PERINATAL GROWTH OF DELPHINOIDS: INFORMATION FROM AQUARIUM REARED BOTTLENOSE DOLPHINS AND FINLESS PORPOISES

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ABSTRACT

The early postnatal growth of bottlenose dolphins and finless porpoises was studied using 97 body length records of 61 individuals born in aquariums. The growth rates observed were similar to those estimated independently for wild dolphins assuming that dentinal growth layers are deposited annually. The perinatal growth parameters thus estimated were also close to those predicted using published interspecific relationships. These results suggest that (1) the dentinal growth layers are deposited annually in these species and (2) the interspecific relationships of the parameters can be used to examine the correctness of growth layer interpretation.

INTRODUCTION

Although some studies use daily or monthly growth layers in tooth (Kasuya, 1977; Myrick, 1980; Myrick, Shallenberger, Kang and Mackay, 1984), most odontocete age determination studies are based on annual growth layers in dentine or cementum (Perrin and Myrick, 1980). This approach limits the precision of individual age estimates, and makes it difficult to study the rapid perinatal growth of dolphins, an important component of their reproductive biology.

Some authors attempted to overcome this problem by defining the interspecific relationship between the growth parameters of better known species. Scott (1949) and Ohsumi (1966) tried to estimate neonatal body length from the size of adult whales. Perrin, Holts and Miller (1977) and Kasuya (1977) defined relationships between neonatal length and gestation time or between neonatal length and fetal growth rate. Perrin, Coe and Zweifel (1976) tried to estimate the early postnatal growth rate of dolphins using gestation

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time and neonatal length. Kasuya (1972), Collet (1981) and Kasuya and Matsui (1984) deduced that delphinoid calves grow about 60 % of the neonatal body length in the first year after birth. However, some of these studies were not free from the age determination problem mentioned above, because growth layer readings were used in the analyses as well as data from known age individuals.

There is still also considerable disagreement concerning the interpretation of growth layers of some toothed whales (Perrin and Myrick, 1980; Jones, Kasuya, Gosho and Miyazaki, 1985). This problem will be solved through examination of growth layers of known age individuals or by comparing growth layer deposition in aquarium-reared individuals and wild individuals assuming that growth does not differ significantly between these two groups at least for the age classes being compared.

In this study, we use data from the bottlenose dolphin, *Tursiops truncatus* (Montagu, 1821), and the finless porpoise, *Neophocaena phocaenoides* (G. Cuvier, 1829), to compare the early postnatal growth of aquarium-reared individuals with that of wild individuals estimated from dentinal growth layer counts assuming an annual deposition rate. We then evaluated published interspecific relationships between the growth parameters as a means of calibrating growth layer readings.

MATERIALS AND METHODS

Body length data of known age individuals were available for 55 bottlenose dolphins and 6 finless porpoises born in aquariums (Tables 1 to 3). Although most body lengths were measured at death, live measurements were obtained from three bottlenose dolphins and two finless porpoises over period of up to 4.7 years. We did not distinguish between deaths due to accident and disease, assuming that the effect of disease might be smaller on body length than on body weight. Parents of these aquarium-reared bottlenose dolphins were obtained from the catch of the drive fishery off the Pacific coast of Japan, and those of the finless porpoise from the intended or incidental take in the Ise Bay or in the Inland Sea (Kasuya, Tobayama and Matsui, 1984). No teeth from the individuals born in aquariums were examined.

Body length frequencies of bottlenose dolphins taken off the Pacific coast of Japan (the same stock as the parents of the aquarium-reared materials) were also available, as well as body lengths and dentinal growth layer counts from bottlenose dolphins from the Iki Island area, which is located in the Tsushima Pass connecting the Sea of Japan and the East China Sea. Although there is no basis for our assumption that these two samples belong to the same population, no significant differences of the body length frequencies, or in the body length at sexual maturity were detected i.e. 50 % of the females off the Pacific coast of Japan were sexually mature at a body length of between 265 and 275 cm (presumably close to the former figure, Fig. 1), while the

TABLE 1. POSTNATAL GROWTH OF MALE *TURSIOPS TRUNCATUS*

Sample No.	Days after birth	Birth yr mo day	Data yr mo day	Body length (cm)	Body weight (kg)	Remarks
1	0	'73. 2. 6	'73. 2. 6.	140.0	29.0	Taiji, Stillbirth
2	0	'76. 6.16	'76. 6.16	126.0	–	Taiji, Stillbirth
3	0	'76. 7.30	'76. 7.30	126.0	–	Taiji, Stillbirth
4	0	'77. 8.12	'77. 8.12	132.0	–	Taiji, Stillbirth
5	0	'84. 6.10	'84. 6.10	116.0	–	Chita, Unknown sex
6	0	'78. 6.14	'78. 6.14	125.0	–	Mito, Unknown sex
7	0	'81. 7.25	'81. 7.25	122.0	–	Taiji
8	0	'77. 7. 5	'77. 7. 5	134.0	–	Misaki
9	3	'81. 7.14	'81. 7.17	133.0	30.0	Taiji
10	4	'84. 6. 3	'84. 6. 7	132.0	23.0	Taiji
11	9	'75. 7.19	'75. 7.28	139.0	–	Taiji, Unknown sex
12	11	'80. 7. 4	'80. 7.15	127.0	–	Taiji
13	21	'82. 9.26	'82.10.17	136.0	–	Taiji
14	63	'78.10.17	'78.12.19	149.0	47.0	Kamogawa
15	147	'75. 7.15	'75.12. 9	181.0	77.0	Taiji
16	154	'77. 6.22	'77.11.24	165.0	–	Taiji
17	189	–	–	183.0	–	Honda (1979)
18	212	'76. 8.17	'77. 3.17	197.5	–	Awashima
19	1164	'79. 2.22	'82. 5. 1	254.0	–	Enoshima
20	297	–	–	197.0	–	Honda (1979)
21	654	'78. 7. 2	'80. 7.16	246.0	–	Shimoda
22	782	–	–	221.0	–	Honda (1979)
23	1418	'77. 8.17	'81. 7. 6	263.0	–	Taiji
24	242*	'76. 9. 9	'77. 5. 9	188.0	–	Kamogawa
	299*		'77. 7. 5	208.0	126.0	
	362*		'77. 9. 6	220.0	136.0	
	422*		'78.11. 5	224.0	161.0	
	472*		'77.12.25	223.0	156.0	
	513*		'78. 2. 4	228.0	–	
	569*		'78. 4. 1	230.0	–	
	595*		'78. 4.27	230.0	–	
	620*		'78. 5.22	234.0	156.0	
	813*		'78.12. 1	245.0	178.0	
	859*		'79. 1.16	–	191.0	
	953*		'79. 4.20	244.0	190.0	
	959*		'79. 4.26	–	190.0	
	1219*		'80. 1.11	250.0	197.0	
	1619*		'81. 2.14	248.0	–	
	1655*		'81. 3.22	265.0	224.0	

*: measured while alive.

TABLE 2. POSTNATAL GROWTH OF FEMALE *TURSIOPS TRUNCATUS*

Sample No.	Days after birth	Birth yr mo day	Data yr mo day	Body length (cm)	Body weight (kg)	Remarks
1	0	'72. 6.19.	'72. 6.19.	120.0	19.0	Taiji, Stillbirth
2	0	'72. 7. 2.	'72. 7. 2.	140.0	30.0	Taiji, Stillbirth
3	0	'77. 7.20.	'72. 7.20.	128.0	–	Taiji, Stillbirth
4	0	'77. 6. 1.	'77. 6. 1.	115.0	–	Misaki
5	1	'79. 8. 2.	'79. 8. 3.	118.7	–	Shimoda
6	1	'81. 7.28.	'81. 7.29.	121.0	–	Shimoda
7	9	'79. 8.30.	'79. 9. 8.	132.0	–	Awashima
8	10	'76. 6.21.	'76. 7. 1.	130.0	25.0	Taiji
9	32	'76. 6.29.	'76. 7.31.	144.0	30.0	Taiji
10	35	'71.10.30.	'71.12. 4.	139.0	35.2	Taiji
11	37	'71. 6.16.	'71. 7.23.	145.0	44.0	Taiji
12	118	'76. 1. 4.	'76. 5. 1.	165.6	68.2	Shimoda
13	194	–	–	179.5	–	Honda (1979)
14	201	'79. 7.26.	'80. 2.13.	194.0	–	Taiji
15	247	–	–	193.0	–	Honda (1979)
16	262	–	–	193.0	–	Honda (1979)
17	275	'80. 9.17.	'81. 6.19.	200.0	–	Awashima
18	370	'74.11. 1.	'75.11. 6.	226.0	–	Awashima
19	398	–	–	204.0	–	Honda (1979)
20	410	–	–	200.0	–	Honda (1979)
21	578	–	–	235.0	–	Honda (1979)
22	627	'77. 5.20.	'79. 2. 6.	200.0	–	Shimoda
23	808	'82. 8.13.	'84.10.29.	252.0	185.0	Taiji
24	1,032	'75. 7.18.	'78. 5.15.	238.0	–	Awashima
25	1,151	'78. 7. 6.	'82. 3.20.	258.0	–	Shimoda
26	1,345	'81. 7. 5.	'85. 3.10.	262.0	200.0	Taiji
27	1,466	–	–	279.0	–	Honda (1979)
28	1,729	–	–	265.0	–	Honda (1979)
29	1,742	–	–	259.0	–	Honda (1979)
30	354*	'79. 7.28.	'79. 7.17.	200.0	–	Kamogawa
	404*		'80. 9. 4.	202.0	–	
	467*		'80.11. 6.	228.0	–	
	510*		'80.12.19.	218.0	–	
	567*		'81. 2.14.	218.0	–	
	724*		'81. 7.21.	228.0	150.0	
	835*		'81.11. 9.	233.0	160.0	
	944*		'82. 2.26.	238.0	–	
	955*		'82. 3. 9.	239.0	150.0	
	986*		'82. 4. 9.	240.0	155.0	
	1,081*		'82. 7.13.	238.0	140.0	
	1,157*		'82. 9.27.	239.0	130.0	
	1,182*		'82.10.22.	238.5	130.0	

(Continued)

TABLE 2. (Continued)

31	635*	'79. 6.28.	'81. 3.24.	236.0	–	Kamogawa
	833*		'81.10. 8.	253.0	170.0	
	865*		'81.11. 9.	–	180.0	
	1,026*		'82. 4.19.	261.0	210.0	
	1,231*		'82.11.10.	271.0	230.0	
	1,237*		'82.11.16.	–	225.0	
	1,257*		'82.12. 6.	260.0	215.0	
	1,332*		'83. 2.19.	264.0	225.0	
	1,357*		'83. 3.16.	–	220.0	
	1,569*		'83.11. 6.	265.0	245.0	

*: measured while alive.

TABLE 3. POSTNATAL GROWTH OF *NEOPHOCAENA PHOCAENOIDES*

Sample No.	Days after birth	Birth	Data	Body length (cm)	Body weight (kg)	Remarks
		yr mo day	yr mo day			
1	0*	'84.4.16	'84.4.16.	77.5	6.6	Yashima, Male
2	4	'77.5. 9.	'77.5.13.	79.0	7.4	Toba, Male
3	17	'76.4.17.	'76.5. 3.	81.5	7.2	Toba, Female
4	28	'81.4.21.	'81.5.19.	83.0	–	Miyajima, Female
5	1,719**	'79.5. 1.	'84.1.14.	159.5	–	Toba, Male
6	864**	'82.4.20.	'84.8.31.	153.5	39.5	Toba, Male

*: stillbirth, **: measured while alive.

corresponding figure for the Iki Island sample was 267 cm (Kasuya, 1985). Body lengths and estimated ages of finless porpoises from the Inland Sea were also used.

The ages of these individuals were estimated from dentinal growth layer counts in decalcified and haematoxylin-stained sections as outlined in Kasuya and Matsui (1984). Growth layer readings were done without biological data.

BOTTLENOSE DOLPHIN

Gestation time and neonatal length

Body lengths of neonatal bottlenose dolphins (measured within 11 days of birth) ranged from 116 to 140 cm. No differences were detected between the length of stillborn dolphins, those that died within two days and those that died on the third to eleventh days. No differences in neonatal body length was detected between the sexes in the present small sample. Combining the data from these 20 neonates, an average of 128 cm was estimated as the mean neonatal length for this species off the Pacific coast of Japan (Table 4).

Scott (1949) found for both mysticeti and odontoceti the following linear relationship between the maximum body length of adult (among both sexes,

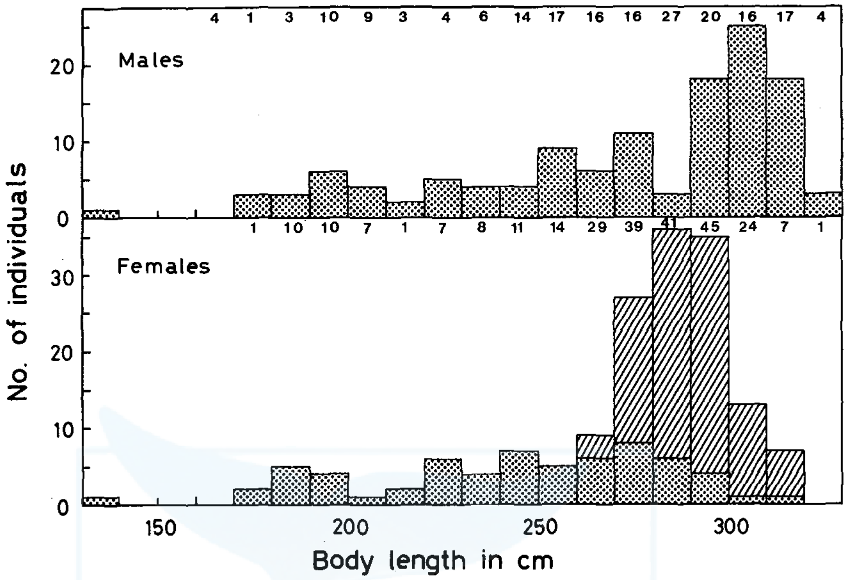

Fig. 1. Body length frequencies of the catch of bottlenose dolphins in the drive fishery off the Pacific coast of Japan (173 males and 165 females sampled from 8 schools driven during 1973 to 1983, represented by the histogram). The parents of the aquarium-reared individuals in the present study were taken by the same fishery. This body length frequency is similar to that of 190 males and 255 females sampled from 6 drivings in the period from 1979 to 1980 in the Iki Island area (indicated by numerals at the top). In the female samples from the Pacific, dotted areas represents sexually immature individuals and shaded areas mature individuals (male maturity was not determined).

X in cm) and the neonatal body length (Y in cm):

$$Y = 0.2441X + 44.3 \qquad \text{Equation 1}$$

Of 165 female and 173 male bottlenose dolphins taken off the Pacific coast of Japan and measured by Kasuya, the largest individual was a male of 328 cm and the next largest 325 cm. The former figure and the above equation suggest a neonatal length of 124.4 cm, which is only 3 % smaller than the figure estimated from the neonates in our sample.

Using data from *Physeter, Berardius, Delphinapterus, Phocoena* and several species of Delphinidae, Ohsumi (1966) suggested the following relationship between mean neonatal body length (Y in m) and mean body length of females at the attainment of sexual maturity (X in m):

$$Y = 0.532X^{0.916} \qquad \text{Equation 2}$$

The Iki Island sample suggests 2.67 m as the body length at which 50 % of females are sexually mature. Using this figure and Equation 2, the mean neonatal length of bottlenose dolphins is estimated as 1.31 m (Kasuya, 1985). This is 2 % larger than the estimate obtained above.

The good agreement between observed and predicted neonatal body

TABLE 4. ESTIMATION OF NEONATAL BODY LENGTH OF *TURSIOPS TRUNCATUS* (cm)

Length of postnatal life	Male	Female	Mean
Stillbirth	126.0	120.0	130.3
	126.0	128.0	–
	132.0	140.0	–
	140.0	–	–
After 0 to 2 days	116.0*	115.0	121.7
	122.0	118.7	–
	125.0**	121.0	–
	134.0	–	–
After 3 to 11 days	127.0	130.0	132.2
	132.0	132.0	–
	133.0	–	–
	139.0	–	–
Mean	129.3	125.6	127.8

*: living on 204th day after birth, **: living on 2364th day after birth.

lengths is probably, in part, due to the fact that Equations 1 and 2 were based on sample sets that include *Tursiops*.

Substituting a neonatal length 128 cm (as estimated above) in the equation of Perrin *et al.* (1977) which describes the relationship between gestation time (Y months) and neonatal length (X cm) for five stocks of Delphinidae:

$$\log Y = 0.4586 \log X + 0.1659 \qquad \text{Equation 3}$$

gives a predicted gestation time of 13.6 months, slightly longer than one year (Odell, 1975) estimated for the Atlantic bottlenose dolphin which has a neonatal length about 10 cm smaller than Japanese coastal population (Nakajima, Takahashi, Ogura and Sawaura, 1963; Hohn, 1980). However, there is no reason at present to conclude that the gestation time of the Japanese population is longer than that of the Atlantic, because above Equation 3 describes the interspecific relationship between these parameter in several delphinoid species rather than the relationship among several populations of a single species.

Kasuya (1977) suggested the following relationship between neonatal length (X in cm) and the daily fetal growth rate for the linear part of the fetal growth phase (Y cm/day) for several species of Delphinidae, *Phocoena* and *Delphinapterus*:

$$Y = 0.001462\ X + 0.1622 \qquad \text{Equation 4}$$

This equation and the neonatal length 128 cm calculated from neonates give a fetal growth rate as 0.3493 cm/day or 10.63 cm/month for *T. truncatus*.

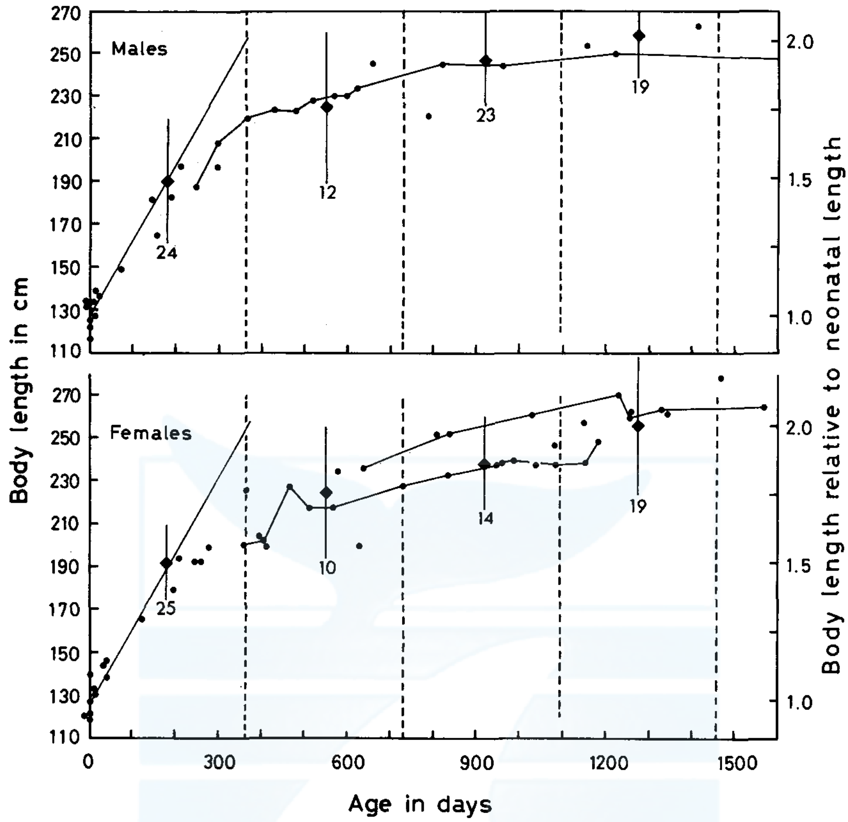

Fig. 2. Bottlenose dolphin body lengths plotted on age. Each independent closed circle represents one aquarium-reared individuals; those connected by solid lines represent repeated measurements of one individual. The diamonds and vertical lines represent the mean body lengths ± 2SD plotted against ages estimated from dentinal growth layer counts (wild individuals taken off Iki Island, for their body length composition see Fig. 1). The numerals indicate the number of individuals whose ages have been estimated. Ages between n and n+1 years were expressed as n+0.5 years (n being integer). The thin solid lines represent extraporation of the linear part of the fetal growth curve through the mean neonatal length (128 cm). Left scale indicates body length in cm and the right scale body length relative to mean neonatal length.

Early postnatal growth

Individual body lengths of aquarium reared individuals and the mean body length of the species from Iki Island area are plotted against age in Fig. 2. The agreement between the two data sets is good, suggesting that (1) the growth in a given range is similar between wild and aquarium-reared individuals and (2) deposition of dentinal growth layers is annual as shown for the Atlantic stock of the species using aquarium reared specimen (Sergeant, Caldwell and Caldwell, 1973).

The rate of increase in neonatal body length decreased with increasing age, and except for some individuals less than 40 days old, the data for most neonates came below the line of the mean fetal growth curve extended through the mean neonatal length. Furthermore, the size of individuals older than 200 days significantly diverged from the line (Fig. 2). These data suggest that the growth rate of postnatal individuals never exceeds that of a fetus during the linear part of its growth.

The mean body length of the present sample of aquarium-reared calves at one year of age falls within the range of 200–220 cm or 1.56–1.72 times the mean neonatal length (Fig. 2). This is in good agreement with the range of 1.55–1.64 times found for five species of Delphinidae (discussed by Kasuya and Matsui, 1984). Perrin *et al.* (1976) deduced, using data of *Physeter, Phocoena, Delphinapterus, Globicephala* and *Stenella*, the following relationship between mean fetal growth rate (X in cm/month), mean postnatal growth rate during the period equivalent to the length of gestation (Y in cm/month) and neonatal length (Z in cm):

$$\log(X-Y) = -1.33 + 0.997 \log Z \qquad \text{Equation 5}$$

Using this equation, a mean fetal growth rate of $X = 128/12$ or $128/13.6$ and a mean neonatal length ($Z = 128$), suggests a mean body length of 184.6 cm at age 12 months or 192.0 cm at 13.6 months. These predicted values are about 10 % smaller than the observed figure and come below the range of individual variation (Fig. 2).

Sexual maturity

A male that lived for 1,655 days (4.5 years) in captivity had left and right testis weighing 15.0 and 14.0 g, respectively. It showed no behavioral signs of puberty, and was considered as sexually immature based on the similarity of its testis weight to those of the immature Atlantic bottlenose dolphin (Harrison, Brownell and Boice, 1972).

The oldest female in the present material lived for 1,182 days (3.2 years) and attained a body length of 238.5 cm, smaller than the smallest sexually mature wild individuals (Fig. 1). There were no corpora in the ovaries. In the Iki Island area, the youngest mature and oldest immature females appeared at ages of 3.5 and 8.5 growth layer cycles (years), respectively (60 individuals in the age range). This material suggested that 50 % of the females were sexually mature at an age of 7 years (Kasuya, unpublished).

FINLESS PORPOISE

Gestation time and neonatal length

Kasuya and Kureha (1979) listed 14 Japanese records of neonates of this species with body length ranging from 68.8 to 97.6 cm ($\bar{x}$ = 78.6 cm). Their ages at death were usually unknown. The lengths of four known age neonates

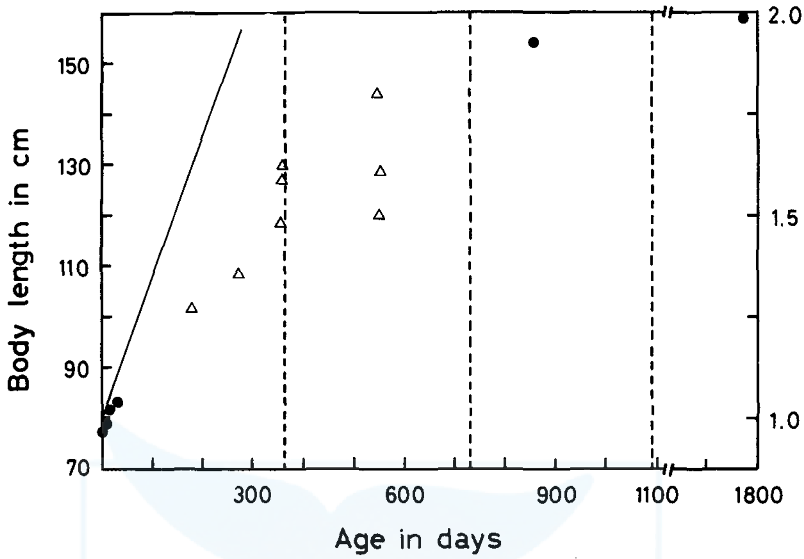

Fig. 3. Body lengths of known-age individual finless porpoises plotted against age (closed circles) and body length of fishery-caught individuals plotted against ages estimated from dentinal growth layer counts (triangles). The ages of the latter were estimated to nearest 1/4 year for animals 1 year or younger and to the nearest n+0.5 years for individuals between n and n+1 years (n being integer, n ≥ 1). The thin solid line indicates the linear part of the fetal growth curve extraporated through the mean neonatal length (80 cm). Left scale indicates body length in cm and right scale body length relative to mean neonatal length.

(some of which were listed in Kasuya and Kureha (1979)) are now available. They range between 77.5 and 83.0 cm (died within 28 days) ($\bar{x}$ = 80.0 cm) (Table 3 and Fig. 3).

Although this sample size is small, the largest individuals available to us were 187 cm (out of seven adult or subadult males) and 164 cm (out of seven adult females). The neonatal body lengths predicted using Equation 1 and either of the above adult sizes, 89.9 or 84.3 cm, seem to be overestimates. This equation may not give reliable prediction for small species such as the finless porpoise. There are no data on the mean body lengths of finless porpoise at the attainment of sexual maturity to use in Equation 2. Therefore we decided to use the mean of the four neonates of known age (80.0 cm) as the mean neonatal length of the finless porpoise in Japanese coastal waters.

The Equation 3 and the above neonatal length suggest a gestation time of 10.9 months. Assuming an error of ±5 cm in this neonatal length estimate, the resultant range in the gestation period is 10.6 to 11.2 months. The error in our estimate of neonatal length has only a negligible effect on the gestation period of small delphinoids calculated using Equation 3.

Using Equation 4, the growth rate at the linear part of fetal growth was estimated using a neonatal length of 80 cm as 0.279 cm/day or 8.49 cm/month.

Early postnatal growth

In Fig. 3 the body lengths of both known age aquarium-reared and wild finless porpoise (which ages have been estimated from dentinal layer count) are plotted against age. All the values for wild individuals fall between those of aquarium-reared individuals suggesting that the dentinal growth layers are deposited annually. All the values are far below the extended fetal growth curve suggesting that the decline in the neonatal growth rate after birth is faster in this smaller species than in the bottlenose dolphin.

Assuming that growth layers are deposited annually the mean body length at one year of age is estimated between 120 and 130 cm or 1.50–1.63 times the neonatal length (Fig. 3). This fits the general rule deduced by Kasuya and Matsui (1984) for delphinoids. The mean neonatal length, 80 cm, and Equation 5 suggest a body length at an age equivalent to the gestation period (about 11 months) as 116.1 cm with a range of 113–126 cm due to the uncertainty about the neonatal length estimate. Although the agreement is possibly better in this smaller finless porpoise than in the bottlenose dolphin, the calculated figure is still smaller than the corresponding figure directly estimated from age determined from dentinal growth layer counts (Fig. 3).

Sexual maturity

Of two individuals still living in the Toba Aquarium, a male which measured 153.5 cm at 2.4 years of age (No. 6 in Table 3) shows no behavioral sign of sexual maturity. Another 4.7-years-old 159.5 cm long male (No. 5) often indulged in sexual play with his mother (but not with other adult females in the tank). His penis was erect but no intromission was confirmed. We regard the maturity of this male as questionable.

Among the six males over 140 cm caught in the wild, four had sperm in their epididymides (body lengths 144, 148, 157 and 187 cm), but two (body length 155 and 165 cm) had no sperm (Kasuya, unpublished). Of nine females taken in the wild, eight individuals measuring between 141 and 164 cm in body length were sexually mature. One immature female was 118 cm long. These are not inconsistent with our observations of aquarium specimens.

DISCUSSION

Our analyses show that the bottlenose dolphin and possibly the finless porpoise have annual cycles of dentine deposition usable for age determination. The growth of the aquarium-reared individuals was, at least in their early postnatal stage, similar to that of the naturally grown individuals. This allows a detailed analysis of early postnatal growth which was not possible based on age determination using annual growth layer counts from wild individuals.

This study showed that the early post natal growth of bottlenose dolphins and finless porpoises follows the established pattern for Delphinoidea and indeed for Odontocetes in general. Some unknown growth parameters of these species can be predicted with various degrees of precision using published equations describing the interspecific relationship of these parameters. The use of these equations enhance our ability to interpret dentinal growth layers deposited in the early postnatal stage. Such layers are often difficult to interpret correctly without data from known age individuals.

The recommended procedure is firstly to examine if the age determination technique for the species being examined suggests an average increase of 55 to 70 % of the neonatal length in the first year after birth. If the neonatal length is not available, it can be estimated from the adult size, preferably using the mean body length of females at the attainment of sexual maturity. The technique of age determination should be questioned if the resultant estimate of postnatal growth exceeds the growth rate of the fetus during the linear part of the fetal growth stage as estimated using Equations 4 and 5.

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