Validation of Age Estimation in the Harp Seal, *Phoca groenlandica*, Using Dentinal Annuli

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We investigated the validity and accuracy of age estimation in harp seals, *Phoca groenlandica*, using a sample of 155 known-age teeth from seals age 3 mo to 10 yr. Under transmitted light, transverse sections of harp seal canine teeth showed distinct incremental growth layers (IGLs) in the dentine. The first growth-layer group (GLG), representing 1st-year growth, consists of two IGLs: an outer layer of opaque dentine, bounded by the neonatal line, and an inner layer of translucent dentine. Subsequent GLGs, each representing 1 yr of growth, generally consist of three IGLs: an outer layer of interglobular dentine deposited during the annual molt in April, a middle layer of opaque dentine formed during the northward spring migration (May–June), and an inner layer of translucent dentine formed from July to March. We show that dentinal GLGs can be used to estimate the absolute age of harp seals. The accuracy of the method decreases with age. Only 72.4% of estimates of 0-group seals were correct using only transverse sections. These errors were virtually eliminated (99.0% correct age determination) when the tooth root was examined. Based on a single examination of a transverse section, the probabilities of correctly estimating age are 0.983, 0.889, 0.817, and 0.553 at ages 1, 2, 3, and 4+ yr, respectively, when clearly inaccurate tag-tooth associations are omitted. The respective probabilities are only slightly higher when age is based on the average of five blind readings, being 1.0, 0.889, 0.833, and 0.625. Beyond age 3 yr, existing data are insufficient to estimate reliably the accuracy of age determined by counting GLGs.

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Le présent rapport porte sur l'étude de la validité et de la précision de la méthode de détermination de l'âge des phoques du Groenland, *Phoca groenlandica*, à l'aide d'un échantillon de 155 dents prélevées de phoques âgés de 3 mois à 10 ans. L'examen de coupes transversales de canines a révélé la présence de couches distinctes de croissance (CC) dans la dentine. Le premier groupe de couches de croissance (GCC), qui représente la croissance de la première année, se compose de deux CC, soit une couche externe de dentine opaque limitée par la ligne néo-natale et une couche interne de dentine translucide. Les GCC suivants, dont chacun représente une année de croissance, se composent généralement de trois CC: une couche externe de dentine interglobulaire déposée pendant la mue annuelle, en avril, une couche mitoyenne de dentine opaque formée pendant la migration vers le nord, au printemps (mai et juin), et une couche interne de dentine translucide formée de juillet à mars. Les auteurs démontrent que les GCC peuvent être utilisés pour évaluer l'âge absolu des phoques du Groenland. La précision de la méthode diminue en fonction de l'âge. Pour le groupe d'âge 0, seulement 72,4 % des estimations au moyen des coupes transversales étaient correctes. Ces erreurs ont été presque complètement éliminées (précision s'élevant à 99,0 %) avec l'examen de la racine de la dent. Les probabilités d'estimation correcte de l'âge s'élèvent

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à 0,983, 0,889, 0,817 et 0,553 pour les âges 1, 2, 3 et 4+ respectivement quand on examine seulement une coupe transversale et qu'on omet les données clairement inexactes sur les dents et l'étiquette. Les probabilités respectives ne sont qu'un peu plus élevées quand l'âge est basé sur la moyenne de cinq lectures par un tiers, soit 1,0, 0,889, 0,833 et 0,625. Après 3 ans, les données actuelles ne permettent pas d'évaluer sûrement la précision de l'âge déterminé par le dénombrement des GCC.

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THE ability to determine accurately the age of an animal is essential to the study of population dynamics. Incremental growth of cementum, dentine, and bone has been used for age determination in many species of mammals (Klevezal and Kleinenberg 1967; Jonsgard 1969; Morris 1972; Spinage 1973; Grue and Jensen 1979; Scheffer and Myrick 1980), including over 20 species of pinnipeds (Laws 1962). The technique is based on the assumption that such tissues are deposited in a cyclic manner, producing histologically distinct and permanent layers that can be related to the actual age of an animal. As there is no resorption of calcium from teeth (Johansen 1967; Scott and Symons 1974), the structure and appearance of the dental tissues should accurately reflect the history of growth of an individual.

Incremental growth layers in the teeth of marine mammals were described or illustrated by zoologists as early as 1840 (Owen 1840–1845; Scheffer and Myrick 1980). However, it was not until about 1950 that the value of dental layers for determining the age of marine mammals was generally recognized (Scheffer 1950; Laws 1952, 1953; Nishiwaki and Yagi 1953). Laws (1962) reviewed methods of age determination in seals with special reference to dental growth layers.

Several methods have been proposed to determine the age of harp seals, *Phoca groenlandica*. Plekhanov (1933) found transverse growth ridges in the claws of harp seals which enabled him to estimate the age of animals up to 13 yr. He was working with specimens of unknown age, however, and was unable to check his conclusions. Chapskii (1952) used the number of layers in the periosteal zone of the lower jaw to estimate the age of harp seals.

The method of age determination in harp seals using dentinal annuli was first described in detail by Fisher (1954). He examined about 3000 canine teeth, half taken from seals on the southward migration in January, and the remainder from whelping and molting concentrations in March and April, respectively. Based on this material he deduced the annual pattern of dentine layering and its value in estimating age.

Although incremental dental growth layers have been widely used to determine the age of many mammals, validation of the method using known-age animals has been possible in only a limited number of species. Among pinnipeds, the teeth of a number of known-age animals have been examined in the northern fur seal, *Callorhinus ursinus* (Scheffer 1950; Anas 1970); Cape fur seal, *Arctocephalus pusillus* (Fletemeyer 1978); grey seal, *Halichoerus grypus* (Hewer 1964; A. W. Mansfield, Arctic Biological Station, Ste. Anne de Bellevue, Que., personal communication); southern elephant seal, *Mirounga leonina* (Carrick and Ingham 1962); and hooded seal, *Cystophora cristata* (Øritsland unpublished data).

Harp seals are commercially important (Sergeant 1976) and a method of accurate age determination is important in understanding the influence of the harvest on the dynamics of the population. In this study, we use a sample of 155 known-age specimens to investigate the validity and accuracy of age estimation in harp seals based on dentinal annuli.

Materials and Methods

The canine teeth of 155 known-age harp seals from 0 to 10 yr of age were studied (Table 1). All animals were tagged or branded within 2 wk of birth making it possible to determine age to the nearest month. For convenience in determining known age, a birth date of March 1 was assumed. This introduces little error, as harp seals in the White Sea give birth in late Feburary and early March, in the northwest Atlantic population a few days later, and in the Jan Mayen population in late March (Sergeant 1976). About 92% of the material comes from the northwest Atlantic population (Table 1).

Lower jaws were boiled in water for ~1 h to facilitate extraction of canine teeth. Transverse sections of teeth were cut just below the enamel cap (Fig. 1, zone A) at 200–250 μm. Sagittal sections were also prepared to illustrate the internal gross anatomy of the dentine and, in particular, to illustrate the position of the neonatal line. Ages were estimated from transverse sections only because incremental growth lines were difficult to differentiate and interpret in most sagittal sections. Teeth and thin sections were stored in a solution of equal parts of water, 70% ethanol, and glycerine.

All sections were examined with transmitted polarized light using a 6× to 50× binocular microscope. Generally, thin sections were placed in a petri dish containing a small quantity of water to prevent desiccation of the sample, as dry sections become opaque making examination difficult and unreliable. A small number of transverse sections were mounted on glass slides with Permount. In general this method of storage proved unsatisfactory, because the specimens tended to become opaque.

All measurements of dentine thickness were made with an ocular micrometer. The width of the pulp canal and total length of the tooth were measured with calipers. The standard error is given with mean values unless otherwise stated.

There is considerable variation in the terminology used to describe incremental growth layers in dentine and cementum. To avoid confusion, we have adopted the usage proposed by the International Conference on Determining Age of Odontocete Cetaceans (Perrin and Myrick 1980). Incremental growth layers (IGLs) are distinct layers parallel with the formative surface of dentine which contrast with adjacent layers based on their optical density under transmitted light. Growth

TABLE 1. Origin of known-age harp seal teeth examined.

Location marked[a]	Sex[b]	Age (yr) at recapture											Total	Area total
		0	1	2	3	4	5	6	7	8	9	10		
Northwest Atlantic														
Gulf of St. Lawrence	M		4	4	1		1	2		1		1	14	
	F		2	2		1		1					6	87
	Unk	15	23	14	5	1	6	1	1	1			67	
Front	M	4	4	1	2				1				12	
	F	6	5		2		1						14	55
	Unk	12	6	11									29	
Jan Mayen	M													
	F													9
	Unk			4	4	1							9	
White Sea	M		1	1									2	
	F		2										2	4
	Unk													
Total		37	47	37	14	3	8	4	2	2		1		155

[a]Front = northeastern Newfoundland and southern Labrador.
[b]M = male, F = female, Unk = unknown.

layer groups (GLGs) are groups of incremental growth layers which may be recognized by virtue of a cyclic repetition. Such a cyclic repetition of GLGs must involve at least one change between translucent and opaque layers.

Results

General Morphology and Anatomy of Canine Teeth

In some phocids, the milk dentition is reabsorbed in utero and the teeth which erupt after birth constitute the permanent dentition (Bertram 1940). In harp seals, the lower canine teeth erupt within 1 wk of birth and at that time consist of an enamel crown below which is found a short thin-walled cylinder of fetal dentine. The average length of the canine at birth is 15.3 ± 0.53 mm (n = 9) and the average diameter of the pulp canal (Fig. 1) is 6.6 ± 0.6 mm. As in other phocids the canine teeth of harp seals grow rapidly, reaching an average length of 26.1 ± 0.84 mm (n = 11) at about 1 yr of age and 93% of this value by 6 mo of age. The diameter of the pulp canal decreases rapidly over the first 12 mo and, except for a small opening for blood vessels and nerves, is closed by cementum in about 3 yr (Fig. 2), although the pulp cavity itself remains large.

Transverse sections of harp seal canines are oval or broadly elliptical in shape. Measurements of dentine thickness, taken along the major axis of these sections, revealed asymmetrical growth. The mean thickness of dentine was significantly greater (paired t, df 80, $P < 0.001$) along the major axis at the buccal side (991 μm; n = 123) of the section (as the tooth is positioned in jaw) than at the labial side (897 μm). In all subsequent analyses, measurements of dentine represent an average of two measurements, one taken from each side of the tooth along the major axis.

Three different types of tissues are seen in sagittal sections of harp seal canines: enamel, cementum, and dentine. Enamel is of little use in determining age as its growth ceases shortly after the tooth erupts (Scott and Symons 1974). Incremental growth layers have been described in cementum and dentine of many species and in many cases age determined from the cementum layer is considered more reliable than that based on dentine annuli, particularly for older animals. In harp seals only a thin layer of cementum is deposited throughout the life of the animal. GLGs in the cementum were observed but were generally indistinct and could not be used reliably to estimate age. Further discussion is limited, therefore, to the dentine layer.

Dentine

Transverse sections of harp seal canines, examined with transmitted light, show distinct dentinal IGLs. In 62% of known-age teeth each GLG, excepting the first, consisted of three IGLs: an outer layer of interglobular dentine which is seen to be reticulated, a middle band of dark or opaque dentine, and an inner band of light or translucent dentine (Fig. 3E). In the remainder of known-age specimens, the outer layer of interglobular dentine was absent and each GLG consisted of only two IGLs (Fig. 3G). In all teeth examined, the first GLG, representing the 1st year's growth, consisted of an outer opaque IGL and an inner translucent IGL (Fig. 3A, E). There are no differences between male and female harp seals in the pattern of dentinal GLGs, based on the limited known-age material and a large sample of specimens of unknown age.

In determining age from transverse sections, it is often difficult to define the extent of the 1st year's growth in the dentine. Often there are confusing accessory opaque IGLs in the translucent dentine (Fig. 3E) which could be counted. Because of this, the neonatal line is an important reference

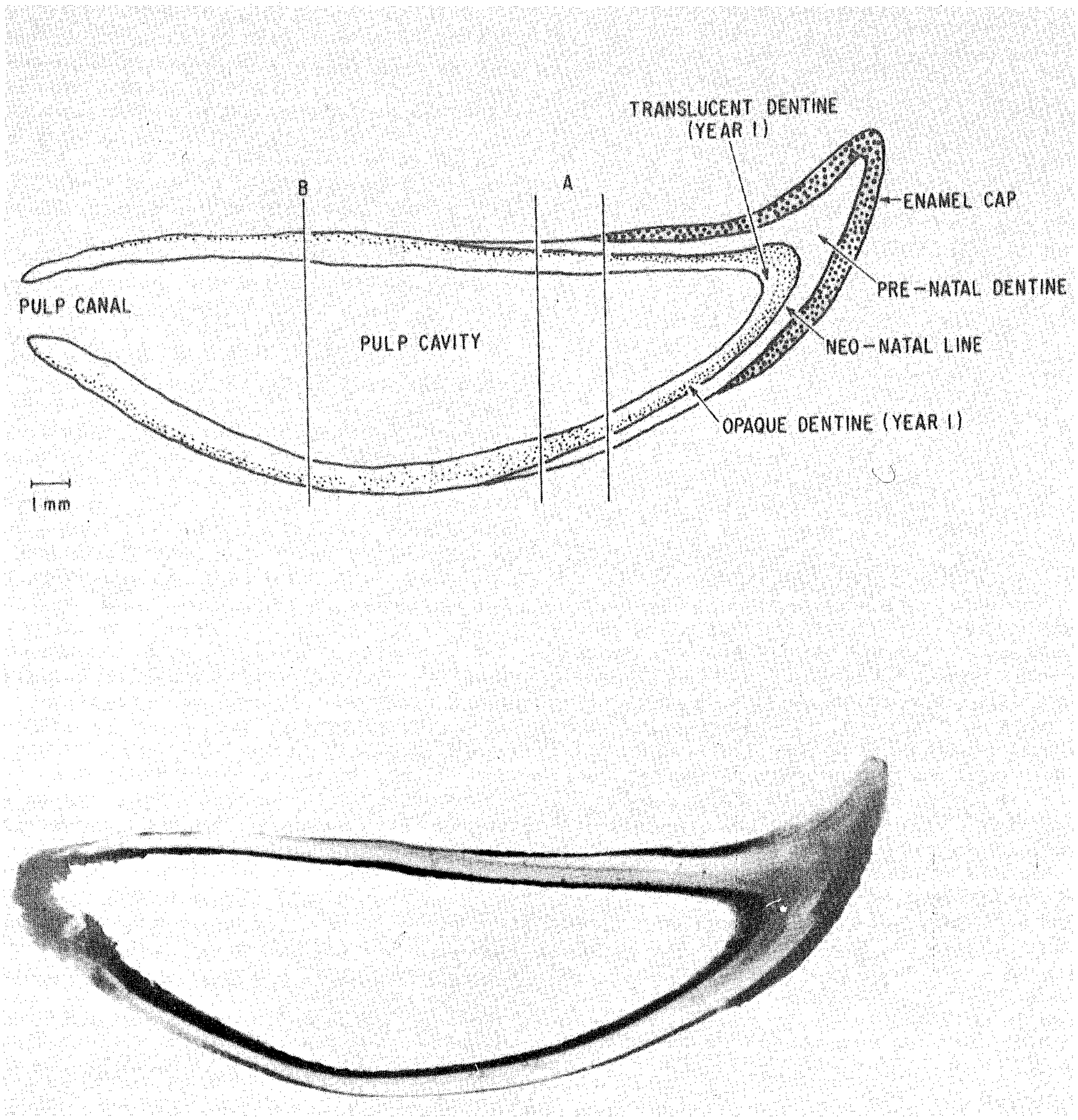

FIG. 1. Sagittal section of lower canine of a 13-mo-old female harp seal.

point in making a judgment about the extent of the 1st-year growth. The neonatal line results from a discontinuity in the growth of dentine which occurs at birth in many mammals. It is usually distinct in transverse sections. The position of the neonatal line in a transverse section will depend on the location from which the section was taken, and will not appear in a section taken close to the proximal end of the tooth, say from position B in Fig. 1. In a transverse section cut from zone A in the distal half of the tooth root (Fig. 1), the neonatal line is located an average of 172 ± 8 μm inside the dentine–cementum junction (Fig. 3A, B).

The thickness of dentinal annuli in transverse sections is shown as a function of age in Fig. 4. The widest dentinal GLG is deposited in the 1st year. Between the ages of 1 and 7+ (7–10) yr there is a linear decrease in the width of successive dentinal GLGs from an average of 489 μm at age 1 to 124 μm at ages 7–10. Although some of the variation in the width of dentinal GLGs can be attributed to variation in the location from which the section was taken, individual variation in dentine growth rate is clearly evident. The thickness of successive dentinal GLGs in nine harp seals is plotted against age in Fig. 5. In only four of these nine animals is the

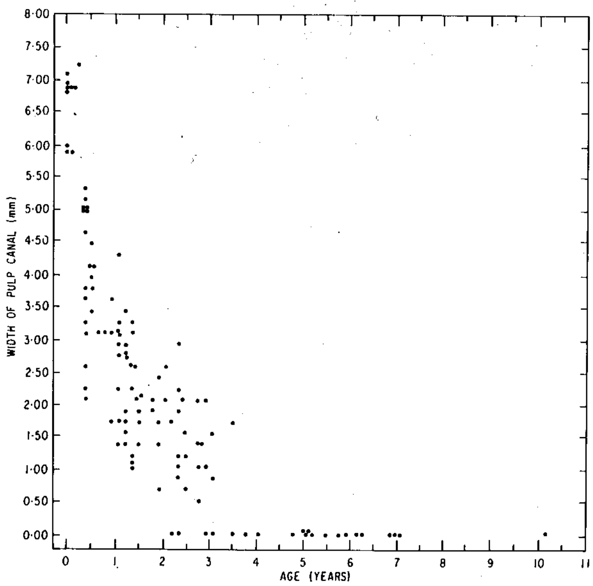

FIG. 2. Decrease in width of pulp canal in lower canine teeth with increasing age in 111 known-age harp seals.

thickness of the first GLG greater than the second and succeeding GLGs. One individual (M964) shows an increase in the width of succeeding GLGs to the age of 4 and another (58) to age 3, with a decrease thereafter. Such variation increases the difficulty of determining true age by making it more difficult to eliminate a false GLG based on its position relative to that of others which are perhaps more distinct.

The total width of the dentine layer from the neonatal line to the edge of the pulp cavity increases linearly with age from 6 mo to 10 yr (Fig. 6). However, this linear growth cannot be expected to continue, as there is only a finite amount of space inside the tooth. Examination of teeth from harp seals of unknown age suggests that the total thickness of the dentine continues to increase beyond the age of 25 yr, at which point the width of incremental growth in the dentine is quite small and magnification of 50× or more may be required to resolve individual GLGs. The pulp cavity in harp seal canines is usually not completely filled with dentine until 25 to 30 GLGs have been deposited, and as many as 34 to 37 GLGs have been resolved in several specimens (Fisher 1954; W. D. Bowen unpublished data).

Evidence for Annual Nature of GLGs

To establish when the various IGLs are formed, it is necessary to observe the nature of the newly formed dentine next to the pulp cavity, in seals killed at all times of the year. There is good seasonal representation of known-age animals among age groups 0 to 2 in the present sample. The thickness of the translucent IGL next to the pulp cavity was measured in 91 specimens. Because the absolute growth increment of dentine is a function of age, within each age group, measurements were standardized by dividing each value by the maximum value in that age group. The resulting scores, ranging from 0.0 to 1.0, were then plotted by month for each age (Fig. 7).

The relative thickness of translucent dentine by July–August in the 1st year is greater than that in the 2nd and 3rd years. However, at each age the translucent IGL begins to form in June–July and reaches its maximum thickness in February–March, corresponding to the time of harp seal births. The outermost IGL in a typical GLG, the interglobular dentine, is formed in April and early May, the period when harp seals undergo their annual molt. The middle IGL or opaque band is formed in May and June, during the time when most harp seals are migrating to their summer feeding range (Fig. 7). There is also an indication from the data on 2nd- and 3rd-year growth of the translucent IGL, that the growth rate of this layer is not constant throughout the year. The most rapid growth appears to occur in winter from January to March (Fig. 7), during which time the seals are feeding heavily. However, more data are required to confirm this.

The annual nature of dentinal GLGs in harp seal canines is illustrated further in Fig. 3A to H. The neonatal line is clearly seen in Fig. 3A, B, and E. At the end of the 1st year of growth, the dentine consists of an outer opaque IGL and a wide inner IGL of translucent dentine (Fig. 3B). Interglobular dentine is deposited during the annual molt in April (Fig. 3C). By late August the second GLG consists of the layer of interglobular dentine and an opaque layer (Fig. 3D), and by December the second GLG consists of all three IGLs (Fig. 3E). A false GLG can also be seen in Fig. 3E. Figure 3F, G, and H illustrate the pattern of GLGs in the dentine in animals ranging from 2 yr and 9 mo to 10 yr and 1 mo of age.

Accuracy of the Method

We next consider how accurate and consistent are ages determined from transverse sections when the actual age of the animal is unknown to the observer.

To examine the accuracy and precision of age determined by counting dentinal GLGs, one of the authors (W.D.B.) estimated the ages of 138 known-age harp seals in five blind replicates. Replicate examinations were done prior to detailed study of the dentinal GLGs of the known-age sample to minimize familiarity with the material.

The results of this experiment are summarized in Table 2. Overall, 83.4% of 675 'readings' resulted in assigning the correct age. However, because the teeth examined were mainly from young animals, the accuracy of the method over a wider range of ages is undoubtedly overestimated. The probability of estimating the age of harp seals correctly varied between ages and generally decreased with age. Only 0.724 of estimates of 0-group seals were correct using only transverse sections as the basis for the determination. Errors generally consisted of counting false annuli near the pulp cavity in animals 9–11 mo of age. However, these errors were virtually eliminated (0.99 correct determinations) when the tooth root was also examined. In animals less than 1 yr of age the pulp canal is generally ≥3.0 mm in diameter and the root has a translucent appearance, resulting from the rather thin layer of dentine that has been deposited. By contrast, in animals 1 yr and older, the pulp canal is usually <3.0 mm in width and the root is opaque. At ages 1 and 2 yr, 0.983 and 0.889, respectively, of readings based on transverse sections resulted

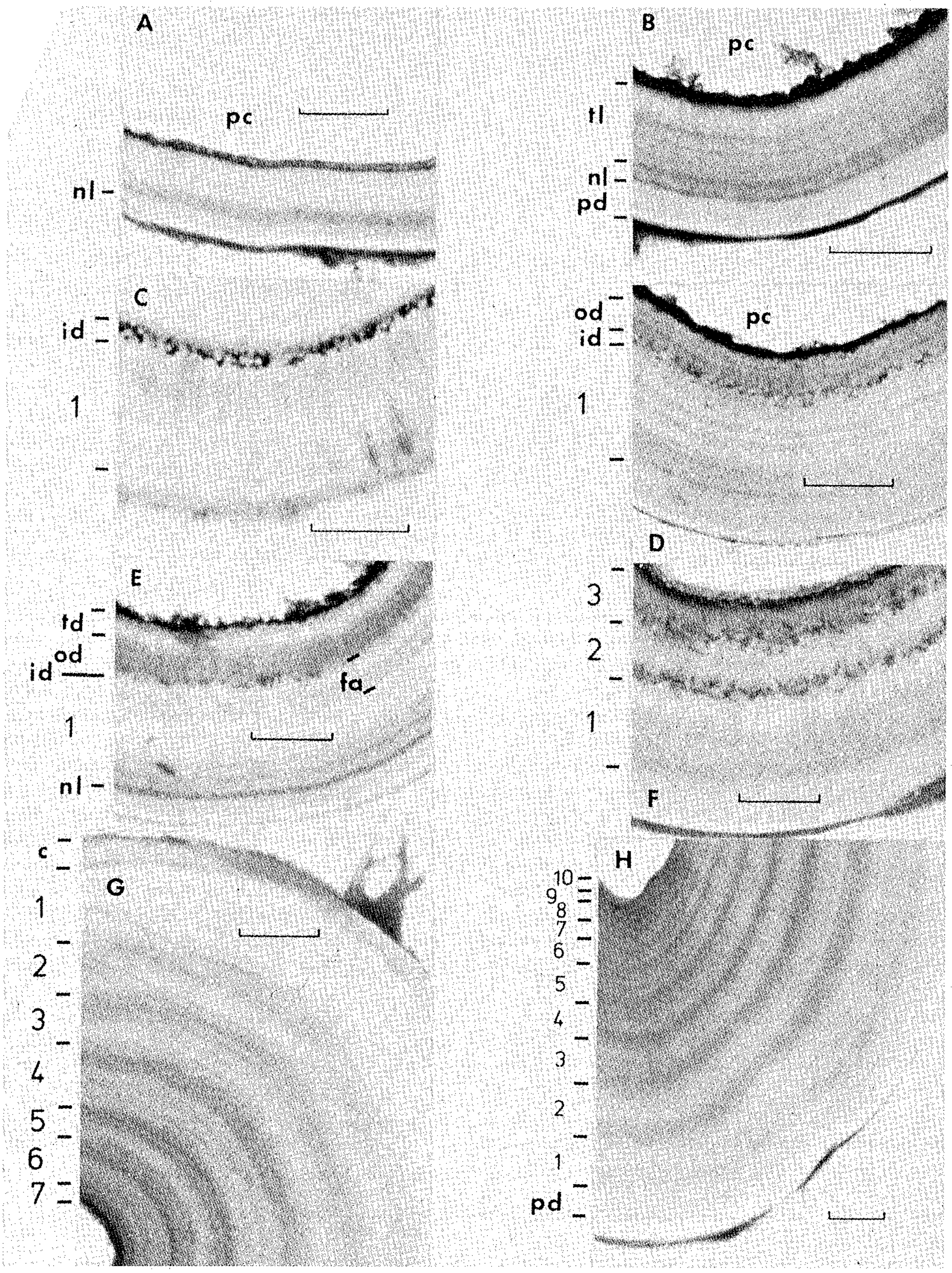

FIG. 3. Transverse canine sections of known-age harp seals examined with transmitted light. Bar scales = 0.5 mm (i.e. magnifications are from about 20 to 30×). (A) A 5-mo-old animal, killed August 11, 1980, (B) An 11-mo-old seal, killed February 10, 1979, (C) A 13-mo-old seal, killed April 18, 1969, (D) A $1\frac{1}{2}$-yr-old seal, killed September 1, 1979, (E) Harp seal 1 yr and 9 mo of age, killed December, 1979, (F) Harp seal 2 yr and 9 mo of age, killed December, 1980, (G) Female harp seal age 6 yr and 11 mo, killed February 18, 1982, (H) Male harp seal age 10 yr and 1 mo, killed April 25, 1982. c, cementum; fa, false GLG; id, interglobular dentine; nl, neonatal line; od, opaque dentine; pc, pulp cavity; pd, prenatal dentine; td, translucent dentine. Numerals denote annual GLGs.

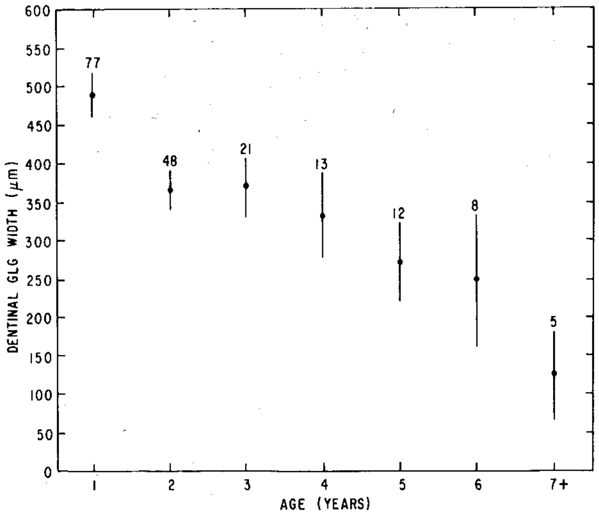

FIG. 4. Decrease in the average thickness of dentinal GLGs in the lower canines of known-age harp seals with increasing age. Vertical lines are 95% confidence intervals and numerals are sample size.

in the correct age being assigned. Age was estimated correctly in only 0.700 of 3-yr-olds. However, the age of two specimens, whose known age was 3 yr, was estimated consistently at 2 yr. Careful examination of both teeth revealed two complete GLGs and a third incomplete GLG, thus making these animals 2-yr-olds. It is likely that an error in tag-tooth association had been made in these cases. In three other cases the wrong tooth was clearly associated with the tag; a 1-yr-old read age 4, and two 8-yr-olds read age 4 and 18–22, respectively. Eliminating the above two specimens, as errors in tag-tooth association, then 49 of 60 or 0.817 (rather than 49 of 70 as in Table 2) of readings of 3-yr-olds resulted in correct age determination. Beyond age 3 yr, the existing data are insufficient to estimate the accuracy of age determined by counting GLGs. Although pooling ages 4 through 10 suggests that only about 0.553 of determinations would be correct, the age of all three 4-yr-old animals was estimated correctly and four of five readings of the 10-yr-old animal (Fig. 3H) were correct (Table 2).

Various rules could be used to decide upon the age of an individual animal using dentinal GLGs. In routine age determination for population dynamics it is usual to base the age of individuals on the result of a single examination of a transverse section. The above estimates of accuracy are what can be expected on average based on this method. However, we could adopt a rule which took, for example, the average of five readings (rounded to the nearest year) as the correct age. Following this method (and this is only one of many that could be proposed), the probability of correctly determining the age of a single animal is 1.00, 0.889, 0.833, and 0.625 for ages 1, 2, 3, and 4+, respectively. These values are slightly higher than those based on a single reading.

We have omitted further consideration of 0-group seals for two reasons. First, their age is based more on examination of the tooth root than on examination of dentine and second, they are usually killed in the commercial hunt at a time when their age can be determined with considerable certainty by body size alone. Thus as a rule, it is not necessary to estimate their age.

Variation in estimated age about the true age can be expressed by the relative percentage error (RPE), defined as:

$$(1)\quad \mathrm{RPE} = \frac{\left(\dfrac{\sum_{1}^{n}(x_i - \mu)^2}{n}\right)^{1/2}}{\mu} \times 100$$

where x_i is the ith reading of n readings and μ is the true age. For example, at age 1 yr there are 235 readings (Table 2). The RPE is 13.0, 16.7, and 14.3% at ages 1, 2, and 3 yr, respectively. Although sample sizes are small beyond age 3 yr, there is no indication of a trend in the RPE with increasing age (Table 3). However, more data are required to confirm this result. In addition to inconsistency in age estimation, there is also a potential bias in determining age by counting dentinal GLGs. The age of young animals tends to be overestimated and that of older animals (ages 5, 6, and 7) underestimated (Table 2).

Discussion

Our results demonstrate the annual nature of dentinal GLGs in the canine teeth of harp seals. In the 1st year two IGLs are deposited and, in most specimens, three IGLs are formed annually thereafter. Fisher (1954) described each GLG in the canine teeth of harp seals as consisting of two parts, an outer layer of reticulate air spaces (interglobular dentine) and an inner layer of opaque dentine. According to Fisher, these IGLs were separated by "areas of clear 'normal' looking dentine." Although Fisher's terminology differs somewhat from that which we have used, the pattern described is similar. This pattern also corresponds to that observed in ringed seals, *Phoca hispida* (McLaren 1958; Smith 1973); crabeater seals, *Lobodon carcinophagus* (Laws 1958); and hooded seals (T. Øritsland unpublished data). The interglobular dentine layer is absent in about 38% of known-age harp seal teeth examined. In these cases, each dentinal GLG consists of an outer opaque IGL and an inner translucent IGL. Variation in the presence of interglobular dentine (also known as vacuolated or reticulate dentine: Fisher 1954; McLaren 1958; Laws 1958, 1962) has also been noted in ringed seals (McLaren 1958) and hooded seals (W. D. Bowen unpublished data). Similar patterns of dentinal laminae are found in the leopard seal, *Hydrurga leptonyx*; the Weddell seal, *Leptonychotes weddelli*; and the Ross seal, *Ommatophoca rossi* (Laws 1962).

The results of this study show that the opaque IGL is formed during the period May to perhaps early July (Fig. 7). This corresponds to the northward migration of harp seals. Lacking known-age material, Fisher (1954) concluded that "the dark or opaque layer is laid down at some time between the moult and the beginning of the southward migration, probably during the summer sojourn in the Arctic." Rasmussen (1957) stated that white (translucent) zones in the dentine are formed in feeding periods, mainly during the summer, and that the dark layers are formed in periods when

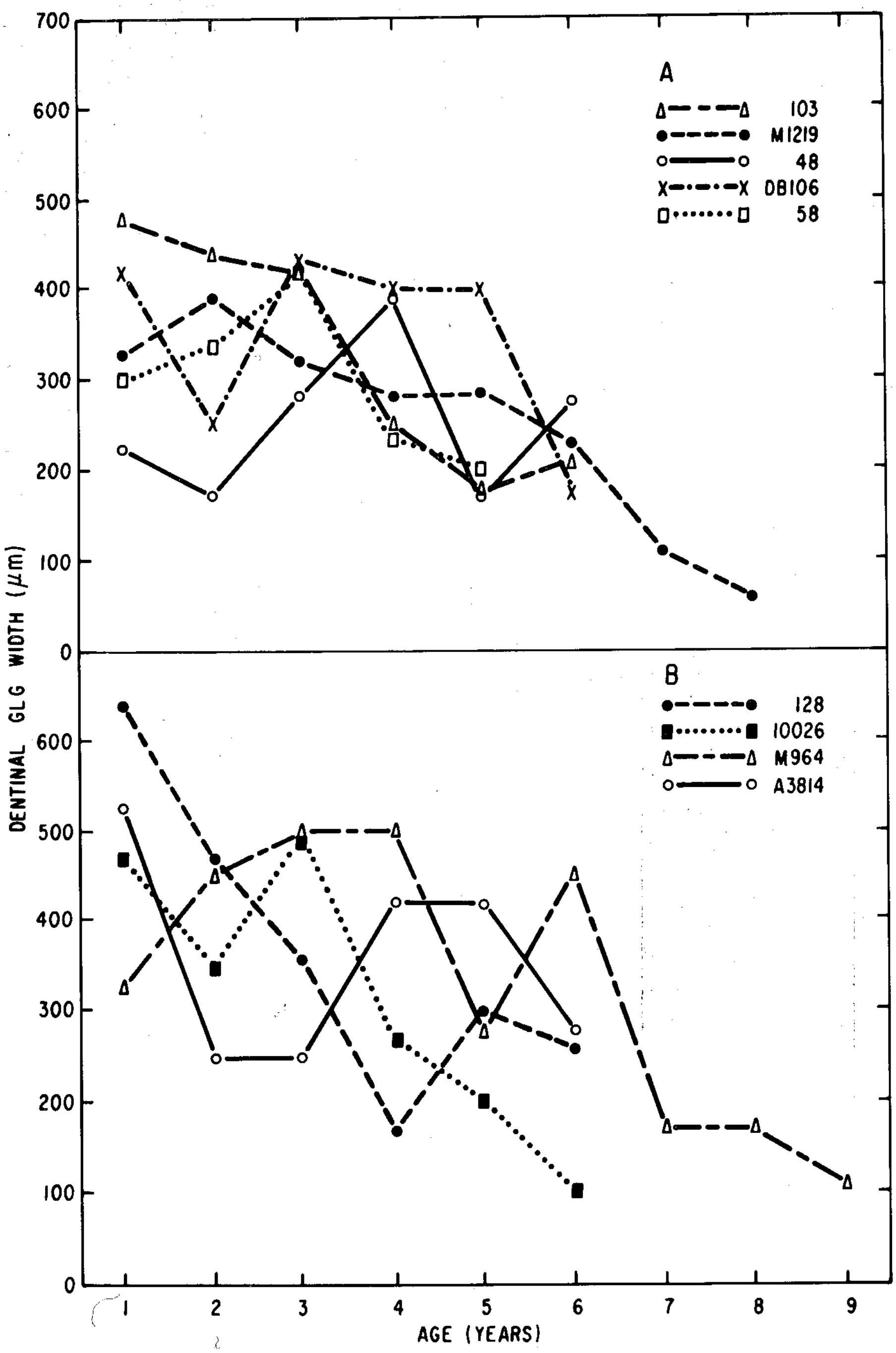

FIG. 5. Individual variation in the width of dentinal GLGs in lower canines as a function of age in nine known-age harp seals.

the animals do not feed, such as during whelping and molting. We conclude that the opaque IGL is deposited more quickly than assumed by Fisher and somewhat later than assumed by Rasmussen.

Yakovenko (1960) stated that a layer of clear dentine is formed during such times as whelping or molting when harp seals are hauled out upon the ice. A dark layer of dentine is formed during the summer and winter periods when animals are in the sea. The contradictory nature of these observations is resolved by noting that the optical density of dentinal IGLs under reflected light is opposite to that seen under transmitted light. Yakovenko examined his material under reflected and

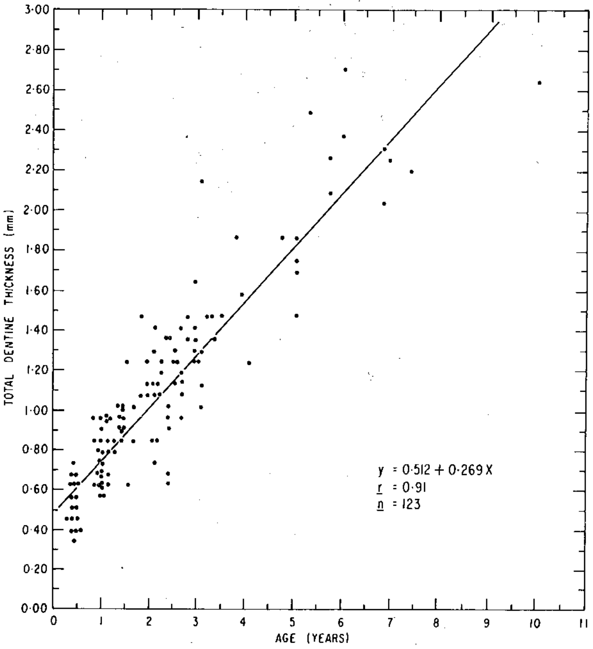

FIG. 6. Relationships between total dentine thickness and age in 123 known-age harp seals.

not transmitted light as was used by Fisher, Rasmussen, and in this study.

Our measurements of the thickness of dentine deposited during the 1st and 2nd year of life are lower than those reported by Fisher (1954). Based on 27 animals of unknown age, Fisher found that 0.7 mm (700 μm) of dentine was deposited from 1 mo of age to the beginning of the first layer of interglobular dentine. This compares with only 489 μm of dentine from birth to the end of 1 yr in our study (Fig. 4). During the 2nd year, Fisher reported that 0.8 mm (800 μm) of dentine was deposited compared to 370 μm in this study. Our measurements of 3rd-year growth (≈ 400 μm) and those of Fishers agree. Furthermore, our data show that the growth of dentine in the 1st year is significantly greater than in the 2nd year of life. This is also the case in ringed seals (Smith 1973). However, Fisher found no difference between the thickness of dentine formed in the 1st and 2nd year of life.

The reasons for this discrepancy are not clear. One possibility is that on average, Fisher sectioned his samples further toward the distal end of the tooth root where the dentine would be thicker. However, if this were the case then we should expect a systematic difference in all GLGs, which was not found. Another possibility is that the growth rate of harp seals born in the early 1950s was greater than that of seals born in the late 1970s. However, this hypothesis is not supported by the limited available data on long-term trends in harp seal growth rate; if anything the reverse seems more likely (Innes et al. 1981). We conclude that the thickness of the first and second GLGs was greater in the 1950s than in the 1970s. However, it is not possible to account for these differences at present.

The factors responsible for the formation of IGLs in the

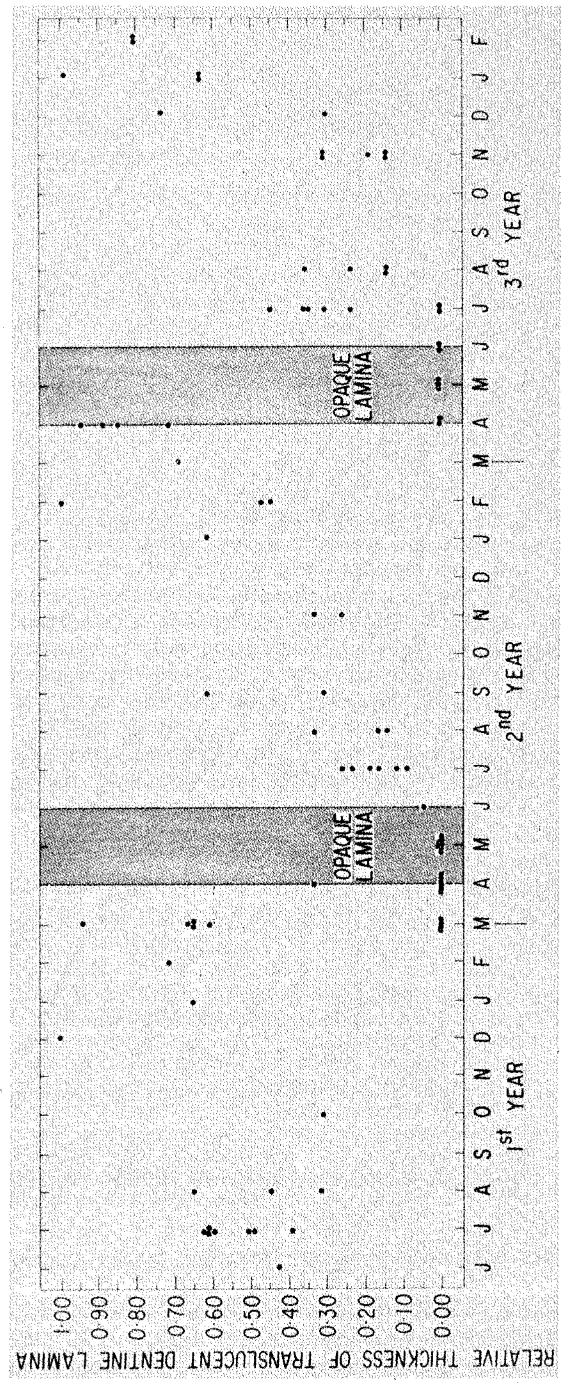

FIG. 7. Monthly variation in the relative thickness of translucent dentine next to the pulp cavity in 91 known-age harp seals between the ages of 4 mo and 36 mo. See text for detail.

TABLE 2. Comparison of estimated and actual age of 135[a] harp seals. Each tooth read five times in blind replicates. Proportion of correct determinations given in parentheses.

Actual age (yr)	Estimated age (yr) 0	1	2	3	4	5	6	7	8	9	10	Readings	n
0	76 (0.724)[b]	29										105	21
1		231 (0.983)	4									235	47
2		9	160 (0.889)	11								180	36
3			20	49 (0.700)[c]	1							70	14
4					15 (1.00)							15	3
5					18	15 (0.429)	2					35	7
6					1	6	12 (0.600)	1				20	4
7						1	8	1 (0.143)				10	2
8													
9													
10										1	4	5	1
Total												675	135

[a]Three of 138 teeth examined were eliminated because of wrong tooth or wrong known-age information.
[b]0.990% if tooth root also used, see text.
[c]0.817% if two problematical teeth eliminated, see text.

TABLE 3. Age-specific estimates of relative percentage error of age determined by counting dentinal GLGs in harp seal canine teeth.

Known age (yr)	n	Relative percentage error
1	47	13.0
2	36	16.7
3	12	14.3
4	3	0.0
5	7	15.1
6	3	7.4
7	2	15.6
10	1	4.5

dentine of harp seals and in other mammals are poorly understood; however, a number of hypotheses have been proposed. These include seasonal variation in hormone balance (Carrick and Ingham 1962), in vitamin D levels (Mellanby 1928; Laws 1953; Fisher 1954; McLaren 1958), and in nutritional state or feeding intensity (Mansfield 1958; Scheffer 1950). Scheffer and Peterson (1967) found a direct correlation between nutrition and postnatal dentinal layering in suckling pups of the Alaskan fur seal. Kubota et al. (1961) felt that differential calcification of the dentine in the canine tooth of fur seals 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 dentinal deposition rate and subsequent hypercalcification (Symons 1967), and deficiency of vitamin A causes the formation of interglobular dentine in rats (Rowles 1967).

Another explanation is that endogenous factors are largely responsible for discontinuous growth. Grue and Jensen (1979) reviewed the available data on 52 species of terrestrial mammals and concluded that the formation of IGLs is governed to a considerable degree by internal rhythms which are coupled to the animal's overall pattern of growth and metabolism. Gaskin and Blair (1977), in their study of the harbor porpoise, *Phocoena phocoena*, concluded that the timing of zone deposition is in some way determined by the date of birth, and maintained by an annual endogenous cycle.

IGLs in the dentine of harp seals and certain other phocids are associated with rather specific events in the annual cycle (Fisher 1954; Rasmussen 1957; Laws 1958, 1962; this study). The deposition of well-calcified dentine in the teeth of odontocetes and many other mammals is generally attributed to good nutrition, whereas poorly mineralized dentine is deposited when feeding is reduced to suboptimal levels or as a result of metabolic disturbances for other reasons (Sergeant 1959, 1962; Johansen 1967). In harp seals interglobular dentine, which is poorly calcified but optically dense in transmitted light (Symons 1967), is deposited in the molting season (Fisher 1954; this study), a period of 3 or 4 wk when little if any feeding occurs. Laws (1958) estimated that interglobular dentine in the canine tooth of crabeater seals is deposited in the period September to October, probably during the pupping season in September. This is also at a time of reduced feeding.

The opaque IGL in harp seal canines is deposited from May to early July during the spring migration. Although the feeding habits of harp seals at this time of the year are not well known, some feeding does take place (Foy et al. 1981). The translucent IGL is formed largely from January to March when harp seals are feeding heavily. Therefore, we might expect that the dentinal GLG would represent a series of layers of increasing mineralization. However, there is considerable conflicting evidence on the relationship between optical opacity, mineral content, and other physicochemical properties of dentine (Hay 1980). For the present, it is not possible to say which of the two inner IGLs is more highly calcified.

The decision as to which features are included in the count as GLGs is made on the basis of an inspection of the overall pattern of dentinal layering, rather than strictly on the basis of the internal structure of the dentine. Inevitably a certain subjective skill is involved in determining age by counting GLGs (Gambell 1977). Therefore, it may be expected that an incorrect age will be determined in a certain proportion of samples examined.

In general, few attempts have been made to assess the accuracy of age estimation procedures (Dapson 1980). The present known-age material is insufficient to estimate the accuracy and precision of the method much beyond the age of 3 yr. Taking the mean of five readings, the probability of correctly estimating the age of an animal decreases with age from 1.0 at age 1 yr to 0.83 at age 3 yr and based on a small sample, to 0.63 at age 4+ yr. Similar results were obtained by Doubleday and Bowen (1980) who studied a sample of 202 canine teeth from harp seals of unknown age. As in the present study, each tooth was examined in five blind replicates by W.D.B. Age was assigned on the following basis: if three or more readings were the same, this value was assumed to be the 'actual' age, and if less than three readings were the same, the mean value was taken as the 'actual' age. They found that the probability of a single age reading being equal to the mean age decreased linearly from 1.0 at age 1 to about 0.2 at age 22. Our results demonstrate, however, that this previous work overestimated the accuracy of age determination based on GLGs. It is clear that repeated examinations of certain teeth are consistent but wrong. Of 22 teeth in which one or more of five readings differed from the true age, 27.3% consistently differed. When the true age of the animal is unknown this type of error cannot be detected.

The bias in age estimation reported herein has been found in other studies. Anas (1970), studying a large sample of known-age northern fur seal canines, found a clear tendency for readers to overestimate the age of 3- to 5-yr-old females and to underestimate, by as much as 70% of the time for one reader, the age of 6- to 10-yr-olds. Doubleday and Bowen (1980) demonstrated that age reading variations can bias estimates of harp seal pup production (using the survival index method) by as much as 10% and natural mortality rates from catch curves by a comparable amount. Inconsistencies in age determination also tend to overestimate mean age of maturity. They concluded that the size of these biases is sufficient to have an impact on management advice for northwest Atlantic harp seals. However, Doubleday and Bowen did not consider error caused by consistent but inaccurate age determinations. Hence the impact of age determination errors on the management of harp seals will likely be greater than that previously anticipated.

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