AGE DETERMINATION AND GROWTH OF THE SHORT-FINNED PILOT WHALE OFF THE PACIFIC COAST OF JAPAN

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ABSTRACT

This study is based on data and specimens from 373 female and 170 male *Globicephala macrorhynchus* collected off the Pacific coast of central Japan and covering eight months of the year. The deposition rate of dentinal growth layers was annual, the haematoxylin-stainable layer being formed from May to October and the unstainable from December to February. The annual deposition of cemental layers continued after dentine deposition ceased, thus enabling the age of old individuals to be determined. The maximum age attained by females was 62 years, that of males 45 years. Females almost ceased growth at sexual maturity (nine years) and reached the asymptotic length of 364.0 cm at age 22 years. Male growth was similar to that of females until age nine years, when the secondary male growth spurt started. Males attained an asymptotic length of 473.5 cm at 27 years. Body length could be converted into age with an accuracy of ±2 years, up to a body length of 280 cm (females; equivalent to age 5 years) or 320 cm (males; age 8 years). The relationship between body weight (W, kg) and body length (L, cm) of fetal and postnatal individuals of both sexes was described by log W=2.8873 log L+log (2.377×10^{-5}).

INTRODUCTION

Sergeant (1959) examined the dentinal growth layers in the tooth of long-finned pilot whale, *Globicephala melaena* (Traill, 1809), and suggested that these layers might be used to estimate absolute age. He used this technique in his analysis of the life history of *G. melaena* in Newfoundland waters (Sergeant, 1962). Sergeant also observed cemental growth layers in this species and suggested that they might be used to age animals in which dentine deposition had ceased. However, he did not use the technique, presumably because of technical difficulties.

Dentinal layer counts have subsequently been used in the study of the life

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Sci. Rep. Whales Res. Inst.,
No. 35, 1984, 57–91

history of several odontocetes as reviewed by Scheffer and Myrick (1980), despite the limitations of the technique for determining the age of old individuals. In recent years, however, the methods of preparing teeth for cemental and dentinal layer counts have been greatly improved (Perrin and Myrick, 1980).

The improved age determination techniques have been used to study the life history of the short-finned pilot whale *Globicephala macrorhynchus* Gray, 1846. We report on age determination and growth in *G. macrorhynchus* in this paper. Related studies on the life history and reproduction of this species (Kasuya and Marsh, in press) and on fundamental anatomy of the ovaries (Marsh and Kasuya, in press) will be published elsewhere.

MATERIALS AND METHOD

Data source

Most of the data and specimen materials were collected between 1965 and 1980 inclusive from 24 schools of *G. macrorhynchus* (Schools 1 through 24 in Table 1) caught on the Pacific coast of Japan by the driving fishery at Taiji (33°34′N, 135°54′E), Futo (34°54′N, 139°09′E), or Arari (34°49′N, 138°46′E), and from one school stranded at Choshi (35°43′N, 140°52′E) in the Chiba prefecture. The

TABLE 1. MATERIALS USED IN THIS STUDY

School no.	Locality	Date of		No. of individuals			
		catch	data collection	driven	examined	aged	lost
1	Arari	20 Oct. '65	21 Oct. '65	33	18	8	15
2	Choshi	13 Dec. '66	15 Dec. '66	ca. 90	9	3	80
3	Arari	— June '67	27, 28 June '67	>30	14	4	16
4	Taiji	22 July '69	July–Aug. '69	31	9	2	22
5	Taiji	27 July '69	July–Aug. '69	46	23	10	23
6	Taiji	24 Feb. '71	24 Feb. '71	24	12	0	12
7	Taiji	17 Jan. '75	18, 19 Jan. '75	28	28	26	0
8	Taiji	21 Jan. '75	21, 22 Jan. '75	52	47	0	5
9	Taiji	24 June '75	25 June–4 Jul.	ca. 230	173	125	57
10	Taiji	22 July '75	22–24 July '75	33	32	18	1
11	Taiji	13 Jan. '76	13–17 Jan. '76	28	26	21	2
12	Taiji	4 Feb. '76	5, 6 Feb. '76	20	20	18	0
13	Taiji	7 Oct. '76	8, 9 Oct. '76	38	38	38	0
14	Futo	20 Dec. '77	21 Dec. '77	25	25	22	0
15	Futo	24 Dec. '77	25 Dec. '77	48	48	45	0
16	Taiji	20 Feb. '78	20, 21 Feb. '78	27	27	27	0
17	Futo	4 Dec. '78	5 Dec. '78	52	52	49	0
18	Futo	13 Dec. '78	13, 14 Dec. '78	28	28	28	0
19	Taiji	6 Jan. '80	6 Jan. '80	26	23	0	3
20	Taiji	17 Jan. '80	17, 18 Jan. '80	14	14	7	0
21	Taiji	2 Feb. '80	2 Feb. '80	19	17	0	2
22	Taiji	20 Feb. '80	23 Feb. '80	15	15	15	0
23	Taiji	21 Feb. '80	24 Feb. '80	23	23	23	0
24	Taiji	30 May '80	31 May–3 June	38	38	38	0

linear distance between the southernmost location, Taiji, and the northernmost, Choshi is about 500 km.

The quality and quantity of data and samples varied between the schools. In the early period of the study (Schools 1 to 6), effort was directed to the collection of materials for taxonomy, and the data obtained for the present analyses were limited and biased to adult individuals. Information from four schools (schools 8, 19, 20 and 21) examined by volunteers was usually limited to sex and body length. The 14 schools (Schools 7, 9 through 18, 22, 23 and 24) caught in the seven years from 1975 to 1980 and examined by Kasuya constituted the major source of data used for the study.

Field procedures

The information and samples listed below were collected by Kasuya, volunteers or both, when the fishermen were flensing. At this stage each pilot whales was assigned a sample number which is a hyphonated combination of the school number followed by the number of the animal within the school.

1. *Sex*

2. *Body length* Measured to the nearest 1 cm on a straight line parallel to the long axis of the body from the anteriormost point to the bottom of the tail fluke notch. Although the tip of the upper jaw is the anteriormost point of the body of juveniles, it lies posterior to the front end of the melon after the whale is about 240 cm long and becomes difficult to distinguish (Yonekura, Matsui, and Kasuya, 1980). Thus the measurement of body length is not exactly comparable for adults and calves less than one year old.

3. *Teeth* One to three contiguous teeth were collected from the center of the lower tooth row with a hammer and chisel and preserved in 10% buffered formalin. The largest available teeth were selected.

4. *Other specimens* Mammary gland, testis, epididymises, ovaries, uteri and stomach contents were collected as detailed in Kasuya and Marsh (in press).

Laboratory procedures

1. *Tooth preparation* The age determination was done by Kasuya who counted the annual growth layers in dentine or cementum. (One growth layer is equivalent to an *annual* Growth Layer Group of Perrin and Myrick (1980)). The bone and connective tissue surrounding tooth selected were removed with a knife. The tooth was then cut longitudinally with a low speed diamond saw. The cut surface was then polished with coarse (about 1,200 mesh) and fine (about 3,000 mesh) whetstones to expose the center of the tooth. The polished surface was dried and glued on a clear perspex plate (1 mm thick) with cyanoacrilate monomer. After the glue had hardened, the other side of the tooth was similarly sawed off leaving a 0.3 to 0.5 mm thick section on the perspex slide. This section was polished with the whetstones to a thickness of 30 to 40 μm. The polished section was then decalcified in 5% formic acid for about 24 hours at room temperature, rinsed in running water for 5 to 12 hours, stained with Mayer's haematoxylin for 30 minutes,

rinsed in running water for several hours and mounted in Canadian balsam. (A complete removal of acid by long rinse or ammonia after staining prevent fading.)

2. *Reading growth layers* The counting of annual growth layers was done under transmitted light with a compound microscope (20 to 100x) using the following procedure. An ontogenetic series of 20 slides was initially prepared for each sex. Factors taken into account in the selection of these slides included the quality of preparation and the relative age suggested by the thickness of dentine and by the size of the pulp cavity. The dentinal and cemental growth layers in the slide of these 40 teeth were counted. In most cases, there was reasonable coincidence between the number of growth layers in both tissues.

However, there were a few cases where the reading did not correspond. These slides were re-examined for indication that dentine deposition had ceased. All counts were then plotted against body length and sexual maturity for males and females separately. The pattern of increase suggested that the growth layer counts were a reliable index of absolute age.

The age of the other whales were then determined based on the standard established above but without reference to biological data. First the cementum was read three or more times. The medium count was then taken as the true value. Then the dentinal layers were counted three times without referring to the cemental counts. The medium value was again used. If the deposition of dentine was considered to have been continuing on at least part of the wall of the pulp cavity, the dentinal count was used. In a few cases the range of dentinal and cemental counts differed on a tooth with open pulp cavity. In these cases the growth layers in both tissues were repeatedly checked until a good agreement was reached between the counts for both tissues. Kasuya used this method to train himself to be able to make accurate cemental layer counts, enabling him to age whales with closed pulp cavities, the age of these animals being determined from cemental layer count only.

The age of each individual was principally expressed as the number of growth layer cycles, which was equivalent to years (see below). The age of individuals below 10 years was roughly estimated to the nearest 1/4 year by considering the thickness and nature of the first and last postnatal dentinal layers of incomplete thickness. For whales over 10 years, the age was grouped into the nearest n+0.5 years (n=integer).

3. *Other procedures* The method used to determine the reproductive status of each whale are detailed in Kasuya and Marsh (in press) and Marsh and Kasuya (in press).

AGE DETERMINATION

Description of dentinal growth layers (Plates I to III)

The prenatal dentine is capped by an enamel layer, which dissolves in the decalcification reagent. In decalcified and haematoxylin stained sections, the prenatal dentine appears as either a moderately or strongly-stained layer in which

10 to 20 indistinct short cycle layers can be detected with careful study. The proximal border of the prenatal dentine is lined with a thin unstainable layer in most postnatal animals. This is the neonatal line (Fig. 2 in Plate I). The thickness of the neonatal line ranges from 16 to 64 μm ($\bar{x}$=38 μm; n=25). The neonatal line could not be distinguished in four newborn individuals ranging from 136 to 142 cm in body length. Two of these whales (males 136 cm and 142 cm long), had an erect dorsal fin, an indication that birth had occurred not less than several hours before (Kasuya, Miyazaki and Dawbin, 1974). In contrast, the neonatal line was clearly seen in the teeth of five individuals from 154 to 190 cm in body length and aged between 0.1 to 0.5 year (estimated from body length). This indicates that the neonatal line in *G. macrorhynchus* is identifiable only after the deposition of ordinary more stainable postnatal dentine.

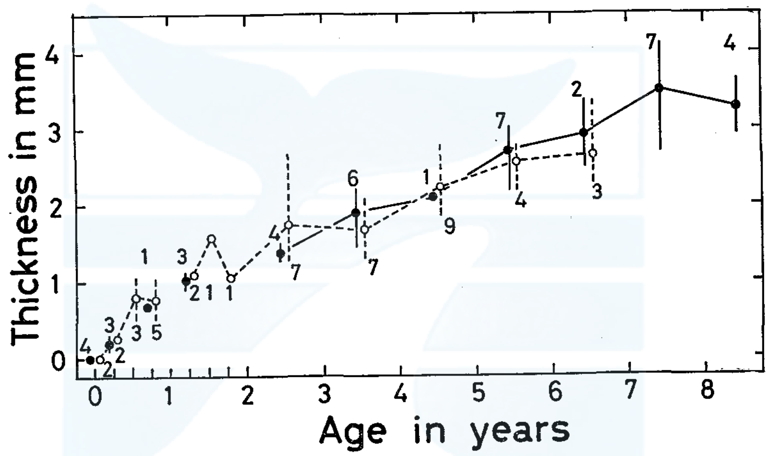

Fig. 1. Thickness of postnatal dentine of *G. macrorhynchus*. The ranges, means and sample sizes are indicated. Open circles and dotted line represent females, closed circles and solid line males.

In decalcified and stained sections, the growth layers in postnatal dentine are seen as layers of alternating stainability. The thickness of the annual growth layers is about 0.5 to 0.6 mm in both the first and second complete layers (measured at the level of the base of the prenatal dentine). This thickness decreases to about 0.1 mm at the 30th and subsequent layers (measured at the midlength of the pulp cavity). No sexual dimorphism was observed in dentine thickness of young whales (Fig. 1). Within one annual growth layer, short cycle layers are usually detectable. These tend to be conspicuous where the growth layers are wide, *i.e.* in the dentine laid down near the tooth apex while the whale is young. Occasionally some of these short cycle layers are as prominent as ordinary annual growth layers.

The appearance of dentinal growth layers is variable within a tooth. The layers deposited in the juvenile stage in the root of the tooth are composed of wide stainable and narrow unstainable layers (Fig. 4 in Plate I). However if a stainable layer is traced to the tip of the tooth its outer border gradually looses stainability, while the stainability of its inner border increases. Furthermore, an accessory layer (Hohn, 1980) of strong stainability may appear in the unstainable layer near the tip. Thus the pattern of stainability of these layers often appears to be reversed with a resultant apparent lag of about half a growth layer cycle between the cusp and the root portions of the tooth. This feature is usually absent or negligible in subsequent layers. The annual growth layer deposited in the root of the tooth in adult whales is usually composed of a narrow stainable layer and a wide unstainable layer (Figs 2 and 3 in Plate II). Although accessory layers are still common in these layers, they are less conspicuous than in the apex.

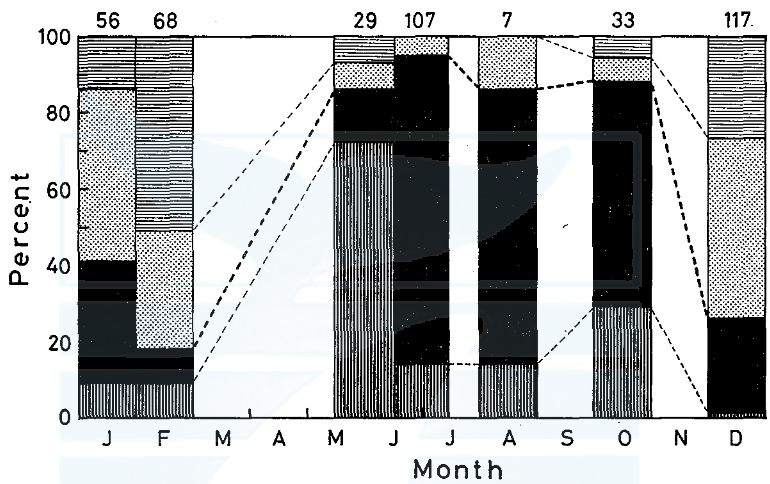

Fig. 2. Seasonal change in the nature of the last incomplete dentinal layer of *G. macrorhynchus*. Numerals at the top indicate sample size. Thin horizontal lines: wide unstainable layer. Stippling: thin unstainable layer. Black: wide stainable layer. Thick vertical lines: thin stainable layer.

Deposition rate of dentinal growth layers

Seasonality of stainability: Data were obtained from 270 females and 147 males in which the deposition of dentine was certainly continuing. The nature of the last incomplete dentinal layer in the root of the tooth was classified as either a thin or a thick, stainable or unstinable layer. The thickness was judged by eye in comparison with the corresponding tissue in the previous cycle. Fig. 2 shows the seasonality of stainability of the last deposited dentine. In May/June most of the 29 individuals (86.2%) have started depositing stainable dentine. This continues in most individuals until October. The number of individuals depositing an unstainable layer increases from 12.2% in December to 82.4% in February. Although data are lacking from March to early May, we suspect that deposition of the unstainable layer peaks in February and March, and suggest that the alternations of dentinal layers from unstainable to stainable and from stainable to unstainable may occur in April to early May and in November, respectively. Thus each of the two major components of a dentinal layer seems to represent approximately six months.

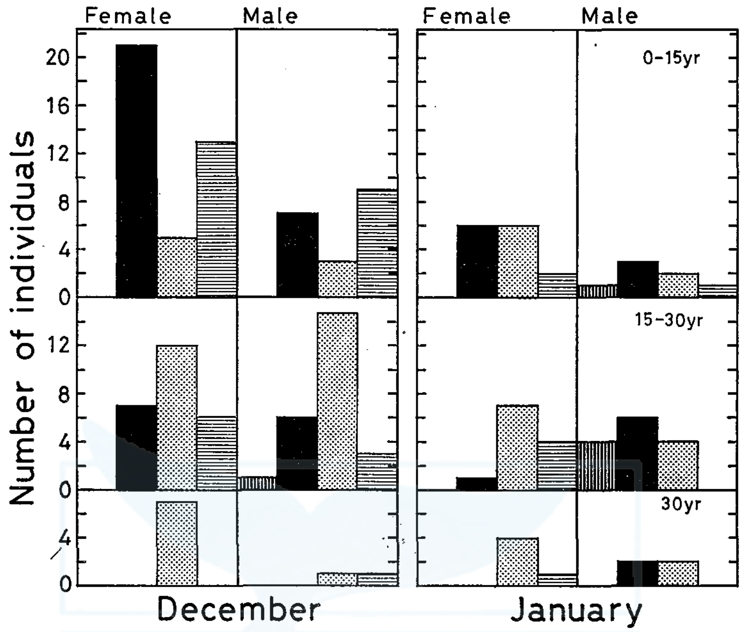

Fig. 3. Age and sex differences in the season when the stainable and unstainable layers within a dentinal growth layer alternate in *G. macrorhynchus*. Thin horizontal lines: wide unstainable layer. Stippling: thin unstainable layer. Black: wide stainable layer. Thick vertical lines: thin stainable layer.

Approximately 10 to 20% of our sample was not depositing dentine in accordance with this pattern. This may have been due to (1) exceptional individuals (2) errors in layer-identification due to the short cycle layers or (3) sex or age differences in dentine deposition. To test the last possibility the data for each month were subdivided according to sex and then into three age groups (1) below 15 years, (2) from 15 to 30 years and (3) over 30 years (Fig. 3). Age/sex differences in the relative frequency of the four deposition stages was then statistically tested for each month (Chi-square test). A statistically-significant difference ($P<0.05$) was found only for samples obtained in December and January. The only combination where a significant difference was obtained between sexes was in intermediate age class (15–30 years) in January ($P<0.01$). Although this result indicates that males of intermediate age were more likely to deposit a stainable layer than females, we consider this is probably an error caused by small sample size because a similar trend was not observed in December (Fig. 3). A significant difference in the proportion of animals of the same sex laying down a stainble layer was also found for the following age combinations in December:

Females young: intermediate, $P<0.01$
intermediate: old, $0.02<P<0.05$
old: young, $P<0.001$

Males young: intermediate, $P<0.01$

Thus as the whales get older, proportionately fewer females tend to be accumulating a stainable layer in December. Although not always statistically-significant, the same trend is also observed in the male. The change in the deposition pattern from stainable to unstainable dentine seems to occur slightly later in younger individuals possibly due to the larger relative width of the stainable dentine in young animals (see "Description of dentinal growth layers").

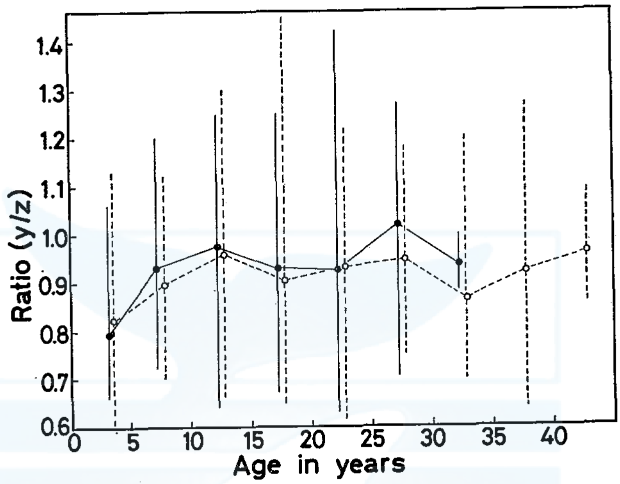

Fig. 4. Rate of decrease in the width of dentinal growth layers indicated by the thickness of the last complete layer (Y) and penultimate layer (Z) in *G. macrorhynchus*. The ranges and means for males (closed circles and solid line) and females (open circles and dotted line) are indicated.

Seasonal changes in dentine thickness: The thickness of dentinal growth layers was measured with an ocular micrometer. The measurement was taken from the center of one stainable layer to the center of the next, except in the case of the last incomplete set, the width of which was measured from the center of the last complete stainable layer to the predentine-dentine boundary near the edge of the pulp cavity (irrespective of nature of dentine being laid down). This latter measurement was often thicker than that of the penultimate measurement because each stainable layer was defined only after the next unstainable layer had been deposited. The uncorrected degree of deposition of the last growth layer (R_n) can be defined as;

$$R_n = \frac{X_n}{Y_n}$$

where X_n is the thickness of the last (incomplete) growth layer of an n-year old whale and Y_n is the thickness of the (complete) penultimate growth layer of the same individual. As the thickness of a dentinal growth layer varies with the whales's age, R_n has to be corrected for this variation. The correction factor C_n for an n-year old whale can be defined as;

$$C_n = \left(\sum_{j=1}^{m} \frac{Y_{n+1,j}}{Z_{n+1,j}}\right) \cdot \frac{1}{m}$$

where m is the number of whales aged $(n+1)$-years and Z is the thickness of the layer one cycle prior to Y. Then the corrected deposition rate for the last incomplete layer of an n-years old individual can be defined as R_n/C_n. This method is only applicable for whales older than two years.

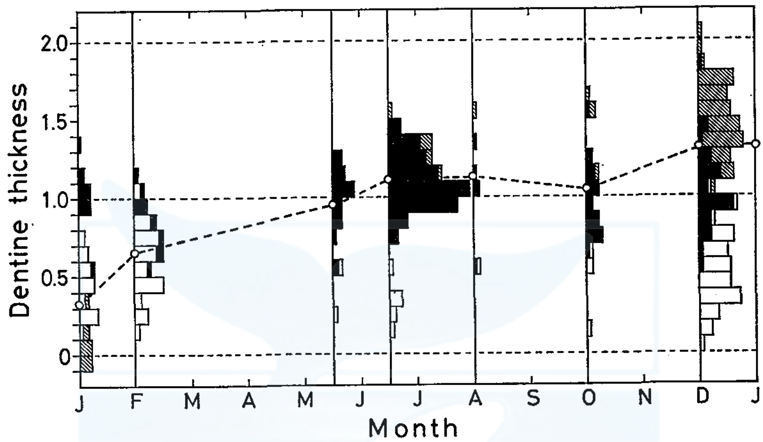

Fig. 5. Seasonal change in the relative thickness of the last incomplete dentinal layer in *G. macrorhynchus*. The dotted line joins the monthly means (open circles). Black squares represent individuals depositing a stainable layer; white squares those depositing an unstainable layer. The shaded areas indicate indiviuals that are moved back (January) or forward (June/July—December) for one cycle in order to correct for the individual variation in the seasonality of dentine deposition.

The relationship between age (n) and Y_n/Z_n is shown in Fig. 4. The means of the five-year age classes increase until the whales are about 15-years old, and stays almost constant thereafter. The values for males are slightly higher than the corresponding values for females indicating that the decline of growth layer thickness with age is slower in males. This may relate to the earlier cease of dentine deposition in males mentioned below (see " Pulp cavity "). Because Y_n/Z_n shows such large individual variation, it is not practical to calculate C_n for each age class and sex. Therefore, we have calculated C_n for both sexes and for four age classes as follows;

2–5 yrs	$C_n=0.804$
5–10 yrs	$C_n=0.902$
10–15 yrs	$Cn=0.963$
≥15 yrs	$Cn=0.922$

The resultant corrected values of the relative thickness of the dentinal layer being deposited at the time of death in various months are shown in Fig. 5. In January, about 40% of the individuals are still depositing stainable dentine while

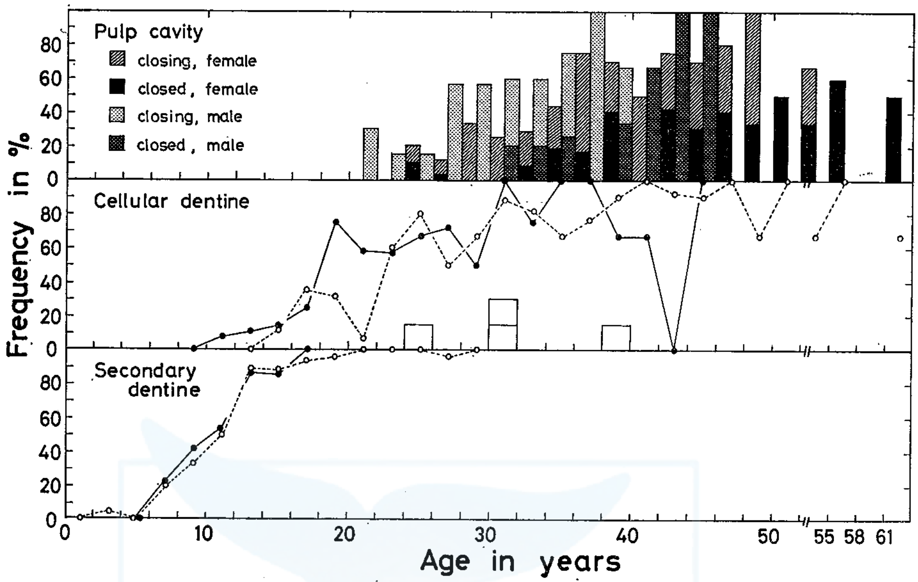

Fig. 6. Growth of *G. macrorhynchus* teeth. Top: condition of pulp cavity. Middle: deposition of cellular dentine. The boxes represent four males whose pulp wall was completely covered by cellular dentine. Bottom: deposition of secondary dentine. The open circles and dotted line represent females, and closed circles and solid line males.

the remainder have already started to deposit unstainable dentine. Therefore the values of the former individuals need to be moved backward for one cycle. In the same way, the values for individuals depositing an unstainable layer after July need to be moved forward one cycle. The mean monthly values of the corrected thickness of the last dentinal layer thus calculated are shown by the open circles in Fig. 5. The values increase from 0.3 in January to 1.3 in December. The increase is 1.0/year, and indicates that the deposition of the dentinal growth layers is annual.

Growth of dentine

The postnatal growth of dentine is shown in Fig. 1. The thickness is measured on the convex ramus of the tooth section from the proximal end of the prenatal dentine to the pulp wall. Because the apex of the pulp cavity reaches the level of the base of the fetal dentine, this measurement is not possible on some males after 8.5 years of age or on some females after 6.5 years. The deposition of dentine is rapid between 0.25 and 0.5 year of age. This period may correspond with the time of tooth eruption and more indirectly with the start of taking solid food (see Kasuya and Marsh, in press). After 0.5 year of age the thickness increases at a slightly decreasing rate. The mean annual increment of the dentine in the juvenile stage is calculated from Fig. 1 as about 0.95 mm in the first year, 0.40 mm in the second year, 0.33 mm in the 3rd year, and 0.30 mm in the 4th year.

The deposition of secondary dentine starts in some pilot whales of both sexes at the age of seven years, and in most individuals by 16 years of age (Fig. 6). Although secondary dentine starts to form during the years when pilot whales mature sexually, there is no correlation between the two phenomena in individual whales and the age at which secondary dentine first forms varies between different teeth in the same jaw (Table 3). Secondary dentine deposition starts at several points on the pulp cavity wall as discussed by Sergeant (1962), and comprises increasingly more of the tooth tissues as the whale ages. It appears translucent on thin undecalcified sections and is less stainable in the decalcified and stained sections (Plate II, Figs 1, 2, 3, and 6). The annual growth layers in secondary dentine are less regular than in ordinary dentine and the contrast between stainable and unstainable layers is usually less pronounced (Plate II, Fig. 2). However, we consider that secondary dentine is not a real obstacle to age determination in *G. macrorhynchus*, because (1) even in old individuals some small areas of ordinary dentine are usually evident along the wall of the pulp cavity and (2) reading the layers in secondary dentine is not very difficult in the decalcified and stained sections (Plate II, Figs 2 and 3).

Another characteristic of the short-finned pilot whale tooth is the deposition of a tissue on the wall of the pulp cavity that we have tentatively called " cellular dentine " (Plate III, Figs 3 to 7). In decalcified and stained sections, this tissue looks rather like cementum. Although the " cellular dentine " contains minute growth layers, the spacings are irregular making counting almost impossible. The deposition of " cellular dentine " starts at the base of the pulp cavity, but progresses further along the cavity in some individuals 10 years or more in age. The boundary between the " cellular dentine " and cementum is less obvious than between this tissue and both other types of dentine.

While preparing teeth for age determination, it was noted that " cellular dentine " tended to be laid down by unusually fibrous pulp which adhered closely to the wall of the pulp cavity. In few exceptional males, the entire wall of the (still open) pulp cavity was lined with " cellular dentine " making it impossible to count the dentinal growth layers (Fig. 6).

Pulp cavity

We classified the condition of the pulp cavity as follows:

1. *Open pulp cavity* All dentinal growth layers continuous in a longitudinal tooth section, dentine being deposited along the entire pulp cavity wall. Similar numbers of dentinal and cemental growth layers.
2. *Closing pulp cavity* Some of the dentinal growth layers (at least the latest one) discontinuous in a longitudinally sectioned tooth. Growth layers deposited along a limited portion of the pulp cavity wall only, the remainder being lined with a strongly-stainable thin layer of uniform structure, which does not contain cells in it. The number of dentinal growth layers may coincide with the number of cemental layers within the range of reasonable error if the best portion of the pulp wall is used for counting.

TABLE 2. LIST OF WHALES WITH CLOSED PULP CAVITV

Sample no.	Age (yrs)		Gonad*	Reproductive status	B.L. (cm)	Sample no.	Age (yrs)		Gonad*	Reproductive status	B.L. (cm)
	dentine	cement					dentine	cement			
Male						Male					
9- 1	26.5+	30.5	2235	—	510	16- 5	30.5+	33.5	1850	Mat.	473
9-23	30.5+	42.5	1475	Mat.	478	18- 1	31.5+	45.5	1360	Mat.	431
9-75	34.5+	41.5	2150	Mat.	491	18- 3	40.5+	45.5	1750	Mat.	463
13-16	28.5+	34.5	2010	Mat.	479	18-49	40.5+	41.5	880	Mat.	444
15- 8	35.5+	39.5	1570	Mat.	438						
Female						Female					
1-16	33.5+	52.5	—	Mat.	378	15-33	46.5+	57.5	12	Rest.	358
5-N3	22.5+	38.5	1+	Preg.	340	15-37	29.5+	35.5	8	Lact.	339
7- 2	22.5+	26.5	13	Preg.	335	16- 8	47.5+	62.5	—	Rest.	363
7- 4	22.5+	32.5	9	Preg.	354	16-19	38.5+	43.5	16	Lact.	353
9- 3	34.5+	38.5	—	Rest.	360	17-20	33.5+	38.5	5	Rest.	368
9-38	35.5+	38.5	—	Rest.	364	17-41	35.5+	47.5	7	Lact.	353
9-47	29.5+	45.5	—	Lact.	381	20- 7	25.5+	36.5	—	—	375
9-55	29.5+	34.5	—	Rest.	368	22- 2	30.5+	55.5	13	Rest.	381
12- 4	33.5+	48.5	7	Mat.	354	22- 7	34.5+	43.5	14	Rest.	382
12-11	32.5+	43.5	10	Lact.	376	22- 9	40.5+	44.5	9	Rest.	380
12-18	22.5+	37.5	12	Rest.	368	23- 8	32.5+	47.5	14	Rest.	363
13-10	42.5+	42.5	13	Lact.	381	24-12	37.5+	45.5	8	Rest.	365
15- 2	38.5+	42.5	6	Rest.	350	24-14	38.5+	50.5	13	Lact.	382
15- 4	35.5+	55.5	4+	Rest.	382	24-19	41.5+	46.5	6	Rest.	377
15- 5	40.5+	47.5	10	Rest.	352	24-24	24.5+	35.5	15	Lact.	372
15-13	42.5+	51.5	8	Rest.	355	25- 3	37.5+	39.5	17	Rest.	—
15-18	22.5+	25.5	10	Rest.	371	25-30	38.5+	45.5	12	Rest.	352
						26-12	34.5+	48.5	12	Lact.	348

* Weight of one testis in gram or number of corpora in ovaries (Data from Kasuya and Marsh (in press) and Marsh and Kasuya (in press)).

Abbreviations: B.L.: body length; Mat.: mature; Preg: pregnant; Rest.: resting; Lact.: lactating.

3. *Closed pulp cavity* Dentinal growth layers discontinuous in a longitudinally-sectioned tooth. The wall of the pulp cavity entirely covered by a thin uniform layer of stainable dentine. The number of cemental layers equal to or greater than the number of dentinal layers irrespective of where the dentinal layers counted.

A closing pulp cavity may occur in males over 21.5-years old and in females over 24.5-years old, and the closed pulp cavity in males over 31.5-years old and in females over 24.5-years old (Table 2). At ages between 20 and 45 years, the proportion of closing or closed pulp cavities is higher in males than in females suggesting that dentine deposition tends to cease earlier in males. About 25 to 50% of females over the age of 40 years still have an open pulp cavity (Fig. 6).

Figure 7 documents the changes in the (maximum) diameter of the pulp cavity that occur with increasing age. The diameter of the pulp cavity tends to be greatest at the proximal end in animals less than a year old and in the middle region in older whales. There is no sexual dimorphism in this character. The diameter of the pulp cavity decreases from about 10 mm for whales less than two-

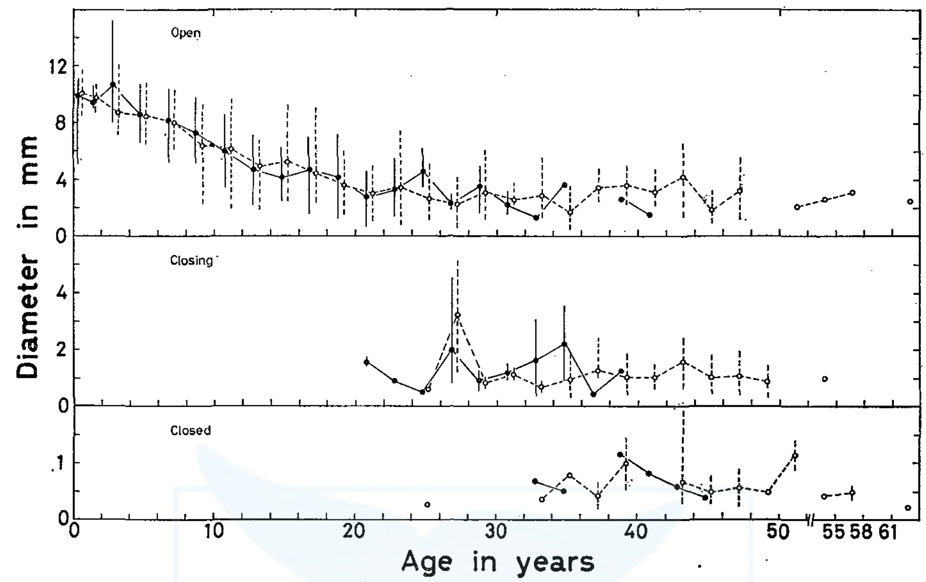

Fig. 7. The mean and range of the diameter of the pulp cavity in *G. macrorhynchus*. Open circles and dotted line represent females, and closed circles and solid line males.

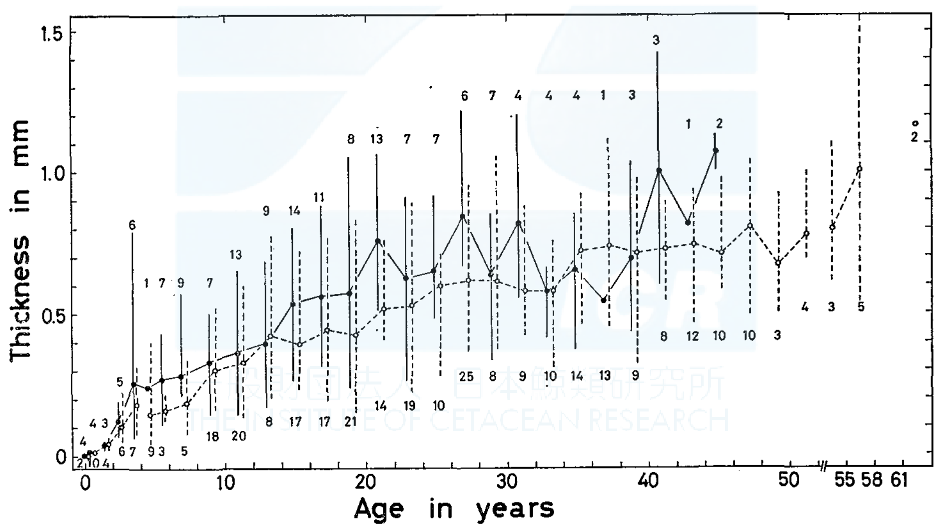

Fig. 8. Thickness of cementum in *G. macrorhynchus* showing means, ranges, and sample sizes. Open circles and dotted line represent females and closed circles and solid line males.

years old to about 3 mm in whales over 20-years old when the cavity starts to close. " Closing " pulp cavities tend to have a relatively constant mean diameter of about 1 mm while the mean diameter of a " closed " pulp cavity ranges from 0.5 to

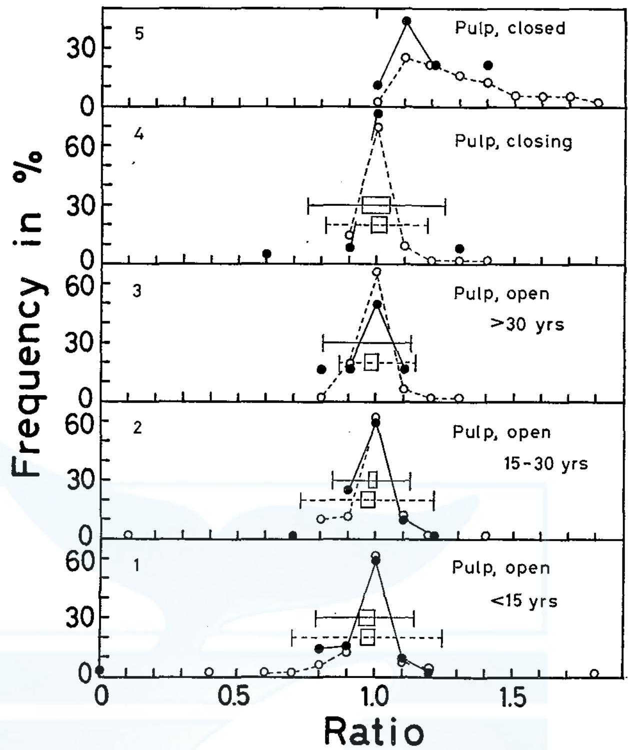

Fig. 9. Ratio of the number of cemental growth layers to the number of dentinal growth layers in *G. macrorhynchus*. 95% confidence interval for the mean (box) and 2×SD range (bar) are indicated on each side of the mean. Open circles and dotted line indicate females, and closed circles and solid line males. 1: 68 males and 61 females below 15 years of age. 2: 53 males and 121 females between 15 and 30 years of age. 3: six males and 45 females over 30 years of age. 4: 22 males (20–40 years) and 46 females (25–52 years). 5: nine males (30–45 years) and 32 females (25–63 years).

1.0 mm and shows no decline with age. These observations are consistent with dentine being deposited only along limited parts of the pulp cavity wall in the " closing " stage and deposition ceasing in the " closed " stage.

Cemental growth layers

Figure 8 shows the maximum cementum thickness plotted against age. Cementum is absent from the teeth of very young postnatal whales. The largest individual without cementum was a male 154 cm long and aged about 1.5 months (age estimated from body length). The smallest individual with a cemental layer was a 163 cm long female (estimated from its length to be two or three-months old). Seven whales less than 200 cm long had tooth cementum. Therefore, we conclude that the deposition of cemental layers starts in *G. macrorhynchus* at a few months of age. Cemental growth is rapid between two and four years of age (Fig.

8). After that the thickness increases at a lower rate, but continues throughout life. After two years of age, males tend to have thicker cementum than females (Fig. 8).

Although the cemental growth layers are much narrower than the dentinal growth layers, the accessory layers are less conspicuous and we consider that the readability of both tissues is about the same (compare figures in Plates I, II, and III). When reading the cemental growth layers it is important to remember that (1) the first or second layer is usually limited to the distal portion of a tooth and (2) in older whales the later layers are usually very thin or absent in the distal part of the tooth. Therefore a whole set of cemental growth layers of an old individual cannot be seen in one cross section of the tooth. It is necessary to read the layers from the inner distal layers to the outer proximal layers as in *Berardius bairdii* (Kasuya, 1977).

Figure 9 shows the number of cemental growth layers expressed as a proportion of the number of dentinal layers. In young whales there is a tendency to underestimate the number of cemental growth layers compared with the number of dentinal growth layers.

For most whales with an open or closing pulp cavity, the counts of dentinal and cemental growth layers were very close. The mean difference from parity of the ratio of cemental layer count: dentinal layer count was only 3.4%, even though there were some exceptional individuals in which the ratio was as high as 1.8 (Fig. 9). We therefore conclude that the deposition of cemental layers is also annual.

Even though we have not otherwise calibrated the cemental layer deposition rate, we consider that cemental layers continue to be deposited after dentine deposition has ceased, for the following reasons. (1) The age at which dentine deposition ceases is very variable and the cessation occurs concomitant with redution of pulp cavity after the transitional " closing " stage. Thus there is no evidence to suspect that cessation is caused by a physiological change which would also affect cementum deposition. (2) The thickness of cemental growth layers decreases constantly throughout life with no indications of an abrupt decline. (3) The technique of reading cemental growth layers was repeatedly standardized by checking young teeth.

Errors in age determination

Errors due to the position of the teeth used for age determination: Hui (1980) reported that in *Tursiops truncatus* the deposition of dentinal growth layers ceases earlier in teeth near the anterior and posterior ends of the row than in the other teeth. In order to test whether this was also true in *G. macrorhynchus*, we counted the growth layers in a series of teeth from five jaws from three whales. Each of the growth layer counts shown in Table 3 is the middle value of three repeat counts. Even though the pulp cavities of all the teeth of the youngest whale (No. 17–7, estimated age 19.5 years) were open, the dentinal growth layer counts of the teeth at the ends of the row were significantly less than those of the other teeth probably because the posterior teeth were smaller and tended to have irregular growth layers. In con-

TABLE 3. COMPARISON OF GROWTH LAYER COUNTS OF SEVERAL TEETH FROM THE SAME WHALE

Sample no.	17–7			23–5			18–3		
BL, Sex	437 cm, male			366 cm, female			463 cm, male		
	C	D	S	C	D	S	C	D	S
Upper teeth (numbered from anterior to posterior)									
1	20	13	11				44	20	11
2	20	20	11				47	32+	11
3	18	20	13				44	31	17
4	17	19	13				44+	27+	7+
5	17	17	9				45+	28+	12+
6	19	19	11				45+	22+	13+
7	19	16	11				45+	19+	—
Lower teeth (numbered from anterior to posterior)									
1	21	17	11	29	30	12	46	32+	12+
2	20	20	9	30	29	13	46	34+	15+
3	19	20	14	29	30	9	46	41	13
4	20	20	13	29	30	7	47	41	15
5	21	20	13	28	31	8	46	35	14
6	20	20	11	30	30	9	48	46	13
7	20	19	12	30	31	9	46	40+	13+
8	19	17	12	25	28+	10+	42	22+	9+
9	19	17	14	—	—	—	—	—	—
10	20	15+	—	—	—	—	—	—	—

Code: C: No. of cemental layers; D: No. of dentinal layers; S: Age (no. of layers) when secondary dentine first deposited; +: Neonatal line or first cemental layer lost by abrasion; BL: Body length.

trast, similar differences were not observed in the 29.5-year old female (No. 23–5). All the teeth of the oldest animal (No. 18–3, 45.5 years) had closed pulp cavities with the exception of the 6th tooth of the lower jaw which had a "closing" pulp cavity. Dentine probably ceased to be deposited in this animal when it had laid down between 36 and 46 dentinal layers. However, only 20 dentinal layers were counted in the anterior teeth.

In contrast, no significant differences were observed between the cemental growth layer counts of different teeth from the same whale except for the two smallest teeth of No. 18–3 (Table 3).

These results suggest that errors in age determination due to tooth position will not occur if the largest tooth near the center of the row is used.

Calibration errors: Errors can occur when the growth layer count is converted into absolute age. The age of *G. macrorhynchus* older than 10 years was expressed as the nearest n minus 0.5 years where n was the number of stainable layers counted (Any incomplete stainable layers in the first or last cycle were regarded as complete and unstainable layers were ignored). As each complete stainable or unstainable layer represents about six months, the true age of an individual with n stainable layers is between $n-1.5$ and $n+0.5$ years *i.e.* a mximum error of ± 1.0 year. For

TABLE 4. INDEX OF ERROR IN AGE ESTIMATION (I, %): DIFFERENCE BETWEEN THE MIDDLE COUNT AND ITS CLOSEST COUNT IN THREE READINGS OF THE SAME TOOTH EXPRESSED AS PERCENTAGE OF THE MIDDLE COUNT

Error (I)	Age (yr) and Tissue used[1]			
	0–15 (D)	15–30 (D)	>30 (D)	>30 (C)
Males				
<−5.0	1.2	4.5	0.0	0.0
−5.0∼−2.5	0.0	7.6	7.1	0.0
−2.5∼+2.5	95.1	87.9	85.8	55.6
+2.5∼+5.0	2.5	0.0	0.0	44.4
≥+5.0	1.2	0.0	7.1	0
Total, %	100.0	100.0	100.0	100.0
No. of whales	81	66	14	9
Mean	+0.07	−0.52	+0.27	−1.97
SD	1.22	1.57	1.93	2.04
Females				
<−5.0	1.9	3.1[2]	3.4	0.0
−5.0∼−2.5	0.0	6.2	5.7	6.5
−2.5∼+2.5	97.2	80.6	78.3	80.6
+2.5∼+5.0	0.0	7.0	11.5	9.7
≥+5.0	0.9	3.1	1.1	3.2
Total, %	100.0	100.0	100.0	100.0
No. of whales	107	129	87	31
Mean	−0.10	+0.10	+0.02	+0.60
SD	1.38	2.18	2.24	1.88

[1] Age based on counts of growth layers in dentine (D) (teeth with open or closing pulp cavities) or cementum (C) (teeth with closed pulp cavities).
[2] One reading of cemental layer included.

G. macrorhynchus less than 10 years of age, the number of growth layers was counted to the nearest 0.25 deposition cycle by estimating the thickness of the first and last incomplete layers. The maximum error of this is 0.5 cycle (=year).

Counting errors: Since three repeat counts were done by the same reader for both cementum and dentine with the middle value considered the best, the index of error (I, %) is calculated by the following formula:

$$I=\frac{C-M}{M}\cdot 100$$

where M indicates the middle reading and C the reading closest to the middle reading. The result is shown in Table 4 arranged by sex, age, and tissue type. The standard deviation of the index or error increases with the age of animals from less than 1.4% to over 2.2%. The error expected for repeat counts done by the same person has a standard deviation of about 2%, giving a 95% confidence range of about 2%×2=4% of the middle reading.

If the errors due to calibration and counting are added together, the 95%

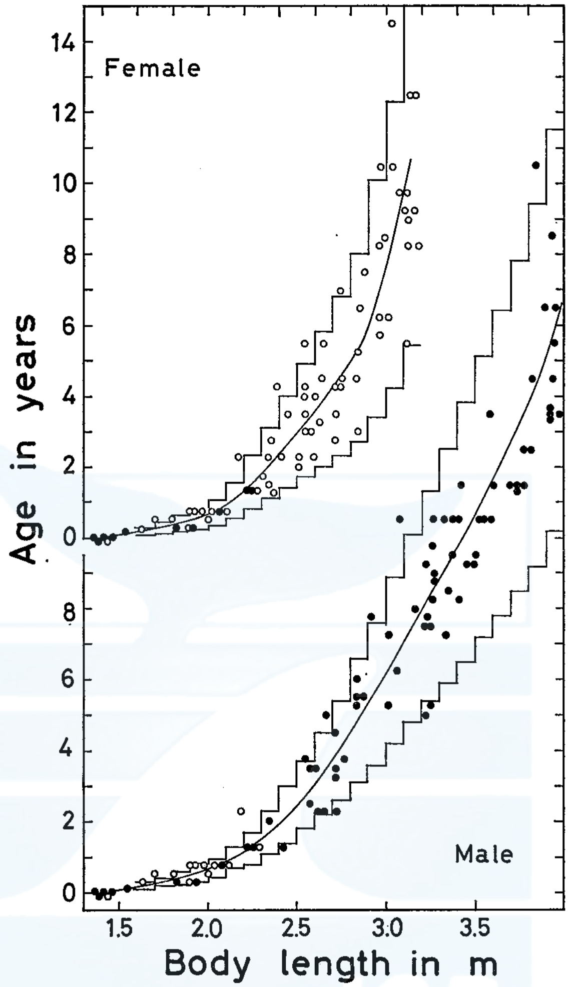

Fig. 10. Conversion of body length into age in *G. macrorhynchus*. Means and 95% confidence intervals are indicated. Open circles represent females and closed circles males.

confidence range for the age estimates at ages 10, 20, 40 and 60 years are estimated to be ±0.9, ±1.8, ±2.6, ±3.4 years respectively. The confidence range for the youngest ages may be slightly narrower than indicated, because the value of *I* tends to be overestimated in this instance.

Conversion of body length into age

The ages of juveniles from which teeth for age determination were not available were estimated from their body lengths as follows. For whales in each 10 cm size-class below 400 cm (males) and 320 cm (females), the mean and coefficient of variation of the ages were calculated. (For whales less than 230 cm long, data for both sexes were combined). As these mean ages fluctuated due to sampling error they were smoothed by eye as in Fig. 10. For females, the coefficients of variation were nearly constant and had a mean of 0.234. In the male, the coefficients of variation tended to decrease with increasing age (because males tend to be larger) and had a mean of 0.182. The 95% confidence interval of the age corresponding to each size class was calculated (assuming that age was normally distributed for each size class and that the coefficient of variation was constant) as:

(smoothed age)$\pm$(smoothed age)$\times$(coefficient of variation)$\times$2

The results are shown as squares in Fig. 10. In females and males less than 330 cm long, the confidence interval approximately coincides with the range of observed values. In larger males the observed range tends to be smaller than the confidence interval, probably because the coefficient of variation was actually decreasing not constant as assumed.

Using this technique it is possible to estimate age within two years for females below 280 cm (mean converted age about 5 years) or for males below 320 cm (mean age about 8 years).

GROWTH CURVE AND BODY WEIGHT

Body length frequencies

The body length frequencies in Fig. 11 are based on the data from 18 schools (Schools 7 through 24). The frequencies are biased, because the catch of a driving fishery may under-represent the juveniles in the population (see Kasuya and Marsh, in press) and because the whales below length 320 cm are missing from one large school (School 9) (see Kasuya and Marsh, loc. cit.).

The largest of the 449 females was 405 cm long. The next longest females were two animals of 400 cm. The adult female length frequency has a single mode at about 360 cm (Fig. 11).

The maximum male body length measured in the present study was 580 cm (No. 9–171), which was followed by much smaller males of 525 and 520 cm. The largest individual, which was measured by Ms C. Goebel, had testes weighing 1.7 and 1.8 kg but no other biological data were collected. We consider that this individual was exceptional among the 201 males examined and may have belonged to the larger of the two types of pilot whale recently recorded from Ayukawa*, and that the maximum body size expected for males of the form usually taken off central Japan will be 525 cm. The male length frequency is more diffuse than

* Since completing this study, Miyazaki and Kasuya (unpublished) have observed two types of pilot whales off Ayukawa (38°20′N) on the Pacific coast of northern Japan in November. This is near the northern boundary of the range of *G. macrorhynchus* at this time of year. Both types have skull feature characteristic of *G. macrorhynchus* as described by Bree (1971). The smaller type is identical to those taken off central Japan and studied in this paper. The other type is possibly a boreal form. It is from one to two meters larger, and has more pronounced saddle mark. The forehead of the adult male is roundish rather than square as in the smaller type. The two forms are presumably geographical races corresponding to those reported by Polisini (1980) from the eastern North Pacific.

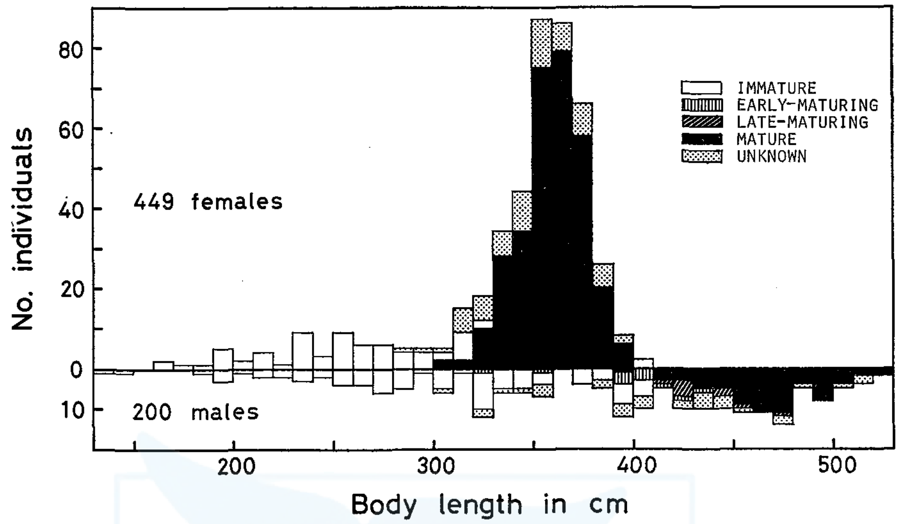

Fig. 11. Frequency histogram of body lengths and growth stages in *G. macrorhynchus*. All data from schools 7 to 24 are included. In school 9, individuals below 320 cm are underrepresented. " Early-maturing " stage represent males with testes where more than 0 but less than 50% of tubules are mature, " late-maturing " those males with testes where from 50% to 100% (exclusive) of tubules are mature, and " mature " those males whose seminiferous tubules are all mature (equivalent to social maturity) (Kasuya and Marsh, in press). For further description of the stages of sexual maturity see Kasuya and Marsh (in press).

that of the female with a possible adult mode at about 470 cm body length. Both the maximum and modal lengths of males are about 110 to 120 cm larger than the corresponding figures for females.

Growth curve

In Fig. 12, the mean body length of each age group is plotted against the corresponding age for each sex. The mean growth curve between the mean birth length of 139.5 cm (Kasuya and Marsh, in press) and asymptotic length has been drawn by eye for each sex as an indication of the general growth trend. The coefficients of variation of body length for each age group for each sex are shown at the bottom. Age-length keys for the samples have been included as Appendices 1 and 2.

The mean growth curves are divided into the four phases; (1) a phase of rapid neonatal growth, (2) a juvenile phase of less rapid but almost linear growth, (3) growth between puberty and mean asymptotic length, and (4) a phase of no increase in body length.

The first phase, in both sexes, is similar and seems to end at about 1.25 years of age. The mean growth in this period (mean length at 1.25 years (230 cm)—mean length at birth (139.5 cm)=90.5 cm) represents a mean annual growth rate of 72.4 cm, slightly smaller than that in the first year after birth (225 cm—

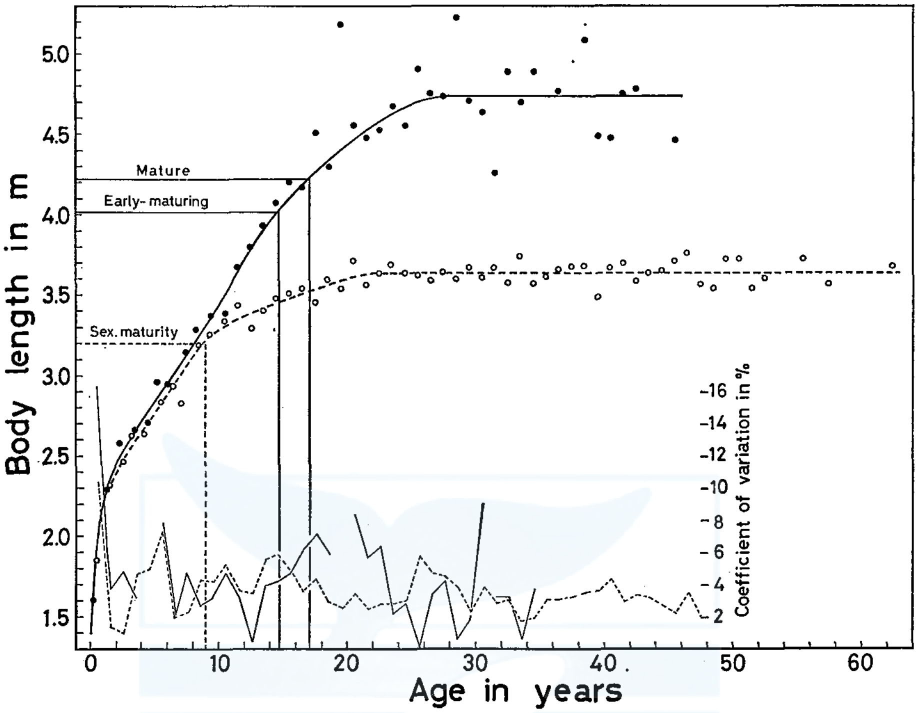

Fig. 12. Mean growth curve of *G. macrorhynchus*. Open circles and dotted line represent females, and closed circles and solid line males. The mean ages and body lengths at the onset of sexual maturity (females), of the " early-maturing " stage (male), and of the ' mature " stage (male) are indicated. Curves between birth and asymptotic length are fitted by eye. For description of the stages of sexual maturity see Fig. 11.

139.5 cm=85.5 cm or 62.1% of the neonatal length). This phase may last slightly longer in males because by the age of 2.5 years, males average 254 cm long, 6 cm longer than females.

The second growth phase lasts, in females, until about the mean age of first ovulation (9.0 years, see Kasuya and Marsh, in press). During this phase the body lengths of females tend to be several centimeters smaller than those of males of similar age. The mean growth rate for females between 2.5 and 9 years is 11.4 cm per year ((322−248) cm/6.5 years). In males, this second growth phase lasts slightly longer until about 10 years of age but the mean growth rate is fairly similar, about 12 cm per year ((344−254) cm/7.5 years).

The third growth phase ends, in females, at about 22 years when the growth curve reaches the mean asymptotic length. The mean growth rate for females during this phase is (364−322) cm/(22−9) years=3.2 cm per year. In males, the corresponding growth phase begins at about 10 years of age with slightly accelerated prepubertal growth followed by a gradual decrease in the growth rate until the growth curve reaches the asymptote at about 27 years. Under these circum-

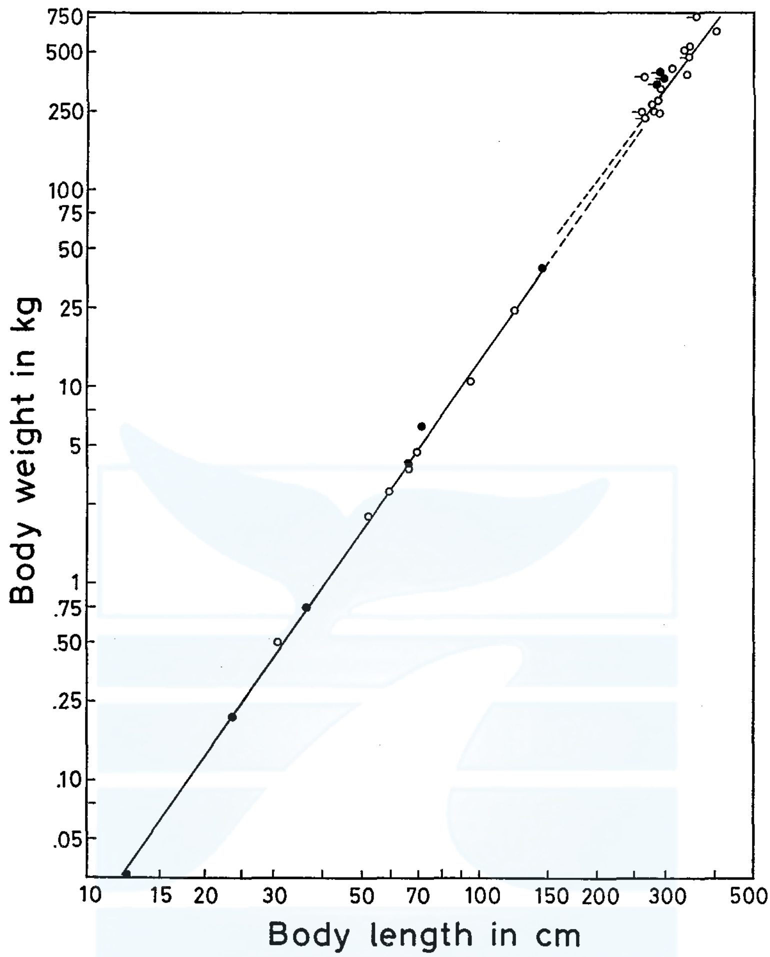

Fig. 13. Relationship between body length and body weight in *G. macrorhynchus* plotted on a double logarithmic scale. Open circles indicate females, closed circles males, and circle with bar individuals which died in an aquarium.

stances, calculation of a mean growth rate over this entire period is not meaningful. The mean growth rate for males between ten years and fourteen years of age is (397−344) cm/4 years=13.3 cm per year while that of males between 23 years and 27 years of age is (473.5−461) cm/4 years=3.1 cm/year.

The last phase starts at 22 years in females and at 27 years in males, when all individuals stop growing. Presumably some individuals will cease growing at a younger age and the proportion of individuals ceasing growth will increase with age until the ages mentioned above. The " mean asymptotic lengths " (in the sense usually accepted for cetaceans) for *G. macrorhynchus* are as follows:

Sex	Number of samples	Mean asymptotic length	95% confidence interval of mean
Female	181	364.0 cm	±1.9 cm
Male	35	473.5 cm	±9.1 cm

These figures are close to the modal lengths in the body length frequencies.

TABLE 5. BODY WEIGHT OF *G. MACRORHYNCHUS*

No.	Body length (cm)	Body weight (kg)	Sex	Remarks
1	12.5	0.0328	♂	Fetus
2	23.3	0.2112	♂	"
3	30.6	0.500	♀	"
4	36.5	0.750	♂	"
5	52.0	2.20	♀	"
6	59.5	2.94	♀	"
7	65.5	3.97	♀	"
8	66.5	4.15	♂	"
9	69.5	4.75	♀	"
10	72.0	6.40	♂	"
11	95.0	10.70	♀	"
12	123	24.50	♀	"
13	144	40.20	♂	"
14	275	275	♀	At capture
15	275	250	♀	"
16	285	285	♀	"
17	286	245	♀	"
18	290	325	♀	"
19	310	410	♀	"
20	330	520	♀	"
21	335	380	♀	"
22	340	530	♀	"
23	400	650	♀	"
24	260	255	♀	At death after 547 days in captivity
25	263	237.19	♀	" 270 "
26	265	377.90	♀	" 225 "
27	281	348	♂	" 311 "
28	290	406	♂	" 362 "
29	291	379.22	♂	" 192 "
30	335	484.60	♀	" 11 "
31	355	751.90	♀	" 228 "

Body weight

Table 5 shows the intact body weights of 13 fetuses and 18 postnatal individuals. As shown in Fig. 13, whales weighed at death after being kept in the museum tend to be heavier than those measured at capture. We considered this to be the result of over-feeding and/or lack of exercise, and excluded those data from the following analyses.

Figure 13 shows the relationship between body length (L, cm) and body

TABLE 6. BODY WEIGHT OF *G. MACRORHYNCHUS* AT SEVERAL GROWTH STAGES CALCULATED FROM BODY LENGTH-BODY WEIGHT RELATIONSHIP

Growth stage and sex		Mean body length (cm)	Body weight (kg)
Birth	(♀♂)	139.5	37.0
Sexual maturity	(♀)	315.6	391
Asymptotic length	(♀)	364.7	593
Early-maturing stage*	(♂)	401.1	781
Mature stage*	(♂)	422.1	904
Asymptotic length	(♂)	473.5	1260

* For definitions see Fig. 11, and for detailed descriptions of these stages see Kasuya and Marsh (in press).

weight (W, kg) of specimens of *G. macrorhynchus* plotted on logarithmic scales. The least squares regression of 10 postnatal females is,

$$\log W = 2.6642 \times \log L + \log (8.403 \times 10^{-5})$$
$$275 \leq L \leq 400 \qquad r = 0.93$$

The similar relationship of 13 fetuses of both sexes is,

$$\log W = 2.8772 \times \log L + \log (2.432 \times 10^{-5})$$
$$12.5 \leq L \leq 144 \qquad r = 0.99$$

The gradients of these equations are not significantly different (T-test, P> 0.3). Although a larger sample may provide evidence of significantly different gradients for the fetal and postnatal stages, we consider that a single equation fitted to fetal and postnatal individuals is more appropriate with the present sample size. This equation is,

$$\log W = 2.8873 \times \log L + \log (2.377 \times 10^{-5})$$
$$12.5 \leq L \leq 400 \qquad r = 0.85$$

This equation does not include postnatal males, which as adults develop a bulbous melon larger than that of females (Yonekura, Matsui, and Kasuya, 1980). Yonekura *et al* (1980) described the changes in shape which occur in *G. macrorhynchus* from a slender head with a pointed rostrum during early postnatal life to the moderately bulbous head of adult females or subadult males. This change does not significantly affect the body length-body weight relationship mentioned above. Therefore, we suspect that the above equation will approximately describe the body length-body weight relationship throughout life for both sexes and have accordingly used it in calculating the body weights shown in Table 6.

DISCUSSION

Our technique of determining the age of *G. macrohynchus* by counting dentinal and/or cemental growth layers in haematoxylin-stained *longitudinal* tooth sections proved very satisfactory. We were able to age all 543 animals in our sample using this technique.

In contrast Perrin and Myrick (1980, p. 19) recommended that cemental layers in *G. macrorhynchus* should be counted in transverse tooth sections. Even though they appreciated that it was possible to lose the first cemental layer using this technique, Perrin and Myrick (1980) considered that transverse sections were superior to longitudinal sections because they were both easier to prepare and to read.

However, our study indicates that, even when the position of the section was carefully selected, more than one cemental layer (either the earliest or latest layers) could be missed from the transverse section of a relatively old tooth (Plates I to III). We consider that the cemental layers are easier to read in longitudinal sections. A wider range of tissue can be scanned in longitudinal sections thus enabling us to eliminate the accessory layers from the count. The variability of repeated cemental layer counts was similar to that of dentinal layers. The difficulty of preparation was minimal by using the method we have developed. In addition, if transverse sections are used for counting dentinal layers, the count is often difficult in older teeth in which secondary dentine is being deposited (Perrin and Myrick, 1980). However, using longitudinal sections enabled us to observe whole pulp cavity and to choose the most readable portion of the tooth (Plates II and III).

Our result indicated that the stainable growth layers in dentine was formed in spring to fall and unstainable dentine in winter to spring, although the time of alternation of dentinal layers was not precisely defined. This seasonality of dentine deposition in *G. macrorhynchus* coincides with that of *Tursipos truncatus* studied by Sergeant (1959) and *Pontopori blainvillei* studied by Kasuya and Brownell (1979), but differs from that of *Stenella attenuata* in the western North Pacific reported by Kasuya (1976). The seasonality of deposition of haematoxylin stainable dentine and/or correspondence of the stainability with optical density can be different between species.

Ogden, Lee and Conlogue (Ms.) listed body lengths of 46 male and 108 female *G. macrorhynchus* stranded on the east coast of the North America. In males, the highest body length frequencies were in the ranges 470 to 480 cm (three individuals) and 480 to 489 cm (three individuals). The largest male had a body length of 535 cm, while the next largest was 525 cm long. In females, the highest body length frequency was in the 360 to 369 cm range (18 individuals). The largest female was 397 cm long and the next largest 392 cm long. These figures are identical to our results from central Japanese coastal waters. Alagarswami, Bensam, Rajapandian and Fernando (1973) reported the body length frequency of 77 whales in a mass stranding of 147 *G. macrorhynchus* in the Gulf of Manar on the southeast coast of India. The identification of the species was based on the skull, teeth and flipper length. The body lengths ranged from 220 to 575 cm (sex was not given). There were two modes in the length frequency, one at 375 to 425 cm, the other at 525 to 550 cm. We suspect that the smaller and larger modes may correspond to the asymptotic lengths of females and males respectively. Because these body lengths are larger than those of known *G. macrorhynchus* but almost identical with those of *G. melaena* as reported by Sergeant (1962), we initially suspected that the method of measuring body length (not detailed in the report) differed from ours. However Alagarswami (pers. comm.) has since confirmed that the body lengths were measured on a straight line from the tip of upper jaw to the notch of flukes. Thus there exists a possibility that the body length of *G. macrorhynchus* in the Indian Ocean may be intermediate between the two geographical forms in the western North Pacific (see footnote on page 75).

Kasuya (1972, 1976) showed that the increase in body length in the first year after birth is between 55 and 65% of neonatal length in several odontoceti *i.e.*, *Stenella coeruleoalba*, 64%; *S. attenuata*, 60%; *Tursiops truncatus*, 55%. Collet (1981) obtained a corresponding value of 61.3% for *Delphinus delphis*. Thus the value we estimated for *G. macrorhynchus*, 61.2%, is in good agreement with the results for other species.

Perrin, Coe, and Zweifel (1976) found for several odontocetes the following relationship between body length at birth (X, cm) and the difference between the fetal growth rate during the linear phase and the average growth rate during an initial postnatal period equal to the gestation period (Y, cm/month),

$$\log Y = -1.33+0.997 (\log X)$$

Substituting the appropriate values for *G. macrorhynchus* (*i.e.*, gestation time 452 days, neonatal length 139.5, and fetal growth rate in the linear phase 10.3 cm/month (for values see Kasuya and Marsh, in press), the above equation predicts a body length of 197.4 cm, 452 days after birth. The corresponding figure, roughly estimated from the growth curve (Fig. 12), is 228 cm.

Ralls, Brownell and Ballou (1980) concluded that males of polygynous cetacean species will have larger body size and higher natural mortality rate compared with the females of the same species. The result of present study (males growing 1.30 times larger than females and living 17 years shorter) and the polygynous social structure of the the species reported by Kasuya and Marsh (in press) agree with their conclusion.

Sergeant (1962) obtained for *G. melaena* the following body length (L, cm)-body weight (W, kg) relationship,

$$W=0.000025\ L^{2.895}$$

using fetuses and juveniles below 235 cm in body length. This relationship is almost identical with the corresponding equation that we have obtained for *G. macrorhynchus*.

ACKNOWLEDGEMENTS

We wish to extend our sincere thanks to all who helped in this study. The cooperation of the dolphin hunting teams at Taiji, Futo, Kawana and Arari made the work possible by allowing the senior author to examine whale carcasses, and to collect the necessary samples. The hunters also provided information on the schools which they had driven.

The Taiji Whale Museum provided laboratory facilities. Dr N. Miyazaki collected the body-length frequency data for one school. The field study was done with the help of many biologists including Dr R. L. Brownell Jr., Dr S. Ohsumi, Mr K. Kureha, Dr N. Miyazaki, Dr T. Otake, Ms E. Miyahara, Mr S. Shiraga, Dr T. Kajihara, Dr K. Hirose and Dr S. Tanaka. Dr D. E. Sergeant kindly cooperated in the cross-reading of several tooth slides of *G. macrorhynchus*. We thank Ms C. Goebel for her collaboration. This study was initially prepared for the Report of the International Whaling Commission (special issue on cetacean reproduction) as a part of a paper on the life history and reproduction of the species, but it had to be split by the financial difficulties. We wish to express our thanks to the two anonymous referees and editor of the IWC volume for their suggestions and criticism. Dr H. Marsh critically read the manuscript and corrected the English. Their cooperation largely improved this paper.

The histology slides were prepared by Ms M. Oya. Ms T. Shirai, Ms M. Nakagiri, Ms Y. Oka and Ms S. Wada assisted in data analyses, typing and drawing.

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APPENDIX TABLES

APPENDIX TABLE 1. AGE-LENGTH KEY OF *G. MACRORHYNCHUS*, FEMALE

Age	Body length																														
n	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	No.	Mean	S.D.
0		1		1	1	1	4	2	1																				11	185.45	19.26
1										1	3																		3	231.00	3.26
2									1		2	1	2	1	1														8	245.50	15.61
3												1	3	1	1	1													7	262.00	12.07
4											1		2	2	3	1													9	264.00	12.85
5													1	1		1	1		1										5	282.60	20.71
6																1	1	1											3	294.33	6.01
7															1	1													2	281.50	6.50
8																	1	1	2	3		1							8	317.50	13.81
9																		1	4	1	3	2							11	325.27	13.18
10																	1	1		1	3	4	1						11	332.81	17.33
11																				1	3	1	3	1					9	343.33	12.25
12																			1	2		1							4	328.75	11.29
13																			1			1	1	2					5	340.22	18.90
14																		1		1	2	4		2	2				12	346.58	20.27
15																				1	1		1	1	1				5	350.00	16.67
16																					2	2	3		2				9	352.66	12.78
17																				1	3	1	1	1	1				8	345.00	14.73
18																					1	1	4	4	3				13	359.30	10.36
19																					1	2	3	4					10	354.10	8.87
20																							1	2	1	1	1		6	370.66	12.53
21																					1		7	2					10	355.60	8.74
22																							5		3	1			9	363.55	10.32
23																							2	4	4		1		11	369.00	10.15
24																							3	1	1	1			6	364.33	10.97
25																					1		1		1		1		4	363.00	20.59
26																				1	2		3	4	4		1		15	359.46	16.74
27																						3	2		4	2			11	363.81	16.23
28																						1	1		2				4	360.25	13.53
29																							1	3		1			5	367.20	8.42
30																						2		1	1	1			5	360.80	13.80
31																							2		2				4	366.50	10.57

32	1		4	1	2			8	358.12	10.79
33				1	1	1		3	373.66	6.34
34		1	3	4				8	357.12	6.75
35	1		2	3	2			8	360.75	10.75
36		1	1	2	2	1		7	365.00	10.92
37		1		3	1	1		6	367.33	11.79
38		1		3	3		1	8	367.37	13.04
39	1			1				2	348.50	12.50
40		1		1	1	1		4	367.25	15.78
41			1	1	1	1		4	369.75	10.70
42		1	2	1		1		5	359.40	11.72
43		1	2	2	1	1		7	363.85	11.30
44			1	3		1		5	365.40	9.62
45				2	1	2		5	371.40	8.21
46				2	1		1	4	375.75	13.32
47		1	3	2				6	356.83	6.84
48			2					2	354.50	0.50
49					1			1	373.00	
50				1	1	1		3	373.33	6.94
51			1					1	355.00	
52		1		1	1			3	361.33	12.39
53								0		
54								0		
55			1		1	2		4	373.25	9.62
56								0		
57			1					1	358.00	
58								0		
59								0		
60								0		
61								0		
62				1	1			2	369.00	6.00

Age: n≤Age in years<n+1. Body length: 10 n≤Body length in cm≤10 n+9.
SD of this table $=[\sum(x-\bar{x})^2/n]^{0.5}$

APPENDIX TABLE 2. AGE-LENGTH

Age																						Body
n	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
0	2	2	1			1	1	1														
1										2		1										
2											1		1	2	1							
3													2	1	3							
4															1							
5														1		3		1		2		
6																1		1				
7																	1	2		3	1	
8																			1	2	1	1
9																				3	1	2
10																		1		1	2	1
11																						1
12																						
13																						
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42																						
43																						
44																						
45																						

Age: $n \leq$ Age in years $< n+1$. Body length: $10n \leq$ Body length in cm $\leq 10n+9$. SD of this table $= [\sum (x-$

KEY OF *G. MACRORHYNCHUS*, MALE

length

35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	No.	Mean	S.D.
																		8	161.62	26.31
																		3	229.00	8.52
																		5	258.00	12.29
																		6	265.50	8.51
																		1	271.00	
																		7	296.00	20.06
																		2	294.00	13.00
																		7	314.28	14.52
																		5	328.00	8.85
1																		7	337.42	10.67
3																		8	339.37	15.91
	1	4																6	366.50	11.91
		1	1															2	379.50	1.50
1				4	1	1												7	393.14	15.18
			1	1	2		1	1										6	406.50	16.89
				1	2			1	2									6	420.00	19.85
				2	1		1	1			1							6	417.16	25.85
						1	2				1	1			1			6	451.33	31.95
				1		1	3			1		1						7	430.00	25.16
																1		1	519.00	
			1							1	1	1		1				5	455.80	37.64
						2		2		2			2					8	447.75	25.66
							1		1	1				1				4	452.75	28.64
										1		2						3	468.33	10.20
									2	1	1	1						5	456.20	12.79
														2				2	490.50	0.50
										1				1				2	474.50	15.50
									1		2	1			1			5	473.60	19.94
																	2	2	522.50	2.50
											2	1	2					5	470.80	8.54
					1					1				1		1		4	463.50	41.65
							1											1	427.00	
												1			1			2	488.50	15.50
											1	1						2	470.00	3.00
											1	1		1		1		4	489.00	18.31
																		0		
												1						1	477.00	
																		0		
															1			1	509.00	
								1		1								2	448.50	10.50
									1									1	448.00	
										1				1				2	474.50	16.50
												1						1	478.00	
																		0		
																		0		
								1			1							2	447.00	16.00

$\bar{x})^2]^{0.5}$.

EXPLANATION OF PLATES

PLATE I

All scale bars represent 0.1 mm.

FIG. 1. Decalcified and haematoxylin-stained section from a newborn female *G. macrorhynchus* (No. 17–46, 163 cm, 0.25–year old, tooth length 22 mm). N indicates the neonatal line in the dentine, and 2 and 3 the positions enlarged in Figs 2 and 3 (this plate) respectively.

Fig. 2. Higher magnification of position 2 in Fig. 1 (this plate). Arrow indicates neonatal line in dentine, and E, cast of dissolved enamel.

Fig. 3. Higher magnification of the position 3 in Fig. 1 (this plate). Arrow and circle indicate a stainable cemental layer (annual layer).

Fig. 4. Decalcified and stained tooth section of an immature male *G. macrorhynchus* (No. 9–73, 326 cm, 5.25 years old with five annual stainable layers of full thickness and 6th (last) stainable layer of incomplete thickness (circles), tooth length 38.4 mm). N indicates the neonatal line, and 5 through 7 the positions enlarged in Figs 5 through 7 of this plate.

Fig. 5. Higher magnification of position 5 in Fig. 4 (this plate), showing cemental growth layers near the neck of the tooth. Circles and arrow indicate 1st to 4th annual stainable layers.

Fig. 6. Cemental layers at position 6 in Fig. 4 (this plate). The 2nd to 5th annual stainable layers are indicated by circles.

Fig. 7. Cemental layer at position 7 in Fig. 4 (this plate). Circles indicate the 3rd to 6th annual stainable layers.

PLATE II

All scale bars represent 0.1 mm.

Fig. 1. Decalcified and haematoxylin-stained tooth section from a lactating female *G. macrorhynchus* (No. 24–22, 366 cm, 27.5–years old, tooth length 42.8 mm). Dentine is still being deposited along the entire pulp cavity wall. C indicates cementum, E cast of dissolved enamel, N neonatal line in dentine, and the numerals the positions enlarged in Figs 2 through 4 of this plate. The dots indicate the annual stainable layers in dentine.

Fig. 2. Higher magnification of position 2 in Fig. 1 (this plate). Annual growth layers are clearer in ordinary dentine (circles) than in secondary dentine. P indicates predentine.

Fig. 3. Higher magnification of position 3 in Fig. 1 of this plate. Annual growth layers are clear in secondary dentine (circles). P indicates predentine.

Fig. 4. Cemental layers at position 4 in Fig. 1 (this plate). Dots indicate 1st to 28th annual cemental layers.

Fig. 5. Cemental layers at position 5 in Fig. 6. (this plate). Dots indicate 2nd to 36th annual cemental layers.

Fig. 6. Decalcified and stained section of a tooth from a resting female *G. macrorhynchus* (No. 17–36, 35.5–years old, tooth length 39.5 mm). Deposition of dentine is about to cease. C indicates cementum, E cast of decalcified enamel, N neonatal line, 5 the position shown in Fig. 5 of this plate.

PLATE III

All scale bars represent 0.1 mm.

Fig. 1. Higher magnification of pulp of the tooth in PLATE II Fig. 6. P indicates predentine. Deposition of dentine is limited to this portion of the pulp wall.

Fig. 2. Cemental layers at position 2 in Fig. 7 (this plate). Dots indicate 1st to 51th annual growth layers.

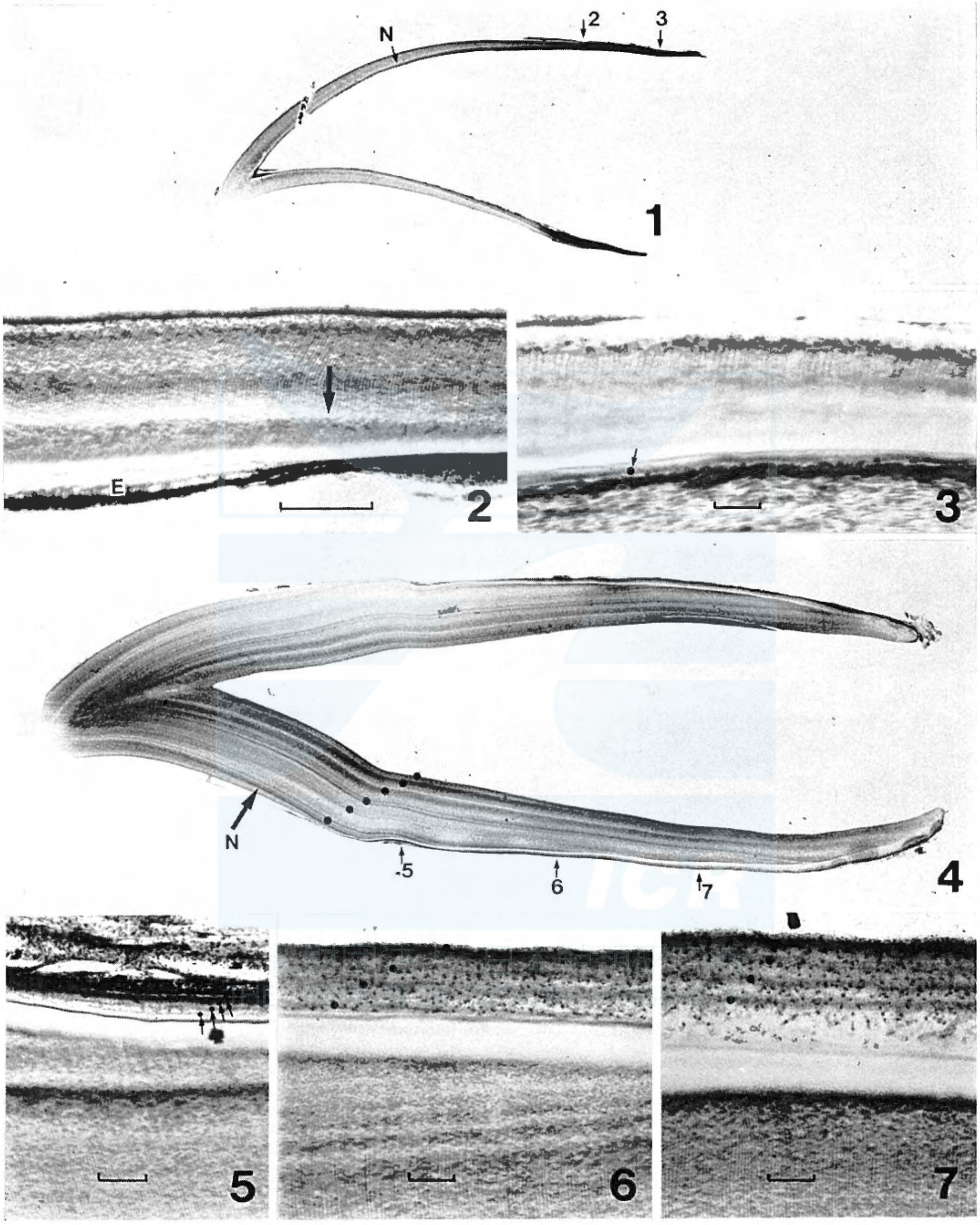
Fig. 3. Top of the pulp cavity of tooth in Fig. 7 (this plate). A strongly-stainable uniform thin layer of dentine (S) indicates the cessation of dentine deposition along most of the wall of the pulp cavity, but thin predentine (P) is still visible at the top and an irregular thin unreadable layer of " cellular dentine " (C) is being deposited. Formation of the cellular dentine has started secondarily on the pulp wall.

Fig. 4. Middle portion of the pulp of tooth in Fig. 7 (this plate). The last two dentinal layers merge in the pulp wall cavity which is covered by thin strongly-stainable uniform dentine (S). Secondary deposition of " cellular dentine " (C) is also visible.

Fig. 5. Base of the pulp cavity of tooth in Fig. 7 (this plate). The last readable dentinal growth layer was deposited as indicated by the arrow. " Cellular dentine " (C) is still being deposited.

Fig. 6. Higher magnification of position 6 in Fig. 7 (this plate). Thick " cellular dentine " is being deposited.

Fig. 7. Decalcified and stained section of a tooth of a lactating female *G. macrorhynchus* (No. 24–14, 382 cm, 50.5–years old, tooth length 38.3 mm). There are 39 annual stainable layers in the dentine and 51 in the cementum. C indicates cementum, E cast of dissolved enamel, N neonatal line in dentine, and 2 and 6 the positions shown in Figs 2 and 6 of this plate respectively.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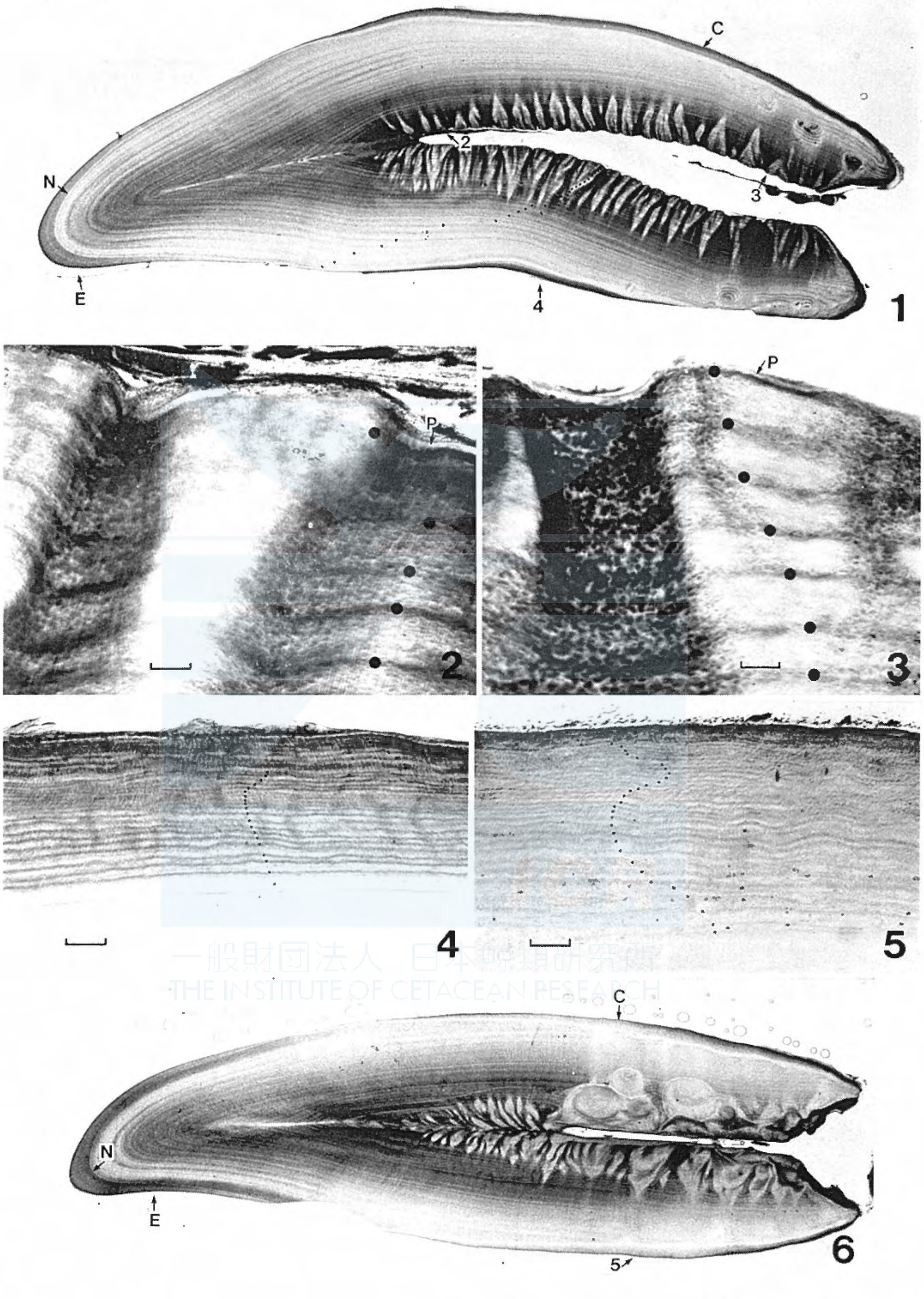
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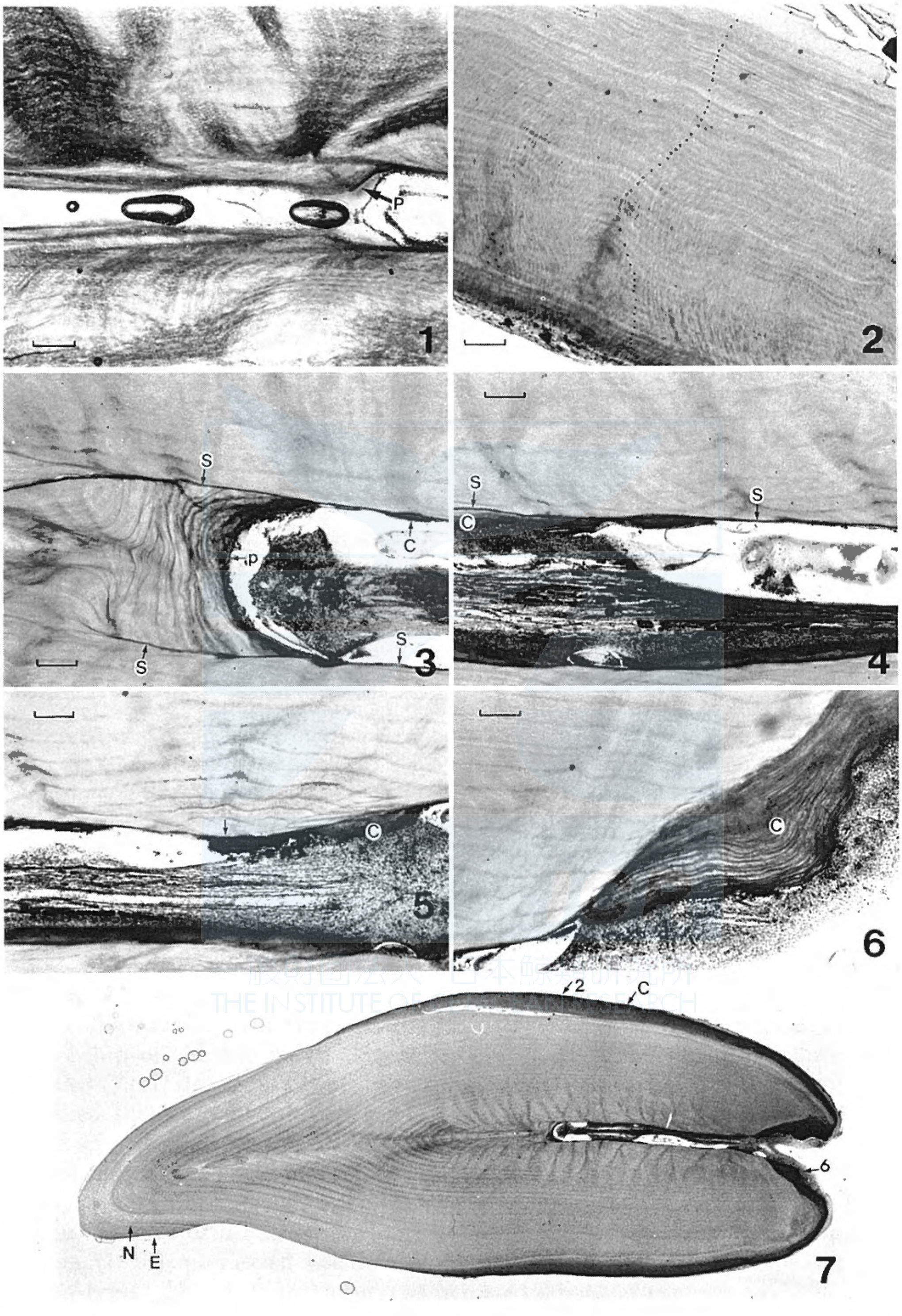
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