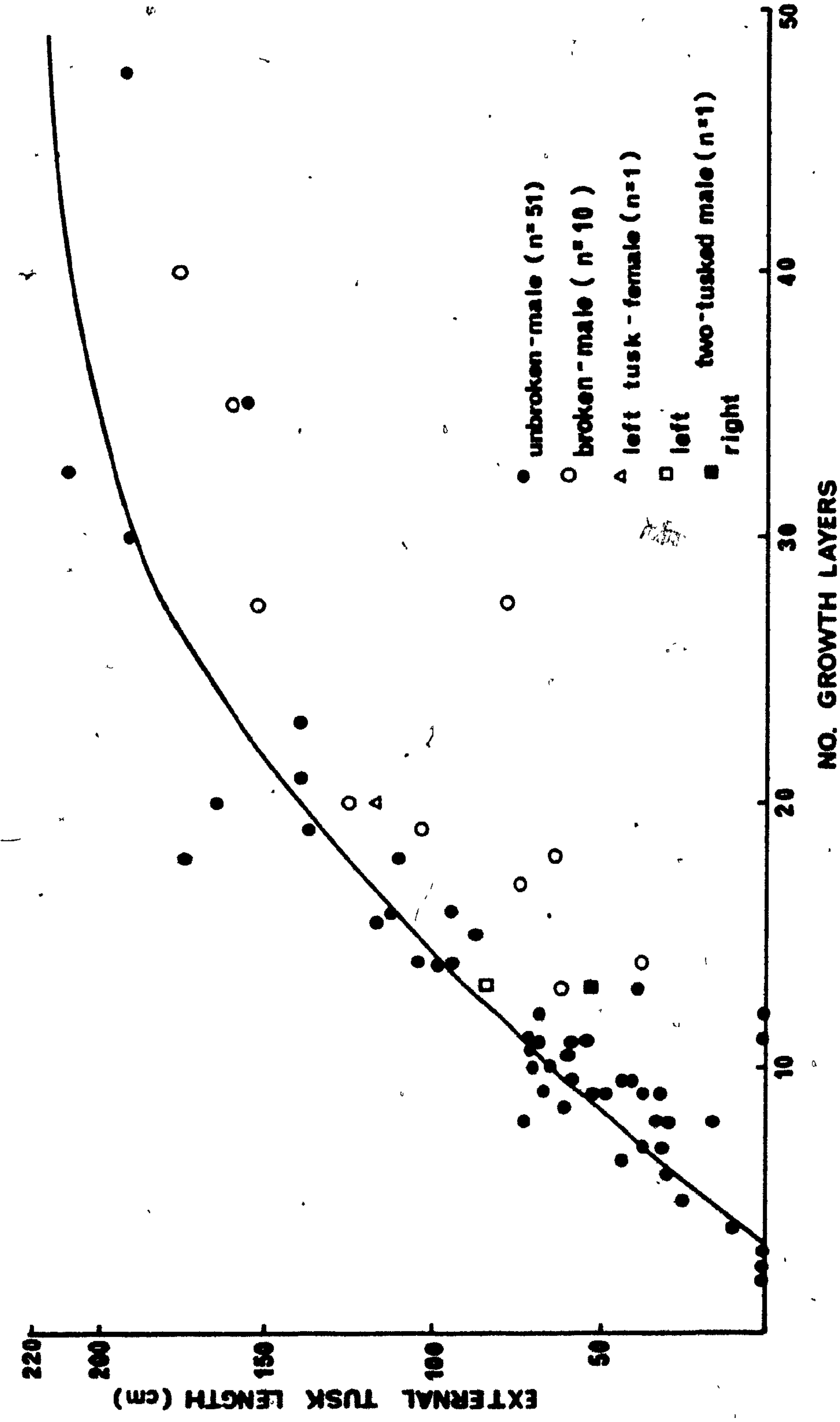


Figure 8. External tusk length plotted against number of growth layers in dentine or mandible in the narwhal. Curve was fitted by eye to the points representing unbroken tusks.

mandibular periosteal layering in *Delphinus delphis* as a means of determining age in this species. Petersen and Born (1982) used mandibular growth layers to determine age of the walrus *Odobenus rosmarus*.

Layering was examined in thin sections taken from the mandible between the mental foramina, where the periosteal bone is thickest (Plate IV, a). The periosteal growth layers are most pronounced on the ventro-labial and mid-labial aspects of the mandible and are virtually absent in the dorsal and lingual regions (Plate IV). In all regions of the cross section, haversian canals surrounded by concentric systems of osteocyte lacunae and resorption cavities are abundant (Plate IV). In old animals, this secondary bone formation causes some discontinuity and irregularity of the periosteal layers, thus interfering with interpretation and counting.

The periosteum deposits intramembranous bone on the surface of the mandible, a discontinuous process as revealed by the laminated appearance of the bone (Plate IV). The intramembranous trabeculae enlarge rapidly by further bone deposition so that periosteal bone soon becomes compact. Bloom and Fawcett (1975) provide a good description of the formation of periosteal bone.

The innermost, first-formed postnatal periosteal bone consists of alternating wide opaque and narrow translucent zones; these initial layers have a corrugated or irregular appearance (Plate IV). Later layers are more narrow and flattened as the rate of bone deposition decreases. The narrow translucent zones are called adhesion lines by Klevezal and Kleinenberg (1967). The corrugated appearance of the growth layers, particularly the first-formed, seems to be associated with the development of parallel arrays of the haversian systems. The adhesion lines are relatively wide in the later-formed, more compact layers.

In many mandibular sections a presumed neonatal line is evident near the mandibular canal (Plate IV, c). This clear, narrow line separates the prenatal and postnatal bone which are optically translucent and opaque, respectively. However, this line disappears as periosteal bone formation progresses, due to resorption by the enlarging mandibular canal. In addition, there is substantial resorption of tissue within the periosteal bone. The presence of only a few growth layers and the thinness of bone on the lingual and dorsal aspects of the anterior part of the mandible seem to be indicative of either negligible appositional growth and internal resorption or else a balance between relatively rapid rates of apposition and resorption. The retention in the lingual-dorsal region of the mandible of a few layers, similar to the early labial layers, favours the first alternative. Appositional growth exceeds resorption on the labial surface of the lower jaw, where old animals may lack the wide, irregular layers which are deposited in early postnatal life, and the layers adjacent to the mandibular canal are therefore narrow and flattened. Further evidence for internal resorption in old animals is indicated by the fact that the layers adjacent to the enlarging mandibular canal are discontinuous or interrupted.

The rates of periosteal deposition and internal resorption by the marrow cavity are greater in the mid-labial area than in the ventro- labial area. In consequence, mid-labial growth layers are quite wide, but the neonatal line and several of the earlier layers may be removed by osteoclastic activity. On the other hand, ventro-labial growth layers are more narrow, but the neonatal line is more often preserved in this area where, however, the slow appositional growth rate results in extreme compression of the late-formed layers, which are thus difficult or impossible to count. In practice, counts of growth layers begin at the first adhesion line in the ventro-labial area and eventually shift to the mid-labial area when the zones of the former area become too compressed. Unfortunately, in old narwhals in which the mandibular neonatal line cannot be detected, the counts of growth layers provide minimum estimates of age.

The most recent periosteal zone at the mandibular surface is usually an adhesion line. However, in a few young animals caught in spring, the most recent zone is opaque. Treatment of thin sections of the mandible with silver nitrate reveals that the narrow adhesion lines are poorly calcified; they are probably formed during the mid-summer period of reduced feeding, at the same time as the narrow dark band in the embedded teeth.

Klevezal and Kleinenberg (1967) reviewed the use of periosteal growth layers for age determination in a variety of mammals. In the taxa that they reviewed or studied, the periosteal adhesion lines stained intensely with haematoxylin and were thought to be heavily-calcified. Having examined several other bones with periosteal growth, they advocated the use of the mandible for most mammals as it shows the least amount of periosteal resorption.

Mandibular periosteal layering in the narwhal is identical to that described for the white whale by Brodie (1969b), who stained thin mandibular sections with aniline blue-acid fuchsin; he attributed the layering to differential calcification of the stainable opaque and unstainable translucent zones. Mandibular periosteal growth in the narwhal is also similar to that described for the sperm whale by Nishiwaki <u>et al</u>. (1961). Examination of thin ground transverse sections of the upper lateral area of the mandible of the sperm whale revealed the presence of a neonatal line which separated the endosteal from the periosteal zones, although it was difficult to confirm this line in most specimens. In older sperm whales, internal resorption had removed the neonatal line and a few of the earliest layers, and the extent of resorption and number of periosteal growth layers varied in different parts of the mandible.

Peabody (1961) attributed the deposition of the narrow, highly-calcified, translucent laminae of the periosteal bone of poikilothermic vertebrates to reduced growth rate during winter or to breeding cycles, and Klevezal and Kleinenberg (1967) put forth the same argument to explain hard tissue layering in mammals. Sissons (1949) demonstrated that the narrow laminae in radiographs of periosteal bone lesions represented a cessation of periosteal activity.

Quantitative analysis of periosteal growth - The thickness of a periosteal layer equals the sum of the thicknesses of one opaque zone and an adjacent translucent zone in the area between the mid-labial and ventro-labial regions of the mandible. The total thickness of periosteal bone, from the inner margin of the earliest-formed postnatal layer to the outer surface of the mandible, was also measured in this area. All measurements were made perpendicular to the surface of the mandible.

Figure 9 indicates that the total thickness of postnatal periosteal bone is proportional to body length in both sexes, and males accumulate a greater thickness of bone (6 to 7 mm) than females (5 mm). In Figure 10, the total thickness of postnatal periosteal bone is plotted against the number of periosteal layers. The rate of deposition of periosteal bone decreases greatly after the accumulation of 18-20 layers in males and 10-12 layers in females, although the growth rates are about the same for both sexes until the accumulation of about 15 periosteal layers.

Successive periosteal bone layer thickness is seen to decrease with number of layers (Figures 11, 13). In males, the mean thickness of each layer decreases from 0.58 mm (layer 1) to 0.18 mm (layer 8) and decreases very slightly thereafter (Figure 11). In females, the decrease in layer thickness from layer 1 to 8 is nearly the same (0.56 to 0.18 mm) as in males, but there is a tendency for layer thickness to decrease slowly from layer 8 to 16 (Figure 13). The rate of decrease of layer thickness with age increases after layer 12 in female narwhals, coincident with the number of layers at sexual maturity.

In males narwhals, cumulative periosteal bone layer thickness increases from 0.58 mm (layer 1) to 4.16 mm (layer 16), after which the rate of deposition of bone decreases greatly (Figure 12). Cumulative layer thickness of the periosteal bone in females increases from 0.56 mm (layer 1) to 3.75 mm (layer 16) but the rate of deposition is much lower after 12 layers have accumulated

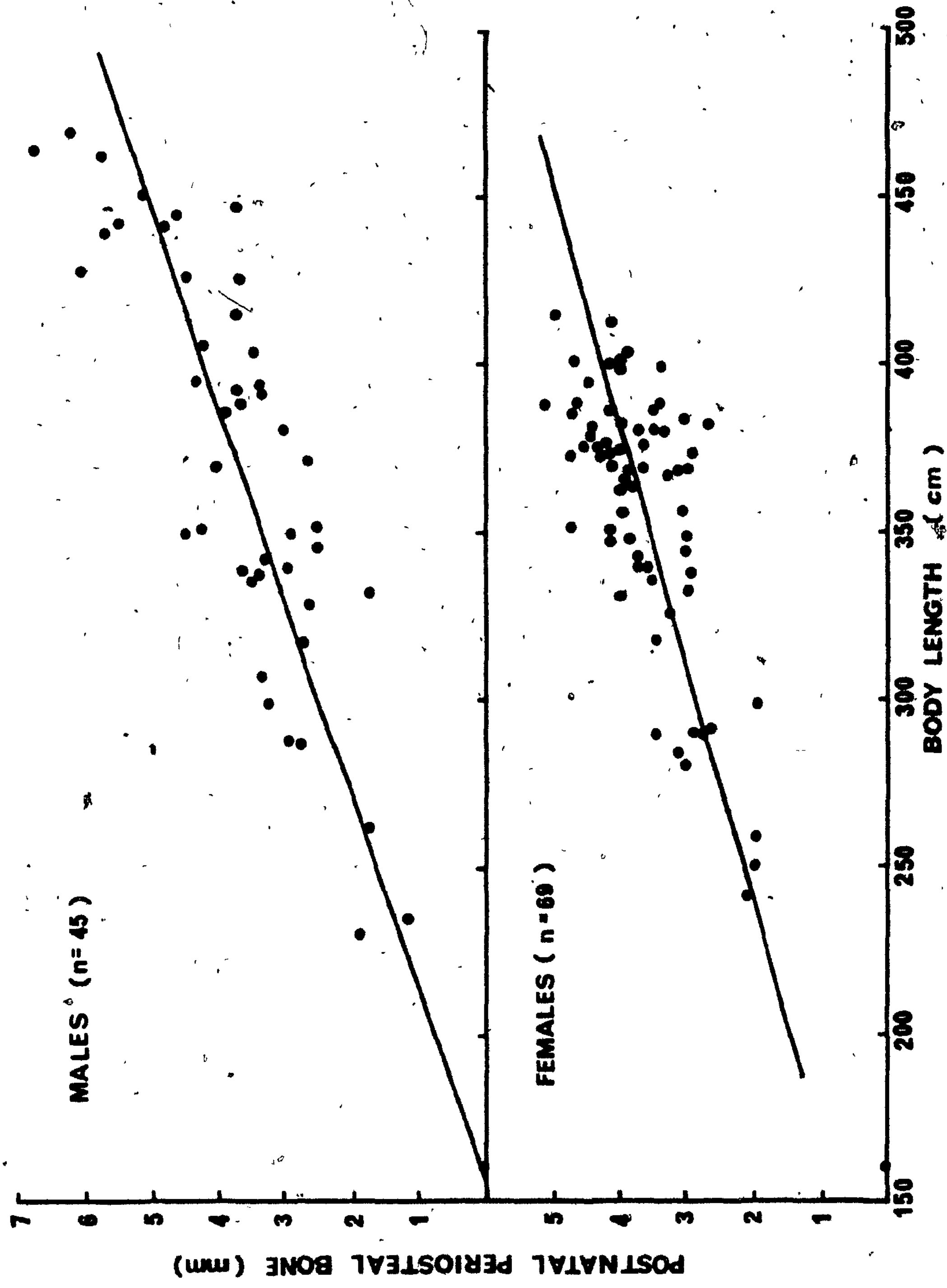


Figure 9. Total thickness of postnatal periosteal bone plotted against body length in narwhals. The linear regressions of periosteal thickness (y) on body length (x) are:

$$y = 0.01694x - 2.58685 \text{ (males) and}$$
$$y = 0.01408x - 1.37494 \text{ (females)}$$

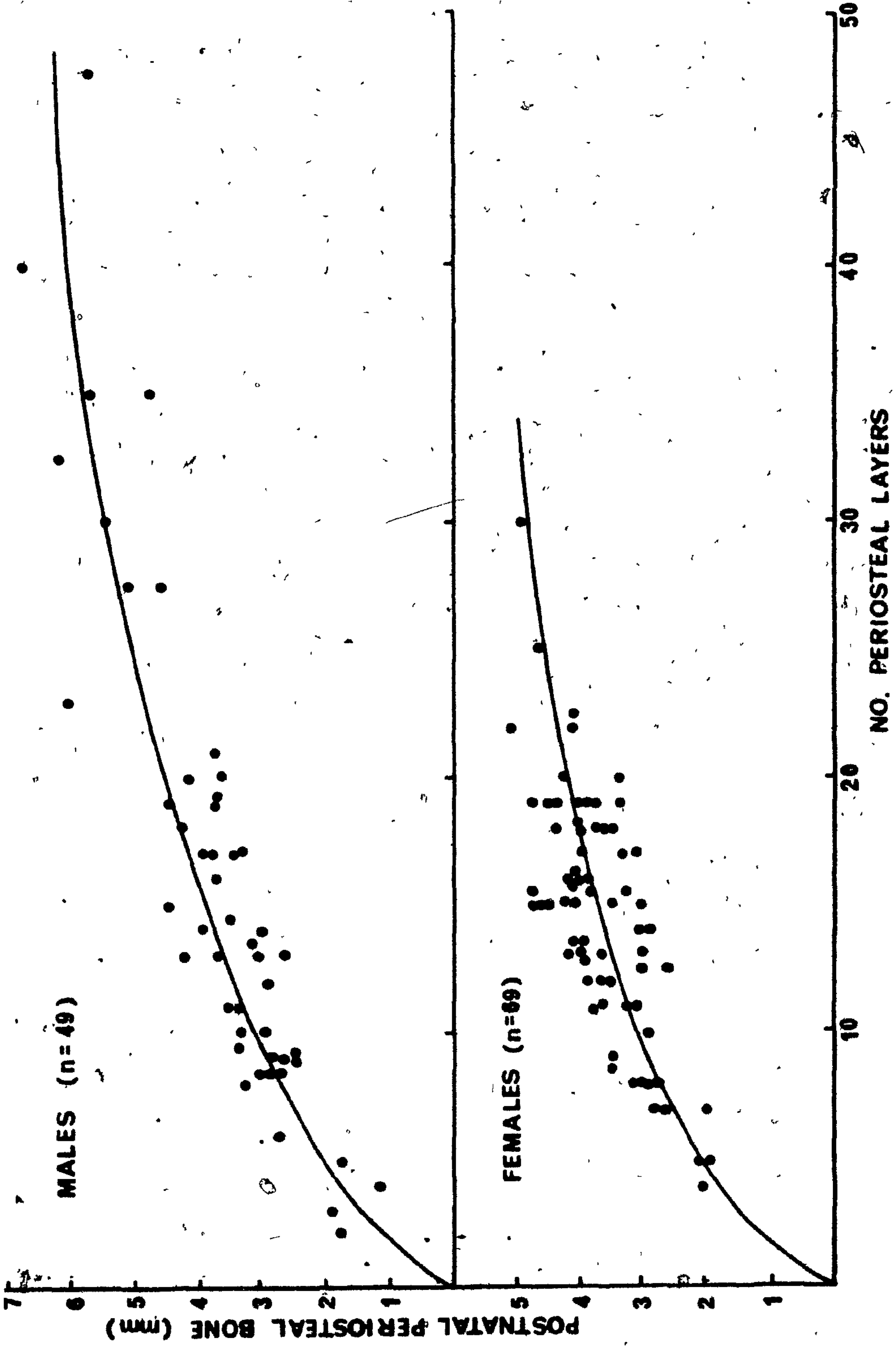


Figure 10. Total thickness of postnatal periosteal bone plotted against number of periosteal layers in narwhals. The curves are fitted by eye.

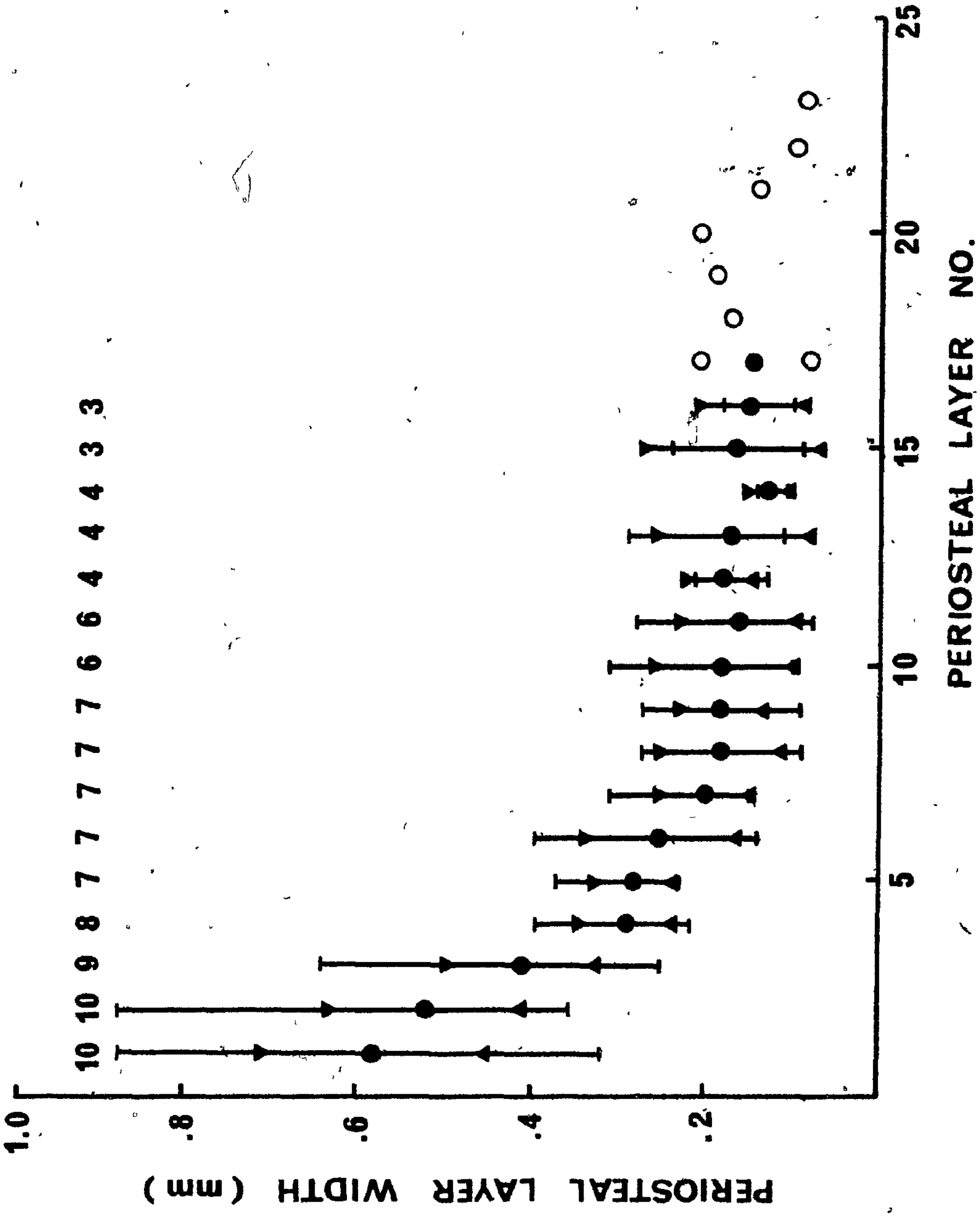


Figure 11. Periosteal bone layer width plotted against layer number in male narwhals. The mean is represented by a closed circle, triangles indicate two standard errors, horizontal lines represent the range, and open circles represent single values. Sample size is given at the top of the graph.

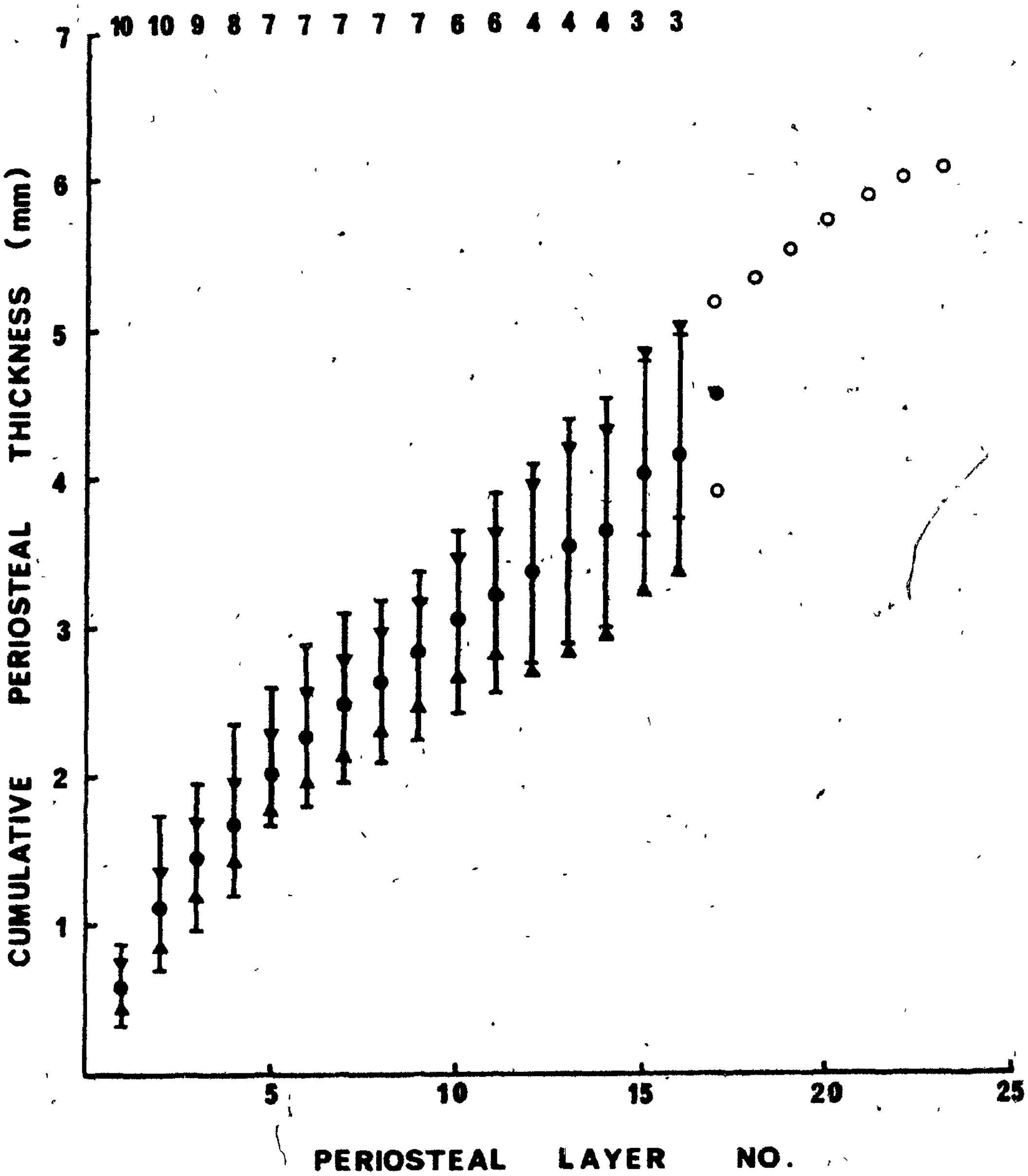
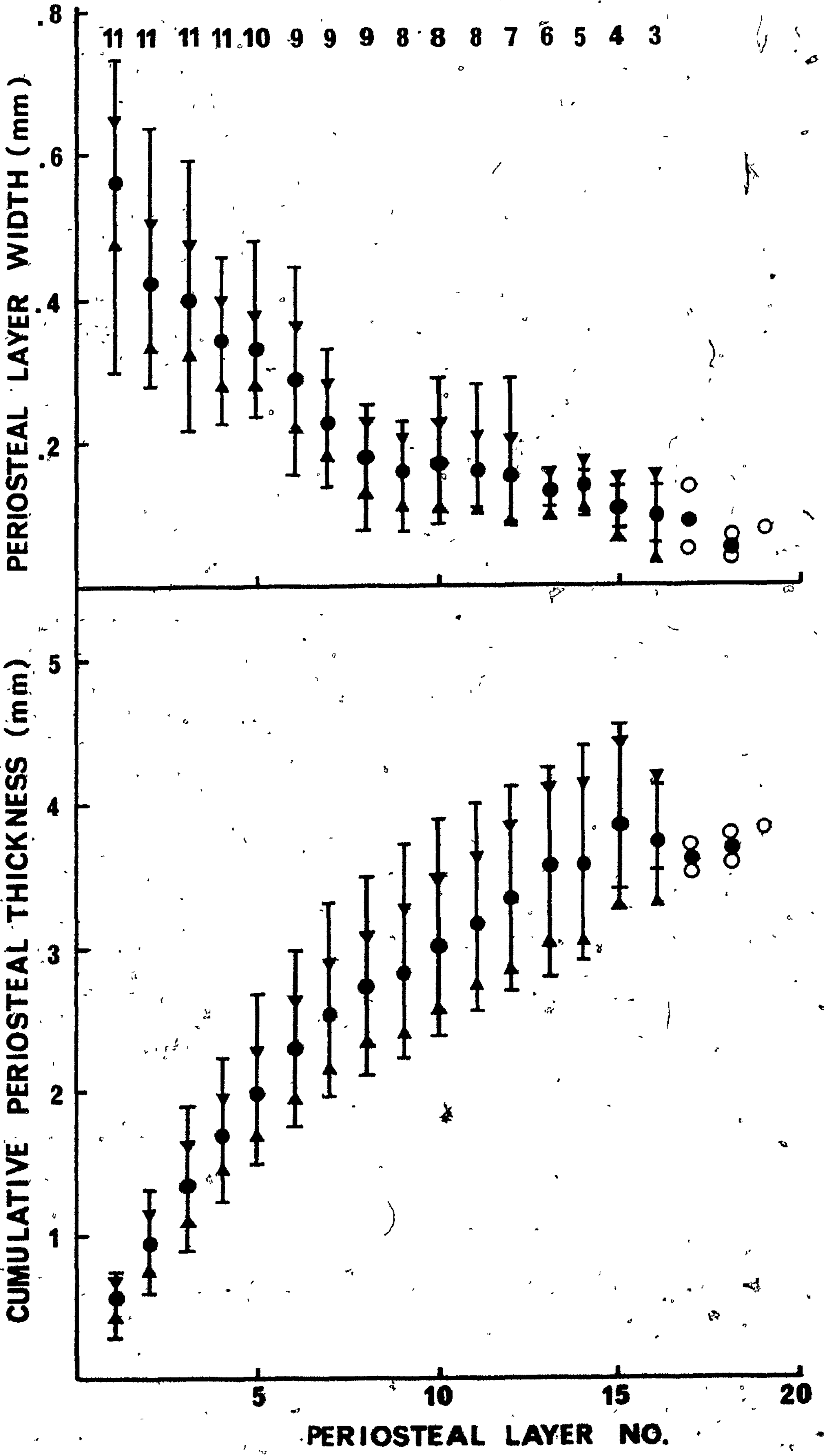


Figure 12. Cumulative periosteal bone thickness plotted against layer number in male narwhals. The mean is represented by a closed circle, triangles indicate two standard errors, horizontal lines represent the range, and open circles represent single values. Sample size is given at the top of the graph.

Figure 13. Periosteal bone layer width and cumulative thickness plotted against layer number in female narwhals. The mean is represented by a closed circle, triangles indicate two standard errors, horizontal lines represent the range, and open circles represent single values. Sample size is given at the top of the graph.


.8
.6
.4
.2
11 11 11 11 10 9 9 9 8 8 8 7 6 5 4 3
PERIOSTEAL LAYER WIDTH (mm)
5
4
3
2
1
CUMULATIVE PERIOSTEAL THICKNESS (mm)
5
10
15
20
PERIOSTEAL LAYER NO.

(Figure 13). The rates of deposition of periosteal bone are nearly the same in both sexes until the accumulation of about 14 layers.

No clear trend emerged from a plot of the ratio of each successive layer thickness to that of the previous layer. A pronounced decrease in this ratio is supposed to be correlated with the onset of sexual maturity (Klevezal and Kleinenberg 1967).

Relation Between Dentinal and Mandibular Layers

Dentinal and mandibular periosteal layers are approximately equal in number until the accumulation of about 14 layers in males (Figure 14); beyond this point, the number of mandibular layers exceeds that of dentinal layers due to dentinal occlusion. In females, the number of dentinal layers increases with the number of periosteal layers until the accumulation of 12 layers, when the incidence of dentinal occlusion increases, resulting in a much larger number of periosteal than dentinal layers in old females. However, in young females with less than 10 layers, the number of periosteal layers is, inexplicably, slightly greater than the number of dentinal layers (Figure 14). The initial equality of dentinal and mandibular layers, with the exception of young females, permits the conclusion that the frequency of layering is the same for both tissues. This conclusion is in marked contrast to the conclusion that two dentinal layers and one mandibular periosteal layer are deposited annually in the white whale _Delphinapterus leucas_ (Brodie 1969b) and in _Delphinus delphis_ (Kleinenberg and Klevezal 1962). On the other hand, Nishiwaki _et al._ (1961) found that, in the sperm whale, dentinal and mandibular periosteal growth layers are equal in number until layer 14, after which the number of mandibular layers is constant because of a balance between apposition and resorption rates, while dentinal layers continue to accumulate. Mandibular and cemental growth layers are equal in number in the Atlantic walrus (Petersen and Born 1982).

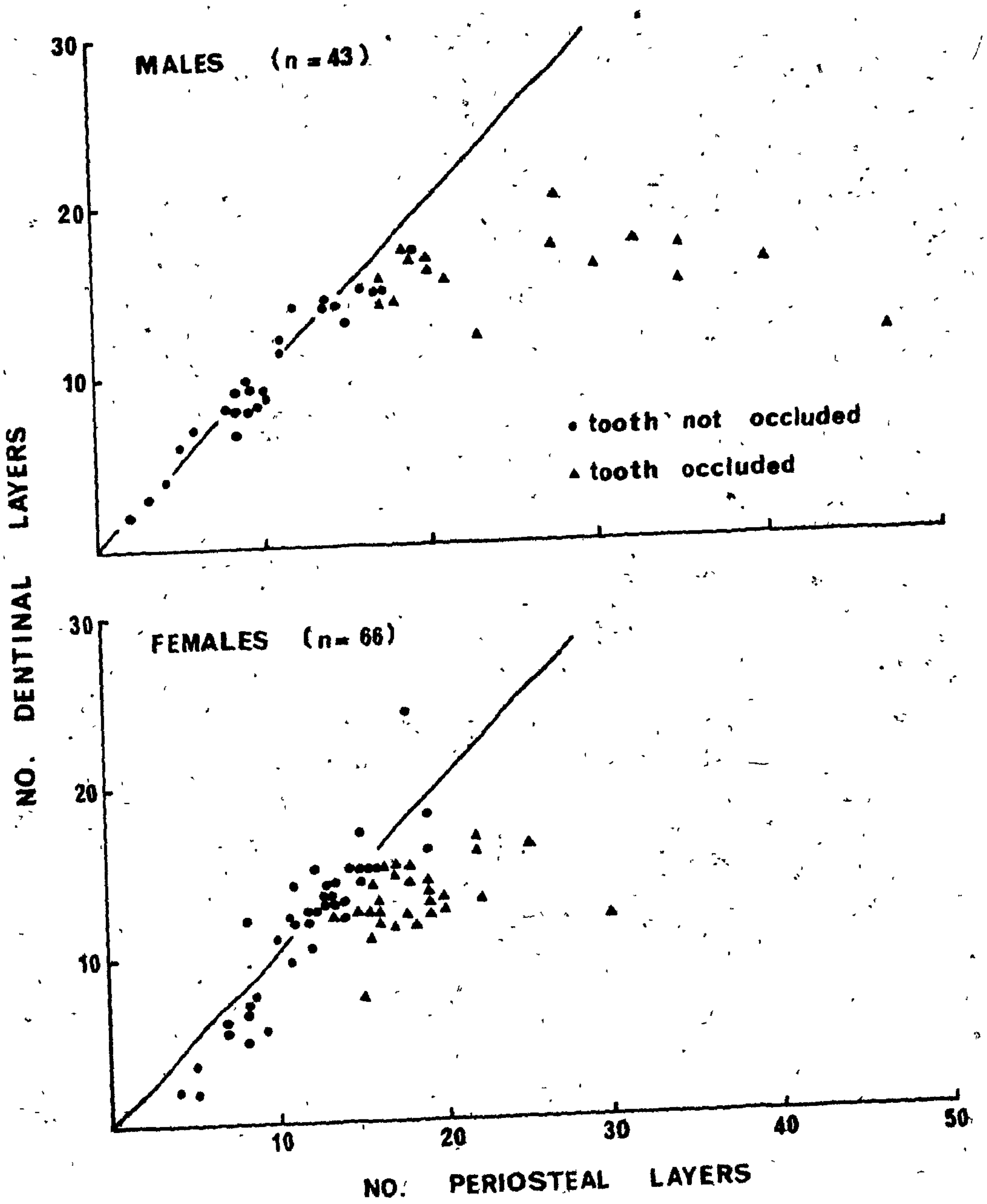


Figure 14. Relation between number of dentinal layers and mandibular periosteal layers in the narwhal. The straight line represents a theoretical 1:1 ratio.

Frequency of Dentinal and Periosteal Layering

The frequency distributions of body length of postnatal male and female narwhals captured from 1963-76 are presented in Figure 15. Most of the newborn calves (represented by the length group 150-180 cm in Figure 15) were taken by netting. Females comprise 55% of the total catch, excluding the animals captured in 1976 at the floe edge where females were selectively sampled.

An analysis of the data in Figure 15 using the method of Cassie (1954) distinguished 3 year-classes: newborns, one-year-olds, and two-year-olds (Hay 1980). However, only the newborn class is obvious from these data while extremely small sample sizes shed doubt on the validity of this analysis (see Fig. 15). Although Cassie's method does provide evidence that young animals have a higher frequency of dentinal layering than older animals (see Hay 1980), no firm conclusion on the frequency of dentinal layering can be made based on these length-frequency data, owing to the uncertainties of Cassie's method as applied to these very small samples (Fig. 15).

The annual ovulation rate is estimated to be about 0.7 and the accumulation rate of corpora lutea is calculated as 0.76 per growth layer (see "Reproduction in the Female"). Assuming that the accumulation rate of corpora lutea may be a slight overestimate due to underestimation of the ages of some very old females (see "Growth"), it appears that one dentinal layer and one mandibular periosteal layer may be deposited annually in mature females. Using growth layer counts in the erupted tusks and aspartic acid racemization ages of two adult male narwhals, Bada et al. (1983) calculate a deposition rate of 0.7-0.8 growth layers per year.

The rate of deposition of growth layers in the teeth and bones of odontocetes is still unknown, mainly because the relationship between the variously-defined growth layers and time (age) has not been examined directly. An exception is the work of Best (1976), who established that one dentinal growth layer is deposited annually in the teeth of captive Lagenorhynchus obscurus, using the technique of time-marking the teeth with tetracycline.

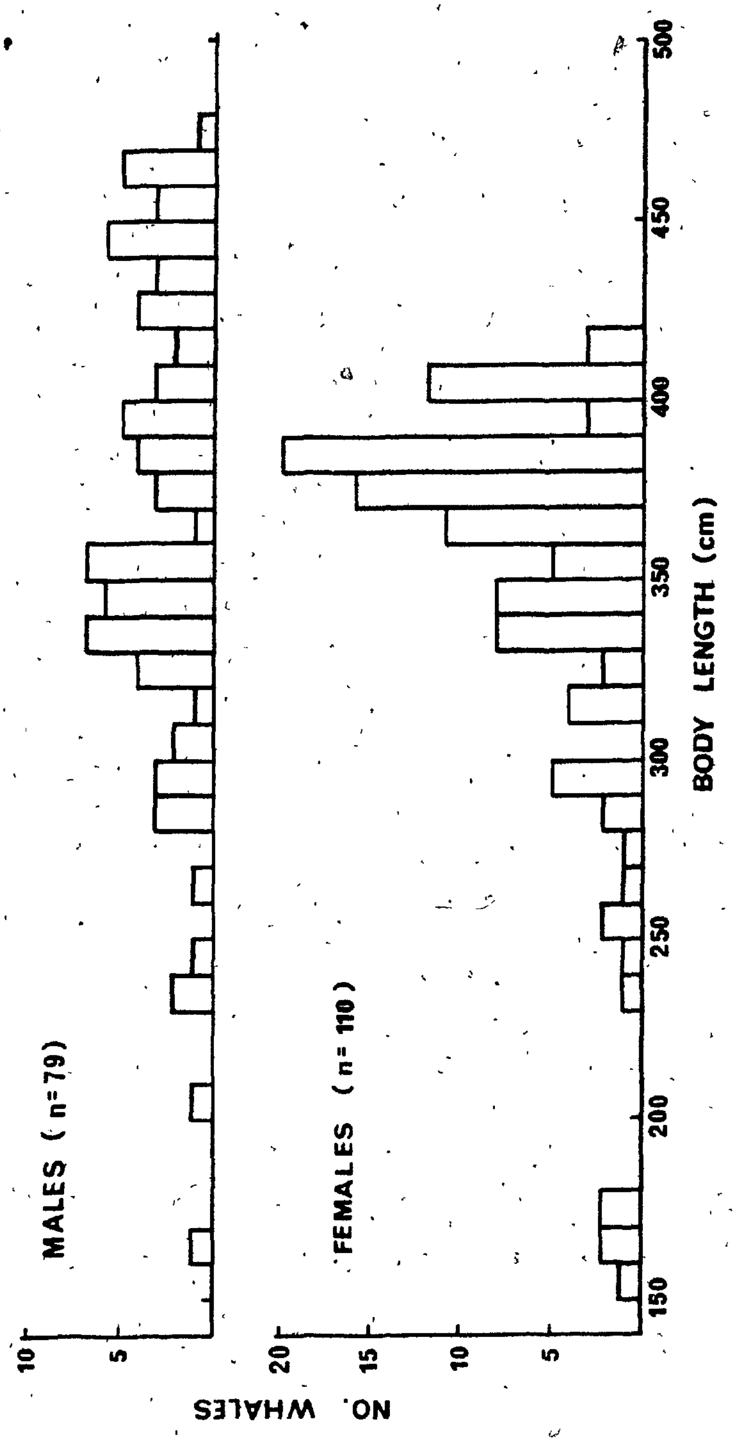


Figure 15. Frequency distributions of length of postnatal male and female narwhals, 1963-65 and 1974-76. Class interval is 10 cm.

Based largely on indirect evidence, dentinal growth layers are believed to accumulate at a rate of one per annum in Globicephala melaena (Sergeant 1962), captive Tursiops truncatus (Sergeant 1959a; Sergeant, Caldwell and Caldwell 1973), Stenella attenuata (Kasuya et al. 1974; Perrin et al. 1976), S. coeruleoalba (Kasuya 1972), S. longirostris (Perrin et al. 1977), wild and captive Phocoena phocoena (Gaskin and Blair 1977; Grue Nielson 1972), Hyperoodon ampullatus (Christensen 1973), and Berardius bairdii (Kasuya 1977). However, two dentinal growth layers and one mandibular periosteal layer are thought to be deposited annually in Delphinapterus leucas (Brodie 1971; Sergeant 1973) and Delphinus delphis (Kleinenberg and Klevezal 1962).

The rate of dentinal layering in the sperm whale Physeter catodon is a matter of considerable controversy. Ohsumi et al. (1963), considering the recruitment rate of the stock, and Best (1970, 1974), considering the ovulation rate, concluded that one dentinal layer is deposited annually in this species. On the other hand, Nishiwaki et al. (1958), considering young whales near weaning, and Gambell and Grzegorzewska (1967), analysing the seasonal deposition of the most recent translucent zone, concluded that two dentinal layers are deposited annually. More recently, Gambell (1977) has concluded that southern hemisphere sperm whales deposit one dentinal layer per year, since all samples showed only one annual peak of formation of each type of lamina (translucent and opaque).

There is considerable evidence that the frequency of deposition of hard-tissue layers is higher or more irregular during early postnatal life of marine mammals. Hay (1980) concluded that young narwhals may have a higher deposition rate than older whales. Brodie (1969b) referred to secondary laminae in the early post-natal growth of the mandibular periosteal bone of the white whale Delphinapterus leucas (his Fig. 1), so that such a possibility exists for this species as well. In addition, Laws (1952, 1953) found that the frequency of dentinal layering was higher and more irregular in immature than in adult elephant seals Mirounga leonina, correlated with the more regular pattern of seasonal haul-out of the adults. Best (1970, 1974) calculated that two dentinal layers are deposited during the first year of life of the sperm whale, although subsequent layers are annual. On the basis of theoretical or indirect evidence, Perrin et al. (1976) and Perrin et al. (1977) have suggested that, in dolphins of the genus Stenella, the frequency of dentinal layer deposition is higher during the first year of postnatal life than in subsequent years. The presence of frequent minor laminae and irregularities in the early postnatal growth layers of the ear plug of southern fin whales is attributed to differences in behaviour and physiology of immature and mature whales (Lockyer 1972). Juvenile fin whales produce only very small amounts of sex hormones which may influence the growth process, and in addition they are little motivated to participate in the regular annual migrations of the adults which are necessitated by the annual cycle of reproduction. For example, juveniles may arrive late at and depart late from Antarctic waters, and some may even overwinter in the Antarctic. Feeding activity of fin whales during winter at low latitudes is usually at a very low level, but those animals found to be feeding are frequently juveniles (Lockyer 1972). As regards the narwhal, there is little knowledge of behavioural and physiological differences between juveniles and adults that could be manifested as differences in hard-tissue structure and deposition rates. During the summer, narwhals occur in groups of different sex and maturity composition (see earlier section dealing with Behaviour) but there is no indication of large-scale spatial segregation of juvenile from adult narwhals. Behaviour of narwhals during the remainder of the year remains unstudied.

In conclusion, the frequency of deposition of growth layers in the dentine and mandibular periosteal bone of the narwhal is not known with certainty. In future studies, it is recommended that attempts be made to determine the rate of layering by direct methods, such as tagging of calves and tetracycline-injections. Larger samples of known mother- calf pairs may also shed more light on age determination for this species.

GROWTH

Foetal Growth

The foetal growth curve is presented in the section "Reproduction in the Female" since it relates to the calculation of gestation period. In this section the relation between foetal weight and length is discussed.

For 21 small foetuses (9.5 to 35.0 cm body length) the relation between weight (W in kg) and length (L in cm) is:

$$W = 0.000039884\ L^{2.86937}$$

For 23 foetuses of all sizes (9.5 to 182 cm) the relation is:

$$W = 0.000056506\ L^{2.75589}$$

Foetal weight ranges from 25 g (9.5 cm) to 80.3 kg (182 cm).

Postnatal Growth

Weight-length relation - The relation between the body weight (W in kg) and length (L in cm) of 41 postnatal animals is shown in Figure 16 and is represented by the following equation:

$$W = 0.0003231\ L^{2.48038}$$

The regression line fits the points quite well, although it is evident that the points representing the largest males are farthest from the regression line. These are probably old males which are approaching physical maturity and therefore growing little in length but continuing to increase in weight, probably by deposition of blubber. Unpublished analyses of weights of meat and blubber obtained from narwhals show that older, larger whales have proportionately more blubber than younger, smaller whales.

Weight and age - Figure 17 presents the relationship between body weight and age of 32 postnatal narwhals. Age is represented by the number of composite growth layers which refers to the number of mandibular periosteal layers if the embedded tooth is judged to be occluded; otherwise, it is the number of dentinal growth layers. There seems to be no difference in growth rate between the sexes, but few males are represented after 12 growth layers, after which age (female sexual maturity) one would expect such a difference in growth

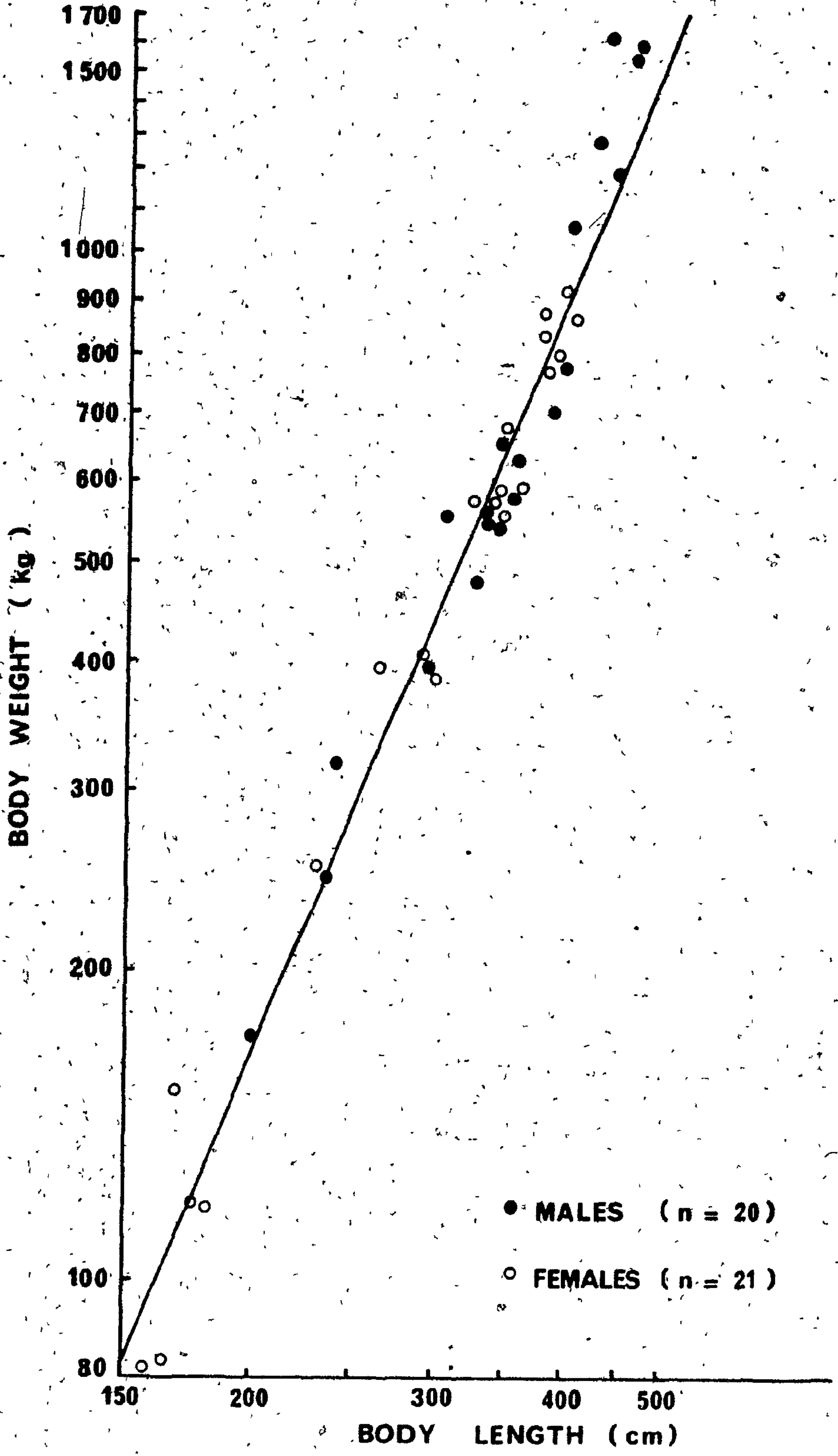


Figure 16. Weight versus length of postnatal narwhals. The relation between weight and length of 41 postnatal whales is:

$$W = 0.0003231\ L^{2.48038}$$

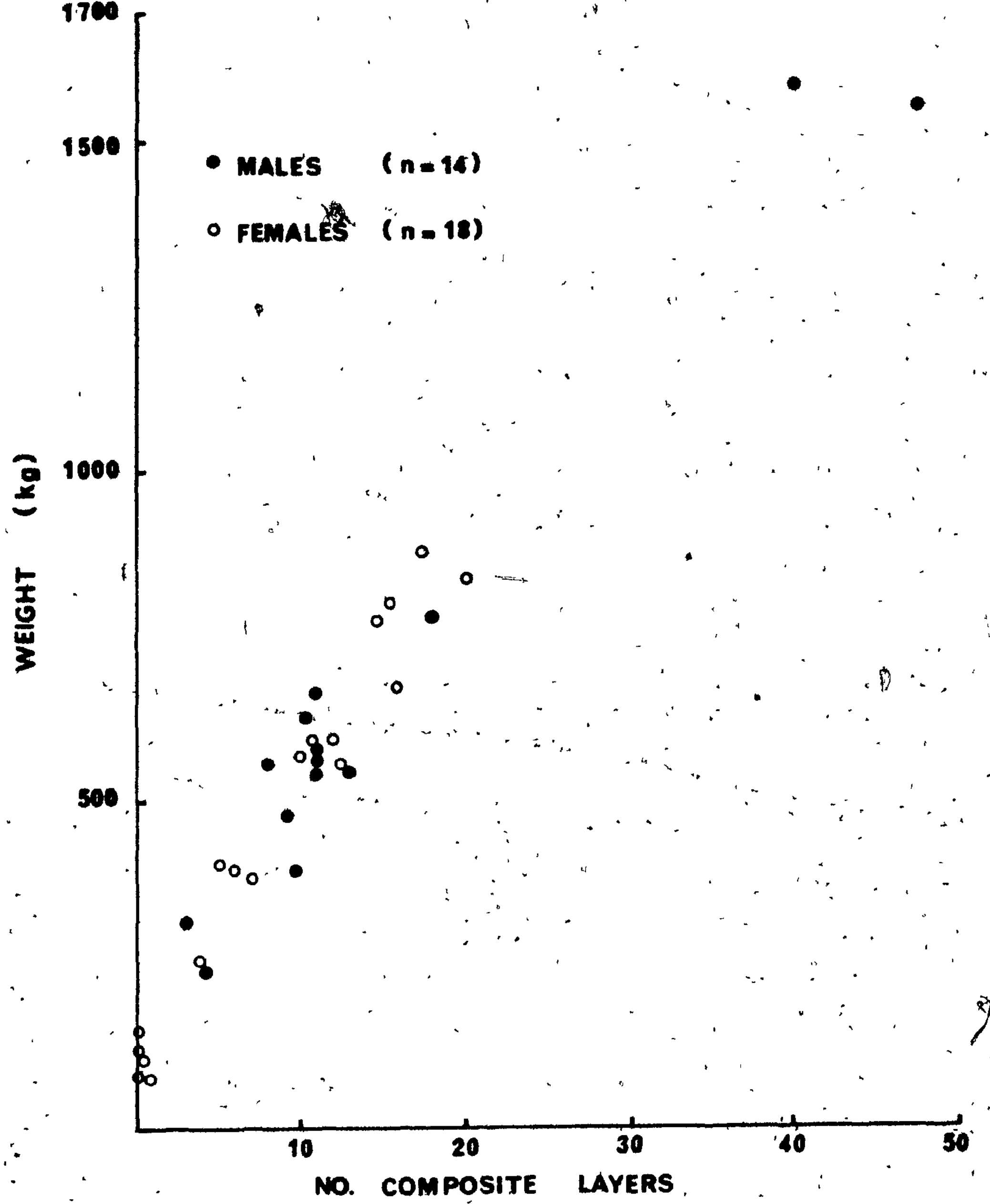


Figure 17. Weight and number of growth layers in the narwhal.

rate. The small sample size precludes any detailed analysis of this relationship.

Length and age - The growth curves of postnatal narwhals are presented in Figures 18 and 19. Growth rates of both sexes are approximately equal until the accumulation of 10 growth layers, after which the growth rate of females declines relative to that of males. There are a large number of females in the sample between 370 and 390 cm in body length with 14-20 composite growth layers (Figure 19); these are probably females that are approaching physical maturity and which comprise the pronounced mode in the length-frequency histogram (Figure 15). This observation suggests either the possibility of a cessation of periosteal activity or the attainment of a balance between the deposition and resorption rates of periosteal growth layers in old females approaching physical maturity. Thus, the ages of many old females may be underestimated and the true growth curve would be further to the right than that indicated in Figure 19, especially after about 370 cm body length. On the other hand, although the sample is small, there is no great number of large, old males over a narrow range of ages, indicating that periosteal layers probably continue to accumulate throughout the life of the male narwhal. This is corroborated by the attainment of as many as 45-50 periosteal layers by males and only 30 by females (Figures 18 and 19). Kasuya et al. (1974) also underestimated the ages of female Stenella attenuata approaching or at physical maturity (12.5 years), at which time poorly calcified postnatal secondary dentine is deposited and age determination becomes difficult. No pubertal growth spurts are evident in the narwhal (Figures 18 and 19).

Physical maturity - Inspection of the growth curves (Figures 18 and 19) reveals that males achieve asymptotic body size (physical maturity) after 30 composite growth layers and females, after 20 growth layers. Table 6 lists the approximate age at physical maturity of some other odontocetes. Some of these values were visually extracted from the length-age curves provided in various publications and are approximations only.

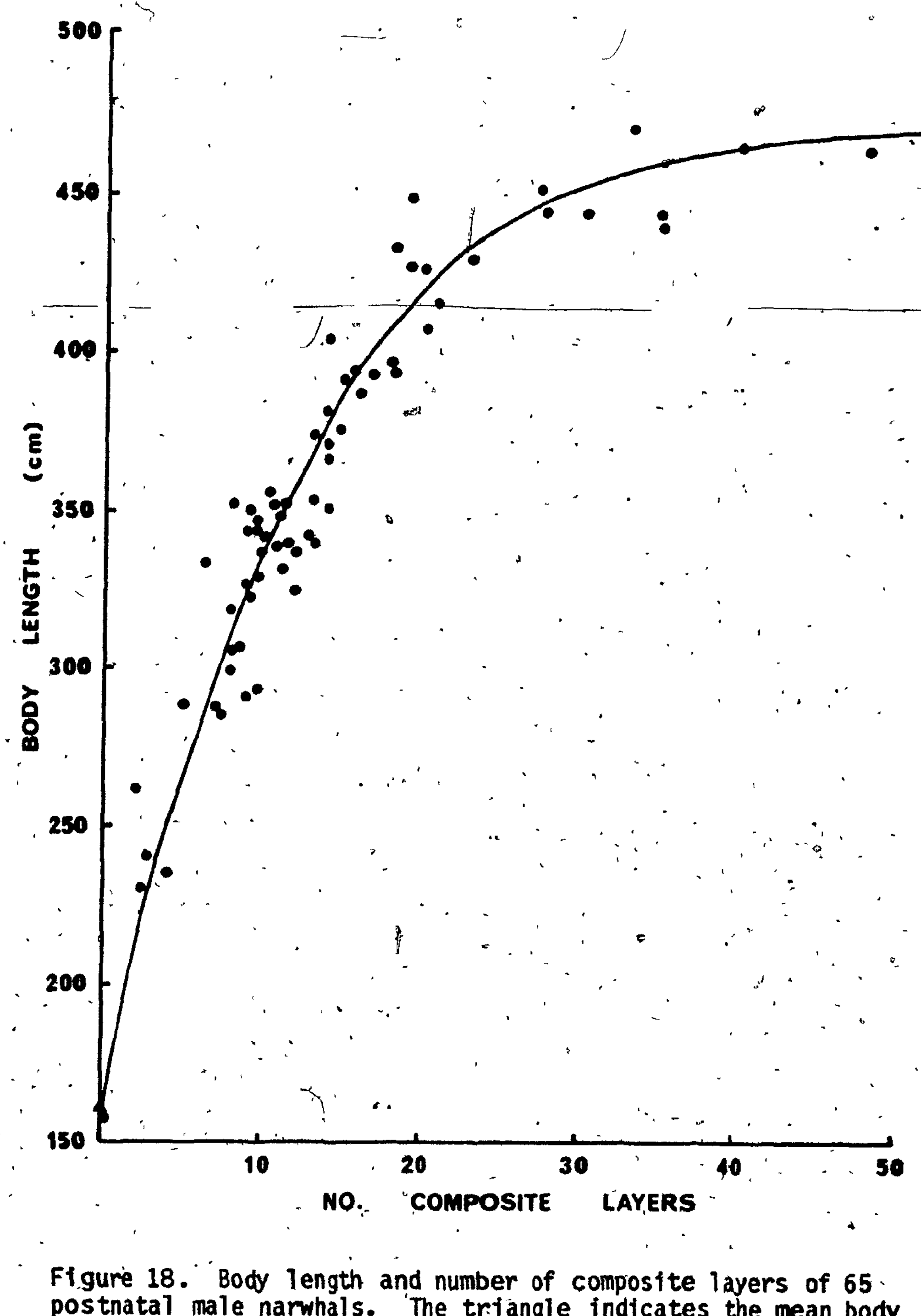


Figure 18. Body length and number of composite layers of 65 postnatal male narwhals. The triangle indicates the mean body length at birth. The curve is fitted by eye.

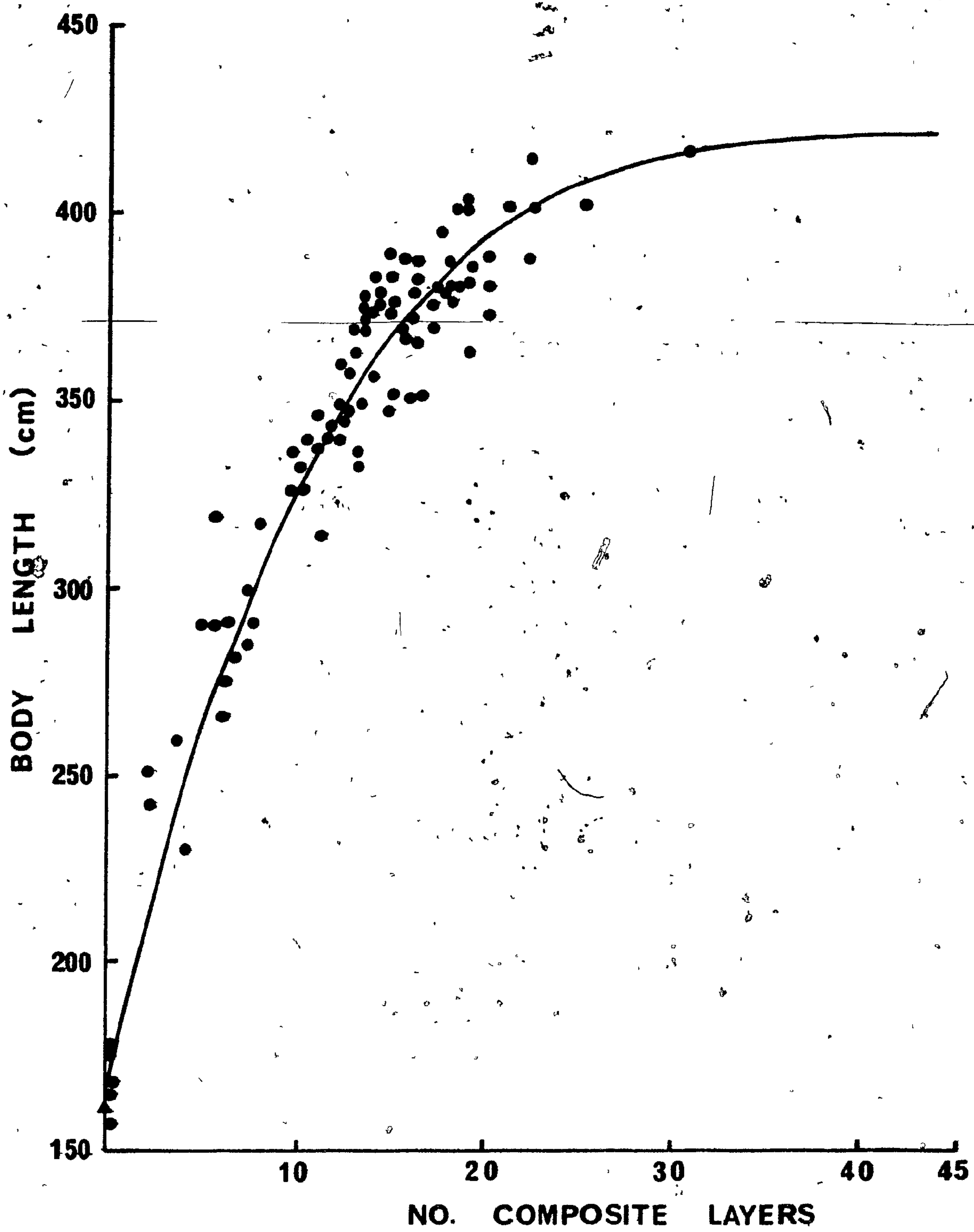


Figure 19. Body length and number of composite layers of 90 postnatal female narwhals. The triangle indicates the mean body length at birth. The curve is fitted by eye.

Table 6. Age at physical maturity of some odontocetes.

	No. dentinal growth layers		
Species	Male	Female	Author
Hyperoodon ampullatus	20	15	Christensen 1973
Physeter catodon	40	30	Nishiwaki *et al*. 1958
	35	28-29	Best 1970
Stenella coeruleoalba	14-15	14-15	Kasuya 1972
	13	11-12	Miyazaki 1977
	21.5[a]	17.5[a]	Kasuya 1976
Stenella attenuata	12	11	Kasuya *et al*. 1974
	13	13	Perrin *et al*. 1976
	22.5[a]	12.5[a]	Kasuya 1976
Stenella longirostris	9-10	7-8	Perrin *et al*. 1977
Delphinapterus leucas	20	20	Brodie 1971
	25	20	Sergeant 1973
Globicephala melaena	16-17	13-14	Sergeant 1962
Phocoena phocoena	7	7	Gaskin and Blair 1977

[a] Number of cemental growth layers.

It is evident (Table 6) that the males of large-sized species grow for a longer time than females, while males of small-sized species (e.g. Stenella) achieve physical maturity at the same age as females, or slightly later. Sexual dimorphism in size is better-developed in the large-sized species, accounting for the great difference in the age at physical maturity between the two sexes.

Longevity

The oldest male narwhal recorded in this study had 45-50 postnatal mandibular periosteal layers and a body length of 463 cm, while the oldest female had 30 layers and a body length of 415 cm. Both whales were probably physically mature. As pointed out earlier, it is probable that large, old females are no longer accumulating periosteal layers. Maximum numbers of dentinal growth layers recorded are 18 (un-occluded) and 20 (occluded) for males and 24 (un-occluded) and 17 (occluded) for females.

For comparative purposes, Table 7 lists the maximum number of dentinal growth layers recorded for various odontocetes. Assuming that one dentinal growth layer is deposited annually, many odontocetes probably have a longevity of about 40 to 50 years. Although the rate of hard-tissue layering in narwhals is not certain, application of this assumption would suggest that the longevity of the narwhal is about 50 years. Bada et al. (1983) give the aspartic acid racemization-determined ages of 4 narwhals as ranging from 25 to 52 years.

A minimum estimate of longevity for the female narwhal is 27.5 years, given the maximum number of corpora albicantia recorded in the ovaries (19) and the annual ovulation rate of 0.69 (see "Reproduction in the Female").

Seasonal Changes in Condition

Seasonal changes in body condition (fatness) are illustrated in Figure 20 for both sexes. Condition index is calculated as maximum

Table 7. Maximum number of dentinal growth layers recorded for some odontocetes.

	Max. no. dentinal growth layers		
Species	Male	Female	Author
Hyperoodon ampullatus	37	27	Christensen 1973
Berardius bairdii	71[a]	71[a]	Kasuya 1977
Physeter catodon	42	35[b]	Best 1970
Stenella coeruleoalba	25[b]	26[b]	Kasuya 1972
	50[a]	49[a]	Kasuya 1976
Stenella longirostris	18	21	Perrin et al. 1977
Stenella attenuata	18[c]	18[c]	Perrin *et al.* 1976
	40[a]	46[a]	Kasuya 1976
Globicephala melaena	21[d]	21[d]	Sergeant 1962
Delphinapterus leucas	41	33	Brodie 1971
	49	50	Sergeant 1973
Phocoena phocoena	13	9	Gaskin and Blair 1977

[a] cemental layers.

[b] possibly occluded.

[c] occluded.

[d] occluded, maximum of 50 cemental layers.

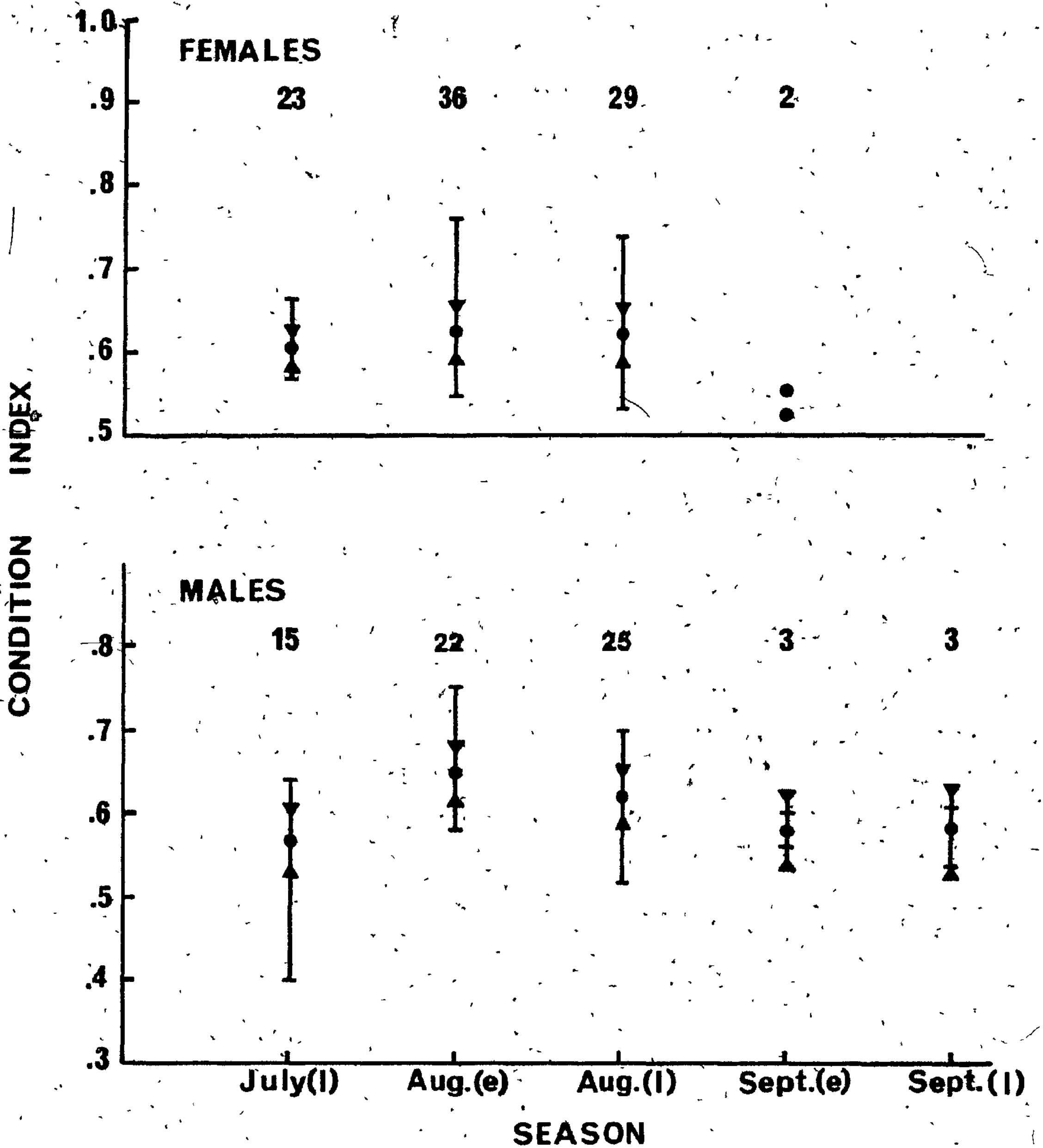


Figure 20. Seasonal variation in condition index (maximum girth/body length) in the narwhal. The mean is represented by a closed point, triangles indicate two standard errors, and horizontal lines represent the range. The letter "e" refers to the first half of each month while "l" refers to the second half. The sample sizes are given at the top of the graph.

girth/body length. This index peaks in the first half of August in male narwhals, and declines slowly thereafter. Males sampled during the first half of August had significantly higher condition indices (at the 5% significance level) than males sampled during late July (F test for homogeneity of variances was not significant at the 5% level, $p > 0.5$; $t = 5.00$, $p < 0.001$) and late August (F test not significant, $p > 0.5$; $t = 2.31$, $0.05 > p > 0.02$). Males sampled in late August were in significantly better condition than males sampled in late July (F test not significant, $p > 0.5$; $t = 3.16$, $0.01 > p > 0.001$). Females sampled during early August had significantly higher condition indices than females sampled in late July (F test significant, $0.01 > p > 0.002$; $t = 2.28$, $0.05 > p > 0.02$), while females sampled in late July were not significantly in better condition than females sampled in late August (F test significant, $0.01 > p > 0.002$; $t = 1.54$, $0.2 > p > 0.1$). Females sampled in early August and late August had condition indices that were not statistically different (F test not significant, $p > 0.5$; $t = 0.70$, $0.5 > p > 0.4$). Therefore, there seems to be no seasonal change in condition index in females, for female reproductive condition is more important in determining body condition. These changes in male condition may be correlated with intensive spring feeding (June and July), followed by fasting during August and September. Finley and Gibb (1982) found that the blubber thickness of female narwhals (but not males) declined over the season; they attributed this to reduced feeding or the additional demands placed on females with calves.

Discussion

Sexual dimorphism in body size and growth rate is evident in the narwhal and many other odontocetes, the males usually attaining a larger size than females. Examples include the bottlenose whale _Hyperoodon ampullatus_ (Christensen 1973), the pilot whale _Globicephala melaena_ (Sergeant 1962), the sperm whale _Physeter catodon_ (Nishiwaki _et al_. 1958; Best 1970), and the white whale

Delphinapterus leucas (Brodie 1971; Sergeant 1973). In these species, the growth rate of the male exceeds that of the female after the age of female sexual maturity. This life history feature, although of lesser magnitude, is characteristic of the striped dolphin Stenella coeruleoalba (Kasuya 1972; Kasuya 1976; Miyazaki 1977) and the spotted porpoise Stenella attenuata (Kasuya et al. 1974; Kasuya 1976). However, females of the beaked whale Berardius bairdii (Kasuya 1977) and the harbour porpoise Phocoena phocoena (Gaskin and Blair 1977) attain greater sizes than the males.

As a consequence of the marked reduction in female growth rate at the attainment of sexual maturity, the body size of females at physical maturity is not much greater than their size at sexual maturity. Laws (1956a) has shown, for several species of marine mammals, that the body length of females at sexual maturity averages 85.1% of the asymptotic body length. The average length of the female narwhal at sexual maturity is 340 cm, which is about 82% of the maximum body length.

Male narwhals do not appear to demonstrate the accelerated growth at puberty found to be characteristic of the males of many other odontocetes, such as the pilot whale (Sergeant 1962) and the sperm whale (Best 1970).

It has been speculated that large-sized odontocetes which demonstrate sexual dimorphism in body size have developed polygyny as a reproductive tactic, and there is good direct evidence that the male sperm whale is polygynous (Best 1969, 1979; Ohsumi 1966). Male narwhals are probably polygynous, each sexually mature male defending several females (a "harem") during the breeding season, but direct observations are not presently available.

REPRODUCTION IN THE MALE

Calculation and Measurement of Testis Volume as a Criterion of Sexual Maturity

Testis volume was measured by water displacement in the field, and if measurements were not available, the volume was calculated from the measured length, breadth, and thickness of the testis, assuming the testis to be cylindrical with hemispherical ends (Brodie 1970). The measured volume usually exceeded the calculated volume by a small amount, and calculated values were corrected using the relationship between the measured and calculated volumes.

Figure 21 indicates a tendency for the left testis to be only slightly greater in volume that the right testis, so that the use of one or the other testis for measurement and study is justified. Where possible, the right testis has been used in this study.

Histological Changes in the Testis and Epididymis

Seminiferous tubules - Plate V shows the appearance of the seminiferous tubules of the narwhal. Immature testis tubules lack a lumen and only a few spermatocytes are present (Plate V, a). Interstitial tissue is quite abundant between the tubules. The testes of maturing narwhals contain both immature and mature seminiferous tubules (Plate V, c and e). These types of tubules may occupy separate lobules of the tissue or they may be in close proximity to one another. The immature tubules of maturing narwhals are identical to those of immature animals, while their mature tubules present an appearance similar to those of sexually mature males.

The seminiferous tubules of mature males are of large diameter with an open lumen; they contain cells in various stages of the spermatogenic cycle (Plate V, e and f), but the disorganized appearance of the epithelium and the sloughing of spermatocytes and spermatids into the lumen (where they degenerate) suggest the cessation of spermatogenesis and the onset of male anoestrous. This is further corroborated by the calculation of the mating season,

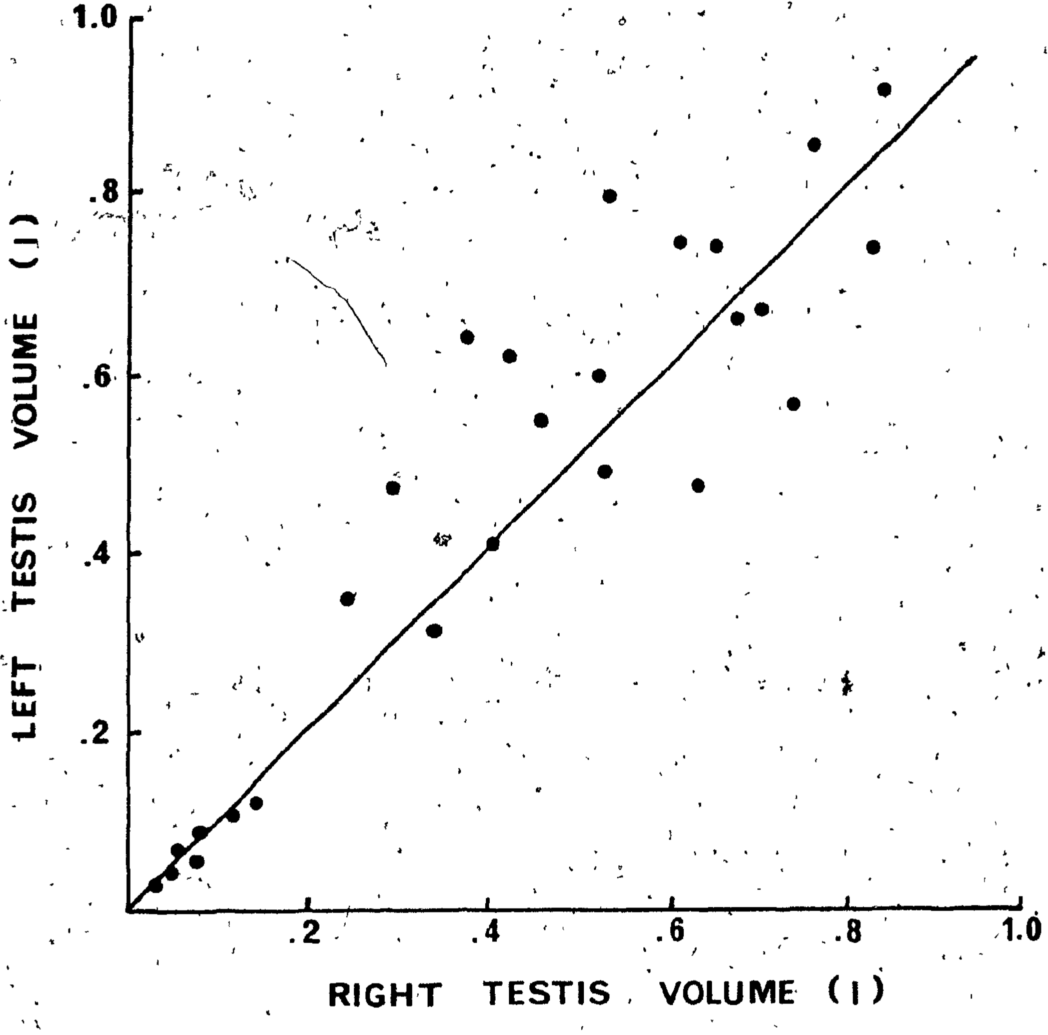


Figure 21. Left versus right testis volume of 26 narwhals. Testes volumes were measured or calculated (see text). The straight line is a 1:1 relation.

which occupies the period March to May, long before the sampling period (see "Reproduction in the Female"). The lumina of mature seminiferous tubules often contain much degenerating cellular debris; interstitial tissue is not as abundant in the mature testis as in the immature testis.

The appearance of the seminiferous epithelium of the narwhal is similar to "phase D" of the post-oestrous seminiferous epithelium of the elephant seal Mirounga leonina (Laws 1956b). In this phase, the seminiferous epithelium is loose-structured and contains many degenerating spermatids and spermatozoa. Brodie (1970) has observed similar degenerative changes in the seminiferous epithelium of mature white whales during mid-summer. Laws (1961), studying reproduction in the fin whale Balaenoptera physalus, cautioned that natural annual cyclical changes in the seminiferous epithelium may resemble post-mortem degenerative changes. The results described here for the narwhal are based on material preserved within 4 hours of death, so that the histological appearance of the testes should not be affected by such post-mortem degeneration.

Epididymal tubules - The epididymal tubules of immature, maturing, and mature narwhals are pictured in Plate V, b, d, and g, respectively. The epididymal epithelium becomes increasingly folded as sexual development proceeds; in sexually mature males, the epididymal epithelium is highly folded and the diameter of the tubules may exceed 1.0 mm. Degenerating cellular debris (with a few spermatozoa) is abundant in the lumina of the epididymal tubules of mature males (Plate V, d). These tubules do not resemble those of oestrous males, in which spermatozoa often fill the lumen (Laws 1956b). In fact, the appearance of the epididymal tubules of the mature narwhal is similar to that described for the anoestrous male elephant seal Mirounga leonina by Laws (1956b). The epididymal tubules of the narwhal present an appearance similar to those of the pilot whale, in which their diameter may exceed 2 mm (Sergeant 1962).

The microscopic appearances of the seminiferous and epididymal tubules suggest that mature male narwhals are not in breeding condition during July to September.

Histological criteria - immature, maturing, and mature narwhals-

Immature males are defined as those in which all seminiferous tubules are immature, while maturing males have both mature and immature seminiferous tubules, and mature males have only fully mature, open tubules. In Figure 22, single testis volume is plotted against the body length of male narwhals of these three reproductive categories. Although there is some overlap of testis volume between the three groups, the following criteria of maturity were established and can be used when only testis volume is available:

	Testis volume (litres)
Immature	<0.140
Maturing	0.140 to 0.535
Mature	>0.535

It is evident from Figure 22 that the attainment of sexual maturity (from the onset of spermatogenic activity) is a protracted process and that the male may be fully mature or fertile only after a further considerable lapse of time. Using the above criteria, it was estimated that of the total sample of 73 male narwhals from 1963-76, 52% were immature, 22% were maturing, and 26% were mature.

Brodie (1970) found that immature white whales had a testis volume less than 0.13 litre, while mature white whales had a testis volume exceeding 0.36 litre. Probably some of the younger mature white whales would be maturing according to the criteria of this study. However, it is possible that the testis volume separating maturing and mature male narwhals was overestimated, since there are few data points between 0.4 and 0.5 litre (Figure 22).

The histological criteria established for the male narwhal are essentially the same as those established by Best (1969) for the sperm whale and Chittleborough (1955a) for the humpback whale

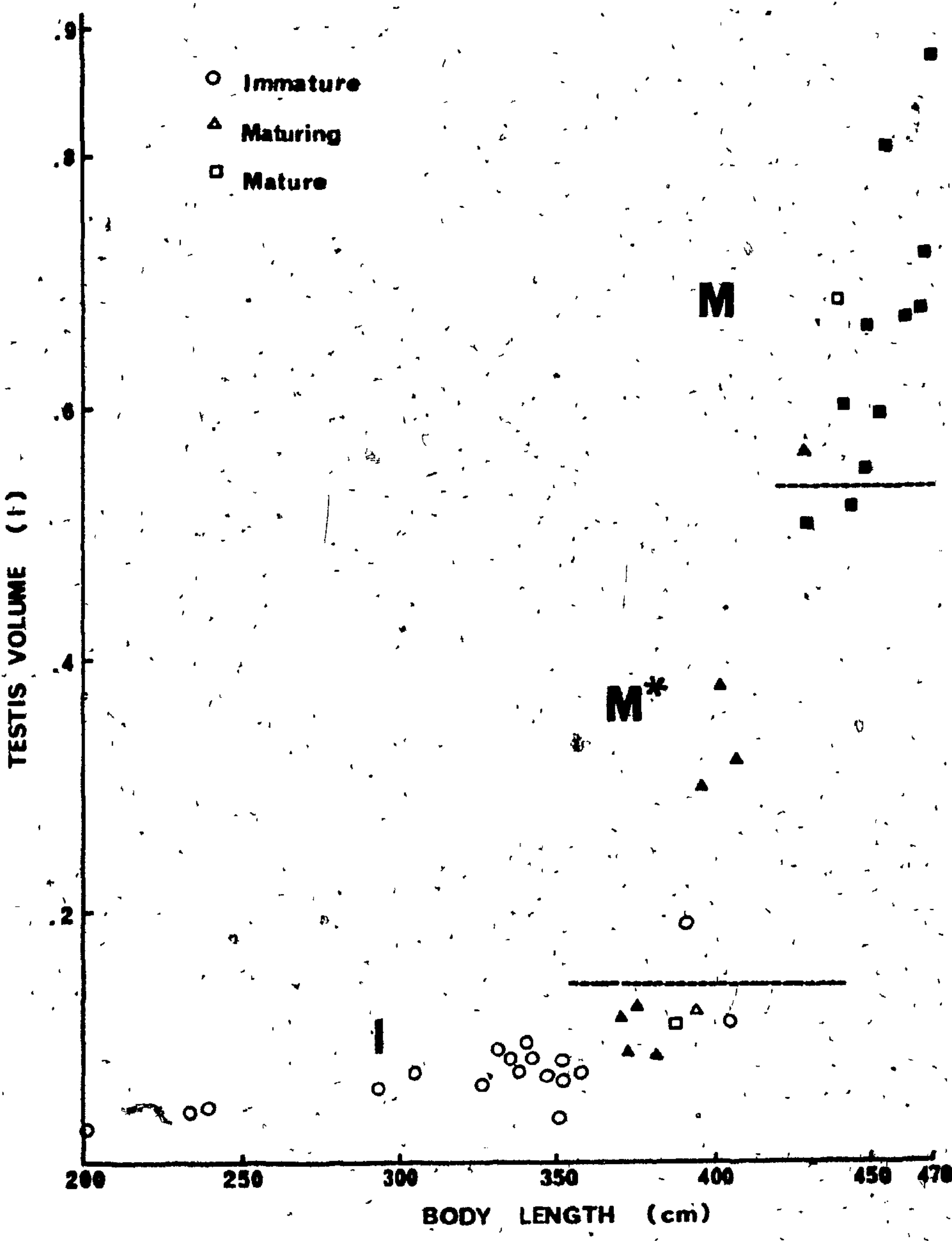


Figure 22. Testis volume and body length of 40 narwhals whose testes were examined histologically. A solid point indicates the presence of spermatozoa. The dashed lines separate immature (I), maturing (M*), and mature (M) narwhals.

Megaptera novaeangliae. Best (1969) showed that the central part of the testis matures earliest; interpretation of reproductive status based on studies of the central part of the testis would lead to underestimation of the age and length at sexual maturity. The histological changes in the testis of the narwhal are similar to those observed in the sperm whale and the humpback whale. Sergeant (1962) noted similar changes in the histology of the seminiferous epithelium of the pilot whale.

Length and Age at Puberty and Sexual Maturity

Testis volume - Testis volume increases greatly after 390 cm body length (Figure 23) and 15 to 16 composite growth layers (Figure 24), indicating that sexual maturity is attained after 390 cm and 15 to 16 growth layers in the male narwhal. The wide variation in the testis volume of mature males could be partly due to individual variation in the stage of postoestrous testicular involution, if indeed there is an annual cycle of testicular growth and regression accompanying the cycle of the seminiferous epithelium.

A similar increase in testis size at puberty has been recorded for the sperm whale (Best 1969, 1974), the humpback whale (Chittleborough 1955a), the pilot whale (Sergeant 1962), and the spotted porpoise Stenella attenuata (Perrin et al. 1976). Testis size may therefore be used in a general though imprecise way to indicate the attainment of sexual maturity by male odontocetes.

Seminiferous tubule diameter - The mean diameter of the seminiferous tubules increases greatly after 390 cm body length (Figure 25) and 16 composite growth layers (Figure 26); these results are the same as those obtained from testis volume data in the preceeding section. The seminiferous tubules of immature males are less than 120 μ in diameter, while those of mature males are greater than 200 μ in diameter.

A marked increase in the diameter of the seminiferous tubules at puberty has also been noted in the sperm whale (Best 1969), the

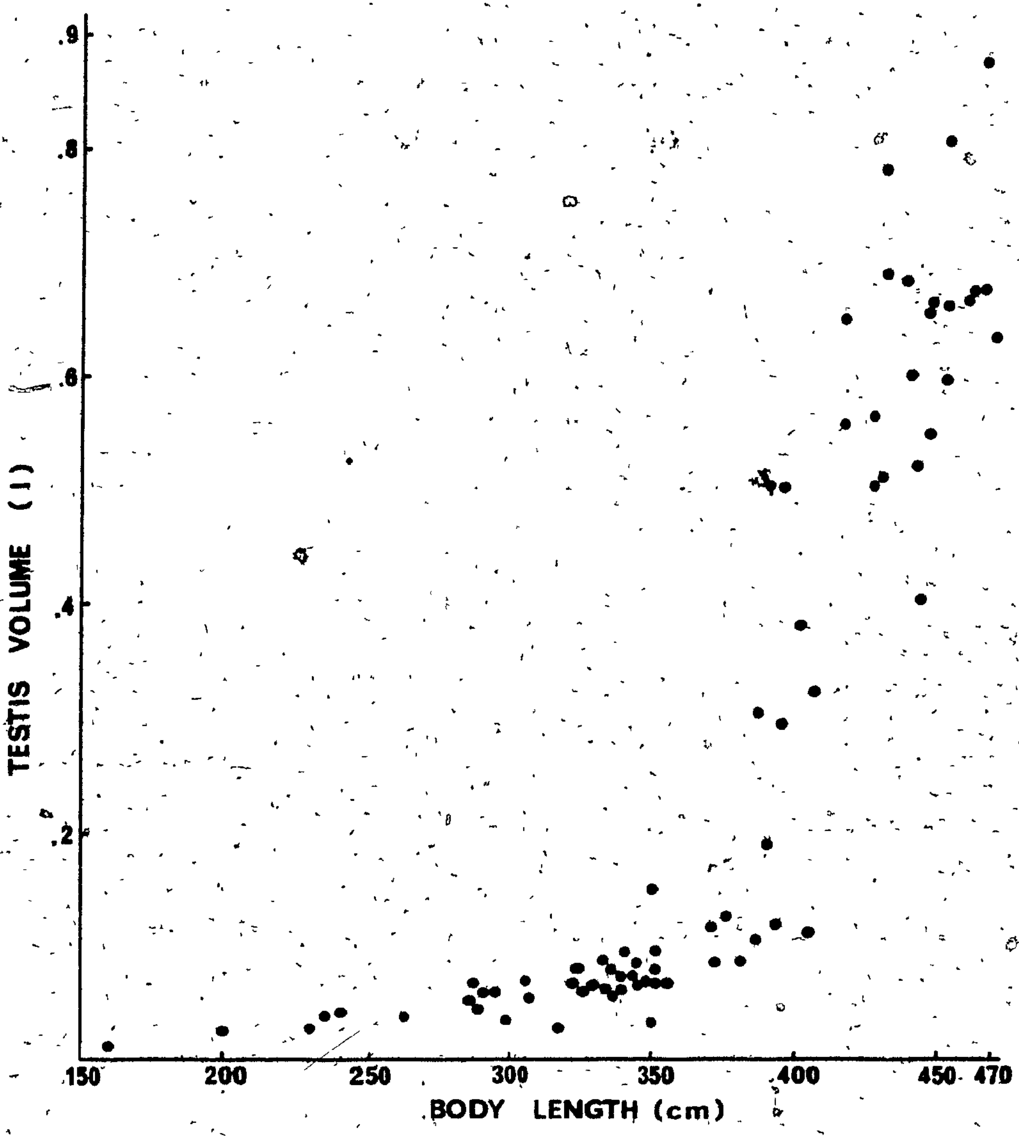


Figure 23. Testis volume and body length of 72 narwhals.

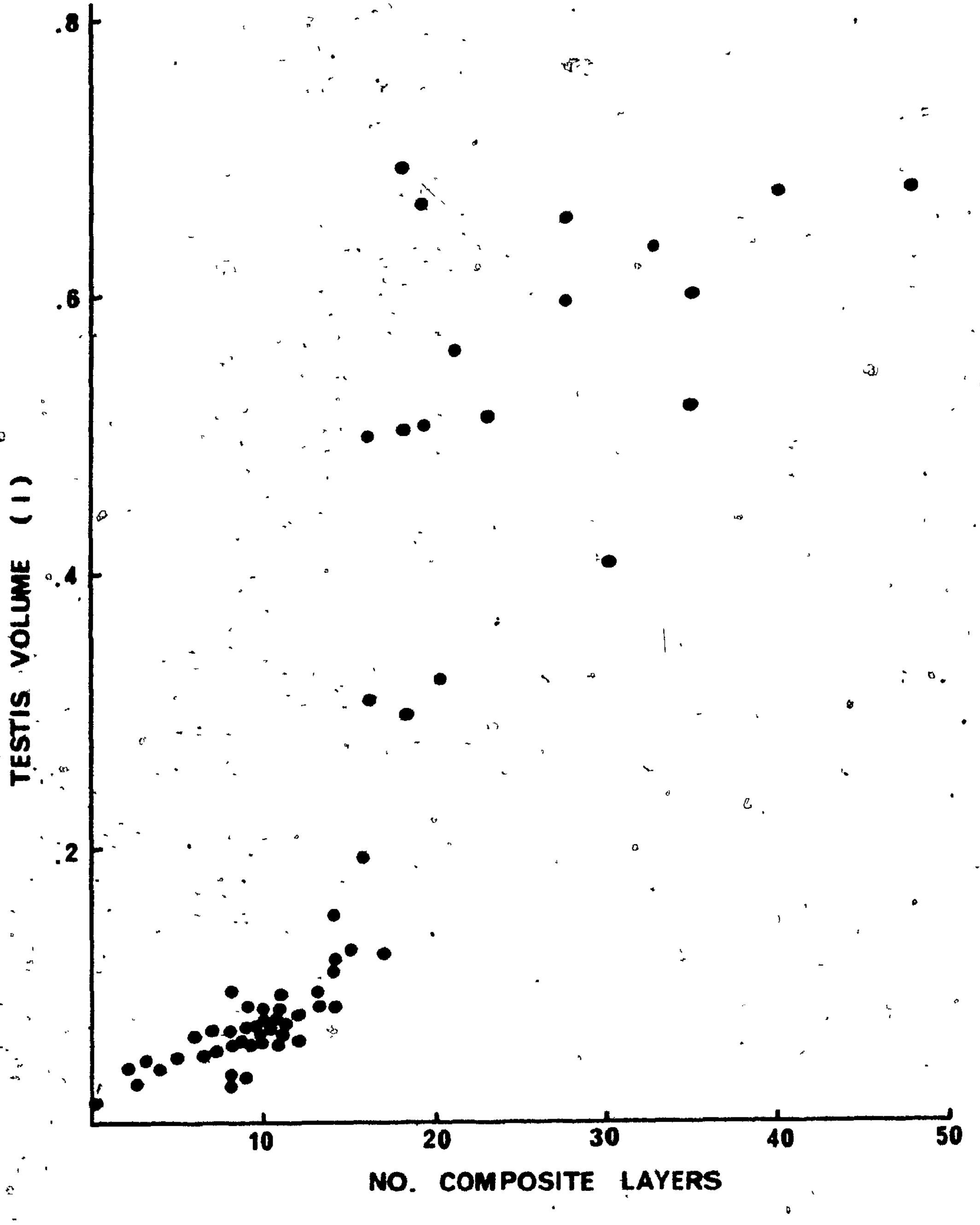


Figure 24. Testis volume and number of growth layers of 61 narwhals.

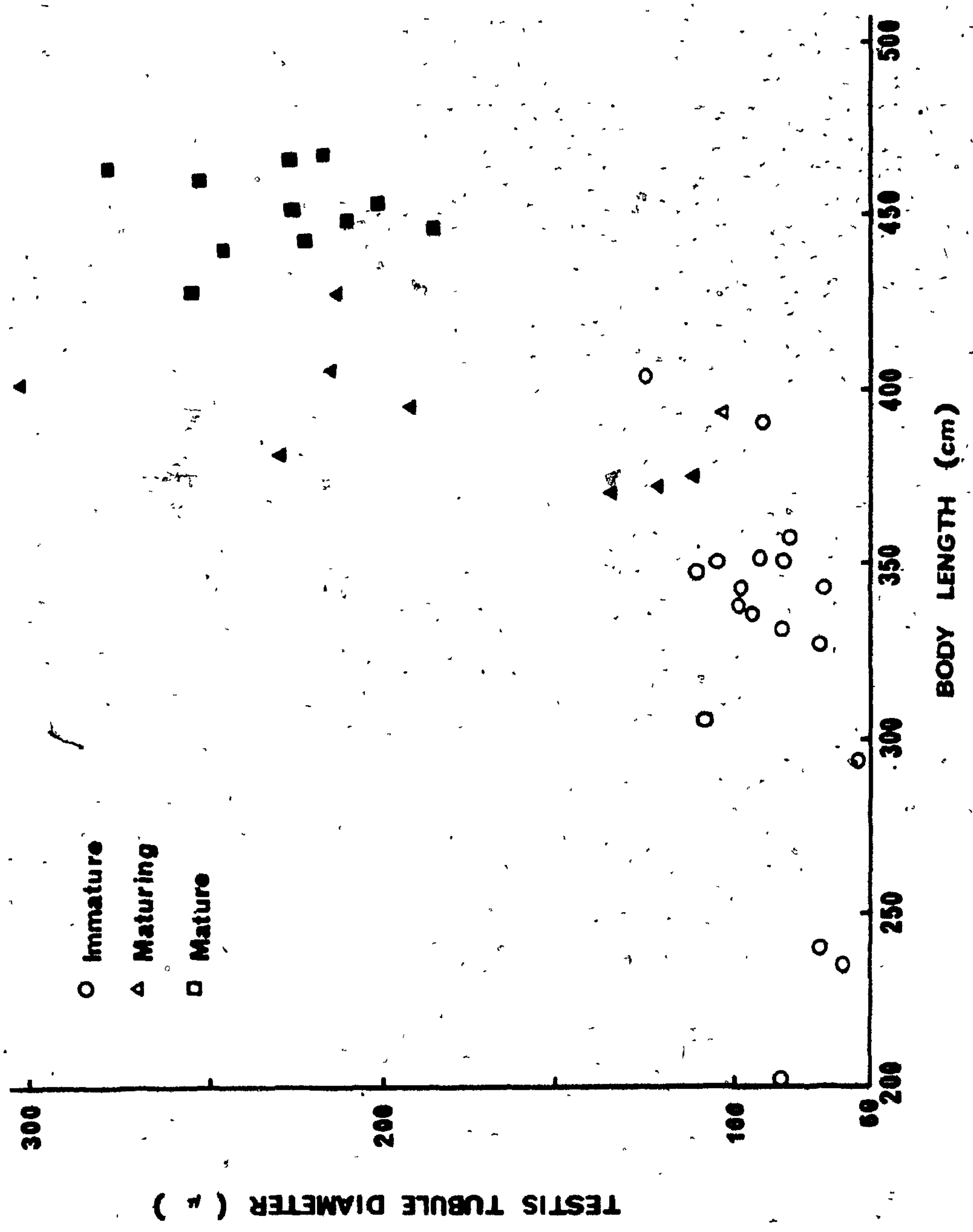


Figure 25. Testis tubule diameter and body length of 38 narwhals. A solid point indicates the presence of spermatozoa.

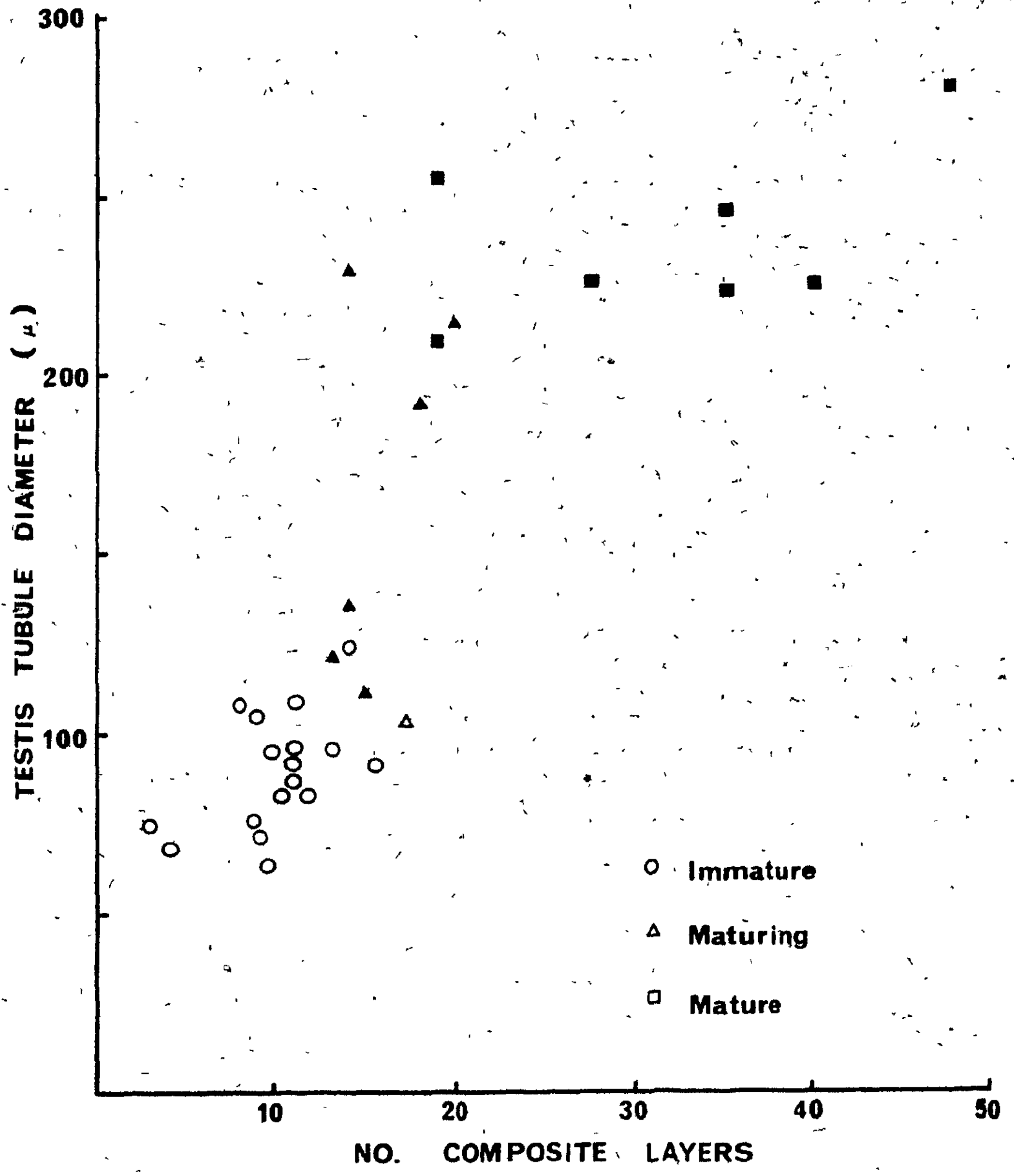


Figure 26. Testis tubule diameter and number of growth layers of 31 narwhals. A solid point indicates the presence of spermatozoa.

humpback whale (Chittleborough 1955a), and the spotted porpoise (Perrin et al. 1976). The diameters of the seminiferous tubules of the narwhal are within the range of values given for the comparable reproductive categories of other male odontocetes (Table 8).

Epididymal tubule diameter - Epididymal tubule diameter increases rapidly after 360 cm body length and 13 composite growth layers (Figures 27 and 28), although it varies widely over a broad range of body length and age; therefore, changes in the diameter of the epididymal tubules seem to be less finely regulated by the sexual maturation process in males, compared to changes in the diameter of the seminiferous tubules.

Length- and age-frequency distributions - According to Best (1969), the length or age at which 50% of males are immature can be taken as the average length or age at puberty (onset of spermatogenic activity) and the length or age at which there are equal frequencies of immature and mature males can be taken as the average length or age at the attainment of sexual maturity. Applying these criteria to the length- and age-frequency distributions of the narwhal (Figures 29 and 30), puberty occurs at 370 cm and 14.2 composite growth layers while sexual maturity is attained at about 395 cm and 17 growth layers. These estimates of mean length and age at sexual maturity are similar to those estimated above using testis volumes and seminiferous tubule diameters. About three growth layers elapse between the onset of spermatogenic activity and the attainment of sexual maturity, which is not necessarily the attainment of full fertility. Chittleborough (1955a) concluded that the interval between puberty and maturity may be about one year in male humpback whales. The attainment of sexual maturity after puberty is an extremely protracted process in Stenella attenuata (Perrin et al. 1976; Kasuya et al. 1974).

The ages at puberty and sexual maturity of the males of several species of cetaceans are given in Table 8. The criteria used by various authors in determining these ages are probably quite diverse. Miyazaki (1977), for example, assumed that puberty is attained when

Table 8. Mean diameter of seminiferous tubules and mean age at puberty and sexual maturity of some male cetaceans.

Species	Mean diameter of seminiferous tubules(μ)			No. dentinal layers at			Author
	Immature	Pubertal	Mature	Puberty	Sexual Maturity	Social Maturity	
Balaenoptera physalus	80		200[a]				Laws 1961
Megaptera novaeangliae	79	103	155				Chittleborough 1955a
Physeter catodon	89		167		25-27		Best 1969, 1970
					10-11		Nishiwaki *et al.* 1958
					12	25	Ohsumi 1966
				9-10	19	25-27	Best 1974
Globicephala meleana					12		Sergeant 1962
Delphinapterus leucas					16		Brodie 1971
					17		Sergeant 1973
Hyperoodon ampullatus					13		Christensen 1973
Berardius bairdii					8-10		Kasuya 1977
Stenella attenuata					10.3		Kasuya et al. 1974
					11.8		Kasuya 1976
				9	12		Perrin *et al.* 1976
S. coeruleoalba					9.0-9.2		Kasuya 1972, 1976
	44	55	131	6.7	8.7	>8.7	Miyazaki 1977
S. longirostris					9-12		Perrin *et al.* 1977
Phocoena phocoena					4		Gaskin and Blair 1977

[a] oestrous condition; anoestrous is 140μ.

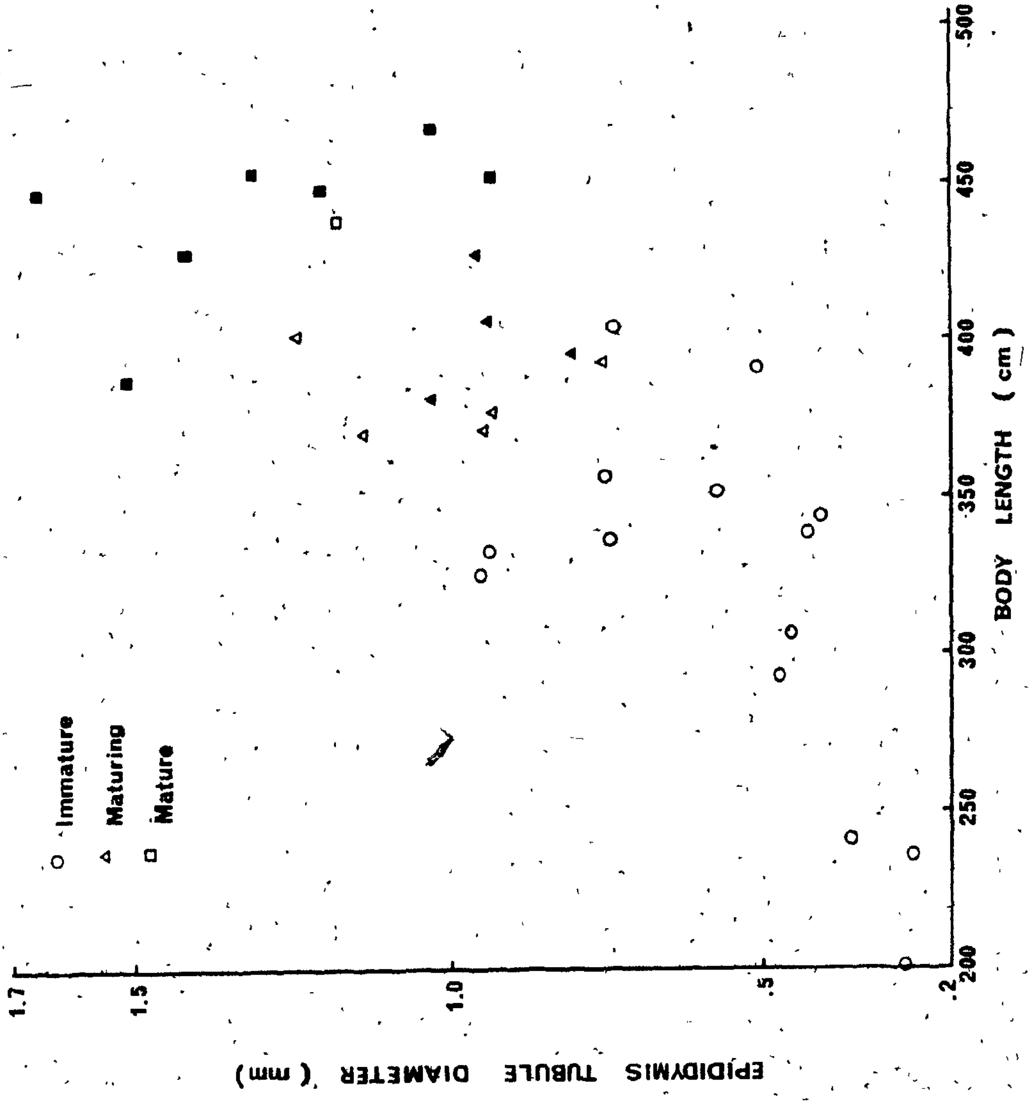


Figure 27. Epididymis tubule diameter and body length of 31 narwhals. A solid point indicates the presence of spermatozoa.

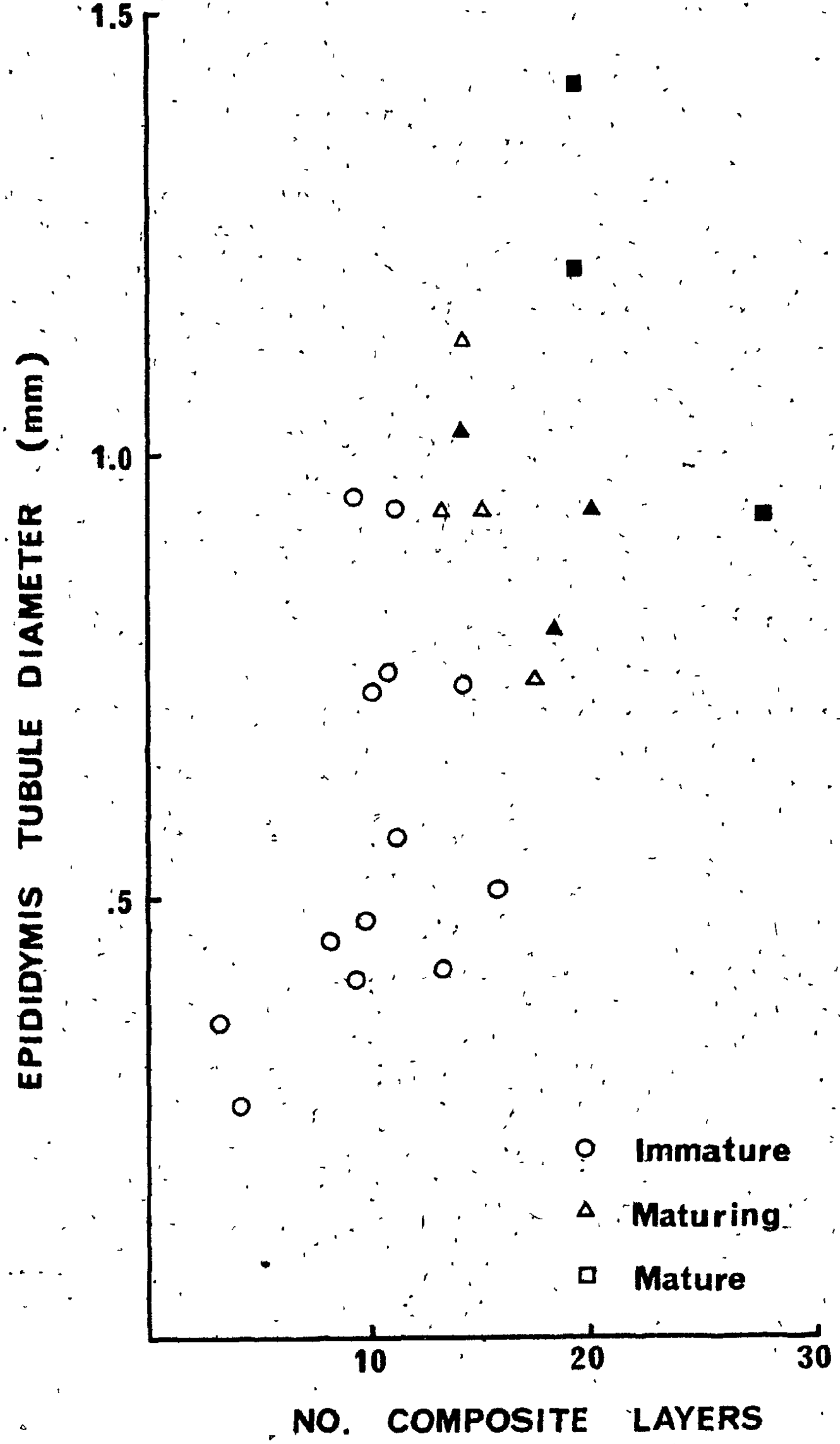


Figure 28. Epididymis tubule diameter and number of growth layers of 23 narwhals. A solid point indicates the presence of spermatozoa.

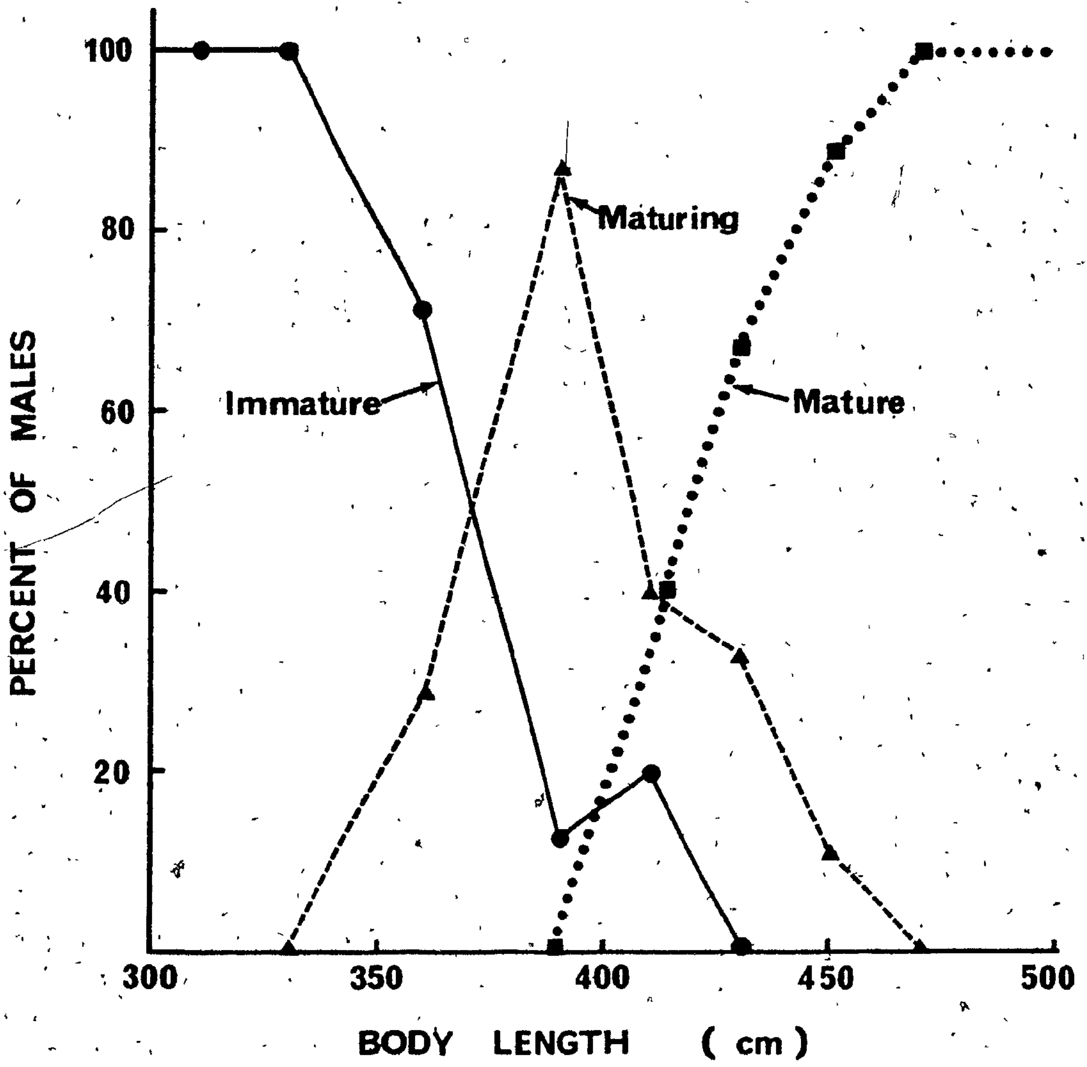


Figure 29. Length-frequency distribution of 72 immature, maturing, and mature male narwhals. Length-class interval is 20 cm.

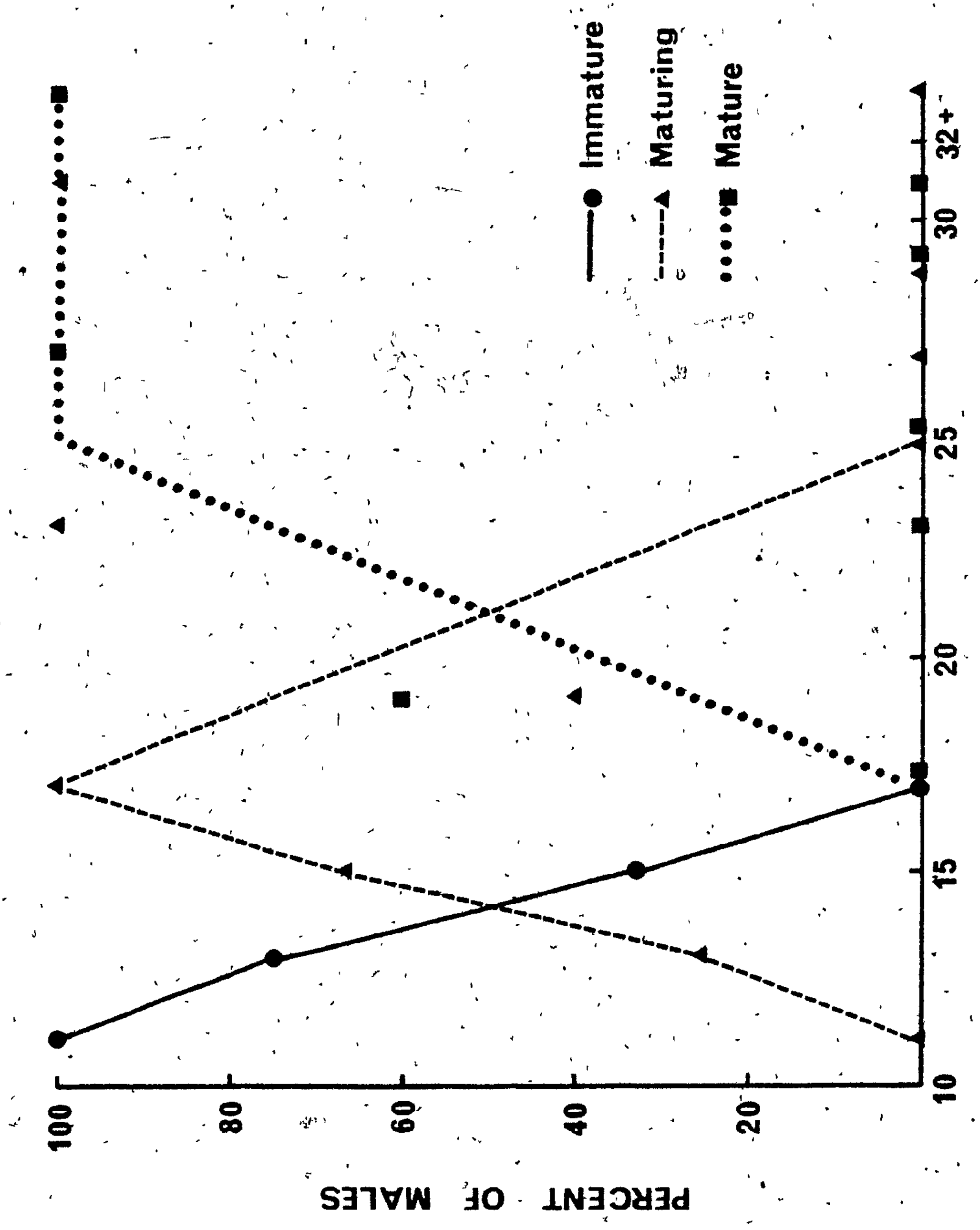


Figure 30. Growth layer-frequency distribution of 61 immature, maturing, and mature male narwhals. Growth layer-class interval is two composite growth layers. Due to small sample sizes in some of the older growth layer- classes, the curves for maturing and mature males were smoothed.

50% of the males are pubertal (maturing), and that sexual maturity is attained when 50% are mature. It is notable that the male white whale Delphinapterus leucas has about the same number of dentinal growth layers at maturity as does the narwhal (Table 8). Brodie (1971) showed that Cumberland Sound, Baffin Island male white whales with 16 or more tooth layers were sexually mature, while Sergeant (1973) found that male white whales from Hudson Bay demonstrated a spurt in testis growth and spermatogenesis at 16 to 18 growth layers. These results suggest that male white whales mature when about 8 to 9 years old, assuming that 2 dentinal growth layers are deposited annually in this species (Brodie 1971; Sergeant 1973).

Seasonal Changes

The single testis volumes of maturing and mature males are plotted against date of capture in Figure 31. There seems to be a decrease in the testis volume of mature males with increasing date, although the range of testis volume is wide at all times. A linear regression of testis volume on time (time=0 is 15 July, the earliest date when a mature testis was recorded) gave the following equation:

$$y = -1.0745\ x + 690.44$$

where y is mature testis volume (ml) and x is time after 15 July (days). The regression coefficient (-1.0745) is not significantly different from zero at the 5% significance level ($t=0.9456$, $0.4>p>0.2$), indicating that mature testis volume is not dependent on date of capture. Maturing testis volumes appear to increase with time, but this could be due to sampling of individuals which are in different stages of the sexual maturation process. A linear regression of maturing testis volume on time (time = 0 is 19 July, the earliest date that a maturing testis was recorded) produced the equation $y = 4.8692\ x + 160.381$, where y is maturing testis volume (ml) and x is time after 19 July (days). The regression coefficient is, however, not significantly different from zero ($t = 2.145$, $0.1 > p > 0.05$), suggesting that maturing testis volume is not dependent on date of capture. In addition, there seem to be no

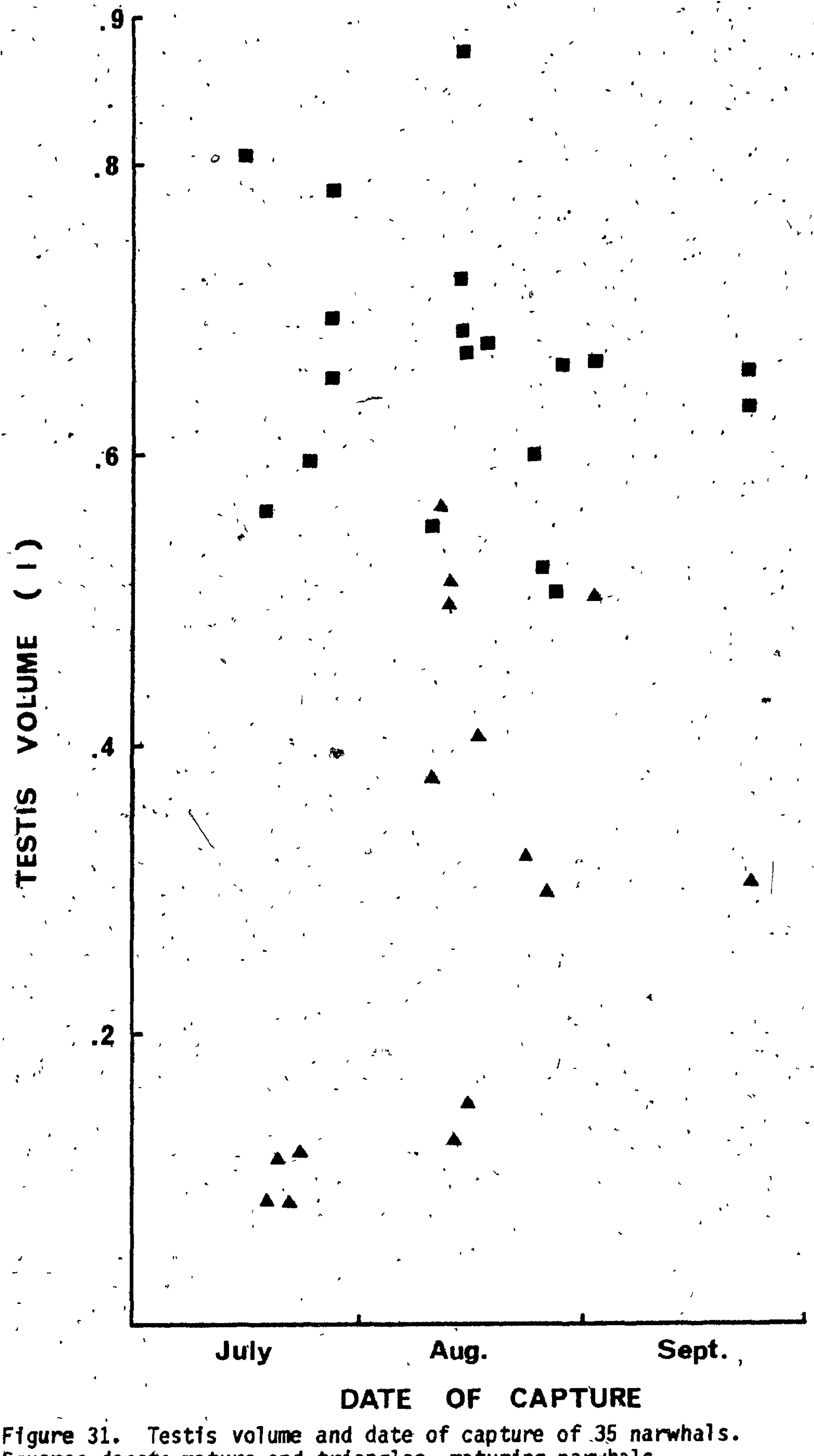


Figure 31. Testis volume and date of capture of 35 narwhals. Squares denote mature and triangles, maturing narwhals.

systematic changes in the diameters of the seminiferous and epididymal tubules with season (Figure 32). The sampling season occurs about three months after the peak of the breeding season, and either the mature testis volumes and tubule diameters have already regressed to annual minimum values or else the sampling period is too short to demonstrate reductions in mature testis size and tubule diameters, given the probable great variation among individuals in the timing of the seasonal development and regression of the testis. On the basis of these data, it is impossible to conclusively demonstrate an annual cycle of reproductive activity in the male narwhal.

Best (1969) did not detect seasonal changes in the size of the testis and the diameter of the seminiferous tubules of the sperm whale, but he had no samples from the spring breeding season. Sergeant (1962) concluded that male pilot whales were anoestrous in late summer and fall after spring breeding and Brodie (1970) came to a similar conclusion for the white whale. Laws (1961) showed that male fin whales were anoestrous from December to February, when seminiferous tubule diameters were lowest. Laws (1956b) demonstrated that the seasonal enlargement of the testes of the elephant seal during the breeding season is due to an increase in the diameter of the seminiferous tubules, with a concomitant reduction of interstitial tissue. There is also a similar cycle of the epididymis in this species (Laws 1956b). Ridgway and Green (1967) demonstrated a marked annual cycle of sexual development and rut in male dolphins of _Lagenorhynchus obliquidens_ and _Delphinus delphis_ off California. The mid- to late summer period of male rut is characterized by: enlargement of testes, seminiferous tubules, and muscles associated with the penis; an increase in spermatogenesis; and production of copious amounts of semen containing viable spermatozoa. However, these authors did not pay much attention to the size and age of the specimens which they compared so that much of the possible seasonal variation which they described could in fact relate to the stage of sexual maturation of these specimens (eg. - see their Table I). It

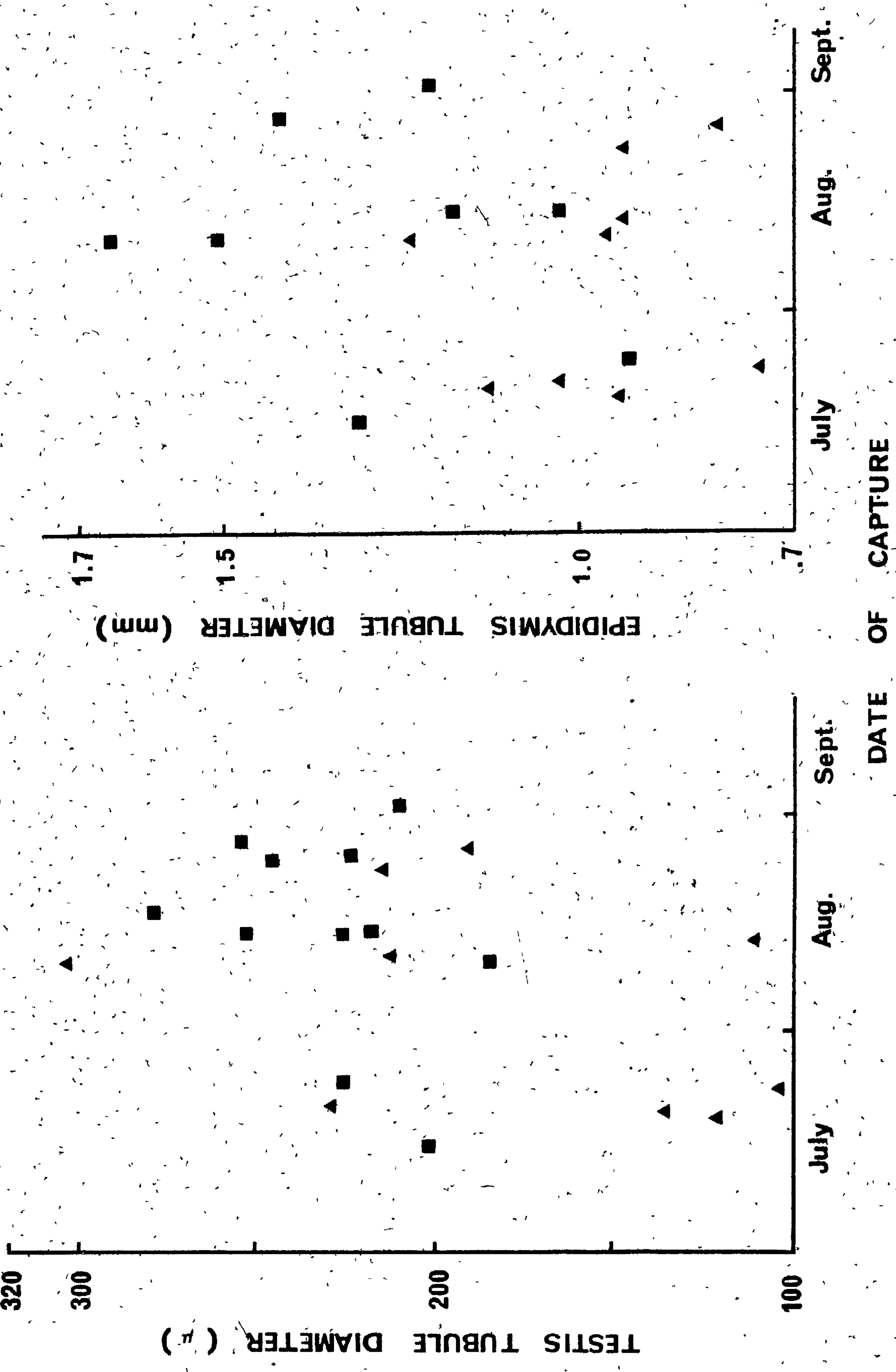


Figure 32. Testis and epididymis tubule diameters and date of capture of 20 and 17 narwhals, respectively. Squares denote mature and triangles, maturing narwhals.

appears that the most serious obstacle to the elucidation of the reproductive cycle of male odontocetes is the often short annual sampling season.

Discussion

The attainment of sexual maturity by male odontocetes is not necessarily accompanied by maximum fertility or the capacity to impregnate females. The male sperm whale, for example, does not attain full fertility and social maturity (ability to breed and maintain a harem) until six to eight years after the attainment of sexual maturity (Best 1974), and maturing or pubertal whales are subfertile (Best 1969). It is not known whether the male narwhal is fully fertile when it attains sexual maturity (400 cm and 17 growth layers), but because of the intense competition for females among the males of a polygynous species, social maturity may be attained only after a further increase in body size and/or testis size. A high level of circulating testosterone and/or large body size may be advantageous to males in securing and defending harems.

Polygyny is believed to be displayed by males of the spotted porpoise (Kasuya et al. 1974) and the sperm whale (Best 1969; Ohsumi 1966). The harem of a male sperm whale may consist of 10 or more females (Best 1969). According to Best (1974), male sperm whales start migrating seasonally to high latitudes when they attain sexual maturity (19 years). In the north Pacific, segregation of male sperm whales to high latitudes starts after the age of 12 years (sexual maturity) and continues to increase until 25 years of age, when dominant males attain social status and remain in lower latitudes with the female schools (Ohsumi 1966). Brodie (1970) believed that mature male white whales are polygynous but they segregate from females outside the breeding season. More direct observation of behaviour during the breeding season is needed to establish the existence of polygyny in odontocetes and its relationship to body size and sexual dimorphism.

Evidence for polygyny in the narwhal includes the larger body size of the adult male compared to the adult female, the presence of a tusk usually only in males, and delayed sexual maturity in males. Further evidence is the high incidence of scars, believed to be made by the tusk, on the heads of adult males (Silverman and Dunbar 1980). Delayed sexual maturity of males leads to a relative excess of mature females: there is an average of 3.06 mature female narwhals for every mature male, excluding data from the Guys Bight floe edge where females were selectively sampled (Appendix Table 3).

REPRODUCTION IN THE FEMALE

Foetal Growth and Gestation Period

The gestation period was calculated by the method of Huggett and Widdas (1951) as modified by Laws (1959). Figure 33 presents the relationship between foetal length and date of capture for narwhals taken in northern Baffin Island from 1963-76. The mean body length at birth is estimated to be 161 cm (the average of the lengths of the largest foetuses and smallest newborn calves) and the mean birth date is 1 August. The mean length of the small foetuses is 24.17 cm on a mean date of 5 August. Using these data, the linear foetal growth rate is calculated as 0.379 cm/da and the gestation period is estimated to be 467 days (15.3 months), resulting in a mean conception date of 21 April. Based on the largest and smallest foetuses observed in August (Figure 33), the extreme limits of the foetal growth curve have been estimated assuming that all foetuses grow at the same rate. Conception is seen to vary from 20 March to 19 May with a peak around 21 April, while the season of births is 30 June to 29 August, with a probable peak on 1 August.

A linear regression of foetal length on time (time = 0 is 17 July, the earliest date when a foetus was recorded) was performed, giving the following equation:

$$L = 0.37794t + 16.91193$$

where L is foetal length (cm) and t is time after 17 July (days). The regression coefficient (0.37794) is essentially the same as the previously calculated foetal growth rate (0.379 cm/da).

Foetal lengths of narwhals from other regions are similar to those from northern Baffin Island. Small foetuses of similar size were recorded during June-August in east Greenland (Eales 1950; Gray 1889) and in west Greenland (Vibe 1950; Bruemmer 1971).

The season of births and neonatal body lengths are constant throughout the range of the narwhal, including the Thule region of northwest Greenland (Vibe 1950; Bruemmer 1971; Raven 1927), the waters of east Greenland (Eales 1950; Gray 1889), and the Arctic Ocean (Rutilevskii 1958). In the Canadian arctic, Degerbøl and

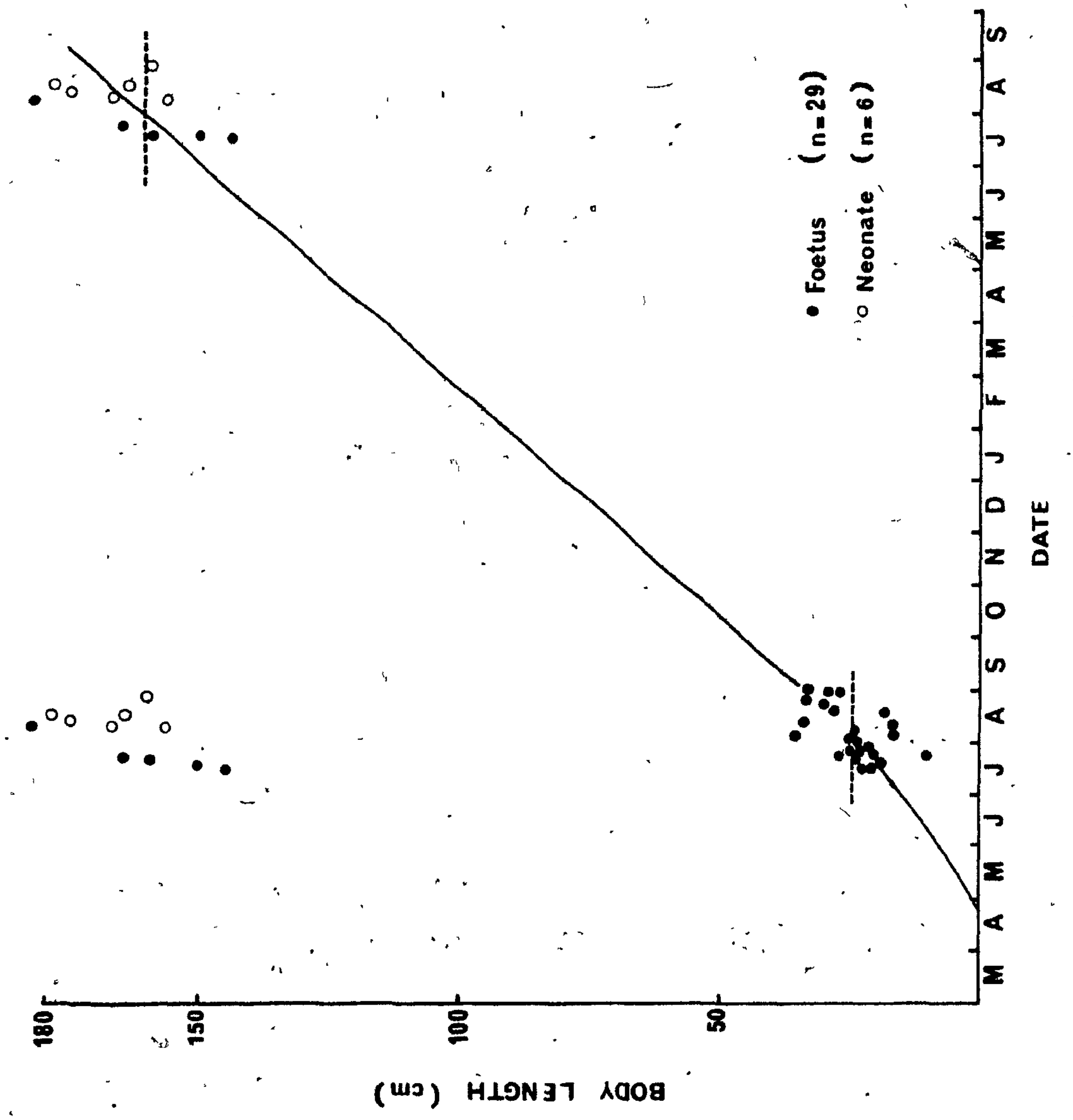


Figure 33. Growth curve of the foetal narwhal, using data from northern Baffin Island, 1963-76. Large foetuses and calves have been plotted twice to produce the growth curve. Dashed horizontal lines indicate the mean birth length (161 cm on 1 August) and the mean length of small foetuses (24.2 cm on 5 August).

Freuchen (1935) observed newborn calves and fully-grown foetuses in Eclipse Sound during July. Finley (1976) observed neonatal narwhals on 18 July 1975 in eastern Barrow Strait, while Greendale and Brousseau-Greendale (1976) recorded neonates at Cape Hay, Bylot Island, from 26 June to 24 July 1976. Johnson et al. (1976) observed 17 neonatal narwhals in Lancaster Sound from 28 June-26 July 1976.

In spite of the fact that the foetal lengths of narwhals taken in July-August comprise two main size groups (10-40 cm and 140-170 cm), the narwhal is assumed by some authors to have no definite breeding season (Porsild 1922; Vibe 1950; Degerbøl and Freuchen 1935). Degerbøl and Freuchen (1935) and Pedersen (1931) claimed that small calves and foetuses of all sizes were present at all times of the year. Gray (1889) concluded that conception occurred in May and June and that the gestation period was 12 months. Best and Fisher (1974) estimated the gestation period to be 14 months, using published data from narwhals captured in Greenland waters and in the eastern Canadian arctic.

The gestation period of the narwhal is similar to that of other large odontocetes. The gestation period is 17 months in the beaked whale Berardius bairdii (Kasuya 1977), 14.6 months (Best 1968) or 16.4 months (Ohsumi 1965) in the sperm whale, 14 to 14.5 months in the white whale (Brodie 1971; Sergeant 1973), and 15.5 to 16 months in the pilot whale (Sergeant 1962). Benjaminson (1972) estimated the gestation period of the bottlenosed whale Hyperoodon ampullatus to be 12 months, but inspection of the foetal growth data for this species indicates a more likely estimate of 15 to 16 months. The smaller odontocetes have gestation periods of 11 to 12 months. For example, the spotted porpoise Stenella attenuata has a gestation period of 11.5 months (Perrin et al. 1976).

Ovarian Structures and the Oestrous Cycle

Gross and histological structure of ovarian corpora - The ovaries of all females were sliced at 3 mm intervals using a scalpel and all corpora lutea and albicantia were identified and counted.

The corpus luteum of pregnancy is a large yellowish glandular structure, 30-62 mm in mean diameter, projecting from the surface of the ovary of pregnant females (Plate VI, a). It is most commonly located at the pole of the ovary. Trabeculae of connective tissue from the theca externa divide the gland into numerous lobes; these trabeculae and a multitude of small fibrous septa carry the blood vessels. A stigma (eruption pit) and corona (everted luteal tissue around the stigma) are usually present on the surface of the corpus luteum. A small central cavity, filled with liquor folliculi or fibrous tissue, is sometimes present.

The granulosa lutein cells are large and polyhedral in shape. Their cytoplasm contains a multitude of small vacuoles and therefore has a frothy appearance, while their nuclei are vesicular (Plate VII, a and b). The theca lutein cells are much smaller and are arranged in small groups at the periphery of the corpus luteum, usually at the bases of the fibrous trabeculae. These cells are polyhedral and contain relatively large, dark-staining granular nuclei. Their cytoplasm appears clear because of the extraction of lipoidal pigments during histological processing. Occasionally, theca lutein cells may be found within the fibrous septa at some distance inside the corpus luteum. The frothy appearance of the cytoplasm of the luteal cells of the active corpus luteum of the fur seal Callorhinus ursinus is indicative of great secretory activity (Craig 1964; Yoshida, Baba, Oya and Mizue 1977). Laws (1961) noted the presence of theca lutein cells at the bases of the fibrous septa and at the periphery of the developing corpus luteum of the fin whale Balaenoptera physalus.

When a corpus luteum ceases secretory activity at parturition, or after its development as a short-lived corpus luteum of ovulation, it beings to involute and to transform gradually into a fibrous scar called the corpus albicans. Whale ovaries are unique in that the corpora albicantia apparently persist for the life of the female (see Laws 1961). Laws (1961) distinguished three stages of regression of the corpus luteum of the fin whale which I have applied to the narwhal. The young corpus albicans is found in the ovaries of recently-parturient females and in females which have recently ovulated unsuccessfully, having produced an infertile ovulation or corpus luteum of ovulation (Plate VI, b and d). It comprises the earliest stage of the regression process, shrinking in size very rapidly. Its luteal tissue appears compact and is yellowish-brown. The young corpus albicans is still prominent externally, having a wrinkled surface appearance due to its shrinkage in size. The core and radially-arranged septa of white connective tissue are not yet extensive. The young corpus albicans is well-vascularized but thick-walled, contorted blood vessels are not macroscopically evident (Plate VI, b). A thickening fibrous capsule with a few thick-walled blood vessels surrounds the young corpus albicans.

Histologically, most of the luteal cells have degenerated and the luteal tissue has been replaced by hyaline connective tissue (Plate VII, c). A few small thick-walled blood vessels are present in the hyaline tissue, and they are becoming increasingly contorted as the corpus albicans shrinks.

Young, regressing corpora albicantia are often seen in close proximity to the corpus luteum of females in early pregnancy. They evidently represent unsuccessful, infertile ovulations prior to the recent conception, indicating that the narwhal is polyoestrous (see Plate VI, d). Benirschke, Johnson and Benirschke (1980) report that infertile ovulations are frequent in dolphins (Stenella sp.) and that ovulation may often be spontaneous rather than copulation-induced. They caution that macroscopic diagnosis of corpora lutea may therefore be frequently erroneous.

The medium corpus albicans occupies an intermediate stage of regression (Laws 1961). The fibrous core and septa are becoming more extensive while the residual light-brown hyaline connective tissue is diminishing. A thickening fibrous capsule with thick-walled vessels surrounds the corpus albicans, and prominent surface wrinkling is still evident. However, it bulges to a lesser extent from the ovary than a young corpus albicans. Thick-walled, contorted blood vessels are found throughout the hyaline tissue, and some of the small calibre vessels are now occluded and non-functional. The walls of these vessels consist largely of loose, acellular collagen, although van Lennep (1950) claimed that elastic tissue was predominant.

The old corpus albicans represents the fully-regressed corpus luteum and does not shrink any further in size (Laws 1961). Diagnostically, the large white connective tissue core and septa are prominent, and the residual hyaline luteal tissue is thin and coloured a deep orange-brown due to concentration of lipoidal lutein pigments by phagocytes that progress inward through the structure (Plate VI, c). A thick white capsule containing thick-walled fibrous blood vessels, some of which are occluded, surrounds the corpus albicans; there is little external evidence of an internal structure, except for a very slight wrinkling of the ovarian surface. Very old coropora albicantia consist almost entirely of scar tissue and fibrous thick-walled, coiled blood vessels, many of which are occluded. Old corpora albicantia are often flattened parallel to the ovarian surface. Coagulated blood and blood pigment granules may also be present (Plate VI, c; VII, d). This blood must be due to rupture of the functional vessels. The core and septa consist of loose connective tissue with few fibroblasts or blood vessels (Plate VII, d).

These involutional changes in the corpus luteum of the narwhal are essentially the same as those described for the fin whale by Laws (1961) and for the sperm whale by Best (1967).

The earliest signs of degeneration of a corpus luteum are nuclear pyknosis and vacuolation of the granulosa lutein cells, both of which are seen in early pregnancy Callorhinus ursinus (Craig 1964) and Mirounga leonina (Laws 1956b). The pinniped corpus luteum regresses throughout pregnancy and is non-functional by the time of birth (Craig 1964). On the other hand, the corpora lutea of blue whales Balaenoptera musculus and fin whales B. physalus do not regress until parturition (van Lennep 1950), while in Phocoena phocoena the corpus luteum begins to regress during late pregnancy

(Fisher and Harrison 1970). Chittleborough (1954) found a degenerating corpus luteum in only one late-pregnancy female humpback whale.

The corpora lutea of near-term female narwhals are the same size as those of females in early pregnancy (40-50 mm), but no histological data on the former group are available to indicate whether or not pre-partum degeneration does occur.

The regressing corpora lutea of the narwhal are histologically similar to those of _Platanista gangetica_ (Harrison 1972), _Neophocaena phocaenoides_ (Harrison and McBrearty 1973-74) and many other odontocetes (Harrison, Brownell and Boice 1972). Van Lennep (1950) described the process of degeneration of the corpora lutea of the blue whale and fin whale in some detail. Initial degeneration is lipoidal, whereby the lipids within the vacuoles of the granulosa lutein cells change from a yellowish to a yellow-brown colour. According to van Lennep (1950), the pigmented hyaline collagen (degenerated luteal tissue) is produced by theca lutein cells which have transformed into fibroblasts, while the main mass of collagen is formed by fibroblasts from the theca externa, the fibrous core and septa, and the fibrous walls of the blood vessels. As regression continues, the blood vessels become increasingly coiled and their walls thicken by growth of collagen, smooth muscle, and elastic tissue, while their lumina are progressively reduced in diameter. A very old corpus albicans apparently consists mostly of elastic fibers. Van Lennep (1950) could not histologically distinguish between regressing corpora lutea of ovulation and those of pregnancy. However, Fisher and Harrison (1970) believed that they could distinguish between corpora albicantia of infertile ovulations and those of pregnancy in the harbour porpoise, but it is clear that they were distinguishing between early and late regression stages, for the latter consisted mainly of coiled, occluded blood vessels with clusters of degenerating cellular elements, while the former consisted of lobular acellular connective tissue and fewer vessels.

Luteinized follicles are corpora lutea derived from unruptuted follicles; they may be partially-luteinized, with the gel-filled cavity surrounded by orange luteal tissue which is likely produced by the hypertrophied theca interna (Yoshida et al. 1977). Some of these structures appear similar to the corpora lutea atretica of the ovary of the sperm whale (Best 1967).

If the follicle luteinizes completely, it may persist throughout gestation as an accessory corpus luteum (Plate VI, a). Histologically, the structure is the same as that of the functional corpus luteum of pregnancy, although the two accessory corpora lutea (pictured in Plate VI, a) are thought to be regressing. These two luteinized follicles would probably be fully-regressed by the time of parturition and would not then be recognizable. Luteinized follicles contain islands of theca lutein cells in the fibrous septa and near the periphery. It is possible that accessory corpora lutea in the narwhal persist only during early pregnancy, as few are seen in the ovaries of late-pregnancy or recently-parturient females.

Regressing luteinized follicles are often present in the ovaries of mature females, especially those in early pregnancy which have ovulated recently during March to May. These follicles are inconspicuous externally, with no surface wrinkling and no eruption site, and they may protrude very slightly from the surface of the ovary (Plate VI, e). They consist of lobules of greyish-brown or greyish-yellow hyaline connective tissue separated by white collagenous septa. The mode of regression seems to be the same as that of the corpora lutea of pregnancy, although they usually become fibrous very soon and coiled thick-walled vessels are not numerous. In addition, regressing luteinized follicles are surrounded by a thin fibrous capsule which contains a few thick-walled open vessels. The lack of clotted blood and blood pigment granules may be diagnostic of regressing luteinized follicles. They probably do not shrink much in size during regression, as evidenced by the lack of surface wrinkling and the presence of a few coiled vessels. It is possible that such small structures are eventually completely resorbed.

The structure of a 15 mm luteinized follicle (or accessory corpus luteum) in very early regression is shown in Plate VII, e and f. The degenerative changes described by Craig (1964) for the fur seal corpus luteum are seen in a few granulosa lutein cells. Plate VII, e shows a granulosa lutein cell with pyknotic nucleus and deep-staining, acidophilic cytoplasm. Fibrous septa are enlarging (Plate VII, f) and fibrous tissue has replaced part of the gland, although much healthy luteal tissue is evidently still present. Well-regressed luteinized follicles are seen to consist largely of vacuolated hyaline connective tissue with a low density of fibroblasts, although a few degenerating granulosa lutein cells may be present. Healthy or degenerating theca lutein cells may persist at the periphery and in the fibrous septa. In fact, the presence of theca lutein cells suggests that some of these regressing bodies may be corpora lutea atretica or their regression products (Best 1967).

Follicles in various stages of development and atresia are present in the ovaries of all mature female narwhals. They are usually filled with fluid (the liquor folliculi) and they are thin-walled. The largest follicles are usually found near the ovarian poles.

Haemorrhagic follicles are small and filled with blood (Plate VI, f). They apparently represent the normal mode of degeneration of small follicles (Best 1967). Some theca-derived orange luteal tissue may form at the periphery and liquor folliculi may still be present in the cavity of the follicle. Collagenous tissue ultimately replaces the blood, forming an invisible fibrous scar.

Enlarging follicles exceeding a diameter of 10 mm are present in the ovaries of mature females of several reproductive categories. Two possibly erupted follicles of diameters 15.3 mm and 11.2 mm were found in the left and right ovaries, respectively, of a maturing female (with 12 dentinal growth layers). These follicles were collapsed, devoid of liquor folliculi, and located at the poles of their respective ovaries. It is therefore possible that the mature follicle attains a size of about 15-20 mm at the moment of ovulation.

Cystic follicles have also been found in some ovaries. A 19 mm follicle in the ovaries of a female in very early pregnancy (foetus not found) was thick-walled, empty, and invisible externally. Its wall consisted of a thin inner membrane and a thick, vascularized, fibrous outer layer. The outer edge of this follicle was about 2 mm from the ovarian surface. A 5.2 mm follicle filled with a brown paste-like substance was present in one of the ovaries of the same female. Such cystic follicles may be partly-luteinized, as Laws (1956b) found for the elephant seal Mirounga leonina. Cystic follicles are also present in the ovaries of some physically-mature humpback whales, some of which have recently ovulated (Chittleborough 1954).

A possible recently-erupted follicle was found in the right ovary of a female thought to be in very early pregnancy (foetus not found), since the left ovary contained a corpus luteum of diameter 33 x 33 mm and there was no evidence that this female was recently-parturient. This 15.9 mm follicle had a wrinkled surface appearance (due to follicular collapse) and was blood-filled (Plate VI, f). It was surrounded by a thick fibrous capsule; connective tissue was invading the blood clot and a few thick-walled blood vessels were present. No luteal tissue was detected. Patches of yellow-brown pigment granules were seen within the blood clot. It is difficult to explain the occurrence of ovulation by a pregnant female, since progesterone from a functional corpus luteum prevents follicular maturation. If the female was recently-parturient, then this would be a case of a post-partum ovulation. Whatever the interpretation, this follicle must have erupted and partially luteinized, and was now involuting.[1]

The corpus incognitum (my term) is a structure whose origin and significance are obscure. It is often present in the ovaries of old, likely physically-mature females. The corpus incognitum is up to

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[1] See footnote at the end of this chapter

15 mm in diameter, and it consists of loose-structured, dark or black tissue which is probably clotted blood (Plate VI, h). All of these structures have a prominent eruption site which may take the form of an open pit on the otherwise smooth surface of the ovary. A thick white fibrous capsule surrounds the corpus incognitum. These corpora have a collapsed appearance, and they also have a central slit-like cavity which is filled with gel or fibrous tissue, but which is often empty. Some loose-structured pigmented (yellow, brown or orange) tissue may be found near the periphery or within the dark tissue. White fibrous tissue is often present within this pigmented tissue, but thick-walled coiled blood vessels are not evident macroscopically.

These structures are similar to the corpora atretica "a" of the sperm whale (Best 1967) and to the corpora aberrantia and "anomalous corpora of lactating females" of the fin whale (Laws 1961). The <u>corpus incognitum</u> is certainly a regressing structure, and it could be derived from a recently-ovulated follicle that failed to luteinize. Some evidence for the suggestion that the corpus incognitum is a haemorrhagic medium or old corpus albicans will be presented later.

All <u>secondary</u> or <u>antral follicles</u> that were examined histologically were found to be undergoing <u>atresia</u> (Plate VII, g and h). This is to be expected, since all whales were taken three to four months after the breeding season (peak of ovulations). Best (1967) showed that atresia of follicles in the ovary of the sperm whale is maximal just after the peak occurrence of ovulations.

The general process of follicular atresia has been described in detail by Bloom and Fawcett (1975). The follicular theca interna hypertrophies, the follicle takes on a collapsed appearance, and the follicular cavity gradually becomes obliterated by connective tissue. A collapsed zona pellucida may be evident in the follicular cavity (Plate VII, g). The cells of the hypertrophied and vascularized theca interna become filled with lipoidal pigments, and the follicle at this stage is similar to an old corpus luteum and has been given the misnomer "corpus luteum atreticum". Finally, the theca interna begins to degenerate and is slowly replaced by connective tissue, but residual islands of the theca interna may persist for some time in the ovarian cortex as the "interstitial gland" (Bloom and Fawcett 1975).

Corpora atretica in the ovaries of the narwhal are small and usually situated deep in the cortex (Plate VI, g). The walls of the corpus atreticum shown in Plate VI, g are thickened, highly folded, and composed of loose fibrous tissue. No luteal tissue could be detected macroscopically within this corpus, but there was a small amount of clotted blood in the follicular cavity. Generally, orange-coloured theca lutein tissue is found at the periphery of atretic follicles (Plate VII, g and h). Fibrous tissue eventually fills the follicle after the granulosa cells have been shed and destroyed. Coiled blood vessels do not play a role in follicular atresia, as they do in the regression of the corpus luteum.

The small atretic follicles of the narwhal are similar to those in the ovaries of Neophocaena phocaenoides (Harrison and McBrearty 1973-74). According to Best (1967), corpora atretica "...represent regressing bodies that have undergone atresia at different stages in the development of the follicle.", and since they are derived from follicles that have not undergone normal ovulation, they are excluded from total corpora counts. Corpora atretica and all follicles have been excluded from total counts of corpora lutea and albicantia in this study as well.

In the ovaries of the sperm whale, Best (1967) suggested that medium- and large-sized ruptured or unruptured follicles may become "corpora lutea atretica", in which the luteinized orange theca interna is the most characteristic structure. A thick collagenous layer may separate the degenerating membrana granulosa from the theca interna, which may become engorged with capillaries and dark blood pigment granules. Corpora lutea atretica may persist for some time, but they eventually degenerate into corpora atretica "a" (Best 1967).

The corpora atretica "a" of the sperm whale are relatively large (up to two-thirds of the diameter of a mature follicle) and a stigma or rupture site may be present (Best 1967). The peripheral theca lutein tissue is loose, yellow or white in colour, fibrous, and avascular. This type of corpus atreticum occurs predominantly in recently-ovulated females, as well as in a few resting females. Corpora atretica "b", on the other hand, are derived from very small unruptured follicles. They are situated deep in the cortex, and fibrous orange or yellow degenerating theca lutein tissue is present at the periphery. These corpora are avascular as well and the follicular cavity eventually becomes filled with connective tissue. Corpora atretica of type "b" are more numerous than those of type "a".

Laws (1961) described the corpora atretica of the ovaries of the fin whale. He stated that "...corpora lutea atretica... originate by hypertrophy and hyperplasia of the cells of the theca interna after degeneration of the membrana granulosa...". Corpora atretica are most prevalent in pregnant and resting fin whales (Laws 1961).

The corpora atretica in the ovary of the narwhal are similar to the corpora atretica "b" of the sperm whale (Best 1967) and the copora atretica of the fin whale (Laws 1961).

<u>Incidence of normal and degenerating follicles</u> - Most sexually mature female narwhals appear to have had prooestrous follicular activity at the most recent breeding season, March to May. This applies to all reproductive categories, including post-partum and lactating females. Enlarged follicles, recent unsuccessful (infertile) ovulations (represented by young regressing corpora albicantia), corpora incognita, corpora atretica, luteinized follicles, and haemorrhagic follicles are all products of recent prooestrous ovarian activity; only immature females do not display such activity (Table 9). Two maturing females are present in the sample; both of these had ovarian follicles exceeding 10 mm in mean diameter and one had a luteinized follicle. Of all the categories of

Table 9. Incidence of normal and degenerating follicles and other ovarian structures in female narwhals.

Reproductive Condition	No. of Females	Incidence of females with																	
		Enlarging follicles[a]		Erupted follicle		Corpus incognitum		Corpus atreticum		Luteinized follicles				Haemorrhagic follicles		Cystic follicles		Infertile ovulations at recent oestrous	
										Active		Regressing							
		No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Immature	31													4	12.9				
Maturing[a]	2	2	100.0							1	50.0								
Pregnant[b]	25	1	4.0			1	4.0	9	36.0	3	12.0	5	20.0	4	16.0	2	8.0	12	48.0
Lactating[b]	22	3	13.6			8	36.4	4	18.2	6	27.3	2	9.1	7	31.8			8	36.4
Pregnant and lactating[b]	5			1	20.0	1	20.0	3	60.0	1	20.0	2	40.0	1	20.0			3	60.0
Total pregnant[b]	30	1	3.3	1	3.3	2	6.7	12	40.0	4	13.3	7	23.3	5	16.7	2	6.7	15	50.0
Total lactating[b]	27	3	11.1	1	3.7	9	33.3	7	25.9	7	25.9	4	14.8	8	29.6			11	40.7
Full-term or post-partum	13	1	7.7			3	23.1	1	7.7	1	7.7								
Resting	11	3	27.3			6	54.5	1	9.1	3	27.3	4	36.4	1	9.1	1	9.1	3	27.3
Total mature	76	8	10.5	1	1.3	19	25.0	18	23.7	14	18.4	13	17.1	13	17.1	3	3.9	26	34.2
Total females	109	10	9.2	1	0.9	19	17.4	18	16.5	15	13.8	13	11.9	17	15.6	3	2.8	26	23.9

[a] Follicles greater than 10 mm diameter.

[b] Excluding full-term and post-partum females.

mature females, only those that were near-term or post-partum failed to ovulate at the most recent breeding season (Table 9). Almost half (48%) of females in early pregnancy (but not lactating) ovulated unsuccessfully prior to the recent conception, while 36% of non-pregnant lactating females (with yearling calves) ovulated unsuccessfully. Five females were simultaneously pregnant and lactating; evidence will be presented later to show that these females were probably nursing yearling calves. Three of these females had pre-conception, infertile ovulations during March to May. Overall, 50% of pregnant females and 41% of lactating females had infertile ovulations at the most recent breeding season. Of 11 resting females, three or 27.3% had ovulated unsuccessfully; some of these females may have recently weaned or lost their calves. Best (1974) has provided evidence, based on the occurrence of resting female sperm whales at certain seasons, that some females fail to ovulate or conceive at the first breeding season following weaning of their calves. Overall, 34% of mature female narwhals had ovulated unsuccessfully at the most recent oestrous.

The absence of post-partum ovulations suggests that ovulations may occur only during March to May (the breeding season). This is further substantiated by the observation that no new corpora lutea of ovulation are evident in any mature females, except for the possible recently-erupted follicle of one pregnant, lactating female (Table 9). The possibility of oestrous and ovulation during winter months cannot be excluded, since no samples were available from this time period. Ovulations may be expected to occur during late lactation, which could include the period March to May, since most summer-caught females in early pregnancy had weaned their calves relatively recently (see below).

Late-pregnancy or post-partum females, although they did not ovulate, still show evidence of recent prooestrous activity (Table 9). However, Best (1968) did not record follicular enlargement in late-pregnancy sperm whales, even during the regular breeding season. Chittleborough (1954) found numerous large atretic follicles, due to the latest prooestrous, in the ovaries of late-pregnancy humpback whales. The ovaries of female fin whales in mid-pregnancy were found to contain enlarging follicles during the Antarctic summer, but none had ovulated (Laws 1961). Laws (1961) suggested that increasing light intensities may stimulate (through the hypothalamo-hypophyseal system) prooestrous ovarian activity and ovulation; this may apply to the narwhal, since light intensity and day length are increasing during the breeding season (March to May). However, the prooestrous activity displayed by late-pregnancy female narwhals does not progress to the point of follicle maturation, due to the inhibitory effects of the corpus luteum. Perrin _et al_. (1976) also recorded late-pregnancy and post-partum prooestrous in the spotted porpoise _Stenella attenuata_. Brodie (1970) observed enlarged follicles in a few post-partum, lactating, and resting female white whales captured during summer (maximum follicle diameters of 9.3 to 19.3 mm), and Sergeant (1973) noted follicles of up to 18 mm diameter, newly formed corpora lutea (17 to 24 mm), and regressing corpora lutea of ovulation (14 mm) in the ovaries of white whales captured during mid-summer, some months afer the mating season.

The data presented in Table 9 suggest that most mature female narwhals undergo prooestrous ovarian activity at the breeding season (March to May), but only females which are pregnant at this time seem to be incapable of ovulation. The limited evidence suggests that mid-summer ovulations do not normally occur, although there are several examples of enlarged follicles and one case of an apparently ruptured follicle at this season (Table 9).

Incidence of accessory corpora lutea - The structure of accessory corpora lutea (luteinized follicles) was discussed previously. Only six accessory corpora lutea were present in the ovaries of pregnant and post-partum females; the mean diameters of these corpora were 5.0, 5.0, 6.2, 7.3, 9.0 and 15.0 mm. All of these were presumed to be derived from unruptured follicles, since no stigma or corona were evident. One pregnant female had two accessory corpora, both of which were beginning to regress, while each of the other females had only one accessory corpus luteum.

Four of 30 (13.3%) early pregnancy females and one of 13 (7.7%) late-pregnancy or post-partum females had accessory corpora. This suggests that accessory corpora of early pregnancy may degenerate and they may not be recognizable by the time of parturition. The overall incidence of accessory corpora in these females was five out of 43 or 11.6%.

The 30 early-pregnancy females had a total of 132 corpora lutea and albicantia, of which five (3.78%) were accessory corpora. The 13 full-term/post-partum females had a total of 70 corpora lutea and albicantia, of which one (1.43%) was accessory. Overall, there were six accessory corpora out of a total of 202 corpora, or 2.97%. These percentages are possibly underestimates, since many old corpora albicantia may originally have been accessory corpora lutea. In order to estimate the contribution of accessory corpora to total corpora, the recent ovulations of females in early pregnancy must be considered. The 30 females in early pregnancy had a total of 55 ovulations at the latest breeding season, this number also including accessory corpora. Therefore, at the time of their formation, accessory corpora comprise 9.09% of total corpora, assuming that they are preserved as scars in the ovaries. On the other hand, if accessory corpora disappear quickly from the ovaries, which is possible because of their small initial size, then they only comprise about 3% of total corpora at the time of their formation.

The prevalence of accessory corpora lutea in primiparous females may be significant: three of six primiparous females in early pregnancy had an accessory corpus, while only one of 24 multiparous females in early pregnancy had an accessory corpus.

Accessory corpora lutea occur generally infrequently in the ovaries of cetaceans. They comprise 1.5% of all corpora in the sperm whale (Best 1967) and 3.7% of all corpora in the fin whale (Laws 1961). In the white whale, accessory corpora lutea comprise 11.8% of the recent corpora of pregnant animals (Sergeant 1973) and they occurred in 12.8% of pregnant and post-partum individuals (Brodie 1970). Brodie (1972) has written a good review of accessory corpora lutea in odontocetes.

Ovarian Maturity and Asymmetry

The first ovulation - The ovary that first ovulated can be known only when all corpora are in one of the ovaries or when only a few, temporally-spaced ovulations are present as corpora albicantia. Of 43 females satisfying these criteria, the left ovary ovulated first in 30 (69.8%); the right, in 13 (30.2%). A chi-square test for parity with one degree of freedom indicates a significant difference at the 1% level between the time of maturity of the left and right ovaries ($\chi^2 = 6.72$, $0.01>P>0.001$). Brodie (1971) found no significant difference in time of maturity between left and right ovaries in the white whale. The left ovary matures earlier than the right ovary in Stenella attenuata (Kasuya et al. 1974; Perrin et al. 1976) and in most odontocetes (Ohsumi 1964).

Total corpora - Of 437 corpora of 76 females, 269 were present in the left ovary (61.6%) and 168, in the right ovary (38.4%). A chi-square test for parity with one degree of freedom shows that this difference is highly significant at the 1% level ($\chi^2 = 23.34$, $P < 0.001$). Brodie (1971) did not detect a significant difference in total corpora numbers between the left and right ovaries of the white whale. The left ovary accumulates more corpora than the right ovary in Phocoena phocoena (Fisher and Harrison 1970), Stenella attenuata (Kasuya et al. 1974; Perrin et al. 1976), Stenella longirostris (Perrin et al. 1977), Globicephala melaena (Sergeant 1962), and in most odontocetes (Ohsumi 1964). Ovarian asymmetry does not exist in the sperm whale (Best 1967) and in the humpback whale (Chittleborough 1958).

Most recent corpus - Of 43 pregnant or post-partum females, 27 (62.8%) had a corpus luteum of pregnancy or young regressing corpus albicans in the left ovary, while 16 (37.2%) had the most recent corpus in the right ovary. This difference is not significant at the

1% level ($\chi^2 = 2.81$; 1 d.f.; $0.10 > P > 0.05$). In the female white whale, Brodie (1971) found a significant tendency for the left ovary to contain the most recent corpus more often than did the right ovary.

Alternation of ovarian activity - Until five corpora have accumulated in the ovaries, 41 to 63% of females have all corpora in the left ovary. The percentage of females with all corpora in the right ovary declines from 43% at one corpus to 0% at five corpora, while the percentage of females with corpora in both ovaries averages about 40% until five have accumulated, after which this proportion increases and attains 100% when seven or more corpora have accumulated. The only exception is one female whose right ovary contained all of its ten corpora. The left ovary is therefore dominant until five or six corpora have accumulated; the right ovary then ovulates more frequently, resulting in an increase in the proportion of females with corpora in both ovaries. The left ovary of Stenella attenuata is dominant until the accumulation of 13 to 14 corpora, when the right ovary increases in ovulatory activity (Kasuya et al. 1974).

Using 37 females whose ovaries contained two or more corpora and in which the most recent corpus luteum or corpus albicans could be distinguished from the next most recent one, I determined the probability of two successive ovulations in the same ovary. Of 25 females whose most recent corpus was in the left ovary, 20 (80%) had the second most recent corpus in the same ovary, while of 12 females whose most recent corpus was in the right ovary, eight (67%) had the second most recent corpus in the same ovary. Overall, 28 of 37 females (75.7%) had the two most recent corpora in the same ovary. Therefore, the probability that two successive ovulations will be from the same ovary is about 0.75. This is unlike the situation in pinnipeds, in which there is usually an annual alternation of ovarian activity (Craig 1964; Laws 1956b).

Regression of Corpora Lutea

There seems to be general agreement that corpora albicantia persist in the ovaries of the whale throughout life. In this section evidence will be presented for the persistence of corpora albicantia in the ovaries of the narwhal, although a few small corpora albicantia may escape detection.

<u>Size</u> - The mean diameters of the various categories of corpora albicantia are set out in Table 10. The corpus luteum of pregnancy, with a mean diameter of 42.7 mm, becomes an old, fully-regressed corpus albicans averaging 6.58 mm in diameter (Table 10). This represents a decrease of 84.6% in the diameter of the corpus luteum. The percentage regression is 84.8% in the bottlenosed whale (Christensen 1973) and 82.6% in the fin whale (Laws 1961).

<u>Evidence for persistence</u> - The mean diameters of corpora albicantia of females with different total numbers of corpora albicantia are plotted in Figure 34. Large unregressed corpora albicantia of recently-parturient females are excluded from this plot, since these corpora are just beginning the period of rapid regression and would therefore distort a plot of mean diameters of regressing corpora. An initial reduction in mean diameter with increasing number of corpora with stabilization at the mean diameter of old corpora albicantia would be considered evidence for the persistence of corpora albicantia (Best 1967; Laws 1961). Because of the strong overlap of ± 2 standard errors (approximate 95% confidence intervals) among the first several corpus number classes, such a trend is not evident for the narwhal (Fig. 34), possibly a result of the initially very rapid rate of regression of corpora lutea. In addition, the minimum corpus albicans diameter is 3.0 mm for most corpora numbers (Figure 34), suggesting either that some corpora smaller than 3.0 mm may be missed during the examination of ovaries or that some may regress to become invisible scars. The fact that the ovaries were sliced at about 3 mm intervals favours the first alternative. However, it is felt that few corpora would be missed in this way since most of those smaller than 3 mm should still be

Table 10. Diameters of corpora albicantia.

Stage of Regression	No. of Corpora	Mean diameter (mm)	Range (mm)	Standard deviation (mm)	Percent of total corpora albicantia
Young	35	14.71	5.8-37.0	6.83	8.64%
Medium	64	10.81	6.0-17.6	2.28	15.80
Corpora incognita	65	8.09	3.0-13.0	2,49	16.05
Old	241	6.58	3.0-13.0	2,33	59.51

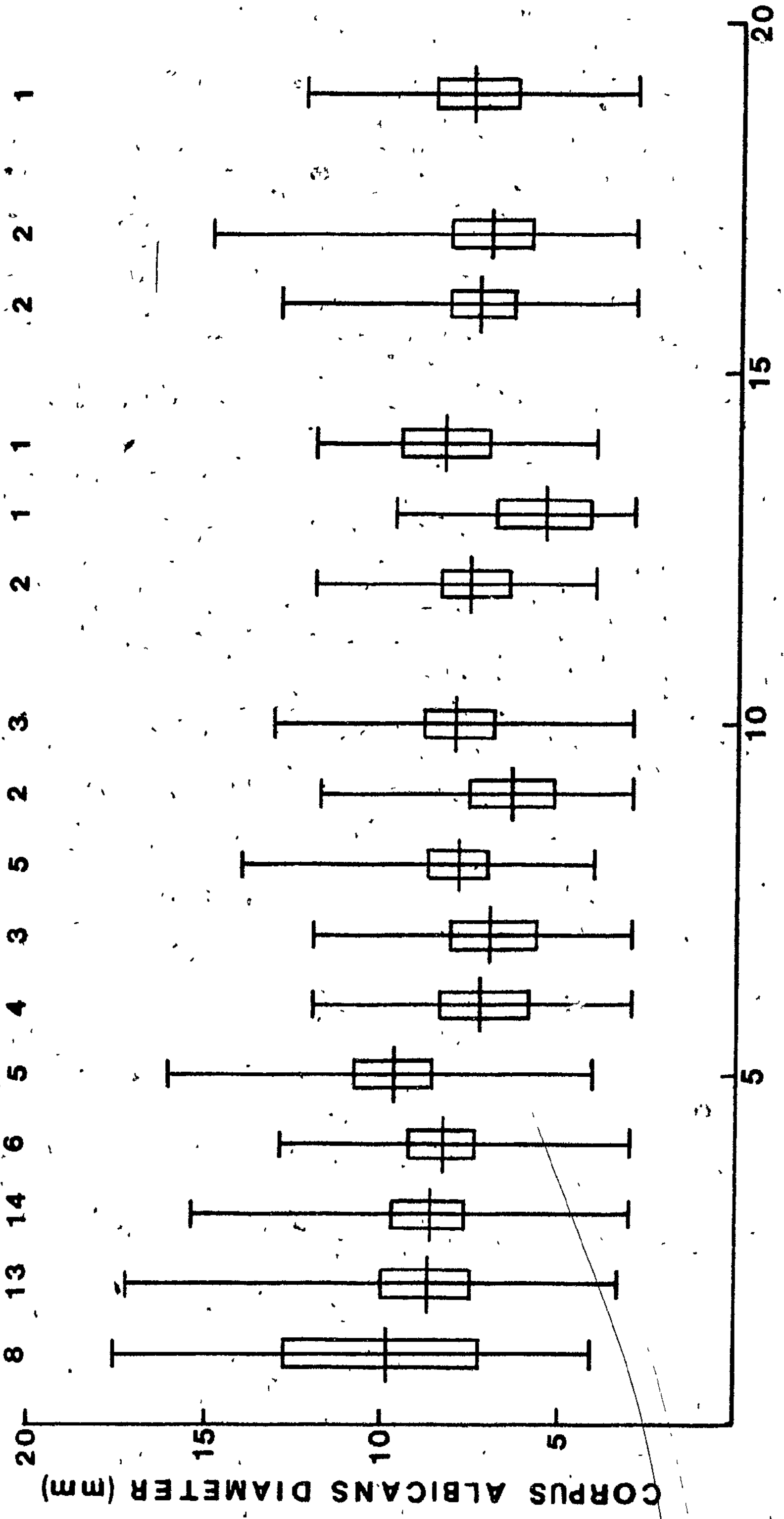

Figure 34. Diameters of corpora albicantia versus total number of corpora albicantia per female. The mean diameter is represented by the central horizontal line, rectangles indicate 2 standard errors, upper and lower horizontal lines represent the range and the sample sizes (no. of females) are given at the top of the figure. Large unregressed corpora albicantia of recently-parturient females are excluded from this plot.

detected by the cuts spaced at 3 mm intervals. Nevertheless, a small, but unknown, number of very small corpora albicantia likely escape detection or are completely resorbed. Of a total of 241 old corpora albicantia, 21 were 3 mm in diameter while 54 were 4 mm or less in diameter. The results of this test are inconclusive as to the macroscopic retention of all corpora lutea in the ovaries, but the possibility that some old corpora are overlooked or resorbed has little bearing on the interpretation of the reproductive cycle which is largely dependent on examination of only the few most recent ovarian corpora and other aspects of the biology of the female narwhal.

The size-frequency distribution of corpora albicantia is presented in Figure 35. The frequency distribution of the diameters of old corpora albicantia is steeply truncated at the left side, again suggesting either the disappearance of those smaller than 3 mm or failure to detect them. A normal distribution of old corpora albicantia is considered to be evidence for their persistence (Laws 1961; Best 1967).

The number of old corpora albicantia per female narwhal is directly proportional to the total number of corpora until 10 have accumulated, indicating the persistencce of old corpora albicantia at least to this point (Best 1967; Laws 1961). However, after 10 corpora have accumulated, the number of old corpora albicantia is highly variable. In females with 12 and 14 corpora, there were four and two old corpora albicantia, respectively, while in other animals with more than 10 corpora, the number of old corpora albicantia increases very slowly with the total number of corpora, suggesting the non-persistence or the non-detection of some old corpora albicantia in the ovaries of these females.

In order to explain the low incidence of old corpora albicantia in the ovaries of some old females, the occurrence of corpora incognita in relation to age was examined. Younger females with 11 or fewer total corpora had from 0 to 1.2 corpora incognita, representing up to 18% of the total number of corpora albicantia.

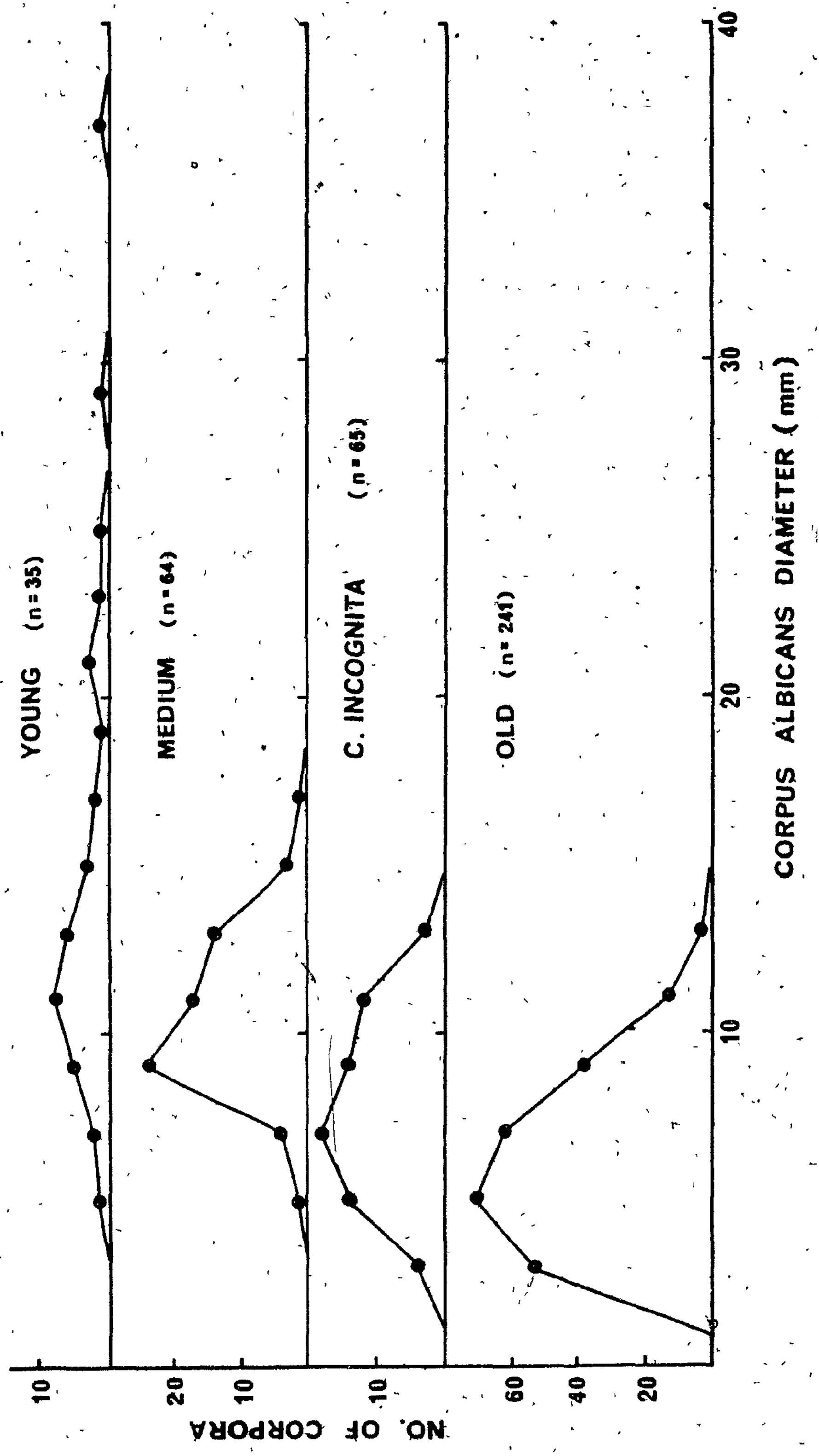

Figure 35. Size-frequency distribution of young, medium and old corpora albicantia and corpora incognita. Size interval is 2 mm.

Older females with more than 11 corpora lutea and albicantia had more corpora incognita, in terms of both number per female and proportion of the total number of corpora albicantia. For example, two females with 12 and 14 corpora each had eight corpora incognita, comprising 57-67% of the total number of corpora albicantia. Females with 13 corpora had a low mean incidence of corpora incognita, but females with 16 to 19 corpora lutea and albicantia had four or five corpora incognita, comprising 21-32 percent of the total number of corpora albicantia.

On the basis of these observations, it is possible that corpora incognita are actually old (or perhaps medium) corpora albicantia that have severely haemorrhaged. The "rupture pit" associated with the corpus incognitum could be caused by a high level of blood pressure within the haemorrhage. Dr. K. Benirschke (in litt. 12 October 1978) has diagnosed a similar ovarian structure from the narwhal as "fresh hemorrhage into an old cystic corpus albicans", adding some support to this interpretation of the corpus incognitum. It may also be significant that corpora incognita are intermediate in size between medium and old corpora albicantia (Figure 35).

Duration of regression - Laws (1961) found that there were twice as many medium as young corpora albicantia in the ovaries of the fin whale, and by assuming that the duration of a regression stage is proportional to its relative abundance in the ovaries, he estimated that complete regression required three years.

The time required for regression of the corpus luteum of the narwhal was estimated in the same way. The ratio of medium to young corpora albicantia in the narwhal is 1.83:1. If a young corpus albicans persists for x amount of time, then a medium corpus albicans persists for 1.83 x time, and the time required for complete regression is 2.83 x. The average number of young and medium corpora albicantia per mature female is 1.303, and these must accumulate in the available time of 2.83 x. Thus, corpora albicantia accumulate at a rate of 0.46 per unit of time x. If the ovulation rate is 0.7 ovulations/yr, as shown in a later section, then each unit of time x is calculated as 0.66 years. Therefore, a young corpus albicans persists for 0.66 yr and a medium, for 1.21 yr, and complete regression requires 1.87 yr. These results are consistent with the observation that the largest, non-recent corpus albicans of lactating females is usually in the medium stage of regression (about 1 year post-partum). In addition, the largest, non-recent corpus albicans of non-lactating females in early pregnancy is usually in the old stage of regression (two years post-partum).

Complete regression of the corpus luteum requires three to four years in the blue whale and fin whale (van Lennep 1950) and up to six years in *Stenella attenuata* (Kasuya *et al*. 1974). Corpora albicantia are thought to persist throughout life in the ovaries of the white whale (Brodie 1970) and *Stenella attenuata* (Perrin *et al*. 1976). Some very small corpora albicantia may be resorbed or escape detection in the ovaries of old female sperm whales, for the corpus albicans declines in size continuously during regression (Ohsumi 1965). Many of the corpora lutea of ovulation of old female pilot whales shrink to 4 mm or less in diameter and these probably escape detection during ovarian examination (Sergeant 1962). Harrison (1949) suggested that corpora albicantia in the ovaries of the pilot whale may eventually disappear entirely.

Corpora albicantia seem to persist throughout the life of the humpback whale (Chittleborough 1954; Dempsey and Wislocki 1941). Dempsey and Wislocki (1941) attributed their persistence to the presence of a cental core of avascular hyaline connective tissue, their initial large size, and the long time required to resorb the luteal elements. In their words, "... the relatively large size of the corpus luteum in the whale may impose certain limitations and restrictions on its vascular supply, with the result that it undergoes marked hyalinization.".

Age at Sexual Maturity

Length-and age-frequency distributions of immature and mature females - Figure 36 shows that 50% of females are sexually mature at

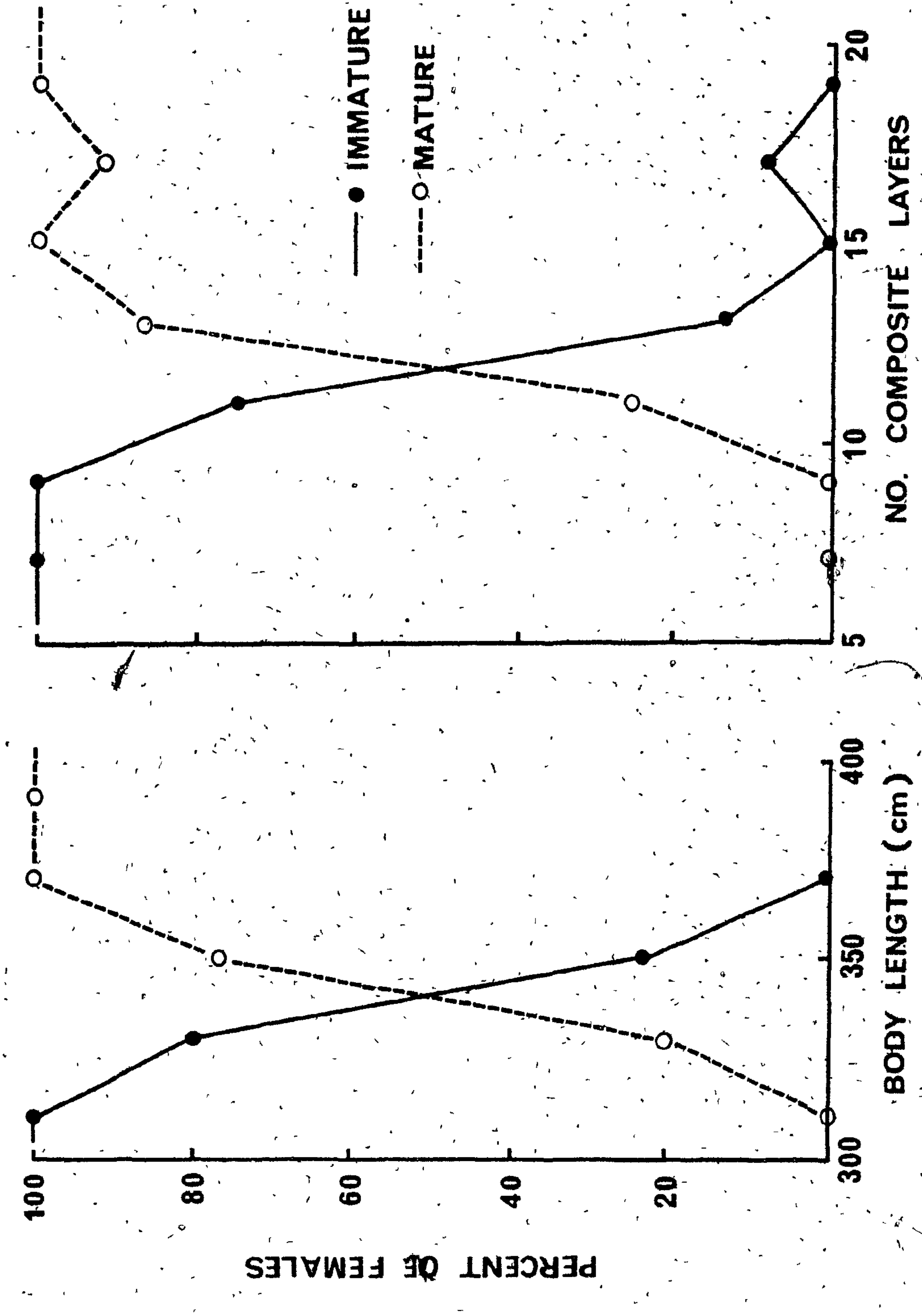

Figure 36. Length- and age-frequency distributions of immature and mature female narwhals. Sample sizes are 33 immature and 78 mature narwhals for body length and 31 immature and 61 mature narwhals for age (number composite growth layers). Class intervals are 20 cm body length and two growth layers.

a body length of 340 cm and at 12 composite growth layers. These values represent the mean size and number of growth layers at the attainment of sexual maturity in the female narwhal. Application of the method of DeMaster (1978) to maturity-at-age data for the female narwhal produces a similar estimate of mean age at sexual maturity of 12.3 composite growth layers (0.36 standard error). This method calculates mean age at sexual maturity as the mean age of the maturing age groups, weighted by the proportion of females ovulating for the first time at each age. The mean number of composite growth layers at sexual maturity in the female narwhal is similar to the number of dentinal growth layers at sexual maturity in some of the larger odontocetes, especially the white whale (Table 11). Brodie (1971) found that female white whales from Cumberland Sound, Baffin Island, ovulated for the first time at 9-11 (mean of 10) dentinal layers. For this calculation he utilized females with few corpora and he back-calculated to their ages at first ovulation, accounting for gestation and lactation and assuming that two dentinal layers are deposited per annum. Female white whales from western Hudson Bay ovulate for the first time at 8-13 (mean of 10) dentinal layers (Sergeant 1973). Female white whales thus mature sexually at an average age of 5 years, assuming that 2 dentinal growth layers are deposited annually (Brodie 1971; Sergeant 1973).

Age at first ovulation - Two maturing females with ovarian follicles larger than 10 mm in mean diameter are present in the sample. One of these females had a body length of 340 cm and 11.5 composite growth layers; the other, 350 cm and 16 growth layers.

Data from primiparous females may provide some insight into the age at first ovulation. Six whales were in early first pregnancy; their first ovulations occurred at 11.5, 15, 15, 14, 13.5, and 18 growth layers, or at a mean of 14.5 layers. Two primiparous postpartum females ovulated at their present ages (12.5 and 12 layers) less about a year, or at an average of 12.3 layers less one year. Three females were suckling their first (yearling) calves and had ovulated for the first time two years before capture. Their first

Table 11. Age at sexual maturity of some female odontocetes.

Species	Age at sexual maturity (no. dentinal growth layers)	Author
Hyperoodon ampullatus	10 to 12	Christensen 1973
Berardius bairdii	8 to 10	Kasuya 1977
Physeter catodon	9	Nishiwaki *et al.* 1958
	8 to 9	Best 1970
Delphinapterus leucas	10	Brodie 1971
	10	Sergeant 1973
Globicephala melaena	6 to 7	Sergeant 1962
Stenella attenuata	9	Kasuya 1976
	8.2	Kasuya *et al.* 1974
	9	Perrin *et al.* 1976
Stenella coeruleoalba	8.8	Miyazaki 1977
	8.8	Kasuya 1972
	8.5	Kasuya 1976
Stenella longirostris	5.5	Perrin *et al.* 1977

ovulation ages were 10.5, 20, and 19 layers less two years, or an average of 16.5 layers less two years. These values may be used to estimate the frequency of dentinal and mandibular layering. Comparing lactating and post-partum whales, which are about two and one years post-ovulation, respectively, the rate of growth layer deposition is estimated to be 4.2 layers per year, while comparing lactating and early-pregnancy females, it is estimated that one growth layer is deposited annually. The calculation of these values assumes that all females ovulate successfully for the first time at the same age. The samples are too small and too variable to accurately estimate the age of first ovulation and the rate of layer deposition, but they are not discordant with the estimate of 12 growth layers as the average age at the attainment of sexual maturity by the female narwhal.

The first ovulation of the season of primiparous females seems to be no less successful than that of multiparous females. Two of six (33%) primiparous females and 13 of 24 (54%) multiparous females had ovulated unsuccessfully (one to three times) prior to conception. It was noted in a previous section that the incidence of accessory corpora lutea is higher in primiparous (50%) than in multiparous females (4%). Reduced fertility of recently-mature female whales compared to older females, in terms of the frequency of unsuccessful ovulations prior to conception or failure to conceive at the first breeding season, has been demonstrated for the sperm whale (Best 1968), the humpback whale (Chittleborough 1955b), the spotted porpoise (Perrin et al. 1976; Kasuya et al. 1974), and the fin whale (Laws 1961).

Primiparous female narwhals had two of the smallest foetuses (9.5 and 16 cm) recorded in this study, implying that conception may be later in primiparous than multiparous females, as demonstrated for the fin whale (Laws 1961) and the sperm whale (Ohsumi 1965). Brodie (1970) found that the calf of a primiparous white whale is smaller than that of an older, multiparous female.

The Ovulation Rate

Corpora accumulation and age - Figure 37 presents the relationship between the total number of corpora lutea and albicantia and the number of composite growth layers of 60 mature female narwhals. The ovulation rate is estimated to be 0.76 ovulations/growth layer, assuming that all preserved ovarian scars are derived from ovulations and that these scars do not disappear. It is of interest that, at the mean age of sexual maturity (12 layers), two corpora lutea have formed, suggesting that more than one ovulation occurs at the first breeding season (Figure 37).

Corpora accumulation in relation to body length is shown in Figure 38, where it is seen that the total number of corpora increases rapidly over a narrow range of body lengths. Since corpora accumulation is related to age (Figure 37), Figure 38 represents an approximate growth curve of the female narwhal. From this figure it is estimated that physical maturity is achieved after the accumulation of 10 corpora.

Recent unsuccessful ovulations - Several females (except those in late-pregnancy or post-partum) have had infertile ovulations during the most recent mating season (March-May), and this information permits an independent estimation of the ovulation rate. The macroscopic criteria used to assess the occurrence of recent, infertile ovulations have been previously described.

Young corpora albicantia resulting from infertile ovulations average 12.24 mm in diameter (standard deviation, 2.67 mm; range, 5.8 to 17.6 mm). The size-frequency distribution of young corpora albicantia has two modes (Figure 35); the first (11 mm) represents unsuccessful ovulations and the second (more than 18 mm) represents regressing corpora lutea of pregnancy after recent parturition. The young corpora albicantia of those females which have had two or more recent infertile ovulations vary in size, suggesting that the female narwhal is polyoestrous.

Ovulations at different stages of the cycle - For an independent assessment of the ovulation rate, all of the recent ovulations of

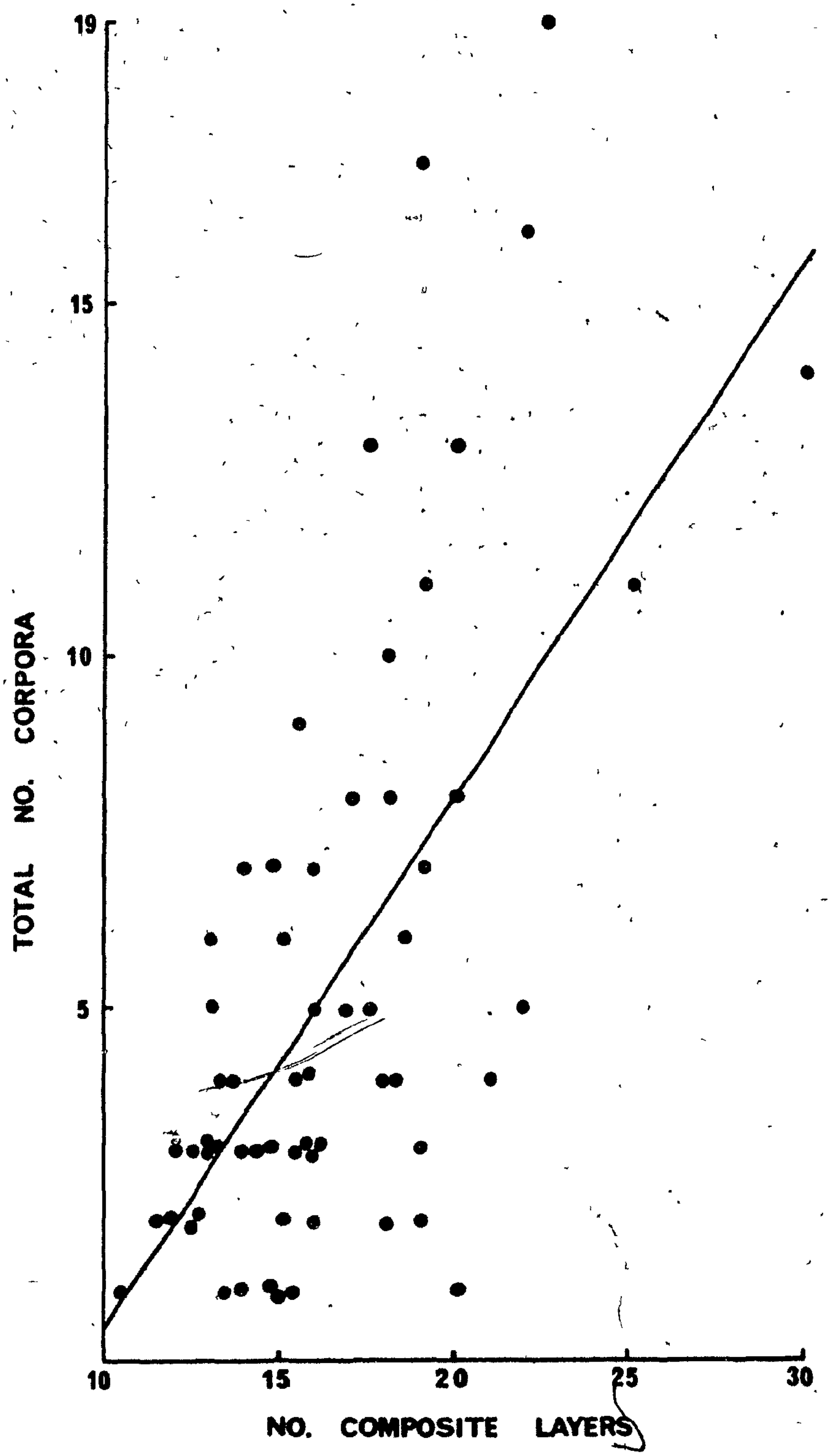

Figure 37. Total number of corpora lutea and albicantia versus number of composite growth layers of 60 mature female narwhals. The relation between number of corpora (y) and number of composite growth layers (x) is:

$$y = 0.75857x - 7.12787$$

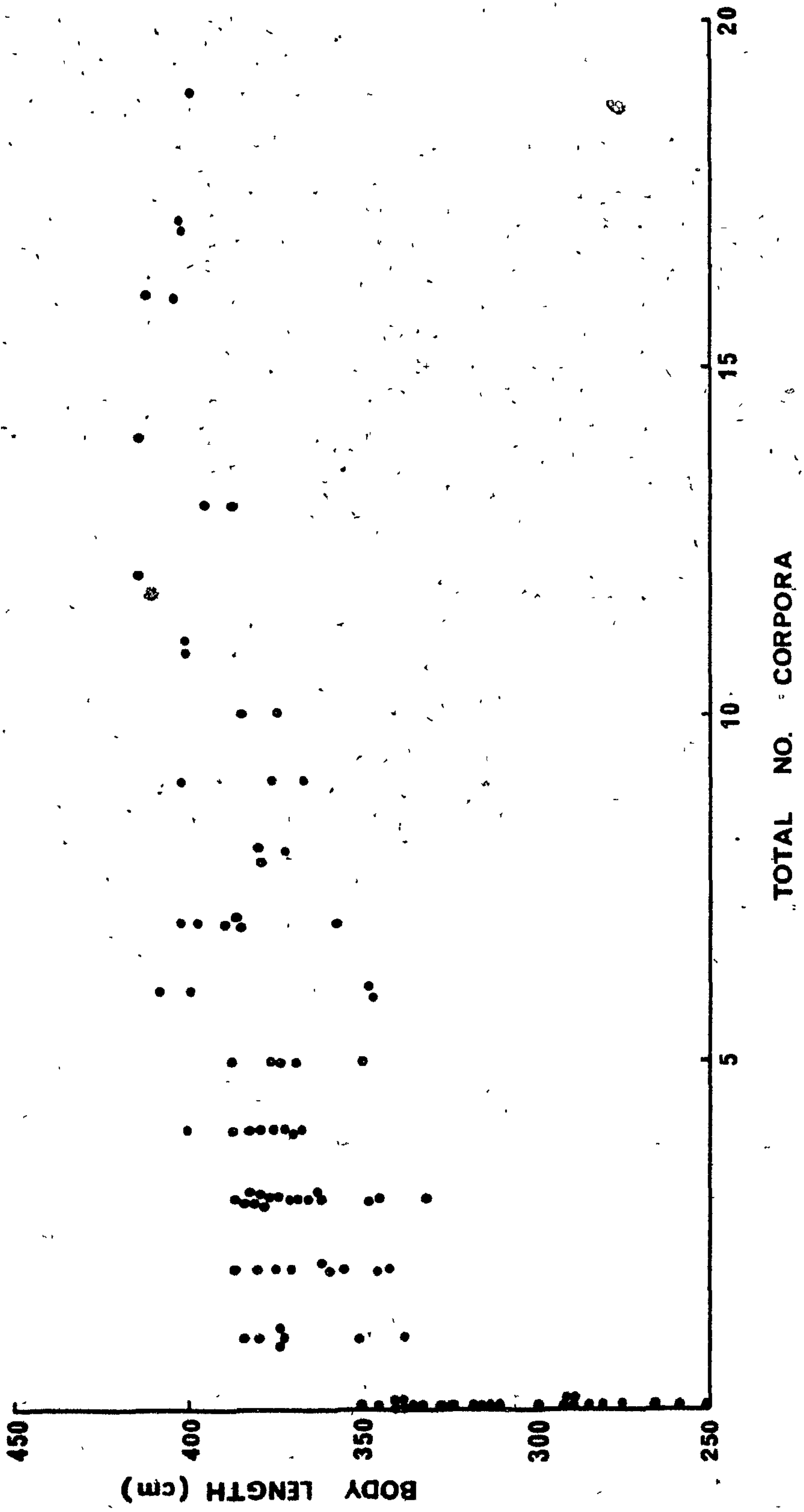

Figure 38. Body length and number of corpora lutea and albicantia of 99 female narwhals (25 immature, 74 mature).

mature females were analysed as follows. It was assumed that the relative numbers of females in the various reproductive classes in the sample are the same as the actual proportions of these classes in the population. Females which are simultaneously pregnant and lactating were assumed to be nursing yearling calves (evidence for this will be presented in "The female reproductive cycle"). In addition, non-pregnant females which are nursing two-year-old calves or which are "resting" were assumed to be in phase with females which are early-pregnant but not lactating. The ovulation rates of females of the different reproductive classes are set out in Table 12.

Early-pregnancy females (non-lactating), resting females (having weaned two-year-old calves), and lactating females (two-year- old calves) were considered together: 38 females had a total of 48 ovulations, or 1.26 ovulations/female. The 25 females which were nursing yearling calves had a total of 20 ovulations or 0.8 ovulations/female. Therefore, the average number of ovulations per female is 1.26 plus 0.8 or 2.06 (over the three-year reproductive cycle), and the annual ovulation rate is estimated to be about 0.69. Since 30 females conceived at the most recent oestrous and 68 recent ovulations were experienced by the total mature female sample, the proportion of ovulations that were successful (resulting in pregnancy) is 30/68 or 0.4412 (Table 12).

Assuming a strict three-year cycle, with no successful ovulations experienced by females in mid-lactation, the calculated ovulation rate is found to not differ appreciably from that calculated above. In this case, early-pregnancy females (not lactating), early-pregnancy females (assumed to be nursing two-year-old calves) and resting females (assumed to have weaned two-year-old calves) were combined: 41 females had a total of 58 ovulations or 1.41 ovulations/female. All non-pregnant lactating females were considered together: 22 females experienced 10 ovulations, or 0.45 ovulations/female. Therefore, assuming a strict three-year cycle, the annual ovulation rate is estimated to be about 0.62. The first estimate of 0.69 is considered to be more accurate

Table 12. Ovulations at different stages of the reproductive cycle.

Reproductive stage	No. of females	No. of females ovulating	Percent of females ovulating	Total no. of ovulations	No. ovulations per		
					Ovulating female		
					Mean	Range	Female
Lactating, 2 yr calf	2	0	0	0	-	-	0
Resting (nulliparous)	11	3	27.3	8	2.67	1-4	0.73
Early pregnancy, not lactating	25	25	100.0	40	1.60	1-4	1.60
Late pregnancy/ post-partum	13	0	0	0	-	-	0
Lactating, 1 yr calf, non-pregnant	20	8	40.0	10	1.25	1-2	0.50
Lactating, 1 yr calf, pregnant	5	5	100.0	10	2.00	1-3	2.00
Total	76	41	53.9	68	1.66	1-4	0.89

since there is evidence for the occurrence of successful mid-lactation ovulations (to be presented in a later section).

Frequency distribution of number of corpora per female - The frequency distribution of total number of corpora per female is presented in Figure 39. There is a pronounced mode at three corpora, which again suggests that more than one ovulation may occur during the first reproductive cycle. A maximum of three ovulations may occur during a three-year cycle, or one ovulation per annum (see Sergeant 1962). This is similar to another estimate of the annual ovulation rate, which is the average number of ovulations experienced by each mature female during the latest breeding season (March to May). The resulting estimate is 68/76, or 0.89 ovulations per annum (Table 12). In addition, from the relationship between the number of old corpora albicantia and the total number of corpora, approximately 1.5 young and medium corpora accumulate before any old corpora appear. These corpora albicantia must accumulate during the time required for complete regression (1.87 yr), producing an estimated ovulation rate of 0.80 per annum.

Crude birth rate and dentinal layering frequency - A preliminary estimate of the crude birth rate (to be discussed in more detail later) can now be made. Using an annual ovulation rate of 0.69 and an ovulation success rate of 0.44, the crude birth rate (pregnancy rate) is estimated to be 0.30 calves/mature female/year. The accumulation rate of growth layers in mature females is estimated to be 0.69 ovulations/yr divided by 0.76 ovulations/composite growth layer, or 0.91 layers/annum. This suggests that one growth layer is deposited annually in sexually mature females.

Discussion - Many odontocetes appear to have polyoestrous breeding cycles, while the baleen whales appear to be monooestrous. Evidence for the occurrence of successive infertile ovulations has been found in the pilot whale (Sergeant 1962; Harrison 1949), the sperm whale (Best 1968), the saddleback dolphin Delphinus delphis (Harrison et al. 1972), the white whale (Sergeant 1973), the spotted porpoise (Kasuya et al. 1974), and the striped dolphin Stenella

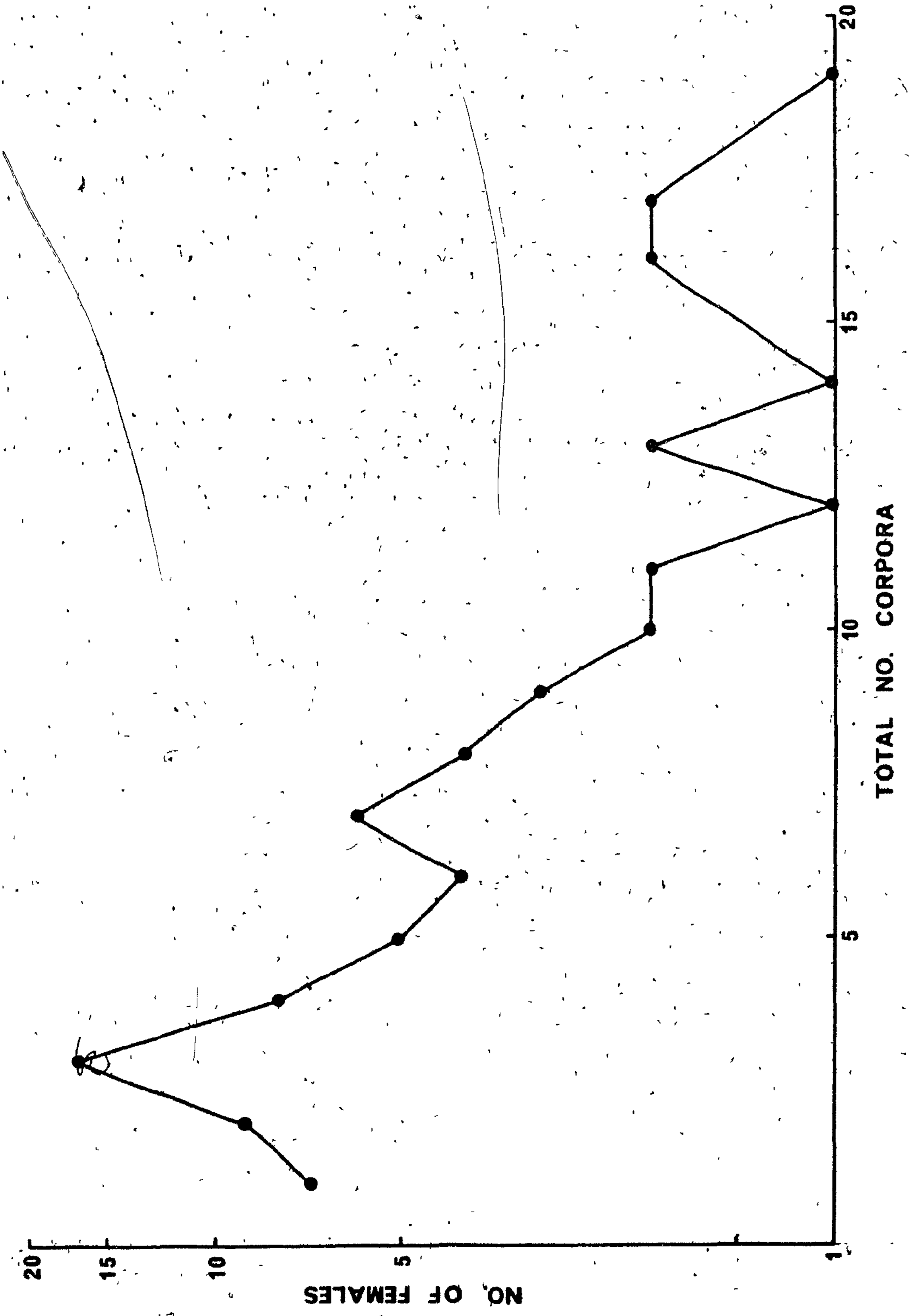

Figure 39. Frequency distribution of number of corpora lutea and albicantia among 76 mature female narwhals.

coeruleoalba (Miyazaki 1977). Comrie and Adam (1938) found a size-graded series of 3 corpora albicantia in early regression in one non-pregnant non-lactating female false killer whale Pseudorca crassidens, suggesting the existence of polyoestrous breeding cycles and spontaneous ovulation in this species as well. On the other hand, evidence for multiple ovulations leading to the formation of accessory corpora lutea has been found in the white whale, in which most corpora albicantia represent infertile ovulations (Brodie 1970, 1971). Multiple ovulations occur frequently in the ovaries of the spotted porpoise, especially newly-mature females (Perrin et al. 1976). As for the baleen whales, multiple ovulations occur occasionally in the humpback whale (Chittleborough 1954) and in the fin whale (Laws 1961). Chittleborough's (1954) observations of the ovaries of the humpback whale show that this species is polyoestrous.

The female narwhal is polyoestrous, experiencing up to four successive ovulations during a two-month-long breeding season which probably comprises the latter part of the lactation period or the period following weaning of the second-year calf (see "The Female Reproductive Cycle"), as in some other odontocetes, such as the white whale (Sergeant 1973) and pilot whale (Sergeant 1962). Non-lactating narwhals which conceive at this season ovulate an average of 1.6 times (Table 12). Female humpback whales usually ovulate once, occasionally up to three times, at the normal oestrous (Chittleborough 1954). Spotted porpoises ovulate an average of 1.41 times during the breeding season, but up to four successive ovulations may occur (Kasuya et al. 1974). Pilot whales ovulate 1-3 times during the usual late-lactation mating season, with a mean of 1.3-1.7 ovulations (Sergeant 1962). Female sperm whales usually ovulate once, but occasionally up to three or four times (mean of 1.6 ovulations), during the usual breeding season. Although ovulations at this season are almost always fertile (Best 1968), a few female sperm whales do fail to conceive (Best 1974), and these are mainly old, possibly senile females (Ohsumi 1965). It is evident that some resting female narwhals fail to ovulate following weaning of their calves; only 3 of 11 resting females had ovulated at the most recent oestrous (Table 12). It will be shown later that this category includes several old, possibly senile females with many ovarian corpora. In addition, two females which were thought to be nursing second-year calves had also failed to ovulate during the most recent oestrous.

Female narwhals do not appear to ovulate after parturition, as is also true of the white whale (Brodie 1971). Post-partum ovulations occur infrequently in the pilot whale (Sergeant 1962) and in the sperm whale (Best 1968), but they are rarely fertile in these species. Infertile post-partum ovulations occur fairly frequently in the spotted porpoise off the coast of Japan (Kasuya et al. 1974), but Perrin et al. (1976) demonstrated that females of this species in the eastern Pacific Ocean occasionally conceived during lactation. Infertile post-partum ovulations occur commonly in the humpback whale (Chittleborough 1954), while about 60% of multiparous, post-partum fin whales ovulate, although only one-third of these ovulations are fertile (Laws 1961).

About 52% of female narwhals which were nursing yearling calves had ovulated at the most recent breeding season, and 38% of these females conceived, with the result that about one-fifth of lactating females conceive one year after parturition (Table 12). Mid-lactation ovulations, although usually infertile, occur in 13.7% of female sperm whales, while late-lactation ovulations occur in 39% of females and some 24% of these are fertile (Best 1968). Post-lactation ovulations prior to the usual breeding season occur in only 2.2% of female sperm whales but these are rarely successful. Oshumi (1965) has demonstrated that lactating sperm whales may ovulate, though usually unsuccessfully, during the normal breeding season. Up to 18% of humpback whales ovulate during late lactation, but most whales ovulate at the usual time following weaning of the calf (Chittleborough 1954). Most fin whales ovulate when their calves are weaned, but these ovulations are usually infertile (Laws 1961).

Sergeant (1962) found that post-lactation ovulations sometimes occur in pilot whales, but these ovulations are usually infertile since the males are anoestrous at the same time.

Female narwhals ovulate at a rate of 0.69/yr or 0.76/composite growth layer, and 44% of ovulations are successful. Ovulation rates in the sperm whale are estimated to be 0.59/yr or 0.44/dentinal growth layer, with 50% fertile (Best 1968), 0.27/yr (Ohsumi 1965), or 0.44/dentinal growth layer (Nishiwaki _et al._ 1958). Ovulation rates are estimated to be 0.51/yr, with 60% fertile, in the pilot whale (Sergeant 1962), 0.70/yr with 68% fertile in the white whale (Sergeant 1973), 0.50/dentinal growth layer in the bottlenosed whale (Christensen 1973), 0.41/yr in the striped dolphin (Kasuya 1976), 1.0/dentinal growth layer in the spinner dolphin _Stenella longirostris_ (Perrin _et al._ 1977), and 0.42/yr in the spotted porpoise (Kasuya _et al._ 1974). Ovulation rates have been estimated to be about 0.5/yr in the humpback whale (Chittleborough 1954) and 1.43/yr, with 33% fertile, in the fin whale (Laws 1961).

The Female Reproductive Cycle

Mother-calf relations - The elucidation of the female reproductive cycle is aided by observations on females captured with their calves. Measurements and observations on mature females captured without their calves can then be compared to these standards, in order to make a reliable assessment of their reproductive status.

Table 13 presents the characteristics of females and calves which were captured together. From this table it is apparent that only post-partum females can be distinguished from females of other reproductive categories, using cornu diameter and diameter of the largest, non-recent corpus albicans. These aspects of the female reproductive cycle will be examined in more detail in the next section, using the total sample of 79 mature females.

Post-partum reproductive events - The post-partum involution of the largest uterine cornu of non-pregnant mature females is shown by

Table 13. Mother-calf relations.

	Reproductive condition of female			
	Post-partum	Lactating (1 yr calf)	Resting[a]	Lactating (2 yr calf)
Sample size	5	3	1	1
Length of calf (cm)	164-200	230-250	262	265
Age of calf (no. dentinal layers)	0	2-4	2	6
Stomach contents	milk	milk	empty	empty
Mother:				
Diameter of largest cornu (cm)[b]	12.0	4.0 (3.5-4.5)	4.0	-
Mammary thickness (cm)[b]	4.9 (4.1-5.5)	4.1 (3.0-5.2)	2.5	4.2
Largest corpus albicans (mm)[b,c]	22.2 (11-37)	9.8 (8.5-12.0)	9.8	10.0
Mammary secretion	milk	milk	post-lactation oil	milk

[a] weaned 1-year-old calf.

[b] mean; range in parentheses.

[c] excluding corpora of recent infertile ovulations.

means of frequency distributions in Figure 40. The largest cornu of post-partum females exceeds 8 cm in diameter; post-partum shrinkage of the cetacean and pinniped uterus is rapid (Chittleborough 1958; Laws 1956b). Lactating females have cornu diameters of 1.5 to 6.5 cm with a mode at about 4 cm. Resting (nulliparous) females have cornu diameters ranging from 2 to 10 cm; most of these have probably weaned (or lost) their calves and have failed to ovulate or conceive at the most recent breeding season. Females with a large cornu and with oily fluids in the mammary gland (Figure 40) may have lost a neonatal calf, but their largest, non-recent corpus albicans is small, suggesting that they are not recently-parturient (Figure 41). The cornu diameters of pregnant females range from 5 to 30 cm, depending on the stage of pregnancy.

The involution of the largest corpus albicans (excluding young corpora albicantia of recent infertile ovulations) is shown in Figure 41. Post-partum females have a large corpus albicans, usually exceeding 20 mm in diameter, which represents the rapidly regressing corpus luteum of pregnancy. Lactating females display a mode at 10 mm, while simultaneously pregnant and lactating females have a similar mode. As most lactating females are probably nursing one-year-old calves, those that are simultaneously pregnant and lactating are also likely nursing yearling calves, and both groups of females must have a largest (non-recent) corpus albicans corresponding to the corpus luteum of pregnancy which has been regressing for about 12 months. Non-lactating, early-pregnant females show a similar mode (11 mm) but the frequency distribution is skewed to the left (Figure 41). Some of these early-pregnant, non- lactating females could have ovulated unsuccessfully some 15 months prior to capture, while they were nursing their previous first-year calves (these corpora would be more than 10 mm in diameter, hence about the same age as those of lactating females), while others have a largest, non-recent corpus albicans which is considerably smaller than that of lactating females and which could correspond to the previous corpus luteum of pregnancy which has therefore been regressing for about

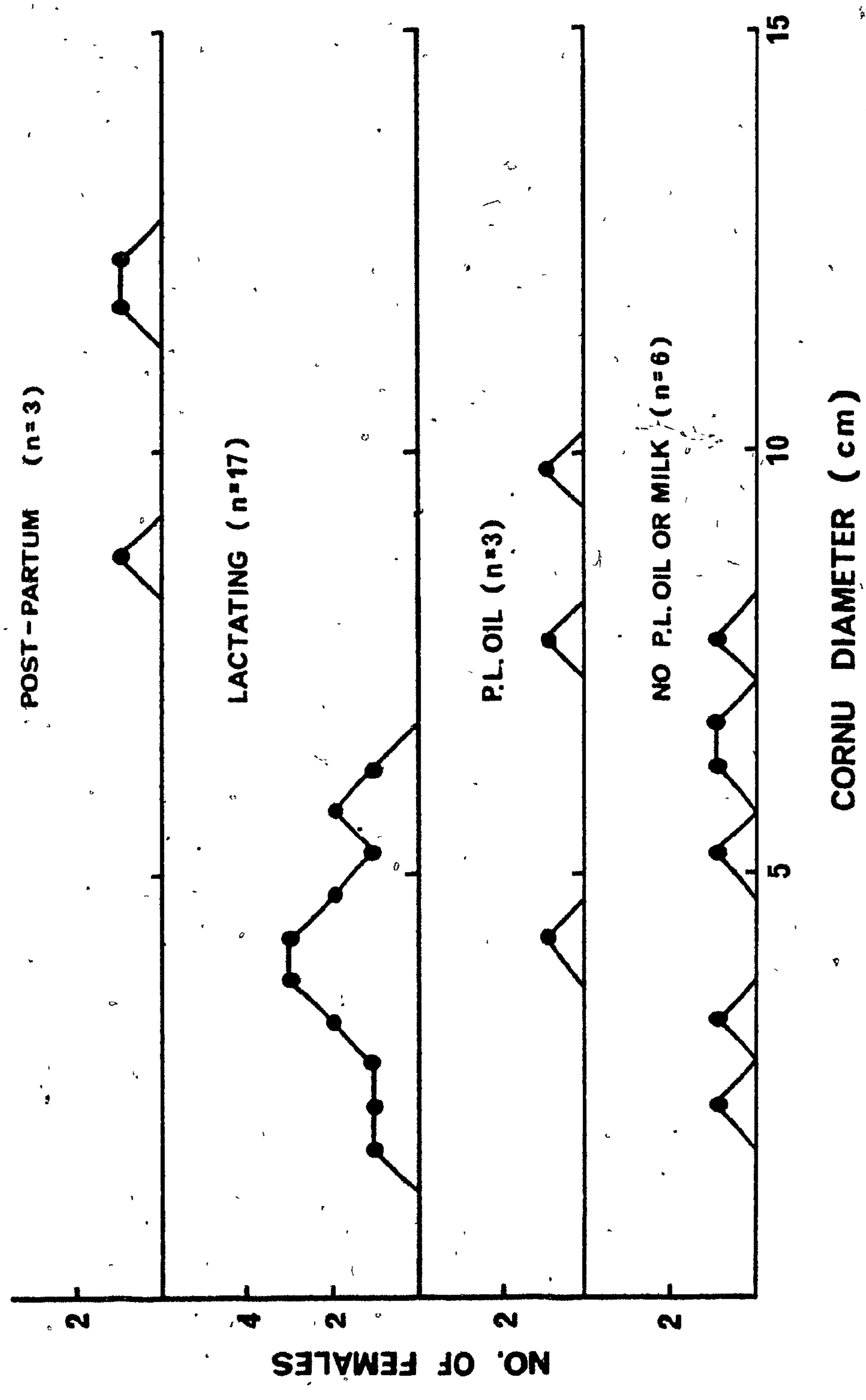

Figure 40. Frequency distribution of the diameter of the largest uterine cornu of non-pregnant mature narwhals. P. L. oil refers to the post -lactation fluid present in the mammary gland after weaning (see text). Class interval is 0.5 cm.

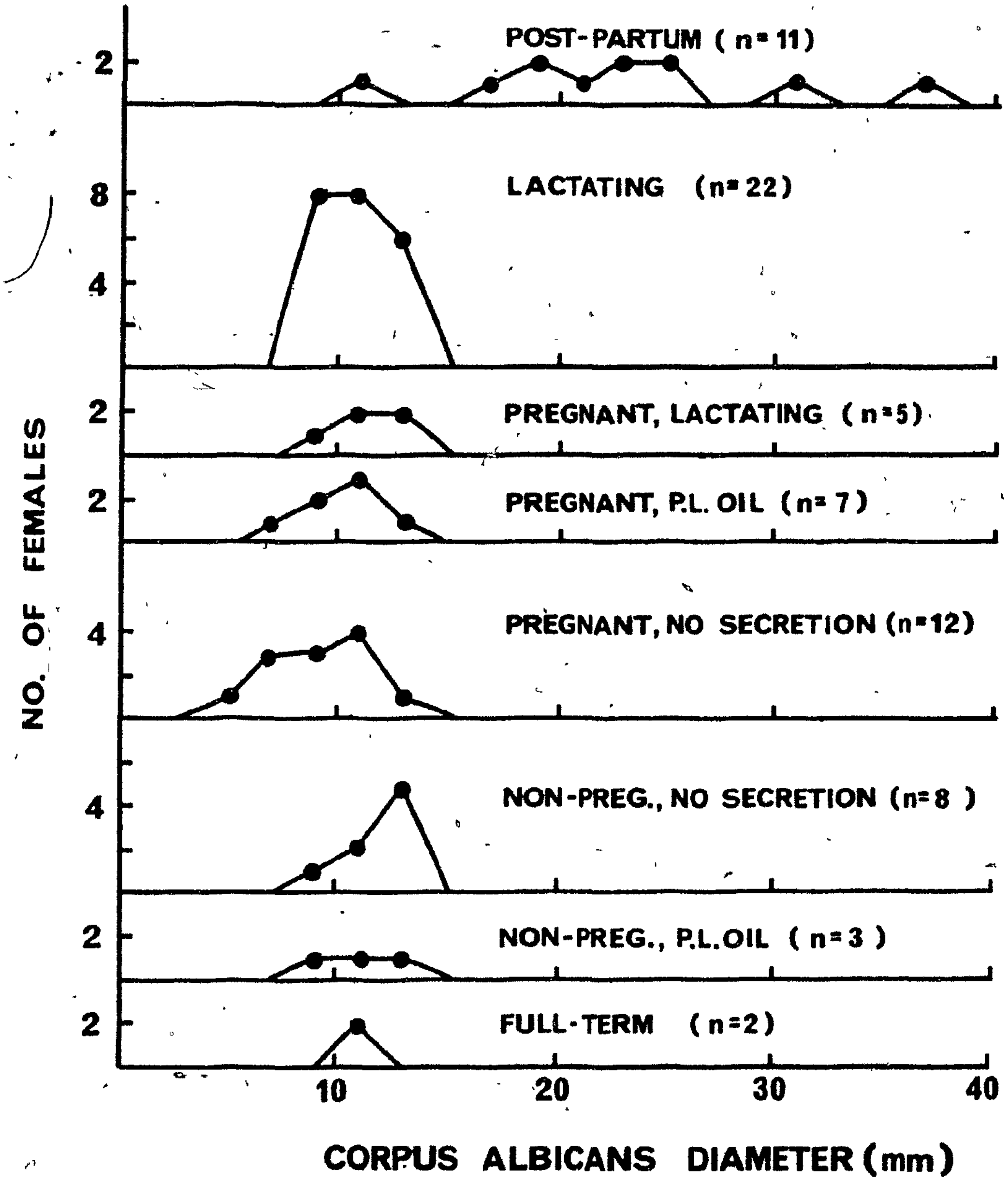

Figure 41. Frequency distribution of the diameter of the largest corpus albicans. Young corpora albicantia representing infertile ovulations at the most recent breeding season are excluded. Class interval is 2 mm.

24 months. This evidence suggests that most early-pregnant, non-lactating multiparous females have weaned two- year-old calves. Resting whales have a largest corpus albicans which varies from 8 to 14 mm in diameter (Figure 41); these are probably females which have weaned (or lost) their calves at various stages of the reproductive cycle, and have not conceived at the latest breeding season. Late-pregnancy females display a modal largest corpus albicans diameter of 11 mm which, considering its large size, could be derived from an infertile ovulation prior to conception (about 15 mo before capture).

Figure 41 and Table 13 indicate that involution of the corpus luteum of pregnancy is rapid during the first few weeks or months following birth. Subsequent regression is much slower, with the result that the diameter of the largest, non-recent corpus albicans is similar in females one and two years post-partum (Figure 41). Some indication of the rapidity of early regression is evident in Figure 42 which presents plots of the age and length of calves against the diameters of the largest non-recent (not derived from the latest oestrous) corpora albicantia of their mothers. Initial regression of the corpus luteum is seen to be very rapid, from a diameter of 37 mm when the neonate is 164 cm to a diameter of 16 mm when it is 178 cm. The modal size of the largest corpus albicans of lactating females is reached when the calf is about 200 cm in length (possibly six mo old). This is close to the point at which the young corpus albicans is transformed into a medium (the young corpus albicans persists for 0.66 yr). These results suggest that the diameter of the largest, non-recent corpus albicans can be used to distinguish only post-partum females, which themselves display a wide range of corpus albicans diameter due to rapid post-partum involution (Figures 41 and 42).

Some multiparous females in early pregnancy had a largest, non-recent corpus albicans of only 4 mm in diameter (Figure 41), suggesting two or more years of regression of the corpus luteum by the time of capture. Some of these females could have weaned their

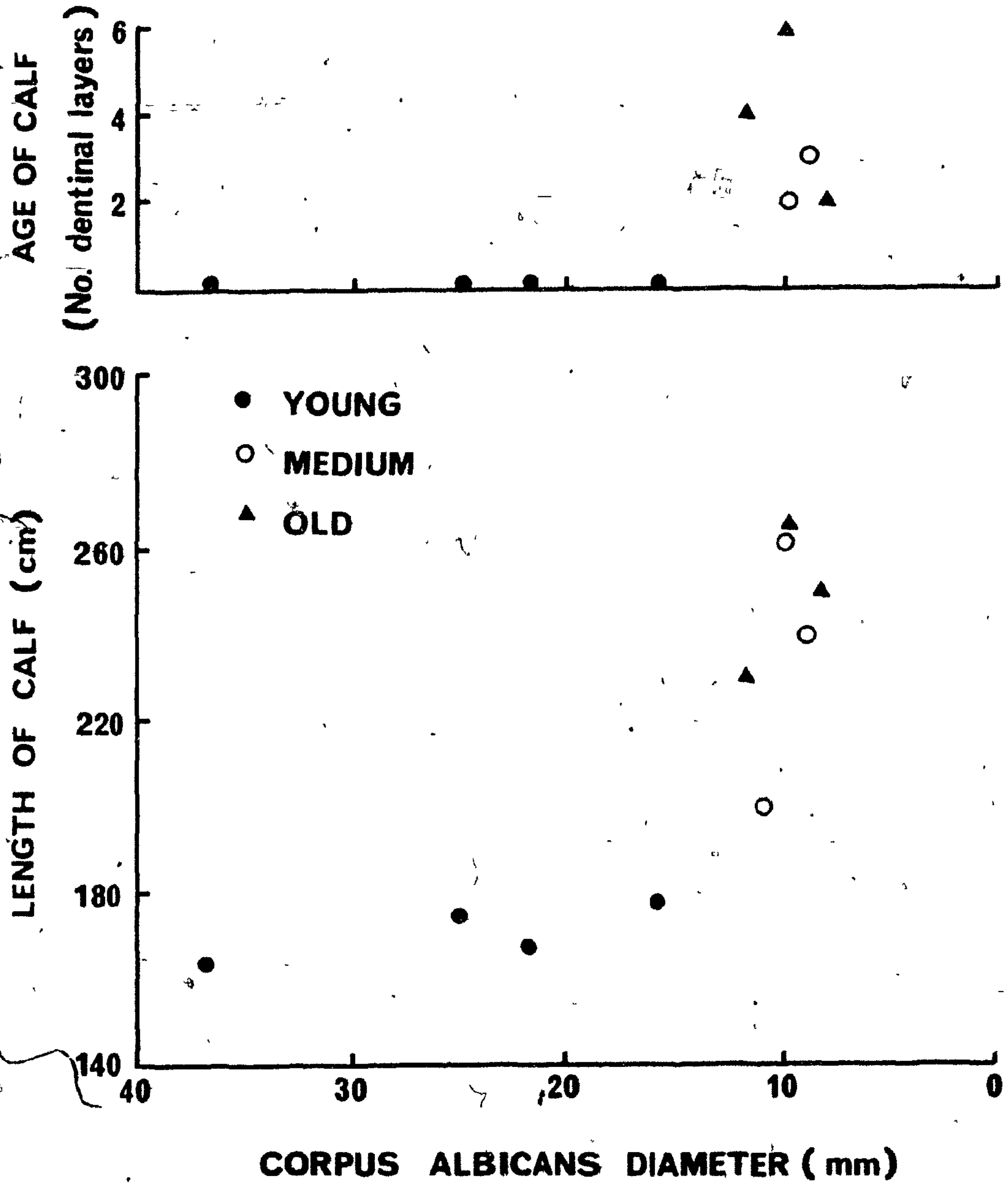

Figure 42. Age and length of calves versus diameter of the largest non- recent corpus albicans of the mature females with which they were associated. The stage of regression is specified (young, medium, and old).

calves about one year prior to conception, thus failing to ovulate at the breeding season in that year, resulting in a prolonged resting period (about one year), followed by ovulation at the next spring season. That some resting females appear to have weaned their calves and had failed to ovulate at the latest season provides some confirmation for this. Best (1970) thought that this might also apply to the sperm whale, in which case the reproductive cycle is extended to five years. It may be significant in this regard that those pregnant females with the smallest corpus albicans also had dry (no oil or milk) mammary glands (Figure 41).

These observations are complicated by the frequent occurrence of ovulations at the first mating season following parturition. For example, of 19 multiparous, non-lactating, early-pregnant females, the largest non-recent corpus albicans of 15 was in old regression (4-12 mm; mean of 9 mm) while the largest corpus albicans of 4 was in medium regression (9-13 mm). Of 17 non-pregnant females nursing yearling calves, 11 had a medium largest corpus albicans (9-14 mm) while six had an old largest corpus albicans (8-12 mm). These corpora are the largest non-recent (not derived from the latest oestrous) corpora albicantia of lactating females, and thus represent one year of post- partum regression. Because these corpora are the same size as the medium largest corpora of pregnant whales and have been regressing for one year, it is suggested that the largest medium corpora of non- lactating pregnant females represent infertile ovulations about nine months after parturition and slightly more than one year prior to capture, by which time they have weaned their two year-old calves. Some confirmation of this is provided by data from three primiparous females nursing their first (yearling) calves: their largest (and only) corpus albicans ranges from 9-12 mm in diameter. Non-lactating pregnant females whose largest corpus albicans is small and in the old regression stage did not likely ovulate at the first oestrous following parturition, but rather their small, old corpora probably represent two years of regression from the corpus luteum of pregnancy. An alternative explanation would be that non-lactating pregnant females with a large corpus albicans in medium regression are only one year post-partum and have weaned or lost yearling calves, and they have therefore conceived at the spring breeding season about nine months after parturition. Resting females also have a largest, non-recent medium corpus albicans of 10-13 mm in diameter; and these females may have weaned (or lost) yearling calves. One female was captured with a presumed yearling calf and she had involuted mammary glands (Table 13), suggesting that some calves may be weaned at the age of one year. The calf of this female was growing particularly rapidly (262 cm; two dentinal growth layers).

Females which conceived early in the season (as shown by size of foetus) have a largest, non-recent corpus albicans which is smaller (8-12 mm) than that of females which conceived later (12-16 mm). Early conception (and parturition) seem to be associated with advanced regression of the corpus albicans since more time is available for regression, but this possibility assumes that an individual animal consistently conceives at the same time of year. On the other hand, the larger corpora of non-lactating early-pregnant females are thought to result from infertile ovulations at the first breeding season following parturition (see above). Corpora albicantia originating over a two or three month season of births would not be expected to differ greatly in size after about two years of regression, further confirming that the larger corpora of pregnant females probably represent infertile ovulations occurring about nine months after parturition.

The post-partum involution of the mammary gland, as indicated by changes in its average thickness, is shown in Figure 43 by means of frequency distributions. A brief description of the various fluids present in the mammary glands will provide a useful background.

The milk of lactating narwhals is a thick turbid green fluid, often seen oozing from the mammary slits when the whale is rolled up the beach. The mammary glands of some females in early pregnancy and those of some resting females (some of which ovulated unsuccessfully)

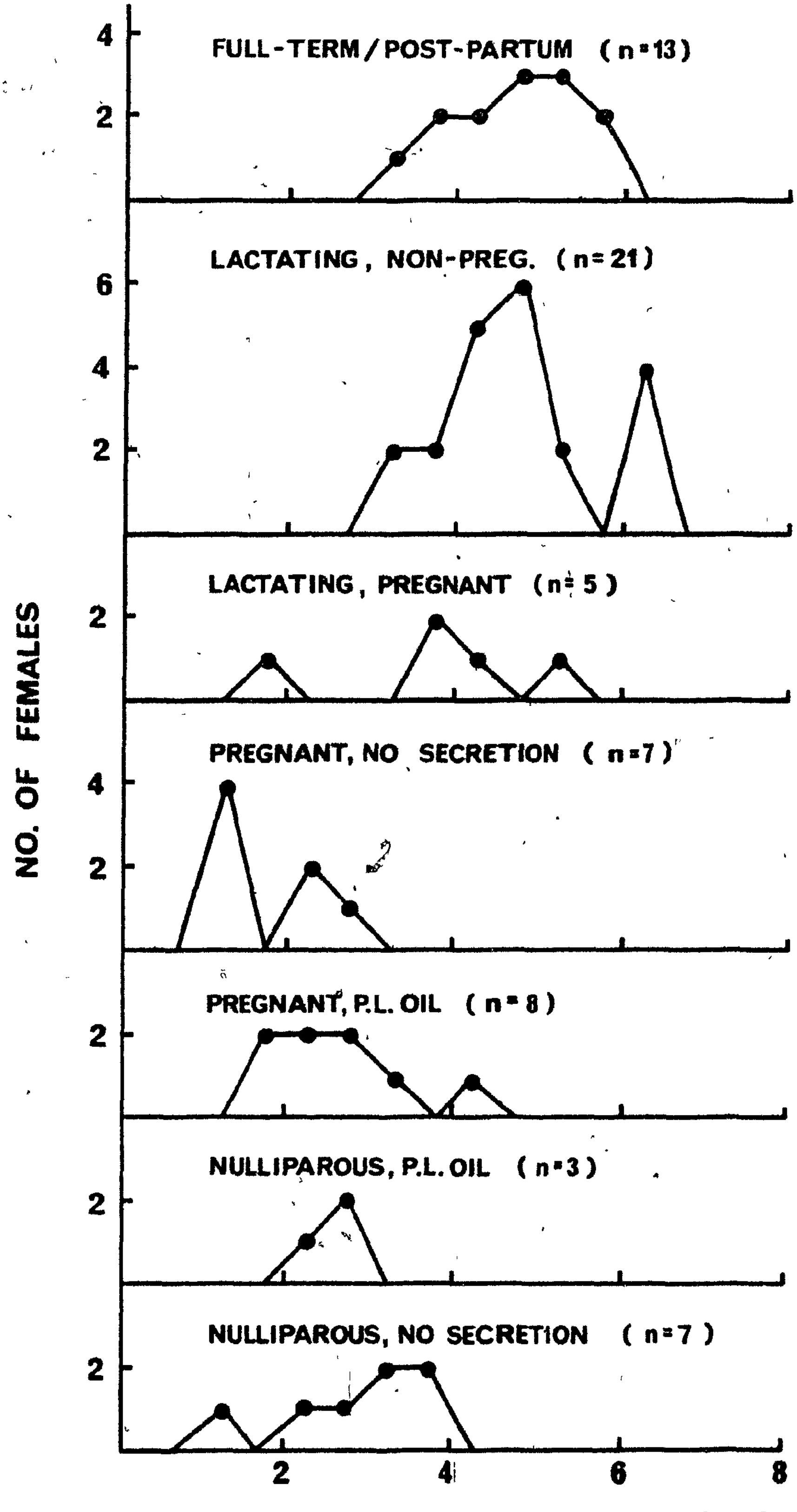

Figure 43. Frequency distribution of thickness of mammary gland of mature females. Class interval is 0.5 cm.

contain a light brownish or greenish translucent oily fluid, which is here referred to as post-lactation oil. The presence of this fluid in only involuting glands (4 cm or less in thickness) and the observation that mammary glands containing this fluid are slightly thicker than those which contain no fluid at all suggest that the presence of post-lactation oil in early-pregnant and resting females indicates recent weaning (or loss) of a calf.

Best (1968) stated that the presence of brown or oily fluids in the mammary gland of the sperm whale is indicative of mammary involution and weaning of the calf. This fluid, often thin and watery, is poor in proteins and fat (Best 1968). Chittleborough (1958) noted a "...rather white watery fluid found in some glands involuting after lactation" in the humpback whale. Laws (1961) described the post-lactation fluid of the mammaries of the fin whale as a "whitish or turbid yellowish thin fluid". Van Lennep and van Utrecht (1953) have identified this fluid as the residual milk of post-lactation glands, and they termed it "corpora amylacea".

Colostrum has been identified in the mammaries of full-term humpbacks, where it is a clear yellow, pale brown, or turbid white fluid (Chittleborough 1958) and in the mammaries of the white whale, where it is a light yellow fluid (Brodie 1970). The mammaries of two post-partum narwhals were recorded as containing "yellow" milk and "pinky brown" milk, while those of a full-term female contained a "turbid-like oily green" fluid. These fluids could be colostrum, but no analyses were carried out to confirm this.

Figure 43 shows that full-term and post-partum females have a modal mammary gland thickness of 5 cm; the lower thicknesses (3 to 4 cm) belong to the developing mammary glands of females in late pregnancy. Non-pregnant lactating females have a main mode at about 4.8 cm and a lesser one at about 6.2 cm, but this separation into two modes could be due to small sample sizes. Lactating females with thin mammary glands (3 to 4 cm) may be in the final stages of nursing their two-year-old calves (Figure 43). Pregnant and lactating females have the same frequency distribution of mammary gland thickness as lactating females, except for one female whose mammary gland was less than 2 cm thick. This female could be in the late stages of the two year lactation period, but the milk of this specimen is described in field notes as a "thick sticky green liquid" which could actually be the post-lactation oil.

Females in early pregnancy have involuted mammaries less than 4 cm thick (Figure 43); those females whose mammaries contain post-lactation oil have slightly thicker glands, suggesting more recent cessation of lactation in these females than in those whose glands contain no fluid at all. Resting (nulliparous) females have involuted or involuting glands less than 4 cm in thickness.

The average mammary gland thickness at the end of lactation can be estimated from Figure 44, which shows a plot of the percentage of females lactating in each 0.5 cm mammary gland thickness interval. Excluding the point representing 1.5 to 2.0 cm, 50% of females are lactating at a mammary gland thickness of about 3.3 cm which is taken as the mean thickness at weaning. This value corresponds well with the discontinuity between the frequency distributions of gland thickness of lactating and non-lactating whales (Figure 43). The point at 1.5 to 2.0 cm belongs to the pregnant and lactating female alluded to above; this female could actually have weaned a two-year-old calf and may not be lactating. Most glands less than 4 cm thick are considered to be involuting (or in the case of full-term females, developing).

Mammary gland thickness cannot be used to distinguish between various reproductive classes, other than between lactating and non-lactating females. The unimodal frequency distribution of the gland thickness of lactating females (Figure 43) indicates that females in different stages of lactation cannot be distinguished (post-partum and one and two years post-partum).

The mammary gland decreases in thickness as the largest, non-recent corpus albicans continues to regress, both in resting females (whose mammaries contain oil or nothing) and, even more pronounced, in non-lactating, pregnant females. In this connection it is

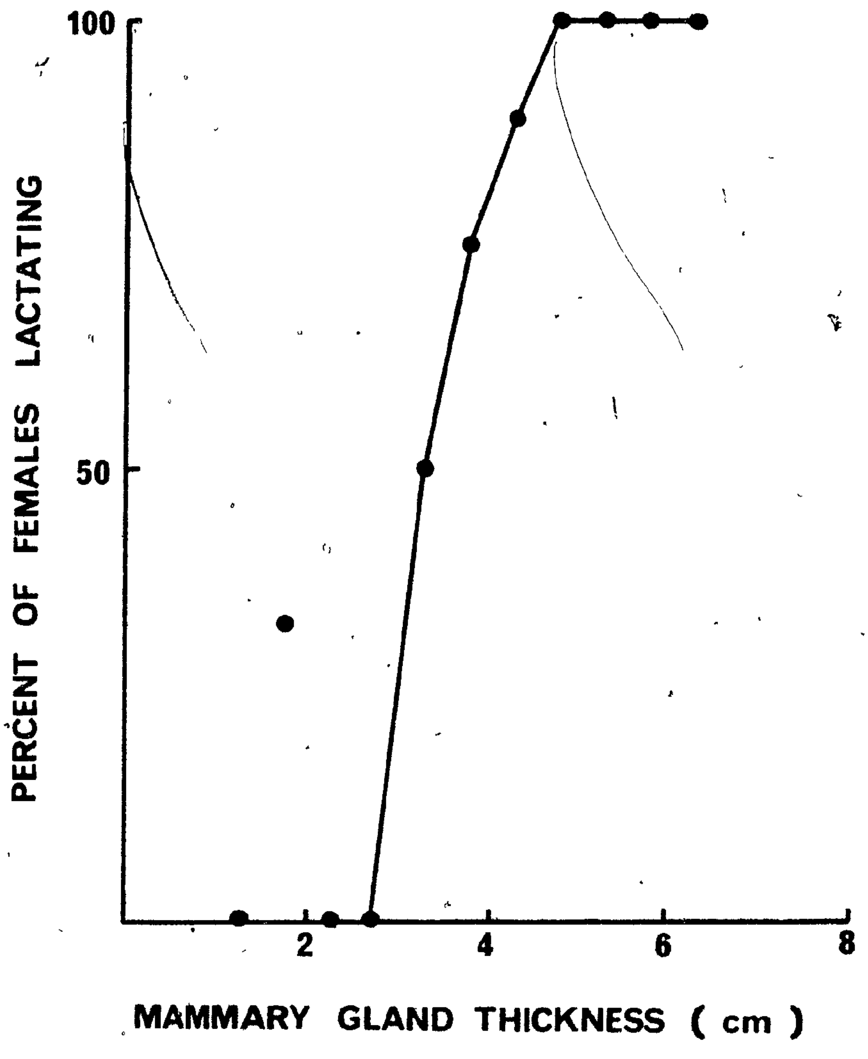

Figure 44. Percent of mature females lactating versus mammary gland thickness. Class interval is 0.5 cm.

interesting that early-pregnant females whose mammaries are dry have smaller, largest corpora albicantia than those whose mammaries contain the post-lactation oil (Figure 41), suggesting that mammary gland thickness is proportional to corpus albicans (largest, non-recent) diameter. If the duration of lactation is constant, then pregnant females which weaned their calves early would be expected to have mammary glands and largest, non-recent corpus albicans in more advanced stages of involution than those females which weaned their calves recently, relative to the time of sampling.

The histological structure of active, involuting, and involuted mammary glands has been described by van Lennep and van Utrecht (1953) and by van Utrecht (1968). Brodie (1970) recorded changes in mammary glands thickness (in relation to reproductive state) in the white whale similar to those described here for the narwhal. Best's (1968) observations of mammary gland involution in the female sperm whale are similar to those described here: mammary involution seems to be a protracted process, beginning when the calf starts taking solid food and being complete at weaning (nutritional independence of the calf).

In summary, the diameter of the largest uterine cornu and the diameter of the largest, non-recent corpus albicans can be used to distinguish between post-partum and lactating (one or two years post-partum) females, while the mean mammary gland thickness of these groups is about the same. Using these criteria, it is impossible to distinguish between non-pregnant, lactating females one and two years post-partum.

Evidence for the occurrence of fertile ovulations about nine months post-partum will now be presented. Five of 30 (16.7%) females in early pregnancy were simultaneously lactating, and they are considered to be nursing yearling calves and to have ovulated at the most recent breeding season when the calf was about nine months old. First, several lactating females (36.4%; see Table 9) had infertile ovulations at the most recent oestrous, indicating that females nursing yearling calves are at least capable of ovulation. Second, most mature female narwhals belong to one of four main reproductive categories: non-lactating, pregnant (weaned two year calf); full-term/post-partum; lactating (one year calf); and resting (non-pregnant; non-lactating; a few have ovulated unsuccessfully at the most recent oestrous). This implies the existence of a basic three year reproductive cycle and further that the lactation period exceeds one year but is less than two years (since most early-pregnant females have weaned their calves). This logically leads to the conclusion that simultaneously pregnant and lactating whales are nursing yearling calves, and therefore that they have conceived about nine months after parturition.

The third piece of evidence relates to the observation that the largest corpus albicans of simultaneously pregnant and lactating females is similar in diameter to that of lactating females, while non-lactating, pregnant females have a slightly smaller, largest corpus albicans (Figure 41). The largest corpus albicans of four of five pregnant and lactating females was in the medium stage of regression. Finally, calves may occasionally be weaned at one year of age (Table 13), and since mammary involution may start long before weaning (Best 1968), the mothers of such calves could conceive at the most recent breeding season, nine months after parturition (during late lactation).

It is of interest that two early-pregnant, lactating females killed at the Guys Bight floe edge during July 1976 had been accompanied by calves which were not taken by the hunters. The field notes state that one had a "calf", while the other had a "large dark calf".

Frequency Distribution of Reproductive States

Table 14 lists the number and percentage of females in each of various stages of the reproductive cycle, as determined by the crtieria established in the foregoing. This information is needed to determine certain aspects of the life history and the reproductive

Table 14. Reproductive conditions of female narwhals.

Reproductive condition	No. of females	Percent of females
Immature	31	27.68
Maturing[a]	2	1.79
Primiparous:		
early pregnancy	6	5.36
full- term	0	0
post-partum	2	1.79
Lactating, yearling	3	2.68
lactating, two year calf	0	0
Multiparous:		
early pregnancy	19	16.96
early pregnancy, lactating	5	4.46
full-term	4	3.57
post-partum	9	8.04
lactating, yearling	18	16.07
lactating, two year calf	2	1.79
Nulliparous, young mature	5	4.46
Nulliparous,-old mature	5	4.46
Nulliparous, senile	1	0.89
Total	112	100.00
Full-term/post-partum	15	18.99
Pregnant only[b]	25	31.65
Lactating only[b]	23	29.11
Pregnant and lactating[b]	5	6.33
Total pregnant[b]	30	37.97
Total lactating[b]	28	35.44
Total resting	11	13.92
Total mature	79	

[a] No corpora present; follicles exceeding 10 mm present.

[b] Excluding full-term/post-partum females.

cycle, to be detailed in the next major section (Life History Parameters).

Reduced Fertility of Old Females

Evidence for reduced fertility of old female narwhals is presented in Figure 45. Female fertility seems to be greatly reduced after the accumulation of 14 corpora or 25 mandibular growth layers. Corpora atretica occur with equal frequency in younger and older mature narwhals (Figure 45); this is to be expected since follicular atresia is a normal post-oestrous phenomenon. However, Best (1967) detected a greater incidence of atretic corpora in female sperm whales with more than 13 ovarian corpora.

Female narwhals with many ovarian corpora tend to be resting or non-pregnant. In addition, older females (with 14 or more ovarian corpora) which ovulated at the most recent breeding season failed to conceive (Figure 45). Best (1967) found that female sperm whales with more than 14 corpora may ovulate but often fail to conceive. Ohsumi (1965) also found low ovulation and pregnancy rates in old sperm whales.

A reduction in female fertility with age has also been detected in the white whale (Sergeant 1973), the pilot whale (Sergeant 1962), the spotted porpoise (Kasuya 1976; Kasuya _et al_. 1974; Perrin _et al_. 1976), the striped dolphin (Kasuya 1976), and the spinner dolphin (Perrin _et al_. 1977). There is no evidence for reduced fertility of old female humpback whales (Chittleborough 1955b), but old female fin whales may be slightly less fertile than young whales, although no true climacteric is reached (Laws 1961).

One resting (nulliparous) female narwhal of body length 415 cm is considered to be senile, on the basis of the observation that no recent ovarian corpora were present (young or medium corpora albicantia). The ovaries of this female contained four old corpora albicantia (5- 6 mm) and eight corpora incognita (7-12 mm). Other old resting females had recent ovarian corpora and were thus not considered to be senile, although their failure to ovulate or

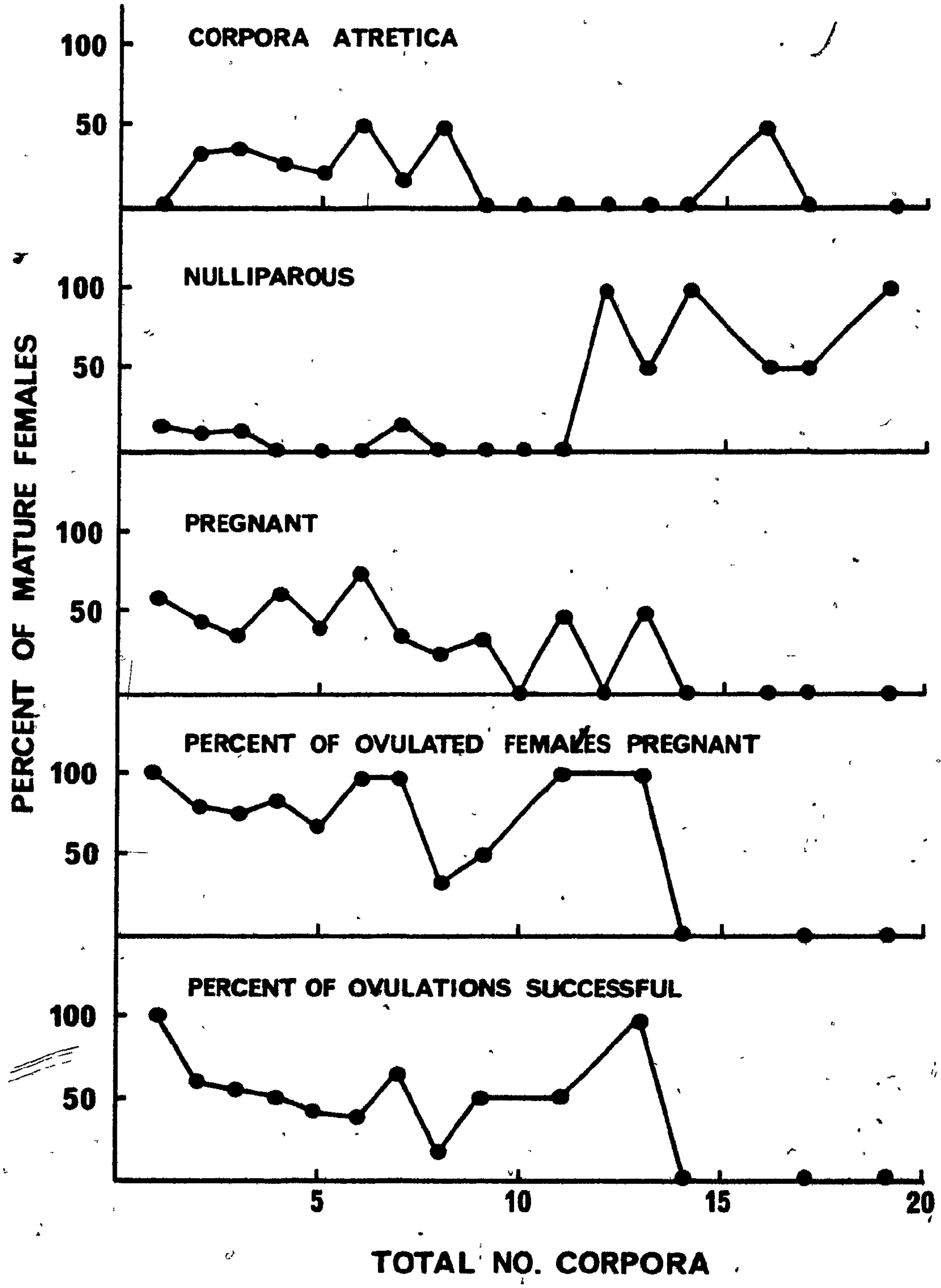

Figure 45. Reduced fertility of old female narwhals. Of 76 mature females, 18 had corpora atretica, 30 were in early pregnancy, and 11 were resting (nulliparous). Fourty-one females had a total of 68 ovulations at the latest breeding season, 30 of which resulted in pregnancy.

conceive at the latest breeding season may be indicative of the approach of a reproductive climacteric. Evidence for the attainment of a climacteric by the female has been recorded in the spotted porpoise (Perrin _et al._ 1976; Kasuya 1976), the striped dolphin (Kasuya 1976), and the pilot whale (Sergeant 1962).

Reproductive Influences on Female Condition

It was shown earlier that the body condition (or fatness) of female narwhals was not dependent on date of capture. Rather, it may depend to a large extent on their reproductive status. Table 15 presents data on the condition of females at different stages of the reproductive cycle. Full-term/post-partum females have significantly higher (at the 5% significance level) blubber thickness than lactating females (F test for homogeneity of variances was not significant at the 5% level, $0.5 > p > 0.2$; $t = 2.55$, $0.02 > p > 0.01$), while pregnant females have significantly higher blubber thickness than lactating females (F test not significant, $0.10 > p > 0.05$; $t = 2.32$, $0.05 > p > 0.02$). All other t-tests comparisons between various reproductive classes of mature females for all 3 parameters were not significant at the 5% level. Lactating females are generally in poor condition due to the nutritional demands of their calves, while full- term/post-partum females are amongst the fattest (Table 15). Brodie (1970) made the same observation on the white whale _Delphinapterus leucas_.

Immature females have significantly higher (at the 5% significance level) condition indices than pregnant females (F test for homogeneity of variances was significant at the 5% level, $0.01 > p > 0.002$; $t = 4.10$, $p < 0.001$), lactating females (F test not significant, $p > 0.5$; $t = 3.90$, $p < 0.001$), and resting females (F test not significant, $0.10 > p > 0.05$; $t = 2.74$, $0.01 > p > 0.001$), but there was no significant difference between condition indices of immature and full-term/post-partum females (F test not significant, $0.5 > p > 0.2$; $t = 1.80$, $0.10 > p \geq 0.05$). Therefore, immature females seem to be in better condition than most mature females.

Table 15. Condition of female narwhals.[a]

		Reproductive condition				
		Immature, Maturing	Pregnant	Full-term/ post-partum	Lactating	Resting
Maximum girth (cm)	N	26	20	12	24	8
	$\bar{X}$	180.5	224.8	233.9	220.5	224.6
	2SE	14.2	4.1	10.3	8.4	16.1
	Range	105-224	210-239	201-255	200-280	190-250
Lateral blubber thickness (cm)	N	26	14	15	25	10
	$\bar{X}$	4.65	5.99	6.09	5.27	5.87
	2SE	0.38	0.34	0.45	0.42	1.04
	Range	2.3-6.9	5.0-7.0	4.5-7.6	3.0-7.3	3.4-8.5
Condition index[b]	N	26	20	12	24	8
	$\bar{X}$	0.65	0.60	0.62	0.59	0.60
	2SE	0.02	0.01	0.02	0.02	0.02
	Range	.55-.76	.56-.66	.56-.67	.52-.70	.55-.63

[a] Sample size (N), mean value ($\bar{X}$), two standard errors (2SE) and range are given.

[b] Maximum girth/body length.

This could be a morphometric difference, or else it could simply reflect the demands of reproductive life on mature females.

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[1] Dr. K. Benirschke (Department of Pathology, School of Medicine, University of California at San Diego) has examined histologically both the corpus luteum and the erupted follicle of this animal. He finds (in litt., 12 October 1978) that the corpus luteum is clearly functional and that "...it might be from a pregnant animal". He has interpreted the haemorrhagic erupted follicle as "...fresh hemorrhage into an old cystic corpus albicans. The "follicular" wall is fibrotic and hyalinized, lacking active granulosa cells".
Dr. Benirschke concludes that "...the animal is early pregnant, too early to have been detected at macroscopic examination. Certainly she has not recently ovulated".

Dr. Benirschke's interpretations differ greatly from mine, but they do confirm my observation that old corpora albicantia sometimes contain blood. Furthermore, his findings give some support to the speculation (see below) that the corpus incognitum represents an haemorrhagic old corpus albicans.

If Dr. Benirschke's interpretations are correct, then the "erupted follicle" of this narwhal is probably derived from an infertile ovulation prior to the successful conception and hence represents the "old cystic corpus albicans" described by him.

LIFE HISTORY PARAMETERS

The Birth Rate

It was shown earlier that segregation by sex and stage of reproduction does exist within the summering narwhal population. This will have implications for the accuracy of estimates of life history parameters which are derived from the relative proportions of females which are engaged in different stages of the reproductive cycle. These calculations normally assume that the proportions of these classes in the sample (catch) are the same as those in the population at large. Because of segregation by stage of reproduction and the small sample sizes, resulting estimates of life history parameters could be seriously-biased. One can assume that the magnitude of the bias will lessen as the overall sample size increases and the sample is spread over more and more groups throughout the summer range of the narwhal.

As an example the birth rate (pregnancy rate) is considered. This can be estimated as the proportion of mature females in early pregnancy or the proportion of mature females that are full-term or post-partum. Because of highly seasonal breeding in relation to a restricted summer sampling season and the gestation period which exceeds one year, only one or the other can be used as an estimate of pregnancy rate; the sum of the proportions of mature females in early pregnancy and those full-term/post-partum would be an invalid estimate of pregnancy rate (see Anderson 1982).

The overall pregnancy rate for the sample from 1963-76 is 0.38 (30 early pregnant females/79 mature females) or 0.19 (15 full-term/post-partum females/79 mature females). In the netted sample of 1963-65, the early pregnancy rate is 0.11 while the full-term/post-partum rate is 0.53; in the Guys Bight floe edge sample of 1976, the early pregnancy rate is 0.56 while the full-term/post-partum rate is 0.11; and in the overall open water hunted sample of 1974-76, the rates are 0.43 and 0.07, for early pregnancy and full-term/post-partum, respectively.

It would thus appear that early pregnant females are prevalent (relative to post-partum females) at the floe edge and in the outer coastal waters (e.g. Kaunak) where the hunted sample was taken. On the other hand, full-term/post-partum females (0.53 of the mature females) are prevalent in Koluktoo Bay where the netted sample of 1963-65 was taken. Koluktoo Bay is situated deep within the fiord complex of Eclipse Sound on northern Baffin Island (Figure 1). Mansfield et al. (1975) and Vibe (1950) also expressed the idea that females with calves tended to select the heads of bays in the innermost fiords as summering places.

Segregation by stage of reproduction, both on a large-scale regional basis and on a small-scale (group composition) basis, does present problems for the accurate estimation of life history parameters. Tentatively, the overall early-pregnancy rate of 0.38 for the total sample is accepted. Because most of the total sample was obtained at the floe edge and outer coasts, this may be an over-estimate; similarly, the full-term/post-partum rate of 0.19 is likely an under-estimate. See Appendix 3 for further discussion and statistical analyses of regional and small-scale segregation within this population.

Another estimate of the birth rate was briefly discussed previously. This is the annual ovulation rate (0.69) multiplied by the percentage of ovulations which are fertile (0.44), or 0.30 calves/mature female/year. Another approach is to calculate the stable distribution of reproductive states starting with all females in early pregnancy, with the assumptions that the reproductive cycle lasts three years and that the probability of the occurrence of a fertile ovulation at nine months post-partum is about 0.20 (see Table 12). This does not take into account females which may fail to conceive at the first breeding season following weaning of their calves or calf mortality. The resulting stable birth rate is estimated to be 0.36 and the stable distribution of reproductive states is 0.29 of females in early pregnancy but not lactating, 0.29 of females nursing yearling calves but not pregnant, 0.06 of females simultaneously early- pregnant and lactating, and 0.36 of females full- term or recently-calved.

The annual pregnancy rate of the narwhal is estimated to be 0.30 to 0.38. The intermediate value of 0.36 is suggested to be the best estimate, since it takes into account the successful ovulations of females nursing yearling calves but it ignores the possible failure of some females to conceive at the first oestrous following weaning of their calves. The pregnancy rates of other odontocete species are as follows: white whale, 0.33-0.5 (Sergeant 1973), 0.33 (Brodie 1971); pilot whale, 0.34 (Sergeant 1962); sperm whale, 0.20-0.22 (Best 1968), 0.29 (Ohsumi et al. 1963), 0.26-0.29 (Ohsumi 1965); spotted porpoise, 0.27 (Kasuya 1976), 0.21 (Kasuya et al. 1974), 0.47 (Perrin et al. 1976); striped dolphin, 0.71 (Kasuya 1976); and spinner dolphin, 0.36 to 0.46 (Perrin et al. 1977). The higher pregnancy rate of 0.71 for the striped dolphin is explained as a density-dependent response to excessive exploitation of this species (Kasuya 1976). The average annual pregnancy rate of killer whales off Vancouver Island is only about 0.10 (Bigg 1982).

The population birth rate (per growth layer) was estimated as follows. Applying the ovulation success rate (0.44) to the corpora accumulation rate (0.76), the pregnancy rate is estimated to be 0.33 calves/mature female/growth layer. Dividing by two (assuming a 1:1 sex ratio at birth), fecundity is estimated to be 0.17 daughters/mature female/layer. The population birth rate is estimated by solving for r in the life history equation

$$\sum l_x m_x e^{-rx} = 1$$

Age-specific fecundities (m_x) are calculated as the proportion of females sexually mature at each age multiplied by the maximum fecundity (0.17). Survivorship (l_x) is set at 1.0, so that r is then the instantaneous birth rate.

A computer program in Caughley (1977) was used to estimate r by an iterative procedure. The instantaneous birth rate (per growth layer) was calculated as 0.056 and the finite birth rate was estimated as e^r-1 or 0.057. If one growth layer is deposited annually in mature females, this figure implies an annual production of about 0.06. These values were calculated using the known duration of female reproductive life (12 to 30 growth layers). Assuming a longevity of 50 growth layers, the instantaneous birth rate is calculated to be 0.069, only slightly greater than that based on a longevity of 30 growth layers.

A second approach to the estimation of the population birth rate is to consider the sex ratio of the catch and the proportion of females which are sexually mature, and applying these values to estimates of the pregnancy rate. The proportion of females which are mature is 0.7054 and the sex ratio is 0.55 females per individual. Applying these values to the estimated annual pregnancy rate of 0.38, a finite annual birth rate of 0.1474 is obtained, or 0.1375 on an instantaneous basis. If the stable annual pregnancy rate is 0.36 (assuming 20% of females conceive nine months post-partum), the finite annual birth rate is estimated as 0.1397 and the instantaneous birth rate, 0.1307. The finite birth rate of the narwhal population is estimated to be 0.057 (per growth layer) to 0.1474 (per year). This latter estimate of the annual population birth rate of the narwhal is similar to estimates for other odontocetes (see below). However, many of these estimates of population birth rate are probable overestimates, since the sex ratio and maturity ratio may be determined from a possibly-biased sample and then applied to the pregnancy rate. For example, mature female narwhals comprise 0.7054 of the total female sample. Since immature females are only partially-recruited to the catchable population, 0.7054 is a substantial overestimate of the actual proportion of females which are mature. Although the sex ratio of 55% females seems to be reasonable, the resulting estimate of annual birth rate (0.14-0.15) is an overestimate of the true birth rate which may be closer to 0.06-0.07.

Population birth rate is estimated to be 0.09 (Brodie 1971) or 0.12-0.14 (Sergeant 1973) in the white whale, 0.10-0.13 in the pilot whale (Sergeant 1962), 0.08-0.10 in the spinner dolphin (Perrin _et al._ 1977), and 0.14 in the spotted porpoise (Perrin _et al._ 1976). The annual population birth rate of killer whales off Vancouver Island is about 0.04 (Bigg 1982).

The number of calves which a female narwhal may produce during her lifetime may be estimated. A maximum of 19 corpora albicantia was recorded, and if 0.44 of ovulations are fertile, then an average of 8.4 calves would be produced. If females have 18 layers of reproductive life (the oldest female had 30 mandibular growth layers and females mature sexually at 12 layers), then with a pregnancy rate of 0.33 calves/mature female/growth layer, 5.9 calves would be produced. This probable underestimate further indicates that the age of old females approaching physical maturity may be greatly underestimated.

In summary, the annual population birth rate of the narwhal is not certain, but could be near 0.07. This is considerably lower than the birth rates estimated for some other odontocetes, but it is likely that many of these estimates are based on biased samples of the mature female population. This estimate of the birth rate of the narwhal is slightly lower than Brodie's (1971) estimate of 0.09 for the white whale; his estimate is based on a solution of the life history equation:

$$\sum l_x m_x e^{-rx} = 1$$

Brodie (1971) determined that female white whales mature at age five years and do not reproduce after 21 years, and that there is three years between births (m_x =0.167 daughters/mature female/year). Using these data as input to the iterative computer program in Caughley (1977), the birth rate of the Cumberland Sound population of white whales was estimated to be 0.077, close to Brodie's (1971) estimate of 0.09. Using vertical aerial photographs of a large herd of white whales occupying Cunningham Inlet during late July 1973, Heyland (1974) estimated that the production of newborn calves by this herd was 17.9%. However, true production may be substantially less, as the immature or non-breeding component of the population may occupy other habitat. The use of potentially-biased population samples and aerial surveys to assess stock production should be critically re-examined.

Duration of Lactation

The duration of the lactation period may be estimated by assuming that the duration of a given reproductive phase is proportional to the relative number of females in that phase. If the duration of one phase in the cycle is accurately known, then the duration of other phases may be estimated. This further assumes that the sample of females in various stages of the reproductive cycle is an unbiased sample of the mature female population.

Nevertheless, the gestation period is known fairly accurately (15.3 months) and a preliminary estimation of the duration of lactation can be attempted. It was shown previously that lactation exceeds one year but is less than two years in duration. Excluding full-term/post-partum females, the ratio of non-pregnant, lactating females to non-lactating, pregnant females is 23/25 or 0.92; lactation period is estimated to be 0.92 multiplied by 15.3 mo or 14.1 mo. A less-biased estimate may be obtained by using the ratio of all non-post-partum lactating females plus one-half of the full-term/post-partum females, to all early pregnant females plus one half of the full-term/post-partum females. The resulting estimate of lactation period is 14.5 months.

The co-occurrence of females and calves also provides some evidence on the duration of lactation (Table 13). The stomachs of newborn calves contained milk, while three possible yearlings were still taking milk and one yearling had apparently been weaned, for its mother's mammaries had involuted and now contained post-lactation oil (Table 13). The mother of a possible two-year-old calf was lactating but the calf's stomach was empty. These results suggest that lactation normally lasts at least one year but less than two years.

There are few comments in the literature as to the duration of lactation in the narwhal. Pedersen (1931) stated that nursing lasts"...at least several weeks", while Vibe (1950) implied that the lactation period was less than one year in duration.

The lactation periods of odontocetes are generally much longer than those of mysticetes. Brodie (1969a) attributed this to the more sophisticated navigational training, kin cooperation, and complex social structure of the odontocetes compared to the mysticetes. Although many odontocetes appear to have lengthy lactation periods (Table 16), the calves of several species may begin to take solid food long before weaning. Captive bottlenosed dolphins Tursiops truncatus nurse their young for up to 18 months, but the calves may begin to take solid food at 5 to 12 months of age (McBride and Kritzler 1951).

The Calving Interval

The interval between births in the female narwhal is usually three years, but it is reduced to two years when a female conceives at the first oestrous following parturition. Some females fail to conceive during the breeding season following weaning, with the result that the calving interval is extended to four or more years. Vibe (1950) claimed that the narwhal gives birth every second year, whereas Degerbøl and Freuchen (1935) attributed a calving interval of three years to this species, but these authors provided no evidence for their statements.

The calving interval can be calculated as the reciprocal of the annual pregnancy rate, which has been estimated to be 0.30 to 0.38; the corresponding calving intervals are 3.33 and 2.63 years. The best estimate of the pregnancy rate is 0.36, which gives an average calving interval of 2.78 years. A second approach assumes that the duration of each phase of the reproductive cycle is proportional to the relative number of mature females in that phase. Gestation and lacation periods have previously been estimated to be 15.3 and 14.5 months, respectively. Using the ratio of resting females to pregnant females, the resting period is estimated as 11/37.5 multiplied by 15.3 or 4.5 months. Therefore, the calving interval is 15.3 + 14.5 + 4.5, or 34.3 months (2.86 yr). In addition, the calving interval may be estimated as the sum of gestation and lactation periods (29.8 mo.), divided by the proportion of mature females which are reproductively active (68/79, or 0.861). The resulting estimate of the interval between births is 34.6 mo (2.88 yr).

The durations of the various phases of the reproductive cycles of some other odontocetes are set out in Table 16. The estimate of the lactation period of the sperm whale by Nishiwaki et al. (1958)must be an underestimate, for with a two year reproductive cycle more females would be expected to be simultaneously pregnant and lactating than is evident in their results, a re-examination of which suggests that the lactation period is about 20 months. The great difference in the reproductive cycles of the spotted porpoise Stenella attenuata and the striped dolphin S. coeruleoalba is attributed to the different degree of exploitation imposed on these two species off the Pacific coast of Japan (Kasuya 1976). The spotted porpoise is unexploited, while the striped dolphin has been heavily exploited since 1955 and has consequently shown marked density-dependent responses in fertility (Table 16). Even very old female striped dolphins are reproductively-active (Kasuya 1976).

The calving interval of odontocetes is seen to range from about 2 to 4 years. The smaller species (e.g. Stenella) have the shorter intervals, while the larger-sized, sexually-dimorphic species have protracted calving intervals. Mature female killer whales off Vancouver Island calve only once every 10 years, on average; the minimum calving interval recorded is 3 years, but many mature females seemingly never calve (Bigg 1982).

Population Size

Utilizing historical catch data, Mitchell and Reeves (1981) have calculated a cumulative catch estimate of population size of narwhals in the eastern Canadian arctic and West Greenland. They calculated that this population exceeded 11,000 individuals in 1914. Mansfield et al. (1975) estimated the current population size of the narwhal in North America to be about 10,000, based on Bruemmer's (1971) estimate

Table 16. Reproductive cycles of some odontocetes.

Species	Duration (yr)				Author
	Gestation	Lactation	Resting	Total	
Delphinapterus leucas	1.21	2		3.21	Brodie 1971
	1.17	1.67		2.84	Sergeant 1973
Physeter catodon		0.7-1.0		2	Nishiwaki *et al.* 1958
	1.37	2.0	0.63	4	Ohsumi 1965
	1.22	2.0	0.78	4	Best 1968
Globicephala melaena	1.31	1.83	0.19	3.33	Sergeant 1962
Stenella attenuata	0.93	2.44	0.82	4.19	Kasuya *et al.* 1974
	0.93	1.99	0.77	3.69	Kasuya 1976
	0.96	0.93	0.28	2.17	Perrin *et al.* 1976
Stenella coeruleoalba	1	1.5	0.4	2.9	Kasuya 1972
	1	0.33	0.08	1.41	Kasuya 1976
Stenella longirostris	0.88	0.84	0.46	2.18	Perrin *et al.* 1977

of 1,500 to 2,500 narwhals in the Thule region of northwest Greenland and Tuck's (1957) count of 6,000 narwhals migrating westward past Cape Hay, Bylot Island. More recently, Greendale and Brousseau-Greendale (1976) counted 6,145 migrating narwhals at Cape Hay from 21 June to 24 July 1976 and, taking into account time periods when observations were limited by fog and other obstructions to visibility, they estimated that 8,000 to 10,000 narwhals passed Cape Hay. The peak of the migration occurred on 15 July when 1,842 whales were seen (Greendale and Brousseau-Greendale 1976).

Other estimates of the numbers of narwhals occuring in various areas of the North American arctic have been made. Vibe (1950) claimed that more than 1,000 narwhals visited Inglefield Bay, northwest Greenland, every summer. Finley (1976) estimated that 200 to 400 narwhals occurred in eastern Barrow Strait during late July 1975, showing that relatively few narwhals migrate to the west of northern Baffin Island.

Several observations of narwhals in the Pond Inlet region have been documented. Anderson (1934) declared that thousands of narwhals passed Button Point, southeast Bylot Island, during July 1928, and he claimed that whalers killed 2,800 narwhals during one season in Eclipse Sound (see Mitchell and Reeves 1981). Miller (1955) noted that 500 to 1,000 migrating narwhals can be seen each year near southwest Bylot Island, while Smith (1969) recorded a movement of 2,000 whales past Pond Inlet on 29 September 1968. A large number of narwhals, up to 2,000 or 3,000, migrated past Bruce Head (Koluktoo Bay) on 17 August 1964 (A.W. Mansfield, pers. comm.).

Davis, Richardson, Johnson and Renaud (1978) concluded that 20,000 or more narwhals migrated westwards through Lancaster Sound in 1976. This estimate was based on the application of aerial survey data to the land-based observations of migrating narwhals at Cape Hay by Greendale and Brousseau-Greendale (1976). Fallis, Klenner and Kemper (1983) report an aerial-strip survey minimum estimate of 9,700 narwhals in southern and mid- Admiralty Inlet on 28 July 1975. The minimum number of narwhals overwintering in northern Davis Strait, southern Baffin Bay, and waters west of Greenland is estimated to range from 7,700-9,100 (McLaren and Davis 1983). These estimates, derived from aerial-strip sample surveys in March of 1981 and 1982, were not adjusted for submerged animals or animals present at the surface but not detected.

Discussion - General Features of Odontocete Life History

As a group, odontocetes have a seemingly complex social organization which pervades all aspects of their life histories. Sergeant (1959b) attributed the pronounced gregarious habit of the smaller odontocetes to potential predation from sharks and killer whales. He felt that the social habit would thus reduce the mortality rate of the calves and younger animals, given that many of these species do not have very high birth rates. On the other hand, Brodie (1969a) concluded that the complex social structure of odontocetes was related to the predatory habits of the whales themselves: the capture of highly mobile prey often requires a cooperative effort among several animals. He attributed the longer nursing period in odontocetes (compared to mysticetes) to the requirement for the young to learn the complex communicational, navigational and cooperative skills which are necessary for successful foraging. On the other hand, the mysticetes are "grazers" and thus do not need to develop these skills on such a highly sophisticated level; therefore, mysticetes have relatively short lactation periods (Brodie 1969a).

Odontocete whales, as a group, do not seem to have very high recruitment rates; the calving interval is on the order of 2 to 4 years, increasing with the size of the species (Table 16). The social habit and prolonged nursing period may, therefore, reduce mortality on calves and young animals (possibly the most vulnerable period of an animal's life), in addition to providing the training which the young need in order to develop the complex and important life skills of their kind.

Sergeant's (1959b, 1982) comparative study of life histories of toothed whales shows that there may be generalized differences of life history and social structure between the two subfamilies of the family Delphinidae, namely the Orcininae (e.g. - pilot whale, killer whale, false killer whale) and the Delphininae (the dolphins, such as Tursiops, Stenella, Lagenorhynchus). Sergeant (1982) concludes that the larger-sized Orcininae are highly social and non-aggressive, tending to form schools of mixed age and sex structure, while the smaller-sized Delphininae are less social and display aggression by adult males towards immature animals which form their own loose schools. Consequently, the Orcininae have a greater tendency to strand en masse (mass strandings) while Delphininae (especially immatures) more commonly strand individually (single strandings). However, the cohesive schools of mature females with calves (of Delphininae) may occasionally mass strand. Both subfamilies are characterized by long lactation periods (about 2 years) and parental care beyond the end of lactation resulting in enhanced survival of calves. Gestation period of Orcininae is 14 to 16 months, while it is 11-12 months in Delphininae.

Sexual dimorphism in body size is well-developed in Orcininae (the male attains a much greater size than females) while males of the Delphininae are only slightly larger than the females. In addition, males of the Orcininae mature sexually at a later age than females, whereas those of Delphininae mature only slightly later than the females. These characteristics of Orcininae, along with the higher mortality rate of the male of some species (e.g. - pilot whales; see Sergeant 1962), lead to an excess of mature females (relative to mature males) and the development of polygyny. Because the most highly social species seem to be characterized by well-developed polygyny, polygyny is not necessarily associated with aggression (Sergeant 1982). He claims that the tooth scarring commonly seen on Orcininae could be mostly made by young animals engaged in "play" behaviour.

The life history characteristics of the narwhal (which, along with the white whale, is in the family Monodontidae) would tend to associate this species with the Orcininae rather than with the Delphininae. A notable exception to this is the less social disposition of the narwhal, as indicated by marked segregation by sex and maturity during the summer. Therefore, Sergeant's (1982) contention that polygyny and lack of aggression are coincident may not be tenable. It is conceivable that the large "mixed" herds of Orcininae in fact consist of sub-groups of different age and sex composition, and that aggression may play a role in this segregation. In addition, polygyny is usually associated with intraspecific competition between adult males for breeding females and hence aggression, at least during the breeding season. Evidence for polygyny in the male narwhal was presented earlier (see "Reproduction in the Male").

Ohsumi (1981) has presented a series of interspecific relationships (some expressed mathematically) among biological parameters concerned with reproduction in both odontocete and mysticete whales. Although the purpose of his paper was to derive such relationships for predictive purposes (to estimate unknown parameter values for a particular species) and for checking the accuracy of reported parameter values for certain species, the data which he assembled clearly demonstrate major differences in life history parameters between the two cetacean orders and trends in these parameters within the odontocetes, which can be correlated with social organization and body size.

Table 17 compares direct estimates of life history parameters of the narwhal with values predicted from interspecific relationships (Ohsumi 1981). The agreement between predicted and observed values is generally very good (Table 17). Ohsumi (1981) used an asymptotic body length of 4.0 m for female narwhals (which he obtained from Mansfield et al. 1975) to produce most predicted values from the interspecific relationships. The predicted gestation period is 12.9 mo., considerably less than the calculated one of 15.3 mo. I

Table 17. Biological parameters of the narwhal.

Parameter	Reported value[a]	Predicted value[b]
Birth length (m)	1.61	1.72
Gestation period (mo)	15.3	12.9
Length at weaning (m)	-	3.04
Lactation period (mo)	>12, <24	20
Length at 1 yr. (m)	-	2.49
Length at male sexual maturity (m)	3.95	3.93
Length at female sexual maturity(m)	3.40	3.68
Age at female sexual maturity	12 growth layers	6.4 yr
Annual pregnancy rate	0.36	0.36
Annual ovulation rate	0.69	0.59
Foetal sex ratio (females/individual)	-	0.50
Litter size	1.00	1.00
Longevity (yr)	40-50	41
Instantaneous annual natural mortality rate (females)	-	0.12
Asymptotic length of males (m)	4.70	4.82
Asymptotic length of females (m)	4.15	4.00

[a] This study.

[b] From interspecific relationships among biological parameters in cetaceans (Ohsumi 1981).

attribute this to the fact that Ohsumi (1981) used a log-log straight line relationship between gestation period and body length at birth, whereas close inspection of these data (his Figure 11) suggests that a curvilinear (log-log) relation is more appropriate and would yield a predicted gestation period closer to the calculated value (i.e. gestation period increases rapidly with size for small species, up to about 1.5 m body length at birth,then levels off at 15-16 mo for species larger than 1.5 m at birth).

From interspecific relationships Ohsumi (1981) estimated that the female narwhal matures sexually at 6.4 yr. With 12 growth layers deposited by the time of maturity, this would imply a frequency of deposition of layers of about 2 per year, or the same as deduced for the closely related white whale (Brodie 1971; Sergeant 1973).

Sacher (1980) developed multiple linear regressions of longevity (as measured by maximum lifespan in captivity) on brain weight and body weight of 239 mammalian species of 12 orders and used these to predict maximum lifespans of cetaceans. He found that for many odontocetes predicted longevity is similar to that deduced from dentinal growth layer counts. Surprisingly, based on theoretical considerations of his multiple linear regression equations, he predicted that odontocetes weighing more than 100 kg should have a constant lifespan, and he suggested that available evidence supports this conclusion (see his Table 1). Using Sacher's (1980) equation no. 1, I calculated that the predicted longevity of the narwhal is 52 yr, which is only slightly greater than the values for longevity in Table 17.

In conclusion, the narwhal seems to be a typical medium-sized, relatively long-lived odontocete with respect to most aspects of its life history. Its characteristics most closely resemble those of species belonging to the delphinid subfamily Orcininae (Sergeant 1982). It has a highly complex social structure (Silverman 1979) which is necessary to the function and maintenance of its life style, which in turn interacts with and shapes the social structure. Figure

46 shows the female narwhal's reproductive cycle graphically. Gestation lasts approximately 15 months and lactation exceeds one year, probably close to 2 years, resulting in a usual 3 year reproductive cycle, a condition which occurs also in its very close relative, the white whale (Brodie 1971; Sergeant 1973). Calving may occasionally occur once every 2 years, a situation which also prevails in the white whale (Sergeant 1973). The complex social structure is manifested not only by the extended parental care of young and the close group (possibly kin) cooperation, but also by the polygynous breeding system, the evidence for which is indirect. Evidence for polygyny in the large sexually-dimorphic sperm whale is conclusive (Best 1979).

Density-dependent effects on reproduction or natural mortality have not been well-documented in odontocete whales. The need for extended parental care (and thus a long lactation period) would appear to preclude a significant shortening of the calving interval in most species. However, the striped dolphin (<u>Stenella coeruleoalba</u>) off the Pacific coast of Japan has a lactation period of only about 4 months compared to about 24 months in the spotted dolphin (<u>Stenella attenuata</u>); this difference is attributed to the heavy exploitation imposed on the striped dolphin since 1955 (Kasusya 1976). Sergeant (1982) has reviewed several other examples of density-dependent reproductive responses to exploitation in odontocetes, and he concludes that the response (only observed in Delphininae) has always been a shortening of the lactation period (and therefore a reduction of the calving interval and increase in pregnancy rate). A decrease in age at sexual maturity in response to exploitation, which is well documented for the baleen whales (Lockyer 1972), has not yet been observed in any odontocete species (Sergeant 1982). Sergeant speculates that the mechanism for a decrease in the duration of lactation is ovulation during lactation by better-nourished females of an exploited population.

Juvenile mortality in an exploited population may remain at a low level, for early-weaned calves may stay within the mature female

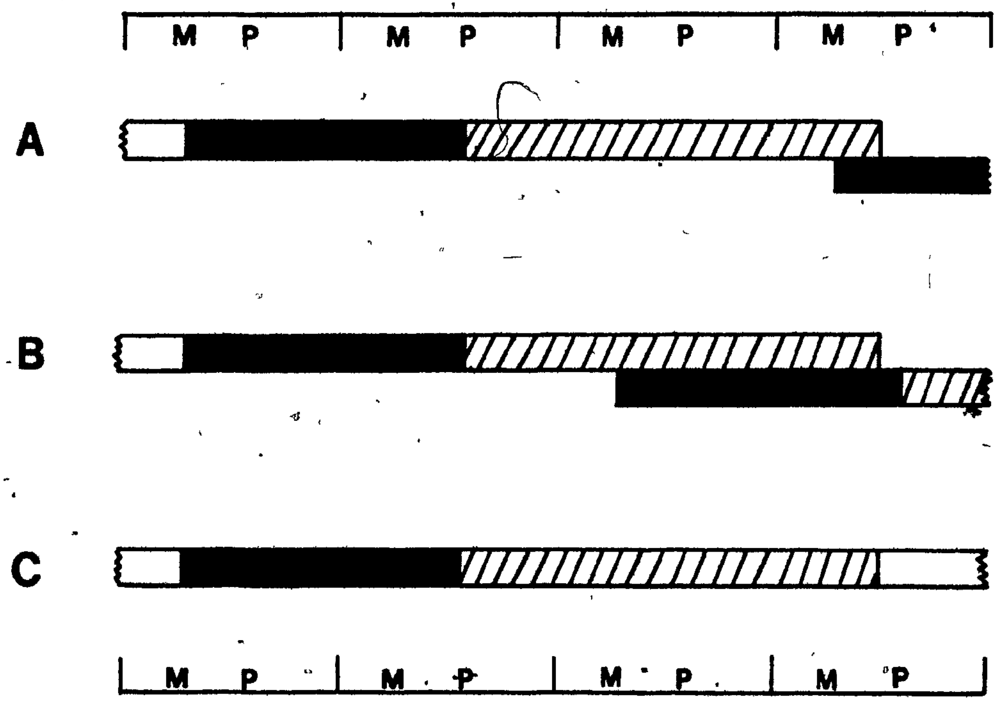

Figure 46. Reproductive cycle of the female narwhal. A-typical 3-year cycle; B- mid-lactation conception produces a 2-year cycle; C- failure to conceive at the regular breeding season extends the cycle to 4 or more years. Solid bar indicates gestation; hatched bar indicates lactation; open bar indicates "resting" condition. Scales at the top and bottom represent calendar years, and mating (M) and parturition (P) seasons are indicated.

The cycles depicted here are initiated by primiparous females. For the typical cycle A, the degree of overlap of lactation and subsequent pregnancy is not certain but it is probably slight.

schools for some time after weaning. In addition, the duration of lactation may not be too critical to calf survival, since the latter part of the normally-protracted lactation period consists of infrequent nursing periods and increasingly frequent foraging episodes by the developing calf (Sergeant 1982).

Sergeant (1982) concludes that the Delphininae demonstrate a density-dependence of reproductive rate, while the highly social Orcininae show density-dependence of natural mortality rate (through mass strandings). For the highly social species which normally have a very low rate of natural mortality, mass strandings represent most of the total mortality and comprise the main mechanism by which their populations are limited (Sergeant 1982).

Mass strandings of narwhals and white whales are unknown, and population regulation mechanisms for these species have not been investigated. If populations of narwhals and white whales are not being controlled or stressed by hunting, is it possible that ice entrapments (or "savssats") are analogous to mass strandings and constitute a density-dependent form of natural mortality?

SUMMARY AND CONCLUSIONS

1. This study has described the life history of the population of narwhals which annually summer in the fiords of northern Baffin Island and which are hunted by the Inuit residents of this area. A total of 194 narwhals was examined, both from a net fishery during 1963-65 (62 animals) and from a hunted sample during 1974-76 (132 animals).

2. An account of the general biology of the narwhal is given, emphasizing earlier studies of morphology, anatomy, distribution, migrations, feeding habits, behaviour, predators, and parasites.

3. Narwhals feed intensively during July in inshore areas where the fast ice is breaking up. Important food items are arctic cod _Boreogadus saida_, the shrimp _Pasiphaea tarda_, and squid _Gonatus fabricii_. During August and September (when little ice is present) almost all examined stomachs were empty.

4. On the basis of an examination of the composition of the summer catch of narwhals, it is concluded that this population consists of groups of pubertal or immature males, groups of sexually mature females with their calves, and small groups of large adult males. There is a significant bias towards the capture of females with calves and young males, suggesting either that these age/sex classes are more susceptible to capture or that they occupy coastal waters while large males remain further offshore. Regional segregation of the summering population by sex and maturity also exists. For example, females with newborn calves frequent the innermost fiords (e.g. - Koluktoo Bay) while early-pregnant females occur at the floe edge during July and at the outer coasts during August.

5. Age determination was investigated by examining growth layers in the dentine and mandible. The postnatal dentine of the embedded tooth of the narwhal consists of a succession of growth layers, each

of which comprises one wide light zone and one narrow dark zone. These layers have a repeatable and consistent structure and are related to age. However, dentinal deposition ceases due to complete coverage of the root by cementum at mean ages of 16 layers in males and 13.8 layers in females. The incidence of dentinal occlusion increases markedly after the mean age of sexual maturity in both sexes. A narrow dark zone occurs adjacent to the open pulp cavity of the embedded teeth of most young whales. This zone is poorly-mineralized and is deposited during August and September when narwhals are feeding lightly.

6. The periosteal zone of the anterior portion of the mandible is laminated. Mandibular periosteal layers are deposited throughout most of an animal's life and may be used to assess the ages of animals whose embedded teeth are occluded. However, the reliability of counts of periosteal growth layers is reduced, especially in old males, by internal resportion and removal of an unknown number of early layers by osteoclastic activity at the edge of the marrow cavity. Counts of mandibular periosteal growth layers are more useful for the estimation of the ages of male than for female narwhals. This is due to the accumulation of periosteal layers throughout the life of the male, whereas a balance between deposition and resorption of growth layers is achieved in the mandibles of old females approaching physical maturity. The maximum number of mandibular periosteal growth layers is about 50 in males and 30 in females.

7. Prior to dentinal occlusion, dentinal and mandibular periosteal layers are equal in number in male narwhals, indicating that both provide a useful index of age, while in young females there are slightly more periosteal than dentinal layers.

8. The time basis of the growth layers is not known with certainty. Consideration of female reproductive data suggests that

one growth layer is deposited annually in the tooth and mandible of adult females.

9. In view of the difficulties involved with the age determination techniques employed in this study (dentinal occlusion, bone resorption), other techniques (including studies of periosteal layering in bones other than the mandible) should be explored. Intensive tagging of calves and other young narwhals, in conjunction with the fishery prosecuted by the Inuit, is probably the most promising approach to elucidation of age determination of the narwhal.

10. The maximum body lengths are 470 cm and 415 cm, for males and females, respectively. Males achieve physical maturity after the accumulation of about 30 growth layers and females, after about 20 growth layers. The maximum life span is estimated to be about 40-50 years.

11. The body condition (as measured by condition index = maximum girth/body length) of male narwhals declines during late August after intense feeding during July when the ice is breaking up. On the other hand, the reproductive status of mature females influences their body condition, since full-term or post-partum females and early pregnant females have a greater blubber thickness than lactating females. Immature females have greater condition indices than all but full-term/post-partum females.

12. The narwhal displays marked sexual dimorphism, as do many other odontocetes. This dimorphism is manifested by the greater size attained by the male (470 cm and 1600 kg) compared to the female (415 cm and 900 kg), and also by the greater growth rate of the male in terms of body size and the accumulation of dentine and mandibular periosteal bone. Sexual dimorphism in rate of growth becomes

evident after the age of female sexual maturity (12 composite growth layers).

13. Based on examination of the histological structure of the seminiferous and epididymal tubules, three categories of maturity of the male narwhal are distinguished. The testis of the immature male is less than 0.140 litre in volume and inactive. The testis of the maturing male is 0.140 to 0.535 litre in volume and contains both immature and mature seminiferous tubules, which are often in close proximity to each other (or in adjacent lobules). The testis of the mature male exceeds 0.535 litre in volume and consists of seminiferous tubules all of which contain spermatozoa. However, most mature seminiferous tubules were degenerating, as evidenced by the disorganized appearance of the epithelium and paucity of spermatozoa. This observation suggests that the male has an annual cycle of breeding activity, corroborated by the fact that these whales were sampled some 2 to 3 months after the breeding season.

14. Testis volume and mean diameter of the seminiferous tubules increase greatly after 390 cm body length and 15 to 16 growth layers. Puberty (onset of spermatogenic activity) occurs at an average body length of 370 cm and and 14.2 growth layers, while sexual maturity (attainment of full spermatogenic activity) occurs at a mean body length of 395 cm (84% of maximum size) and 17 growth layers. Thus there is a considerable lapse of time between the onset of spermatogenic activity and the attainment of full fertility. Assuming that the narwhal is polygynous, social maturity (acquisition of a harem) may only be attained after a further lapse of time, as in the sperm whale.

15. Based on analogy with other odontocetes (especially the sperm whale for which there is much evidence), the mature male narwhal is probably polygynous, securing and defending a harem during the breeding season. Indirect evidence includes: sexual dimorphism in

size, growth rate, and presence of a tusk; delayed sexual maturity in the male resulting in a relative excess of mature females; the occurrence of scars on the head and flanks of some large males, believed to be made by the tusk during aggressive encounters between males in the breeding season; and the segregation of adult males from females outside the breeding season.

16. The gestation period is estimated to be 15.3 months, with mating in March-May and calving during July and August.

17. The various ovarian bodies are described both macroscopically and microscopically, and these are related to the different reproductive activities of females. Criteria for recognizing corpora lutea and the different stages of their regression products, the corpora albicantia, were established.

18. It was found that all reproductive stages of mature females, except those in late-pregnancy or recently-parturient, displayed ovulatory activity at the latest breeding season prior to capture. Infertile (unsuccessful) ovulations occurred in 34% of mature females at the latest oestrous. Mature females in any stage of the reproductive cycle may undergo prooestrous follicular activity during the breeding season, but only females which are pregnant at this time are incapable of ovulation. It is believed that mid-summer ovulations do not normally occur.

19. Accessory corpora lutea rarely occur in the narwhal; four of 30 early-pregnancy females and one of 13 late-pregnancy or post-partum females had accessory corpora.

20. The left ovary matures earlier, accumulates more corpora albicantia, but is not significantly more fertile (with a greater chance of a fertile ovulation) than the right ovary. The probability

that two successive ovulations will occur in the same ovary is about 0.75.

21. It is believed that the majority of corpora lutea persist as detectable scars in the ovaries throughout life, but a small, though unknown, number may regress to become invisible scars or fail to be detected by examination of 3 mm-thick ovarian sections. The time required for complete regression of the corpus luteum is calculated to be about two years.

22. Females become sexually mature at an average length and age of 340 cm (82% of asymptotic size) and 11.8 dentinal growth layers, respectively.

23. It was calculated that ovarian corpora lutea accumulate at a rate of 0.76/growth layer, but this value could be an overestimate since mandibular periosteal growth layer counts of old females are probably underestimates.

24. The narwhal is polyoestrous, as shown by the occurrence of up to four successive ovulations at the breeding season. The macroscopic criteria used to identify corpora albicantia resulting from these infertile ovulations are discussed. Analysis of the recent ovulations (fertile and infertile) of mature females of each reproductive class produces an estimate of the annual ovulation rate of 0.69. About 44% of ovulations at the latest breeding season were fertile.

25. The reproductive cycle of the mature female was examined in detail, using the reproductive data of females captured with calves as "standards" against which other females in the sample can be compared. The diameter of the largest uterine cornu and the diameter of the largest corpus albicans can be used to distinguish post-partum females from those nursing yearling or two-year-old

calves, but the thickness of the mammary gland was similar in all lactating females.

26. Evidence for the occurrence of fertile ovulations in females at the first breeding season following birth of their calves is presented. It was calculated that about 20% of females ovulate successfully at this time.

27. Very old female narwhals, with more than 14 ovarian corpora and 25 mandibular periosteal growth layers, show a marked reduction in fertility; although some of these females had ovulated at the latest oestrous, none were impregnated. Young, newly-mature females are slightly less fertile than older females.

28. Estimates of life history parameters may be biased to an unknown extent because of segregation of narwhals by sex and maturity, on both a large-scale (regional) and small-scale (group by group) basis. This bias may be minimized by using the total sample which is spread over all localities and group types. Taking into account the fertile ovulations of females nursing yearling calves, the pregnancy rate is estimated to be 0.36. The crude birth rate is estimated to be about 0.07. This value is considerably lower than estimates of the birth rate of some other species of odontocete which might be expected to have a birth rate similar to that of the narwhal. These other estimates of productivity have been based on possibly-biased samples of the mature female population and/or aerial surveys, and caution regarding their use is emphasized.

29. Lactation is estimated to last at least one year but usually less than two years. Based on the relative numbers of lactating and pregnant females in the sample and the duration of gestation, the lactation period is calculated to be 14.5 months. The resting period is similarly calculated as 4.5 months, and the interval between births (calving interval) is calculated to be 34.3 months

(2.86 yr). The average calving interval would be slightly lower (2.8 yr) if the fertile ovulations of females nursing yearling calves were taken into account.

30. The life history of the narwhal is similar to those of many other medium-sized odontocetes, especially its close relative the white whale (the only other member of the Monodontidae).

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PLATES I - VII

PLATE I

Plate I. External appearance of the narwhal.

a) Neonatal male, 160 cm, captured at Kaunak on August 29, 1975.
b) Suckling female, 241 cm, two dentinal layers, captured at Kaunak on August 4, 1975.
c) Immature male, 336 cm, 12 dentinal layers, tusk not erupted, captured at Kaunak on August 4, 1975.
d) Maturing male, 372 cm, 13 mandibular periosteal layers, two tusks erupted, captured at Pond Inlet floe edge on July 19, 1976 (photo by H. Silverman).
e) Adult female, 376 cm, 14 dentinal layers, captured at Kaunak on August 20, 1975.
f) Adult male, 452 cm, 20 dentinal layers (occluded), captured at Kaunak on August 28, 1974.

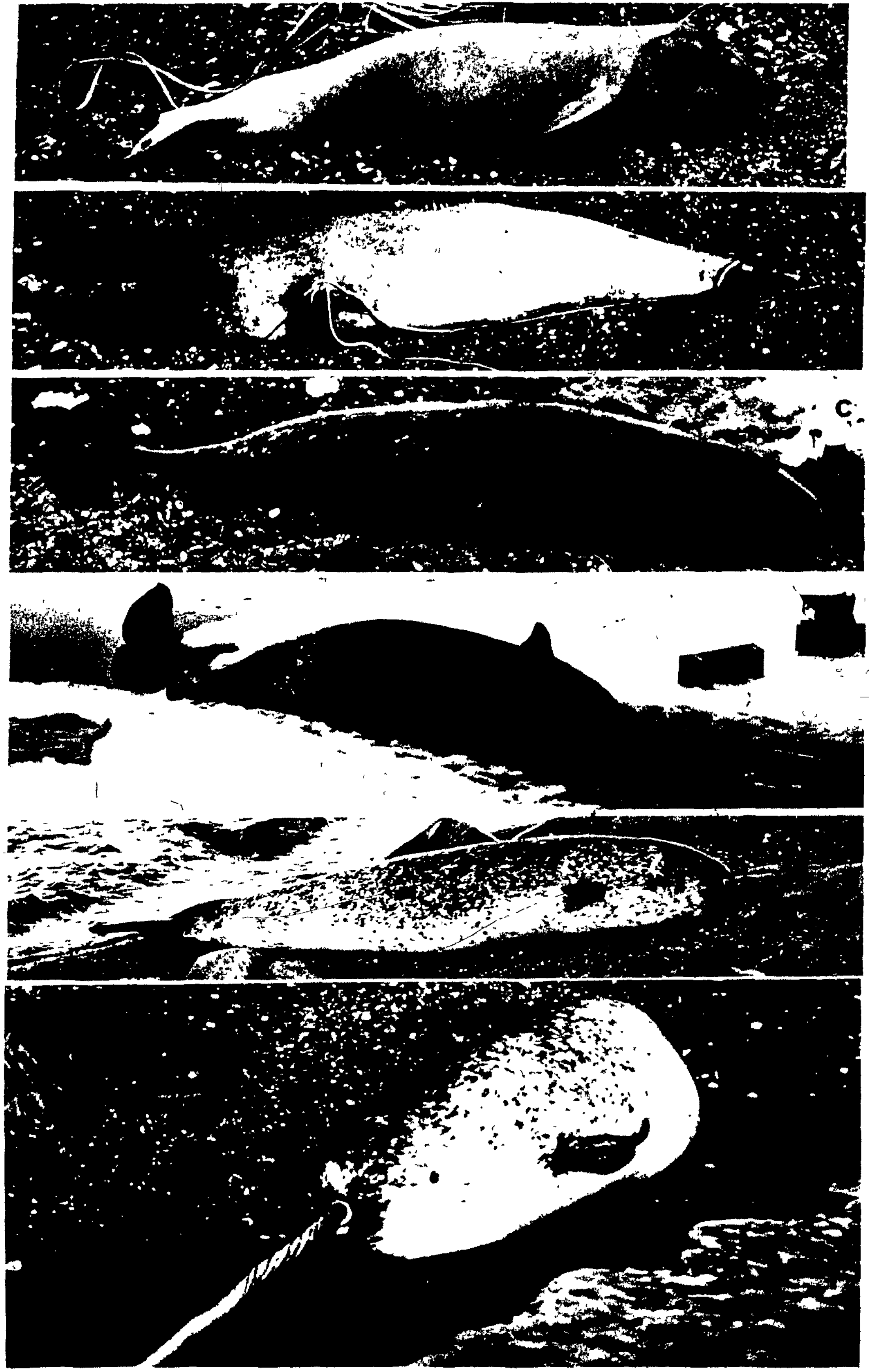

C

PLATE II

Plate II. Polished surface of longitudinally-bisected embedded teeth of the narwhal.

a) Tooth of neonatal male, 160 cm, no postnatal dentinal layers.

b) Left tooth of female calf, 230 cm, four growth layers. A narrow dark band can be seen adjacent to the pulp cavity.

c) Proximal portion of right tooth of a young male, 324 cm, 12 growth layers.

d) Root of right tooth of a maturing male, 393 cm, with 17 growth layers.

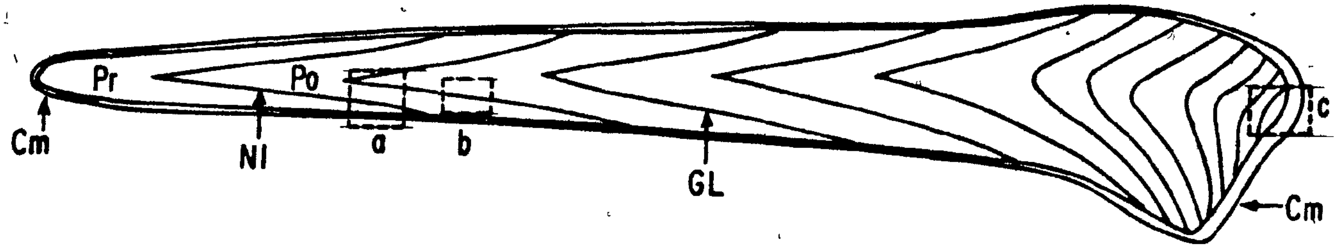
e) Distal portion of right tooth of a maturing male, 443 cm, with 16 growth layers. Dentinal deposition had ceased, and 30 growth layers were present in the mandible.

f) Root portion of right tooth of same animal as in (e) above.

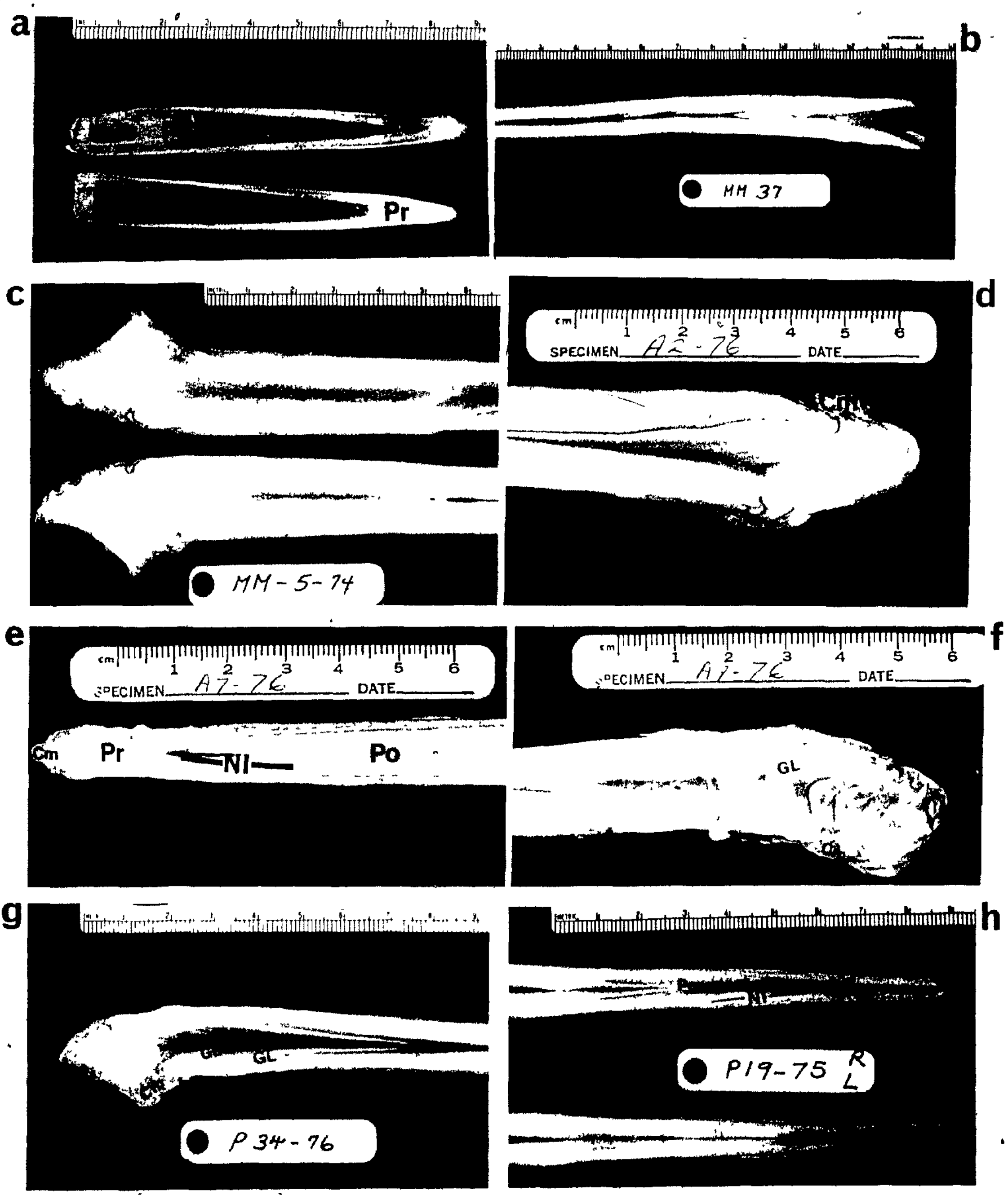
g) Root of right tooth of a mature female, 385 cm, 14 growth layers (occluded), 19 mandibular periosteal layers.

h) Distal portions of the teeth of an immature male, 262 cm, two growth layers.

Schematic representation of an occluded, longitudinally-bisected embedded tooth:



The approximate locations of the thin sections in Plate III (a,b,c) are shown. Tooth structures are represented by the following abbreviations: Cm-cementum; Pr-prenatal dentine; Nl-neonatal line; Po-postnatal dentine; GL-growth layer boundary (used for counting); PC-pulp cavity. The growth layer boundary (GL) is the same structure referred to as "narrow dark band" in the text.


a
Pr
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c
MM-5-74
d
cm 1 2 3 4 5 6
SPECIMEN A2-76 DATE
Cm
e
cm 1 2 3 4 5 6
SPECIMEN A7-76 DATE
Cm
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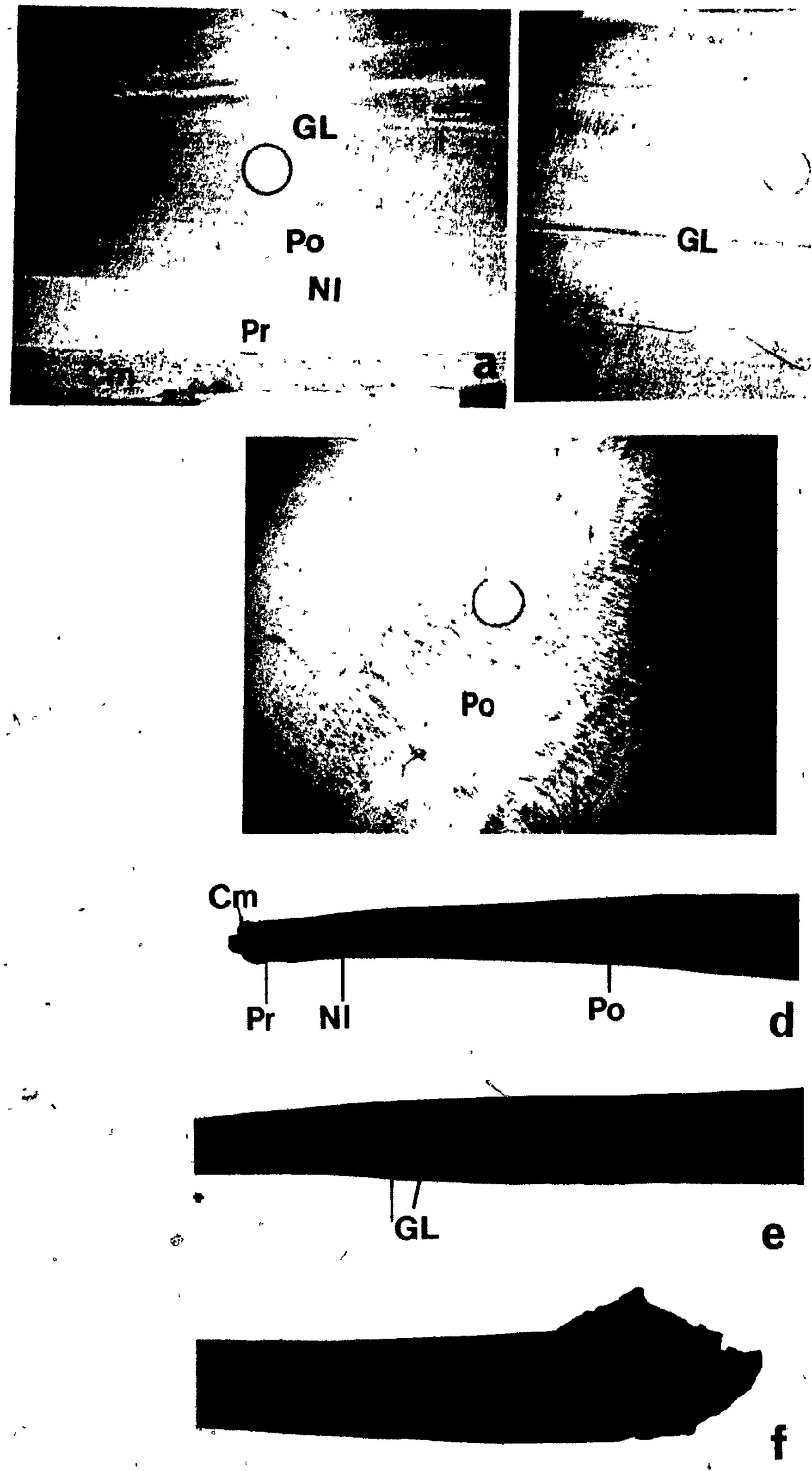
SPECIMEN A7-76 DATE
GL
g
GL
P34-76
h
P19-75
R
L

PLATE III

Plate III. Thin sagittal sections of embedded teeth and silver nitrate-stained bisected embedded teeth.

a) Thin section of anterior portion of tooth. Note translucent neonatal line and optical difference between pre- and post-natal dentine.
b) Thin section of middle portion of tooth. Note optically dense narrow dark band bounded by thin translucent zones.
c) Thin section of root. Note cementum occluding root at the right.
d) Distal portion of silver nitrate-stained tooth. The neonatal line is unstained. (MM-5-74, male, 324 cm, 12 dentinal layers).
e) Middle portion of silver nitrate-stained tooth. The narrow dark bands are weakly stained. (MM-5-74, male, 324 cm, 12 dentinal layers).
f) Proximal portion of silver nitrate-stained tooth. (MM-5-74, male, 324 cm, 12 dentinal layers).

See the legend of Plate II for locations of thin sections (a, b, and c) and for meanings of abbreviations.


GL
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Nl
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Cm
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GL
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Cm
Pr
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e
f

PLATE IV

Plate IV. Thin transverse sections of the ventro-labial portion of the anterior part of the mandible.

a) Location of section cut from the mandible (at arrows) and block of bioplastic containing four mandibular sections.
b) Neonatal male, 160 cm, no postnatal mandibular growth layers.
c) Suckling male, 230 cm, three mandibular layers. Note prominent neonatal line.
d) Maturing male, 381 cm, 14 mandibular layers.
e) Adult female, 382 cm, 12 to 13 mandibular layers.
f) Adult male, 440 cm, 35 mandibular layers. Note internal resorption.

Mandibular structures are represented by the following abbreviations: Nl-neonatal line; MC-mandibular canal; Pr-prenatal bone; Po-postnatal bone; VL-ventro-labial surface; ML-mid-labial surface.

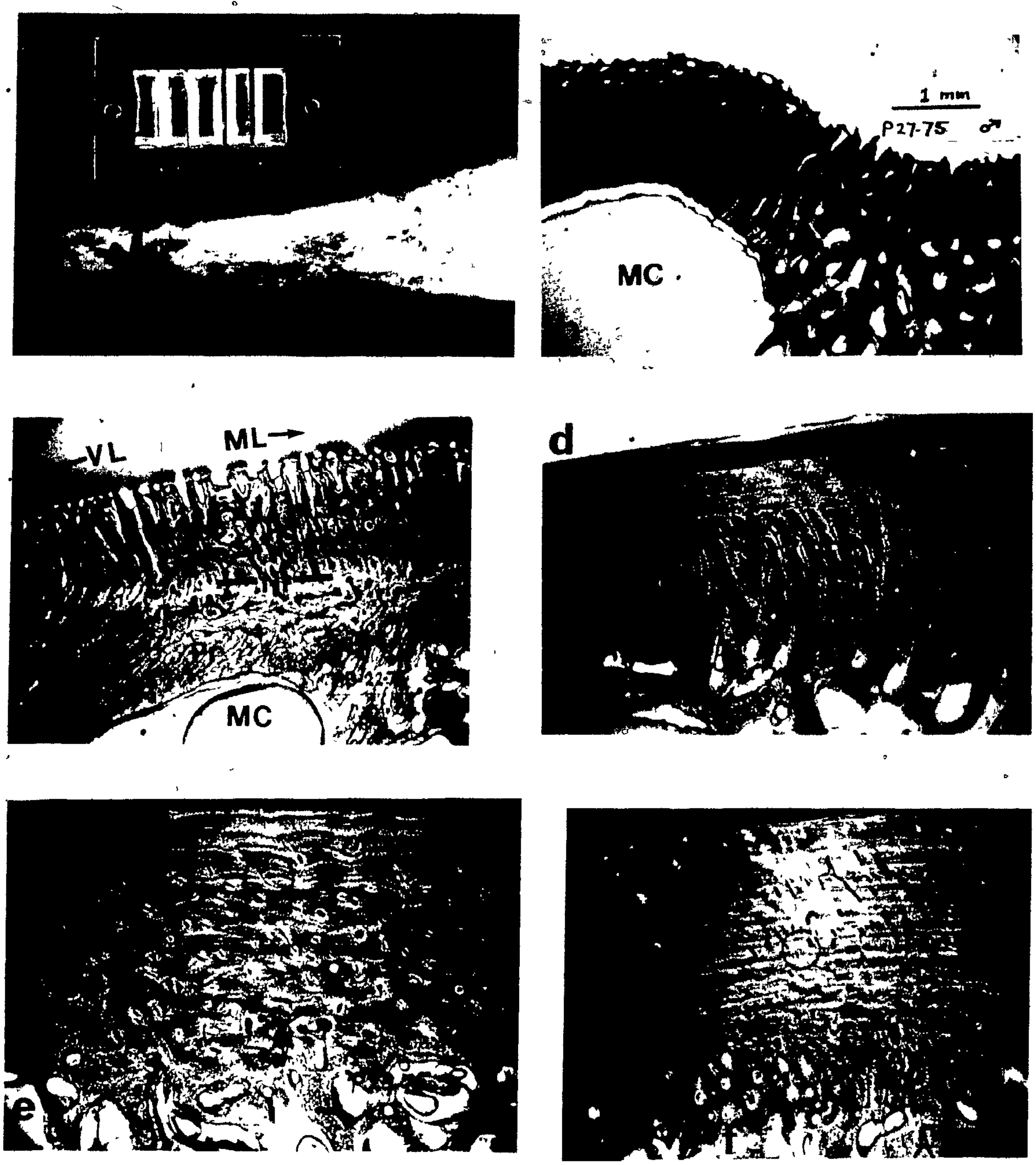

1 mm
P27-75 ♂
MC
VL
ML→
MC
d
e
f

PLATE V

Plate V. Sections of testis and epididymis of immature, maturing, and mature male narwhals. Bars represent 50 μ. Tissues were stained with haematoxylin and eosin.

a) Seminiferous tubules of immature narwhal, 390 cm, 15.5 composite layers. Primary spermatocytes are present.
b) Epididymal tubule of immature narwhal, 340 cm, 13 composite layers. Note the high columnar epithelium and stereocilia.
c) Seminiferous tubules of maturing narwhal, 381 cm, 14 composite layers. Lumina are appearing in some tubules.
d) Epididymal tubule of maturing narwhal, 427 cm, no age available. Note abundant cellular detritus and a few spermatozoa in the lumen.
e) Seminiferous tubule of same male as in (d). Spermatozoa are present, but the epithelium is degenerating.
f) Seminiferous epithelium of mature narwhal, 451 cm, 27.5 composite layers. Spermatozoa are present but the epithelium is degenerating.
g) Epididymal epithelium of same male as in (f). The lumen contains much cellular detritus.

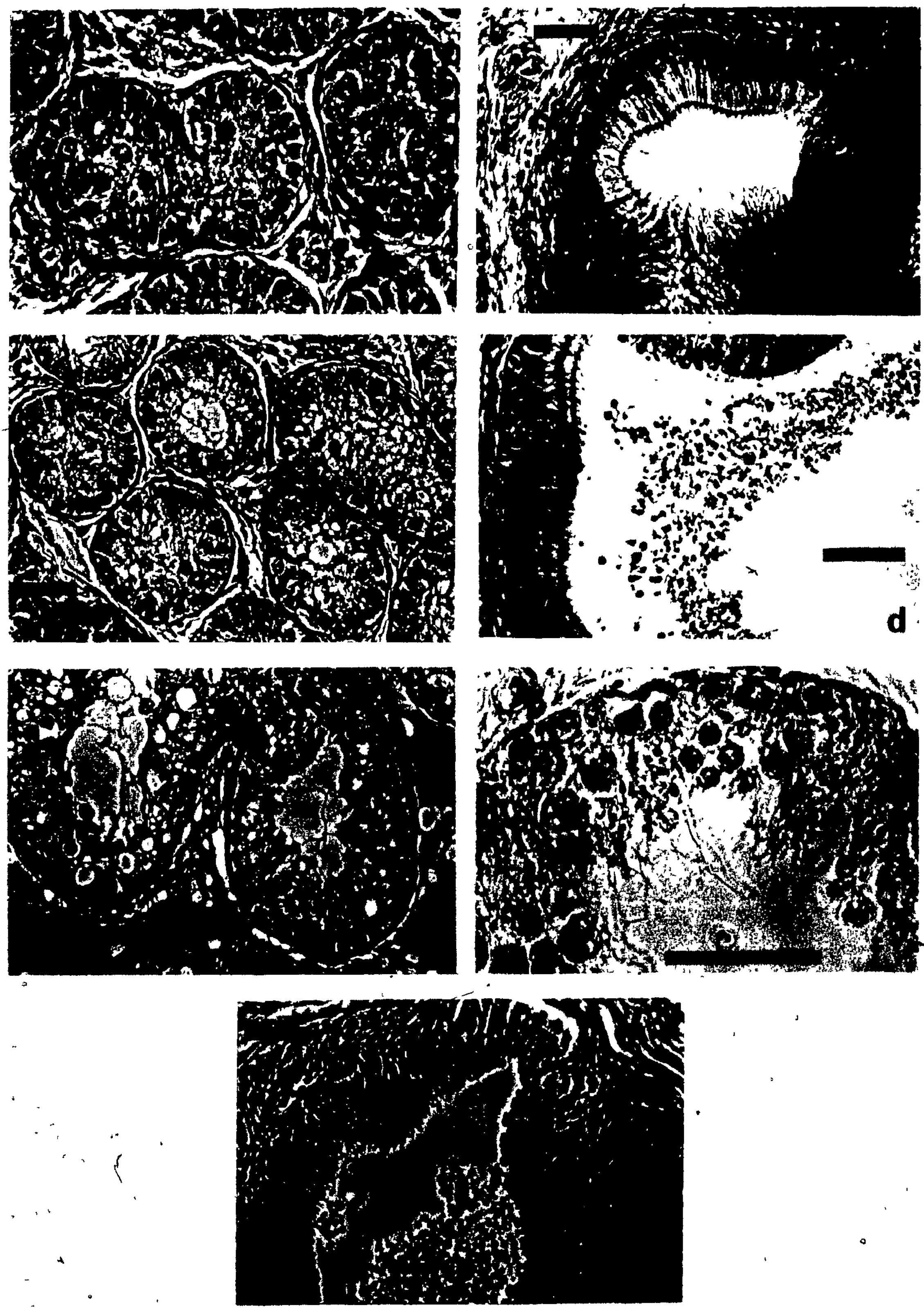

d

PLATE VI

Plate VI. Gross structure of ovarian corpora from female narwhals.

a) Corpus luteum of pregnancy, 40 x 29 mm, and two luteinized follicles (accessory corpora lutea) of 5 and 15 mm, in the right ovary of a primiparous female in early pregnancy (374 cm, 13.5 composite growth layers).

b) Young (early regression) corpus albicans (21.7 mm) in the left ovary of a primiparous post-partum female (345 cm, 12.5 composite growth layers). Note the small amount of fibrous tissue within this corpus.

c) Old corpus albicans (9.3 mm) in the left ovary of a primiparous lactating female (381 cm, 19 composite growth layers). A large core of fibrous tissue is present. Note the clotted blood adjacent to the core.

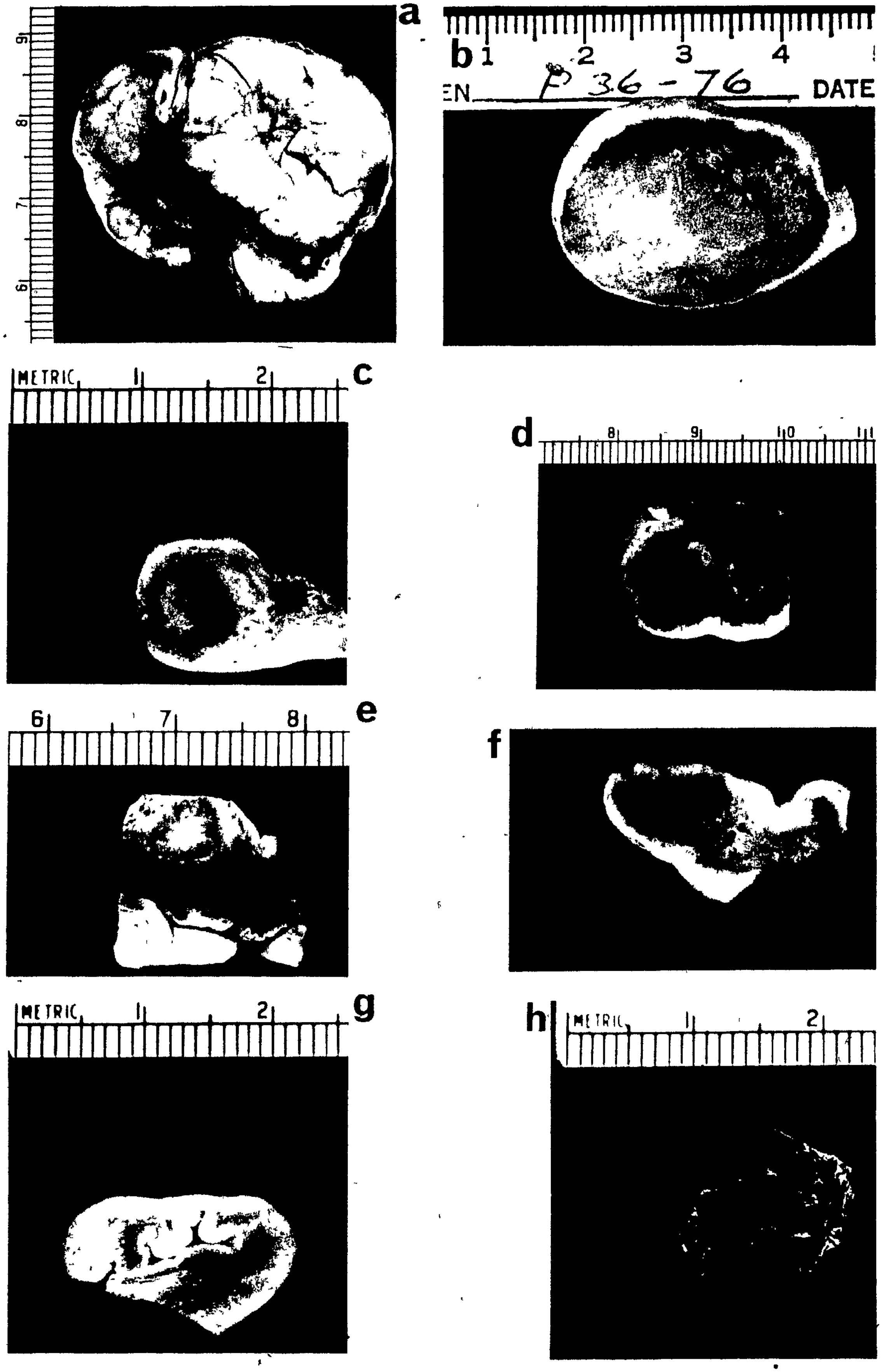
d) Young corpus albicans (12.8 mm) derived from an unsuccessful ovulation at the most recent breeding season. A 10.9 mm gel-filled follicle is also present. Both are in the right ovary of a female in early pregnancy (401 cm, 21 composite growth layers).

e) Regressing luteinized follicle (6.7 mm) in the right ovary of the same female as in (d). Note the fibrous core.

f) Possible newly-erupted follicle (15.9 mm) in the right ovary of a female, in early pregnancy and lactating (388 cm, 22 composite growth layers). The follicle is blood-filled, and a 2.6 mm haemorrhagic follicle is present. The bar represents 10 mm.

g) A corpus atreticum (9.0 mm) in the right ovary of a post-partum female (380 cm, age not available).

h) A corpus incognitum (8 mm) in the left ovary of a lactating female (380 cm, 18 composite growth layers). The tissue had partially dried prior to photography.


a
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8
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PLATE VII

Plate VII. Histological structure of ovarian corpora from female narwhals. Tissues were stained with haematoxylin and eosin.

a) Granulosa lutein tissue in the corpus luteum (35.6 x 29.3 mm) of the right ovary of a female in early pregnancy and lactating (372 cm, 20 composite growth layers). Note the blood vessels within the fibrous septa of the corpus luteum. Bar represents 50 μ.

b) Granulosa lutein cells in the corpus luteum of the same female as in (a). Note the frothy appearance of the cytoplasm and the granular nucleoplasm. Bar represents 25 μ.

c) Regressing young corpus albicans of same female as in Plate VI, b. Note the prominence of hyaline connective tissue and a few degenerating granulosa lutein cells. Bar represents 25 μ.

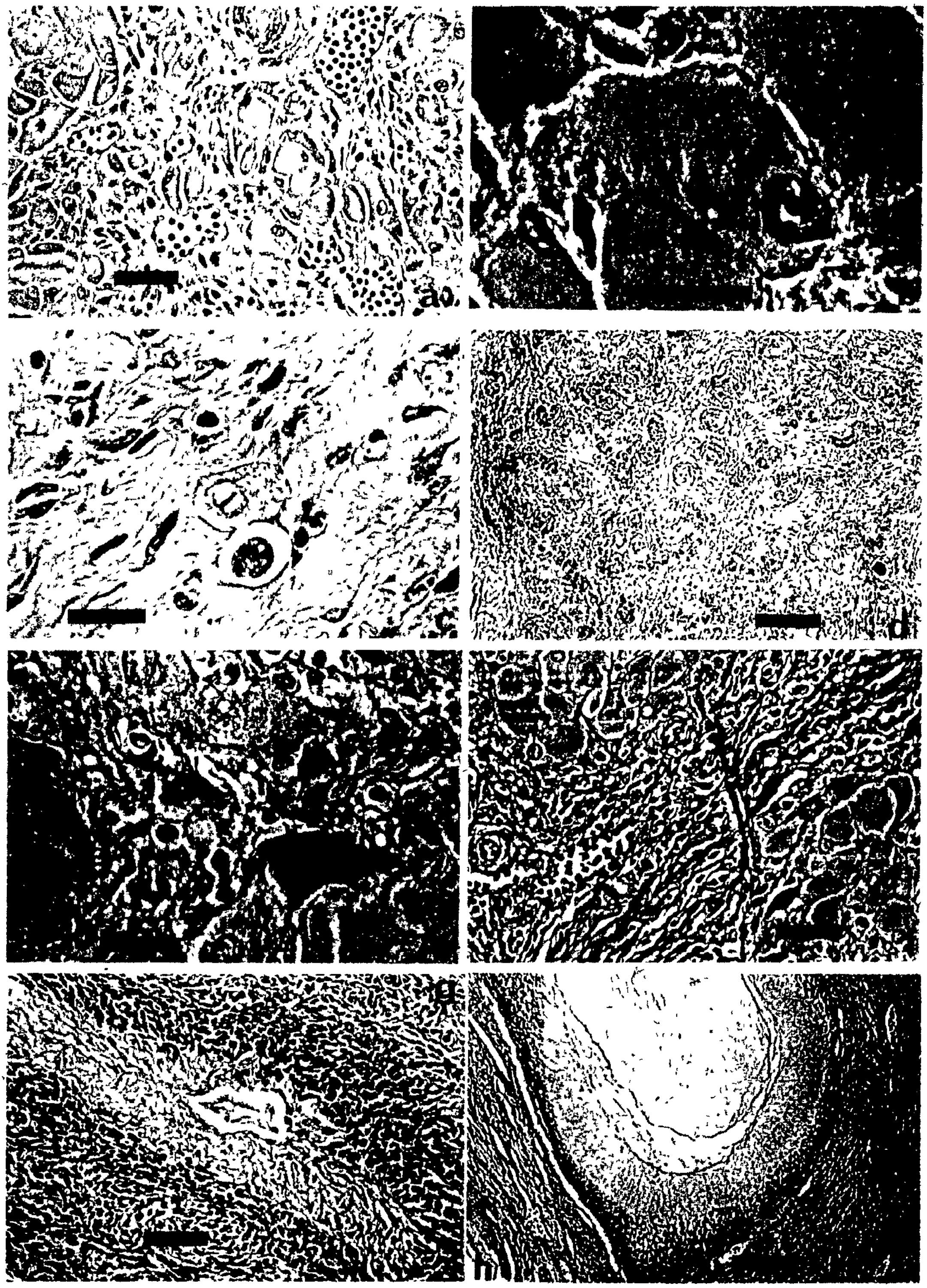
d) Old corpus albicans of same female as in Plate VI, c. Note the abundance of small thick-walled blood vessels and the coagulated blood (with pigment granules) near the collagenous core. Bar represents 200 μ.

e) Accessory corpus luteum (15 mm) in very early regression, in the right ovary of a primiparous, early pregnancy female (374 cm, 13.5 composite growth layers). A degenerating granulosa lutein cell is present in the otherwise normal tissue. Note its pyknotic nucleus and acidophilic cytoplasm. Bar represents 25 μ.

f) Same accessory corpus luteum as in (e). Note the enlarged fibrous septum within the luteal tissue. Bar represents 50 μ.

g) Small atretic follicle in the cortex of the left ovary of a female in early pregnancy (380 cm, 18 composite growth layers). The theca interna has hypertrophied (dark staining cells) and collagen has obliterated the follicular cavity. A degenerate zona pellucida is evident in the cavity. Bar represents 50 μ.

h) Portion of large atretic follicle in the cortex of the right ovary of a primiparous lactating female (381 cm, 19 composite growth layers). The granulosa layer has degenerated and the theca interna has hypertrophied. Fibroblasts are invading the follicular cavity. Bar represents 200 μ.


a
c
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h

APPENDIX 1

International Conference on Determining Age of Odontocete Cetaceans, La Jolla, California, September 5-19, 1978

With the support of the International Whaling Commission, I attended the International Conference on Determining Age of Odontocete Cetaceans, held in La Jolla, California, from September 5-19, 1978. This conference consisted of a three-day symposium (September 5-7) and a ten-day workshop (September 8-19). I presented a paper on age determination of the narwhal and I also participated in the workshop.

The workshop consisted of six sessions, each of which considered a major taxonomic group of odontocetes. I participated in sessions 3 (Monodontidae) and 4 (large Delphinidae). For session 3 which considered the narwhal and white whale, I provided several longitudinally-bisected embedded teeth and thin mandibular sections of the narwhal, and Dr. E.D. Mitchell and Mr. B. Kemper provided the embedded teeth, erupted tusks, and tympanic bullae and periotic bones of two male and two female narwhals.

The counts by several observers of the number of dentinal growth layers seen on the polished cut surfaces of three longitudinally-bisected embedded teeth were as follows:

			No. dentinal growth layers	
Specimen No.	Length (cm)	Sex	Original count[a]	Counts of other participants
MM-74-5	324	M	12	10.5 10.5 11 12 13 13 14
MM-P21-76	329	M	9.5	7 7 10 10.5 12 12
MM-P30-76	451	M	17[b]	14 15 16 17 19
MM-59	265	F	6	1.5 6

[a] by the author

[b] tooth occluded

These results show that there is fairly good agreement among the different observers, but much of the variation could be due to the presence of ill-defined accessory zones in the earliest-formed growth layers. Some problems were also experienced in accurately counting the very narrow growth layers in the proximal portion of the root of the tooth.

The polished cut surfaces of several longitudinally-bisected embedded teeth were exposed to 10% formic acid for 40 hours, washed in running water for two hours, and then dried. This treatment creates a pattern of alternating wide shallow grooves and narrow prominent ridges on the cut surface of the bisected tooth. The neonatal line appears as a narrow inconspicuous ridge while the narrow dark bands of the postnatal dentinal growth layers appear as prominent ridges. The accessory zones which are seen in the earliest-formed postnatal growth layers appear as ridges which are not nearly as prominent as those representing the main growth layers. The narrow growth layers in the root of the tooth are clearly differentiated by acid etching. Growth layers are better-defined on acid-etched than on un-etched bisected teeth.

The counts of the number of ridges seen on acid-etched bisected embedded teeth were as follows:

			No. dentinal growth layers					
Specimen No.	Length (cm)	Sex	Original count[a]	Counts of other participants				
MM-28	178	F	0	0	-	0	0	0
MM-37	230	F	4	3	4	4	2.5	3.5
MM-P10-75	284	F	7	6	4	5	4.5	3.5
MM-43	312	F	11	9	8	8	7	10
MM-P7-75	326	F	9.5	11	12	12	9.5	9.5
MM-62	388	F	13[b]	10	15	14	10	13
MM-P19-75	262	M	2	2	1	1	1	1.5
MM-P23-75	287	M	7	7	6.5	8	6	6.5
MM-74-5	324	M	12	12	-	12	9	-
MM-P15-76	381	M	14	11	12.5	12	10	11
MM-A2-76	393	M	17[b]	15	19	16	13	14
MM-67	442	M	15[b]	13	12	12	10	12.5

[a] by the author on un-etched tooth

[b] tooth occluded

Examination of this table reveals that the counts of the different participants are generally in reasonable agreement and similar to the original count which was made on the polished, cut surface of the bisected tooth. In a few cases, however, the variability among observers is quite large, owing to the presence of accessory zones in the earliest growth layers, and the original count is somewhat higher than the counts using acid-etched teeth.

In addition to the small embedded teeth, two large erupted tusks were examined. These tusks were longitudinally quarter-sectioned and the cut surfaces were polished with no. 400 waterproof sandpaper. A solution of 30% phosphoric acid was applied to the cut surface of one tusk and 10% hydrochloric acid was applied to the cut surface of the other, for a period of one hour. The surfaces were then washed with water for two minutes, air-dried for eight hours, and rubbed with a wide carpenter's pencil of medium hardness in order to highlight the ridges. Phosphoric acid proved to be better than hydrochloric acid in distinguishing between the main growth layers and the accessory zones. The two erupted tusks contained 40 and 29 dentinal growth layers, while the corresponding embedded teeth contained 14.4 and 9.9 dentinal layers, on average, respectively. A neonatal line could not be seen in these erupted tusks, suggesting that there is a significant amount of wear at the tip. Growth layer group counts by several observers for the embedded teeth of these two males and for both embedded teeth of each of two females are provided in the workshop proceedings (Perrin and Myrick 1980).

The group recognized the limited usefulness of the embedded tooth for determining age of the narwhal, owing to dentinal occlusion during early postnatal life, and they also recognized the difficulty of assessing occlusion in the extracted embedded tooth. Scanning electron and light microscopy studies of the tip and root of apparently occluded teeth will be carried out in order to assess the occurrence of cemental growth layers in the tooth and to ascertain the true (microstructural) nature of dentinal occlusion.

The group further recommended that: "Field collectors of unerupted tusks should assess the degree of closure by examining the root end of these teeth and noting the presence or absence of in situ pulp".

The proceedings of the symposium and workshop are now published (Perrin and Myrick 1980).

Reference

Perrin, W.F., and A.C. Myrick, Jr. (ed.) 1980. Growth of odontocetes and sirenians: problems in age determination. Rep. Int. Whaling Comm. (Special Issue 3), 229 p.

APPENDIX 2

Catch Composition of Narwhals Used in this Study, by Year, Area, Method of Capture, and Maturity (Stage of Reproduction)

Appendix Table 1. Composition of the catch of male narwhals used in this study, by year, area, method of capture, and maturity.

		Method	Number of males[a]				
Year	Area	of capture	Immature[b]	Maturing	Mature	Unknown	Total
1963	Mt. Herodier	hunt	-	-	1	-	1
1963	Koluktoo Bay	net	7	3	1	-	11
1964	Koluktoo Bay	net	4(2)	1	1	-	6
1965	Koluktoo Bay	net	2	2	5	-	9
1974	Kaunak	hunt	6	-	1	1	8
1975	Admiralty Inlet	hunt	2	-	3	4	9
1975	Pond Inlet (town)	hunt	1	1	2	-	4
1975	Kaunak	hunt	8(1)	1	3	2	14
1975	Milne Inlet	hunt	1	1	-	-	2
1976	Guys Bight (floe edge)	hunt	6	4	2	-	12
1976	Kaunak	hunt	1	-	-	-	1
1976	Admiralty Inlet	hunt	-	3	-	-	3
Totals			38(3)	16	19	7	80

[a] These categories of male sexual maturity are defined in the section "Reproduction in the Male".

[b] Calves accompanied by mature females in parentheses.

Appendix Table 2. Composition of the catch of female narwhals used in this study, by year, area, method of capture, and stage of reproduction.

Year	Area	Method of Capture	Number of females[a]								
			Immature[b]	Maturing	Early-pregnant	Lactating	Early-pregnant and lactating	Full-term or post-partum	Nulliparous	Total Mature	Total
1963	Mt. Herodier	hunt	-	-	-	-	-	-	1	1	1
1963	Milne Inlet	hunt	-	-	-	1	-	-	-	1	1
1963	Koluktoo Bay	net	5(3)	1	-	1	-	5	1	7	13
1964	Koluktoo Bay	net	6(2)	-	-	3	-	3	-	6	12
1965	Koluktoo Bay	net	2(1)	-	1	2	1	2	-	6	8
1967	Cumberland Sound	net	-	-	-	-	-	-	1	1	1
1974	Kaunak	hunt	2	-	4	-	-	-	-	4	6
1975	Kaunak	hunt	3	1	3	7	-	-	3	13	17
1975	Tremblay Sound	hunt	1	-	-	-	-	-	-	-	1
1975	Milne Inlet	hunt	2	-	-	-	-	-	-	-	2
1975	Admiralty Inlet	hunt	4	-	6	1	-	2	-	9	13
1976	Guys Bight (floe edge)	hunt	3	-	10	3	3	3	5	24	27
1976	Mt. Herodier (ice)	hunt	1	-	1	1	1	-	-	3	4
1976	Kaunak	hunt	1(1)	-	-	1	-	-	-	1	2
1976	Admiralty Inlet	hunt	1	-	-	3	-	-	-	3	4
Totals			31(7)	2	25	23	5	15	11	79	112

[a] These categories of female reproduction are defined in the section "Reproduction in the Female".

[b] Calves accompanied by mature females in parentheses.

Appendix Table 3. Overall catch composition of narwhals used in this study.

Sample	Males				Females							
	Immature[a]	Maturing	Mature	Total	Immature or Maturing[a]	Early-pregnant	Lactating	Early-pregnant and lactating	Full-term/ post-partum	Resting	Total mature	Total
Open water hunt, all areas/years	19(3)	6	9	34	15(2)	13	12	0	2	3	30	45
Guys Bight floe edge plus Mt. Herodier ice crack hunts, 1976	6	4	2	12	4(1)	11	4	4	3	5	27	31
Koluktoo Bay net sample, 1963-65	13(3)	6	7	26	14(7)	1	6	1	10	1	19	33

[a] Calves in parentheses.

APPENDIX 3

Statistical Evidence for Segregation of Narwhals by Sex and Maturity (Stage of Reproduction)

A. Group Composition

The group composition data of Tables 2 and 3 suggest that summering groups of narwhals consist predominantly of animals of one sex and/or maturity class. To establish whether or not segregation into groups of like sex and/or maturity does exist within the population, the following statistical test was carried out. Suckling calves were excluded from these group data because of their close association with adult females.

The null hypothesis to be tested is that captured groups consist of animals brought together by chance (i.e. - random mixing). Segregation by sex, maturity in males, and maturity in females were examined separately, for both the netted and the hunted samples (Appendix Table 4). Binomial probabilities were calculated for each category of segregation using the total sample for each capture method (open-water hunt or nets). These probabilities are listed in column 4 of Appendix Table 4. The binomial expansion of these probabilities was then carried out, for group sizes ranging from one to the maximum number of animals in a group. For each group (Tables 2 and 3), the probability of occurrence of that group (including the one-tailed probability of a more extreme observation for the same group size), under the null hypothesis of random mixing, was determined from the appropriate binomial expansion for that group size, for sex, male maturity, and female maturity (all done separately). For each capture method and category of segregation, Fisher's method for combining independent probabilities (Sokal and Rohlf 1981) was used to evaluate the expression $-2 \sum \ln p$, where p is the probability of occurrence of each group (including the one-tailed probability of a more extreme observation). This expression is a G-value which is distributed as a chi-square with degrees of freedom equal to the number of groups.

All tests for segregation were significant at the 5% level with the exception of segregation by maturity of females captured in the nets (Appendix Table 4). Segregation by sex is significant at the 0.1% level, both for the netted and hunted samples. It is concluded that hunts and nets capture groups which are not random assemblages of animals comprising the summering population, and that segregation by sex and maturity does indeed occur. Groups are most commonly of three types: immature or maturing males, mature males, and mature females, many of which have calves (Tables 2 and 3).

The lack of significance of the test for segregation by maturity of females taken in the nets can be readily explained as follows. The six groups of females captured in nets had the following composition: 1,0; 0,1; 1,1; 0,2; 0,3; 0,4 (no. immature followed by no. mature). Few immatures were thus captured by the nets. Since the capture of an immature is much less probable than that of a mature female (Appendix Table 4), most of these events have relatively high probabilities, and the resulting G-statistic is not significant. On the other hand, immature females are relatively more numerous in the hunted sample than in nets, hence more of the hunting events will have lower probabilities of occurrence.

B. Regional Segregation

Contingency tables were used to test for overall differences in sex and maturity composition of narwhals taken in different parts of the study area by different capture methods. The data used in these contingency analyses are provided in Appendix Table 3. Suckling calves have been excluded from these analyses because of their close association with adult females.

The samples considered for these analyses were the open water hunt (all areas and years), the Guys Bight floe edge hunt of 1976, and the Koluktoo Bay net sample of 1963-65. The maturity composition of males (proportion of males immature, maturing and mature) was not significantly different among the three samples

($\chi^2 = 1.548$; 4 df; $p = 0.818$). The overall sex ratio was not significantly different between the open water hunted sample and the netted sample ($\chi^2 = 0.305$; 1 df; $0.9 > p > 0.5$). The Guys Bight floe edge sample was not used in contingency analyses of sex ratio since females were selectively sampled at the floe edge. The maturity composition of females (proportion of females immature or maturing, early-pregnant, lactating, and full-term/post-partum) was significantly different among the three samples ($\chi^2 = 22.494$; 6 df; $p = 0.001$). For this analysis, the 4 early-pregnant, lactating females taken at the floe edge were assigned equally to the early-pregnant and lactating classes, while the one early-pregnant, lactating female netted at Koluktoo Bay was assigned to the pregnant class. In particular, the netted sample from Koluktoo Bay had considerably fewer early-pregnant females and more full-term/post-partum females than would be expected on the basis of independence of variables, while the open water hunted sample and the floe edge sample had fewer full-term/ post-partum females than expected. In addition, the floe edge sample had more early-pregnant females than expected.

These results indicate that females of different reproductive status may be prevalent in different regions of the study area. In particular, full-term/post-partum females seem to prefer Koluktoo Bay (the innermost small bay of Milne Inlet; see Fig. 1) while early-pregnant females are prevalent at the floe edge during spring.

Reference

Sokal, R.R., and F.J. Rohlf. 1981. Biometry. The Principles and Practice of Statistics in Biological Research. Second Edition. W.H. Freeman and Co., San Francisco.

Appendix Table 4. Results of statistical analyses of group composition of narwhals.

Sample	Segregation by	No. of groups	Binomial probabilities[a]	G-value	Probability
Net	Sex	10	$P_{♂} = 0.47$ $P_{♀} = 0.53$	34.174	$p < 0.001$
Net	Male maturity	6	$P_I = 0.70$ $P_M = 0.30$	15.471	$0.025 > p > 0.01$
Net	Female maturity	6	$P_I = 0.27$ $P_M = 0.73$	9.047	$0.5 > p > 0.1$
Hunt	Sex	17	$P_{♂} = 0.42$ $P_{♀} = 0.58$	53.053	$p < 0.001$
Hunt	Male maturity	12	$P_I = 0.71$ $P_M = 0.29$	21.220	$0.05 > p > 0.025$
Hunt	Female maturity	13	$P_I = 0.30$ $P_M = 0.70$	29.179	$0.01 > p > 0.005$

[a] I = immature plus maturing; M = mature.