RECONSIDERATION OF LIFE HISTORY PARAMETERS OF THE SPOTTED AND STRIPED DOLPHINS BASED ON CEMENTAL LAYERS

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ABSTRACT

Growth layers are visible in both cementum and dentine of the decalcified and stained teeth of *Stenella attenuata* and *S. coeruleoalba*. Their accumulation is annual in young dolphins, but in older animals only the accumulation of cemental layers are detected. Growth of the dolphin lasts longer than expected from previous studies. The maximum age is more than 45 years and sexual maturity is attained at 9 years in females of both species. Annual natural mortality rate of 7.5% in *S. attenuata* and the total mortality of 11.8% in *S. coeruleoalba* are estimated for adult females. In immature animals the mean mortality is lower, and higher in adult males. Annual ovulation rate is about 0.41 in both species. Reproductive parameters are analysed in relation to the age of animals and the present population level.

INTRODUCTION

The age determination of delphinids has been made by counting the growth layers in dentine or cementum. The accumulation of layers was shown to be annual in case of *Tursiops truncatus* based on the animals born and died in an aquarium (Sergeant 1959, Sergeant *et al.* 1973). Sergeant (1962), Kasuya (1972), and Kasuya *et al.* (1974) also indicated the possibility of the same accumulation rate for *Globicephala melaena, Stenella coeruleoalba,* and *S. attenuata* respectively based on the materials covering limited seasons, and analysed the life history of those dolphins.

However, through the analysis of life history parameters of an unexploited population of *S. attenuata*, Kasuya *et al.* (1974) concluded that the accumulation of dentinal growth layers ceases in older animals as already indicated by Sergeant (1962) for *G. melaena*. This made it difficult to study the life history of the species, and even if the life history parameters are estimated by other indirect method the accuracy was unsatisfactory.

The present study was undertaken to reconsider the life history parameters of the spotted dolphin, *S. attenuata*, and of the striped dolphin, *S. coeruleoalba*, which were fomerly estimated through the analysis of dentinal growth layers or by other indirect method (Kasuya 1972, Kasuya *et al.* 1974, Kasuya and Miyazaki 1976). Since the cemental layers abandoned in the study by Kasuya

Sci. Rep. Whales Res. Inst.,
No. 28, 1976, 73-106.

et al. (1974) were found in this study to be readable if the teeth were stained after the decalcification of a thinner ground section.

MATERIALS AND METHOD

All the materials used in this study were collected from the catch of the drive fishery off the Pacific coast of Japan. Though the samples were collected randomly from the catch, as the species have the tendency to form a separate schools in relation to the sex, growth and reproductive stages (Kasuya 1972, Kasuya *et al.* 1974, and Miyazaki 1975) and also some members of a school will be lost during the drive, the samples are not necessarily an unbiased representative of the population. This bias was considered in the analyses.

As shown in Table 1 all the samples of *S. attenuata* are the same as those used by Kasuya *et al.* (1974) except for 2 schools (nos. 8 and 9), which were examined by Mr. S. Matsui of The Taiji Whale Museum and by myself respectively. The data from these two schools were used only for the estimation of the sex ratio at birth.

TABLE 1. SOURCE OF MATERIALS USED IN THIS STUDY

School no.	Species	Date of driving	Place of driving	No. dolphins caught	No. dolphins examined	No. dolphins aged males	No. dolphins aged females
1	*S. attenuata*	23, Oct., '70	Kawana	264	131	17	27
2	„	10, Nov., '70	„	1381	273	9	15
3	„	4, Nov., '72	„	189	48	17	13
4	„	13, Nov., '72	„	192	117	54	54
5	„	16, Nov., '72	Futo	67	23	7	15
6	„	12, Feb., '73	Taiji	146	122	45	67
7	„	2, Jul., '73	„	60	36	9	9
8	„	24, Jan., '75	„	102	102	—	—
9	„	16, Jan., '76	„	91	44	—	—
22	*S. coeruleoalba*	14, Dec., '71	Kawana	903	306[1]	217[2]	62[2]
38	„	17, Nov., '72	„	411	203	37	68
43	„	15, Nov., '73	„	414	250	105	65
44	„	20, Nov., '73	„	1724	470	78	81
45, 46	„	23, 24, Nov., '75	„	1000	399	—	—

1) All immature except 7 sexually mature males.

2) Based on dentine layers read by ordinary method.

The materials of *S. coeruleoalba* were collected from the catch of six drives off the Izu coast. The school numbers in Table 1 are the same as those used by Miyazaki (1975). Though the five schools from nos. 38 to 46 in Table 1 were composed of mature and immature animals of both sexes, the school no. 22 was peculiar in the extreme scarcity of mature animals and the higher ratio of the males as indicated in Table 1 and Figs. 18 and 19 showing the age composition.

From school nos. 45 and 46, only the informations on body length, sex, and ratio of reproductive stages of adult females are available.

The growth layers were counted independently by three methods on a longitudinally sectioned tooth. The first is the ordinaly one (Kasuya *et al.* 1974), or to count the opaque dentinal layers under transmitted light with a stereoscopic microscope (×50 to ×80). The thickness of these sections was 50 to 70μ. For the second and the third methods, the tooth slides used for the first method were ground thinner to a thickness between 10 to 20μ, and decalcified in the 5% water solution of formic acid for several hours. Then they were stained with Mayer's haematoxylin solution and mounted with glycerin. By this preparation the dentinal and cemental growth layers are observed clearly as the well stained and poorly stained layers arranged alternatively. For the age determination by the second method, the number of stainable dentinal layers was counted with a microscope (×100). The fetal dentinal layer is not included in the count. The disagreement of repeated count by this method was less than 5%. The counting of cemental layers, the third method of age determination, was made with a microscope (×150) on a same slide used for the second, and at a part of the thickest cemental layer, which usually situates at a position between cervix and the midlength of the root. Though the arrangement of cementoblasts seems to be correlated with the stainable cemental groundsubstance, the counting of the layer was made on the condition of the latter. Three counts were usually made on the best spot of a slide and the middle figure was used as the number of cemental layers. The disagreement of the repeated counts was usually from 5 to 15%. The discrepancy of the repeated counts is larger in older animals. The fetal cemental layer was not usually detected by the above method, and possibly not included in the count.

As one accumulation cycle of the layers consists of a stainable and an unstainable layer, the real number of the cycles of an animal with n dark layers is expected to be between $n-1.5$ and $n+0.5$. Then the average number of the cycles of the animal is considered to be $n-0.5$, if the samples are obtained evenly from all seasons. Though, it is not actually proved if each kind of layer represent the period of 6 months, the figure $n-0.5$ was used tentatively as the approximate age of the animal.

The presence of corpora in the ovaries was used as the indication of the sexual maturity of the female, and their number was counted by the ordinary method (Kasuya *et al.* 1974). Usually the weight of left testis was measured, and the right testis only when the left is not available. The maturity of the male was determined by the testis weight based on the mean weight of single testis at the attainment of sexual maturity 68 g for *S. attenuata* (Kasuya *et al.* 1974) or 16.5 g for *S. coeruleoalba* (Miyazaki 1975, Kasuya and Miyazaki 1976).

RESULTS

Comparison of the methods

The relationship between the number of dentinal growth lyers counted by ordinary method and that counted on decalcified and stained dentine is shown in Fig. 1. As the stainable dentinal layer seems to correspond approximately with the translucent layer or with the part transitional from opaque to translucent layer of undecalcified dentine, the two counts compared are not indicating the number of same kind of layers. So, the disagreement of only one layer is not significant, and it is suggested that the two methods can give almost same result for the dolphins younger than 8 layers and that after this age the correlation becomes less. The count on undecalcified tooth with more than 12 layers gives, in general, smaller figure than that on decalcified and stained dentine. There is detected no sexual difference in this relationship. The disagreement of the counts of dentinal layers by the two methods will be caused by the difficulty of reading the layers in secondary dentine, or by the difficulty of distinguishing the thin layers of older animals. If so, the count made on decalcified and stained preparation of thinner tooth section can be a better indication of the age, since the layers are more clearly observed by this preparation.

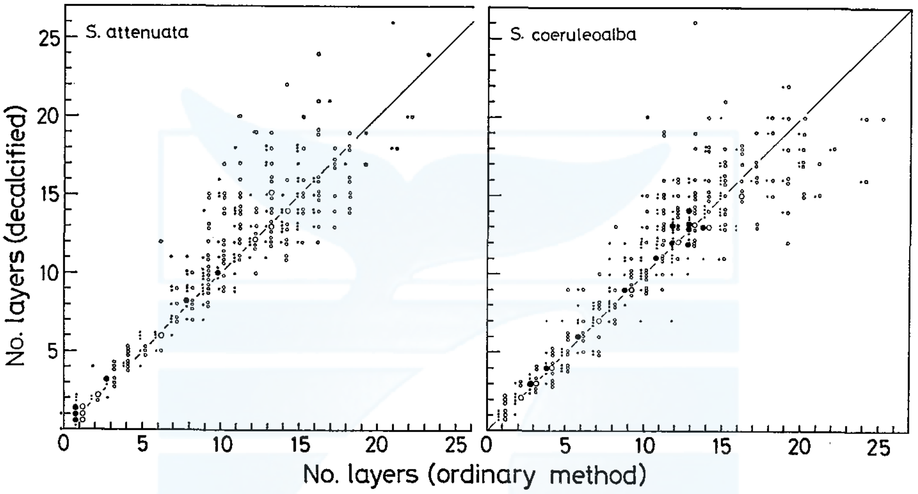


Fig. 1. Comparison of count of dentinal layers made by ordinary method (undecalcified) and that made after decalcification and staining. Open circle indicates female, closed circle male, and solid line the equal accumulation rate. Larger circle indicates five animals, and the smaller one.

However, when the number of dentinal layers in decalcified and stained tooth is compared with that of cemental layers of the same tooth slide, the two coincide extremely well only up to the age of 9 layers in *S. attenuata* or the

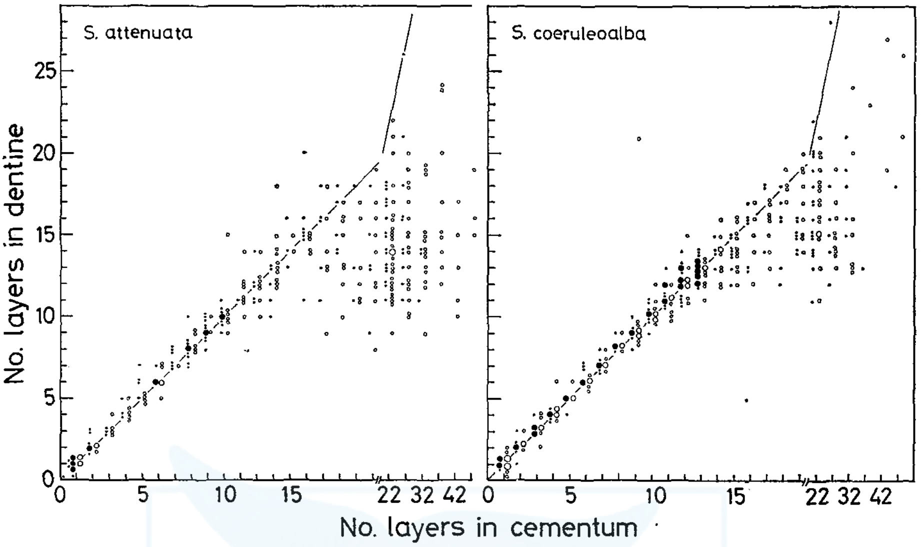


Fig. 2. Comparison of the accumulation rate of dentinal and cemental layers. Layers were counted after decalcification and staining. For other marks see Fig. 1.

age of 11 layers in *S. coeruleoalba* (Fig. 2). After these ages the latter usually gives the higher number, and there is observed almost no correlation between the number of layers in dentine and cementum in teeth with more than 20 cemental layers. This must indicate that the acumulation of the dentinal layers ceases at an large variety of age above 9 layers (*S. attenuata*) or 11 layers (*S. coeruleoalba*), and that the accumulation of cemental layers continues longer as in the case of *G. melaena* (Sergeant 1962). The ages of the oldest animal were 46 cemental layers in *S. attenuata* and 50 in *S. coeruleoalba.* They are about twice as high as those estimated from the dentinal growth layers.

Accumulation rate of layers

As the sample of *S. attenuata* covers wider range of seasons, the seasonal change of the dentinal growth layer was analysed for this species, Table 2 shows the condition of the dentinal growth layers being calcified at the time

TABLE 2. CONDITION OF DENTINE BEING CALCIFIED AT THE TIME OF DEATH OF *S. ATTENUATA*

Dentine* / Date	Stainable layer no. dolphins	%	Unstainable layer no. dolphins	%	Total no.	%
October	16	76.2	5	23.8	21	100
November	62	96.9	2	3.1	64	100
February	40	95.2	2	4.8	42	100
July	1	7.7	12	92.3	13	100

* Stained dark or pale by haematoxylin.

of death. Only the animals younger than 9 growth layers were selected here, because the accumulation of the layer ceases in some animals after this age. The frequency of the dolphins with the stainable layer at the pulp wall is about 75% in the catch of late October, and it increases to about 95% in November and February. However the ratio is reversed in early July. This is an indication of that the formation of stainable layer starts, on the average, in early October and that of the unstainable layer in between March and June.

Kasuya *et al.* (1974) suspected from the observation of undecalcified tooth sections of the same animals that the translucent dentine is formed in the season from December or January to April or May and opaque dentine in the other season. As it is easily expected that Kasuya *et al.* (1974) might have overlooked some of the translucent layers or opaque layers which were too thin to be detected on the thicker and undecalcified section, the seasons when the alternation of the layer occurs can be shown slightly delayed in their study than the result of this study. So the slight difference between the two conclusions is not significant. This is another indication of the fact that the dentinal layers stainable with haematoxylin correspond, as mentioned before, with translucent layers or with the part transitional from the opaque layer to the translucent layer of undecalcified section (Plate III, Fig. 2). As the seasonal change of the condition of the incomplete latest dentinal layers of *S. coeruleoalba* studied by Kasuya (1972) on undecalcified tooth section is same with that of *S. attenuata* reported by Kasuya *et al.* (1974), the seasonal alternation of the dentinal layers of the two species seems to follow the same pattern. The present results on the season of formation of dentinal layers is consistant even with the results on *G. melaena* (Sergeant 1962), *Hyperoodon ampullatus* (Christensen 1973, Mitchell and Kozicki 1975), and *Physeter catodon* (Ohsumi *et al.* 1963).

In order to know the growth rate of dentinal layers, the seasonal change of the thickness of the most recent incomplete layer must be detected. As a preparatory procedure of this, the change of the thickness of the layers accompanied with the age of the animal was checked on the enlarged photographs of the decalcified and stained tooth sections of two *S. attenuata* and two *S. coeruleoalba*, some of which are shown in Plates. In these measurements the first incomplete layer which start from the neonatal line was not included. The measurements of the subsequent layers are shown in Fig. 3. The thickness of the layer of *S. coeruleoalba* decreases rapidly untill 3rd or 4th layers. After this age the decrease is almost constant, and the thickness of a layer is about 95% of that of the preceeding layer. This feature seems to be same even in the case of *S. attenuata*, though the thickness of each layer is larger during the first few years.

The following relationship is lead from this result.

$$T_{n-2} : T_{n-1} = T_{n-1} : T_n$$

when t_n = the thickness of the most recent incomplete layer

T_n = the expected thickness of the same layer at the time of completion

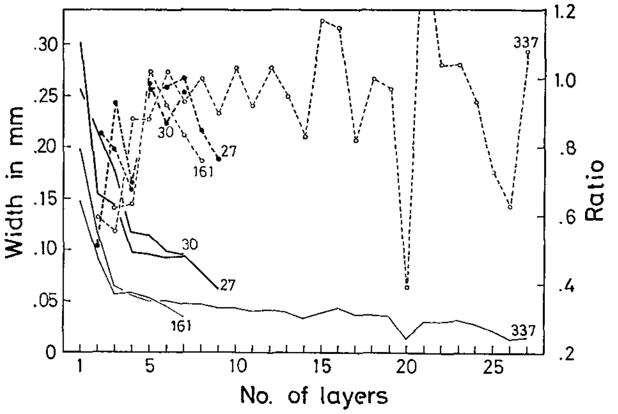


Fig. 3. Thickness of dentinal growth layers shown in relation to the age of the animals. Solid line indicate the thickness of each layer, and circle and dotted line ratio of one layer to the former layer. 27 : *S. attenuata*, 183 cm, male, school no. 7. 30 : *S. attenuata*, 202 cm, female, school no. 7. 161 : *S. coeruleoalba*, 221 cm, female, school no. 38. 337 : *S. coeruleoalba*, 232 cm, male, school no. 44.

T_{n-1}=the thickness of the one cycle earlier complete layer
T_{n-2}=the thickness of the two cycles earlier complete layer

Then, the rate of completion of the most recent incomplete layer, t_n/T_n, is shown as follows.

$$\frac{t_n}{T_n}=t_n\cdot\frac{T_{n-2}}{T_{n-1}^{2}}$$

In the present study the thickness of one layer was measured from the start of a stainable layer to that of next stainable layer, on the selected teeth of *S. attenuata* at the age betwen 4 to 12 layers. These teeth were selected considering the preparation, clearness of layers, the regularity of layers, and in older animals the coincidence of the numbers of layers in dentine and in cementum.

The result is shown in Fig. 4, where 4 schools caught in November are grouped and plotted on the mean date of catch. Though there is observed a smaller peak in October, November and February, they will have been caused by the measurements of young tooth where the thickness changes rapidly. If the highest modes were connected there is suspected a slower growth in the period from November to June. The extraporation of the line connecting the modes in October and November suggests that the starting date of the accumulation of stainable layer is in early October, which coincides well with the estimation has been made from the seasonal change of the frequency of the two kinds of layers being calcified. As the completion rate at the beginning of July is only 45%, the rate of 16.5% per month, which is close to the rate in October 15.0%, must be achieved in the accumulation of unstainable layer formed in the summer months in order to expect the annual formation of the layer. This rate will not be improbable in view of the accumulation rate of opaque layers

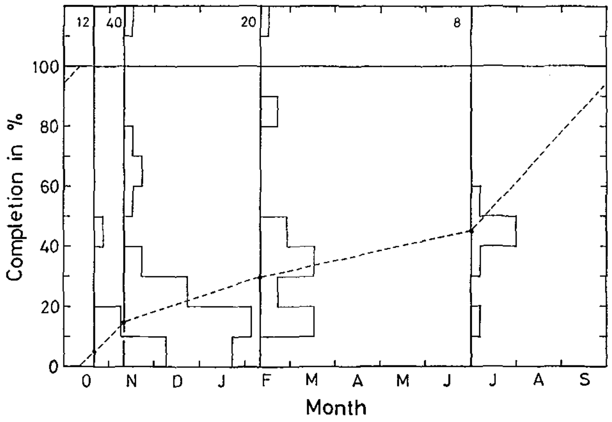


Fig. 4. Seasonal change of the completion rate of dentinal growth layers. The numerals at the top indicate the sample size. The interval of one month corresponds to 5 animals. For further explanation see text.

of *Hyperoodon ampullatus*, about 30% in the fishing season of May and June, suspected by Mitchell and Kozicki (1975, see their discussion) based on the data reported by Christensen (1973). Possibly the growth of dentine in *S. attenuata* is rapid in the summer season when the unstainable layer (≒ opaque layer on ground section) is accumulated, and slower in winter when the stainable layer (≒ translucent on ground section) is accumulated. Though Ohsumi *et al.* (1963) showed a different feature on the growth rate of dentine of *Physeter catodon*, as they measured the layer not on the thin ground section but on the half-cut longitudinal section, the exact comparison is difficult at present.

As the conclusion it will be safe to say that the accumulation rate of the dentinal growth layers is annual in case of *S. attenuata*, and that the similar rate will be expected on the closely related species *S. coeruleoalba*. Since the numbers of layers in cementum and dentine are equal in young animal and the alternation of the layers will be affected by the same physiological change, the accumulation of cemental layer is also considered to be annual.

Mean growth curve

The relationship between body length and age in *S. attenuata* and in *S. coeruleoalba* are shown in Figs. 5 and 6. As the ages are grouped into each n−0.5 years, where n indicate the number of stainable cemental layers, and the stainable layer start to be accumulated in the average in early October, the animals of almost similar age can be grouped into separate age groups affected by the slight difference of the dates of birth and death, or of the formation of stainable layer, even if there is no misreading of the layer. In other words, the difference of one year in the age of each individual is not significant.

The mean growth curves of *S. attenuata* in Fig. 5 were drawn by eye referring the curves of *S. coeruleoalba* where the samples are more abundant,

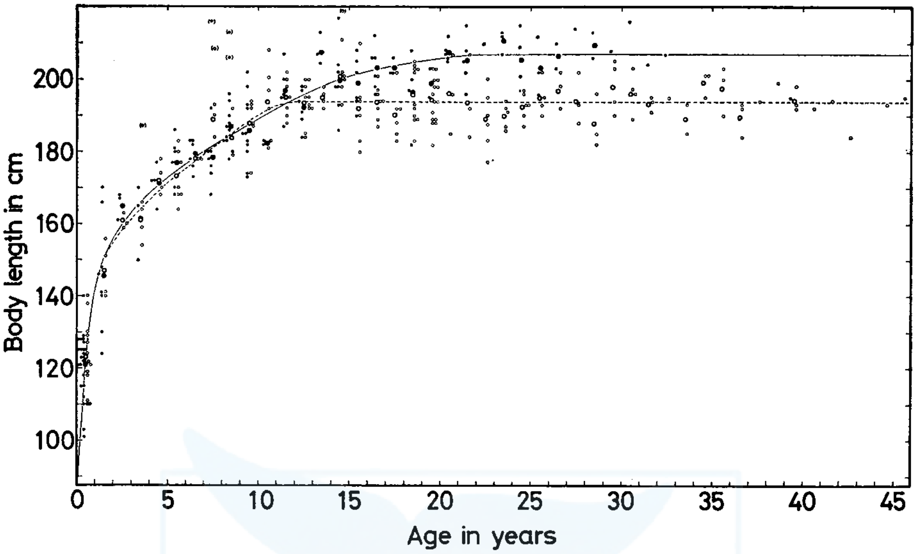


Fig. 5. *S. attenuata*, scatter diagram of the relationship between body length and age estimated from the cemental layers (200 females and 158 males). Open circle and dotted line indicate female, closed circle and solid line male, smaller circle one animal, and larger circle mean body length. Data in parenthesis are excluded from the calculation.

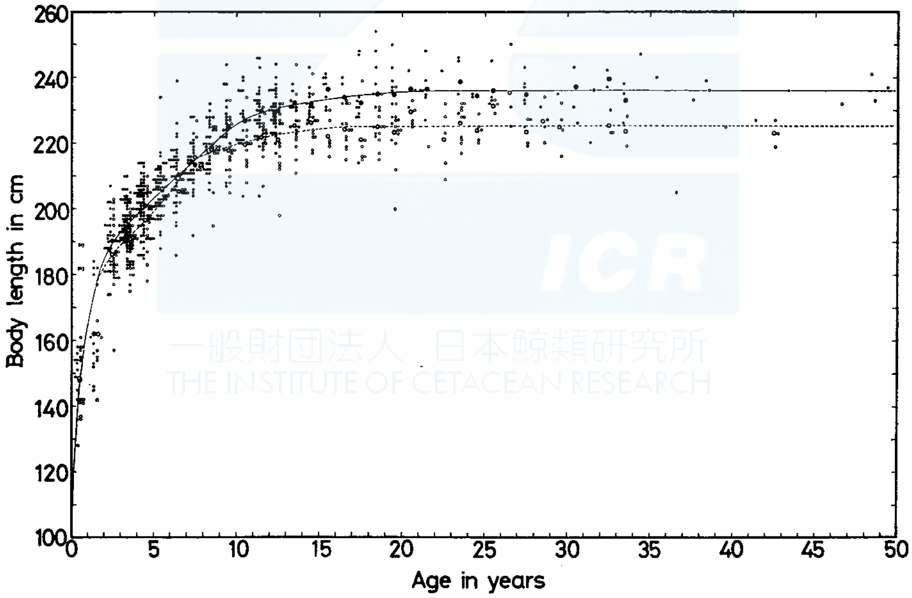


Fig. 6. *S. coeruleoalba*, scatter diagram of the relationship between body length and age (340 females and 488 males). The age data of the school no. 22 estimated by ordinaly method were included. The age of other animal was based on cemental layers. For other marks see Fig. 5.

and are liable to the alteration when more data is accumulated. The body length at birth is about 89 cm (Kasuya *et al.* 1974). The animals of both sexes attain the mean length of 142.5 cm in the first year. Then the male length seems to exceed that of female at the age of two years. Though the data is scanty and the minor change of the growth rate is not clear, there might be again a period, approximately at the age between 9 and 11 years, when the mean length of the female may exceed or equal with that of the male. Apart from these minor and uncertain features, the general trend of the mean growth curve of the immature stage does not differ from that shown by Kasuya *et al.* (1974). But, as reasonably expected from the possible underestimation of the age in their study, the growth in immature period shown in the present study appears slightly slower (Table 7). The mean asymptotic length of the female *S. attenuata* is attained at 11 or 12 years (Fig. 7), and the length is estimated to be 193.9 cm from the mean length of 135 animals at the age more than 12 years. The mean growth curve of the male indicate slower growth after 12 years of age and seems to reach the asymptonic length of 207.1 cm at the age

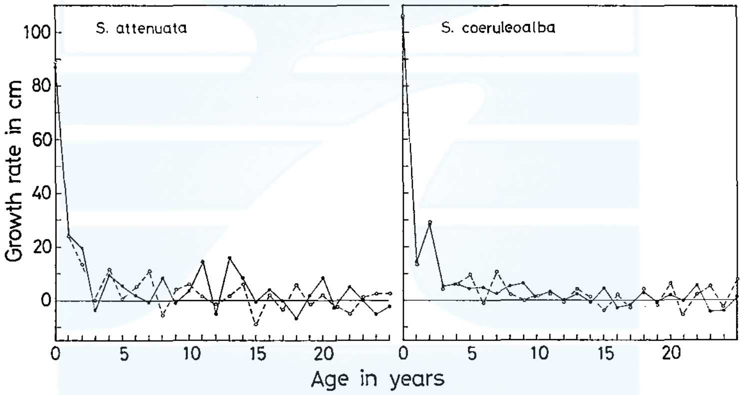


Fig. 7. Annual growth rate of the two kinds of dolphins. The increase in mean body length between n−0.5 and n+0.5 year groups is plotted at n years of age. Closed circle and solid line indicate male, and open circle and dotted line female. The fetal length was cited from Fig. 7 of Kasuya *et al.* (1974).

TABLE 3. ESTIMATION OF THE MEAN ASYMPTOTIC LENGTH

Species	*S. attenuata*		*S. coeruleoalba*	
Sex	Males	Females	Males	Females
Age range (years)	≧22.5	≧12.5	≧21.5	≧17.5
No. of animals	21	135	41	89
Smallest (cm)	195	177	220	200
Largest (cm)	216	211	248	250
Mean (cm)	207.1	193.9	236.0	225.3
Standard dev. (cm)	8.63	4.04	6.14	15.29
Standard error (cm)	1.88	0.35	0.96	1.62

of about 22 years.

The mean growth curves of *S. coeruleoalba* was drawn by eye assuming 99.8 cm for the body length at birth (Kasuya 1972). The age of the school no. 22 was estimated from the number of dentinal growth layers counted by the ordinary method, because this does not seem to give bias since the animals constituting this school are young ranging from 1.5 to 10.5 years of age (Figs. 18 and 19). As the dolphins of larger body length tend to attain the sexual maturity at an age younger than the shorter animals do (see Kasuya 1972 Fig. 4), and other schools are mainly composed of adult animals, it is necessary to add the age-length data of the school no. 22 to eliminate this bias.

S. coeruleoalba attains the mean length of 164.0 cm at the age of 1 year. The sexual dimorphism of the body length appears at the age of about 2 years as in the case of *S. attenuata*, and then the lengths of both sexes increase at an almost constant rate retaining the difference of about 4 cm until the age of 6 years. As shown in Table 7, the growth rate of this period is slightly smaller than that estimated by Kasuya *et al.* (1974). The mean growth rate of the females increases at the age from 6 to 7 years, and attains at age from 7 to 8 years a length slightly exceeding that of the male. After the age of 8 years, which is about one year before the onset of sexual maturity, the mean growth of the female becomes slower, and mean growth curve reaches the asymptotic length of 225.3 cm at about 17 years. Though the growth of the male is slightly faster at the age between 7 and 10 years than the preceeding period, the accelerated growth is not conspicuous. After the age of 10 years the growth of the male becomes slower and attains the asymptotic length of 236.0 cm at the age of about 21 years (Table 3).

The mean growth curves of the two species of *Stenella* discussed here show a similar pattern. The ages when the growth rate changes correspond to the completion of weaning at 1.5 to 2.4 years indicated by Kasuya (1972) and in the latter section of this study, attainment of sexual maturity discussed below, and the completion of the attainment of physical maturity. Though the accelerated growth of the male near the attainment of sexual maturity is not conspicuous, the growth rate of the female seems to become higher just before the attainment of sexual maturity. The fact that the body length of the female near the onset of sexual maturity exceed that of male at the same age is at close resemblance to *G. melaena* (see Sergeant 1962, Fig. 11). The low growth rate preceding the age at asymptotic length might by a reflection of the decrease of the growth rate of each animal and of the increasing ratio of the animals which have attained the physical maturity. The age when mean growth curve attains the asymptotic length will correspond to the age when all the individuals attain the physical maturity.

Attainment of sexual maturity

When the presence of the scar in the ovary or the testis weighing more than 68 g (Kasuya *et al.* 1974) is used as the criterion of the sexual maturity in

S. attenuata, the youngest sexually mature animals are found in the age group of 7.5 years (both sexes) and the oldest immature animals in that of 11.5 years (female) or 15.5 years (male). The following formulae are obtained by the least aquares for the relationship between the ratio of mature animals (y) and the age of the animals (x).

$$\text{Female}: \; y=17.43x-106.93 \qquad 6.5\leqq x\leqq 12.5$$

$$\text{Male} \;\;\;: \; y=10.59x-74.84 \qquad 6.5\leqq x\leqq 16.5$$

The age where 50% of the animals are sexually mature is estimated from the above formulae to be 9.0 (female) or 11.8 (male) years (Fig. 8). These values are slightly higher than those obtained by Kasuya *et al.* (1974), as expected from the limit of ageing by dentinal layers.

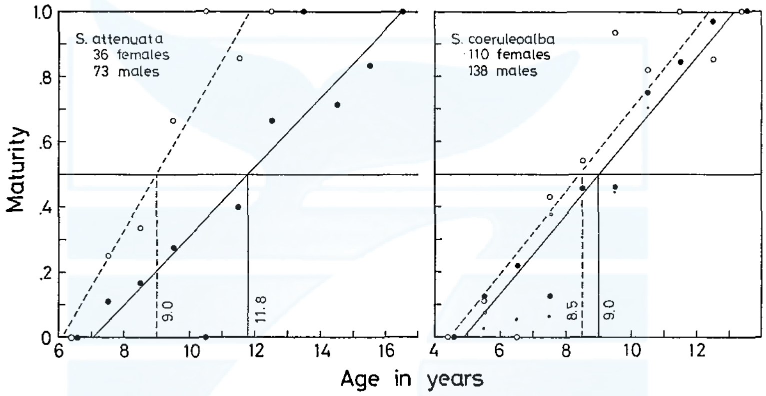


Fig. 8. Relationships between age and the ratio of sexually mature animals. Open circle and dotted line indicate female, and closed circle and solid line male. In *S. coeruleoalba* smaller circles include school no. 22, and the larger exclude it.

In case of male *S. coeruleoalba* the mean weight of testis at the attainment of sexual maturity, 16.5 g, was determined Miyazaki (1975), where the presence of spermatozoa or spermatid in the tissue taken from the center at the midlength of testis was considered to be mature. In spite of this criterion, there were always observed both spermatozoa and spermatid in the mature testis (Miyazaki 1975) as in the case of *S. attenuata* (Kasuya *et al.* 1974). As shown in Table 4, this criterion seems to give a same age at the onset of sexual maturity with the criterion based on the presence of spermatozoa in the epididymal smear. However other criterion may give different results. For the female *S. coeruleoalba,* the maturity was determined by the presence of the corpus in the ovaries.

If the age-maturity data of 152 (146 immature and 6 mature) males and 25 immature females of the school no. 22 are dealt together with the data of school nos. 38, 43 and 44, the ratios of immature males are unreasonably low in the age groups below 9 years and the age of 9.7 years is obtained as the mean age of the male at the attainment of sexual maturity (Fig. 8). However,

TABLE 4. COMPARISON OF DIFFERENT CRITERIONS FOR THE MATURITY OF MALE *S. COERULEOALBA*

No. of	Age in	Testicular smear			Epididymal smear			Testicular weight[1]		
layers	years	imm.	mat.	mat. %	imm.	mat.	mat. %	imm.	mat.	mat. %
2	1.5	2	0	0	2	0	0	9	0	0
3	2.5	8	2	20.0	9	1	10.0	11	0	0
4	3.5	0	1	100	1	0	0	8	0	0
5	4.5	2	1	33.3	3	0	0	7	0	0
6	5.5	3	3	50.0	4	2	33.3	7	1	12.5
7	6.5	1	6	85.7	2	5	71.4	7	2	22.2
8	7.5	4	1	20.0	5	0	0	7	1	12.5
9	8.5	0	7	100	2	5	71.4	6	5	45.5
10	9.5	2	6	75.0	3	4	57.1	7	6	46.2
11	10.5	0	8	100	0	8	100	4	12	75.0
12	11.5	0	17	100	1	16	94.1	4	22	84.6
13	12.5	0	29	100	2	27	96.4	1	32	97.0
14	13.5	0	2	100	0	3	100	0	6	100
15	14.5	0	7	100	1	6	85.7	0	11	100
16	15.5	0	4	100	0	5	100	0	8	100

1) Less than 16.5 g was considered to be immature (Miyazaki, 1975).

as mentioned before, this school is mostly composed of the immature males affected by the special schooling behavior, and the data from this school may not be suited for the present purpose. On the other hand, as the other 3 schools show less specialized age distribution even if the frequency below 9 years is rather low, they will give better estimation of the mean age at onset of sexual maturity. The least squares regressions of the age-maturity relationship calculated for the data of these 3 schools are as follows.

$$\text{Female}: \ y=12.60x-56.51 \qquad 4.5\leqq x\leqq 13.5$$

$$\text{Male} \ : \ y=12.05x-58.94 \qquad 4.5\leqq x\leqq 13.5$$

They give 8.5 years for female and 9.0 years for male as the age where 50% of the animals are sexually mature. Though the figure of the female is slightly lower compared with the corresponding age of female 8.8 years (Kasuya 1972) or 9.1 years (Miyazaki 1975), these difference may not be significant because a slight underestimation is expected from the scarecity of the immature animals below 9 years of age in the 3 schools discussed here. The mean age of the male at the attainment of sexual maturity estimated above shows good coincidence with 9.2 years and 9.0 years estimated by Kasuya (1972) and Miyazaki (1975) respectively.

Fig. 9 shows the relationship between age and the weight of a testis. The weight shows a rapid increase at the age between 9 and 13 years in *S. attenuata* or between 7 and 11 years in *S. coeruleoalba,* which correspond to the age at

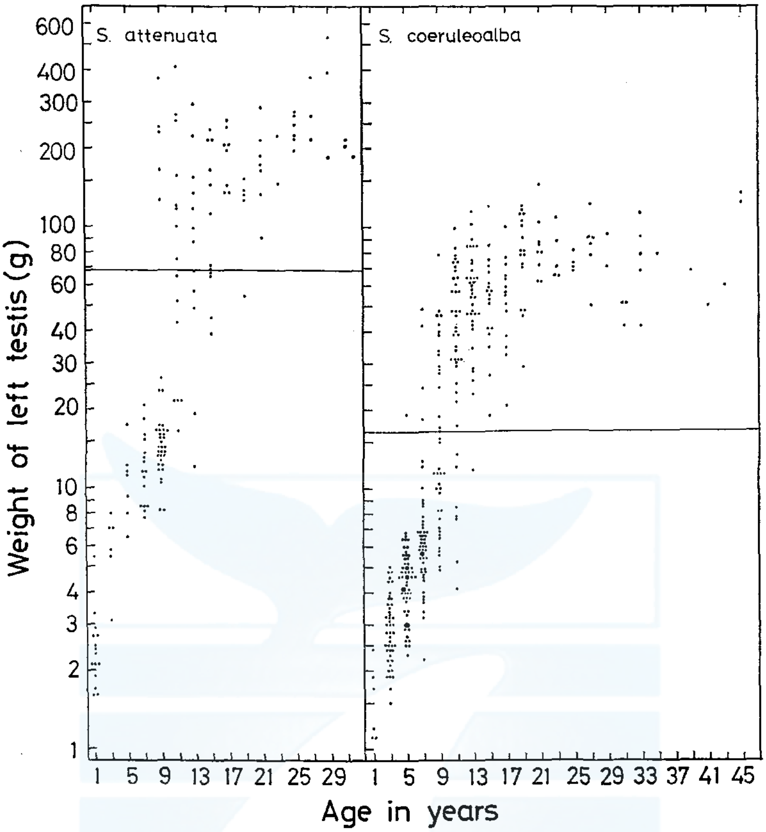


Fig. 9. Scatter diagrams of the relationship between age and the weight of testis. Two age groups are combined. In *S. coeruleoalba* data from school no. 22 are included. Weight of right testis is plotted if the left is not available. Larger circle indicates 5 animals and the smaller one.

onset of sexual maturity. However after the age of 15 years, the weights are distributed between 120 g and 600 g (*S. attenuata*) or between 40 g and 150 g (*S. coeruleoalba*) and there is observed no increase related with the age of the animal. This stage will correspond to the full sexual maturity and probably to the stage of social maturity as suspected by Miyazaki (1975). This feature is completely different from that observed in *Physeter catodon* where the weight of testis increases after the attainment of sexual maturity at or little above the previous rate (Gambell 1972).

Accumuration rate of corpora in the ovaries

The persistency of the corpora for entire lifetime of the female was suggested in *S. attenuata* by Kasuya *et al.* (1974). Possibly this is also true for *S. coeruleoalba* (Hirose *et al.* 1970, Miyazaki 1975).

In *S. attenuata*, though the individual variation is large, there is expected a linear relationship between the number of corpora and the age (Fig. 10). The following regression is obtained by the least squares for the animals older than 7 years of age,

$$y=0.412x-1.97$$

where y indicates the number of corpora, and x the age in years. This indicates the mean annual ovulation rate of 0.412, or 1.62 ovulations in one reproductive cycle of 3.94 years (see page 88). Kasuya *et al* (1974) estimated, through the analyses of corpora diameter, the annual ovulation rates of between 0.407 and 0.595 for 5 age groups classified by the corpora number. And they concluded from these estimates that the annual ovulation rate changes from 0.432 of young animal to 0.487 of the animals with highest corpora number. Though they considered that this indicates the change of the ovulation rate related with the age of the animal, it is theoretically incorrect because the number of corpora in the ovaries is the function of both the age of the animal and of the individual specific ovulation rate, and these two factors could not be separated in their study. It should have been interpreted that the mean annual ovulation rate of the dolphins which may attain higher corpora number is higher than the mean rate of the other dolphins. Furthermore, the diameter of the corpora is not a much reliable indicator of the time elapsed after the ovulation, and the ovulation rate estimated from its analysis is less accurate. Accordingly the ovulation rate of *S. attenuata* estimated in this study will be the present best estimate.

As shown in Fig. 11, the relationship between the number of ovulations and the age of *S. coeruleoalba* may not come on a single linear relation. If the regression lines are calculated separatly for the age classes from 5 to 25 years and for those from 26 to 43 years. The following relations are obtained by the least squares.

$$y=0.414x-2.40 \qquad 5\leqq x\leqq 25$$

$$y=0.115x+6.55 \qquad 26\leqq x\leqq 43\,.$$

However, the first regression line seems to fit to the animals up to 33 years of age. There are expected three reasons for this. The first is the simple sampling error caused by the scarcity of the samples of higher age, the second is the decline of the ovulation rate or the resorption of corpora at higher age, and the third is the recent increase of ovulation rate might have happened as the response of the population to heavy exploitation started since the last war. The possibility of miscounting of the corpora will be neglected, because the counting was made by myself with the same method for both species of *Stenella*. The third possibility is also improbable because the ovulation rate of 0.115 per annum is too low even as the rate at initial population level, and because the ovulation rate of *S. attenuata* possibly at the initial level (Kasuya *et al* 1974) is almost identical with the first rate 0.414 per annum. Accordingly, the possible explanations can be only the first or the second. And, though the first might be more probable, the conclusion on this problem will have to wait until more data are accumulated.

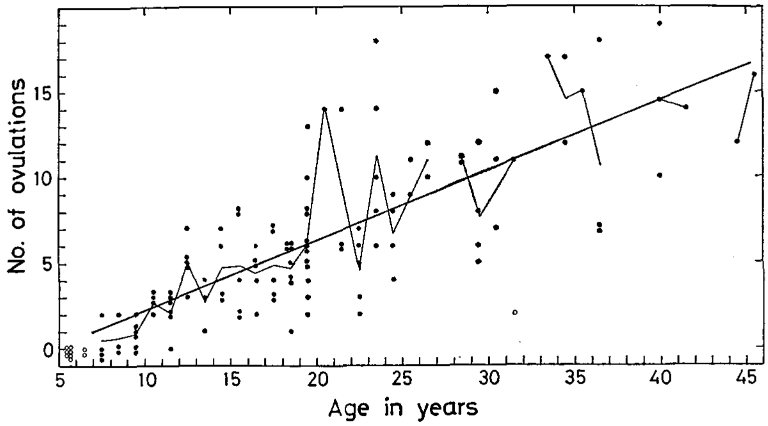


Fig. 10. *S. attenuata*, scatter diagram showing the relationship between age and number of corpora in the ovaries (124 females). Thin straight line and thick straight line indicate mean corpora number and regression line obtained by least squares respectively, for both only the data represented by closed circles are used.

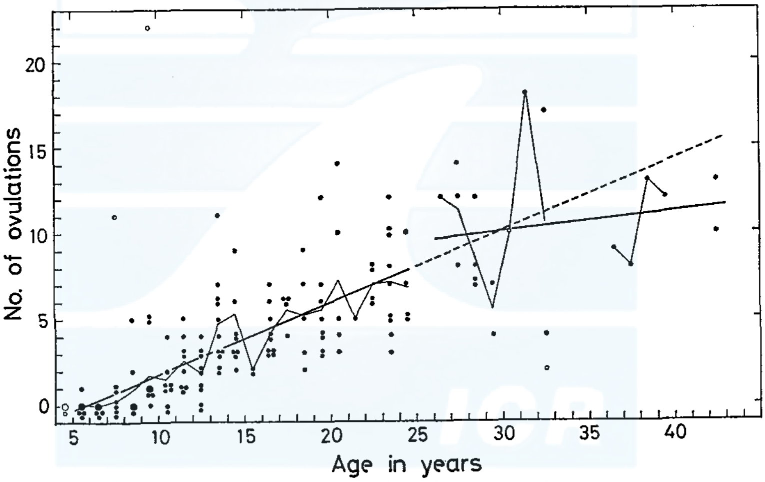


Fig. 11. *S. coeruleoalba*, scatter diagram showing the relationship between age and number of corpora in the ovaries (170 females). The data from school no. 22 are not included. Larger circle indicates five animals and smaller one. For other marks see Fig. 10.

Reproductive cycle

In this section the reproductive parameters of the adult females are analysed in relation to the age of the animals. When the ratio of pregnant females in the total adult females is shown by P, that of pregnant and simultaneously lactating by PL, that of lactating by L, that of resting by R, and the mean length of gestation by G years, the annual pregnancy rate and the mean calving interval in years are estimated as follows.

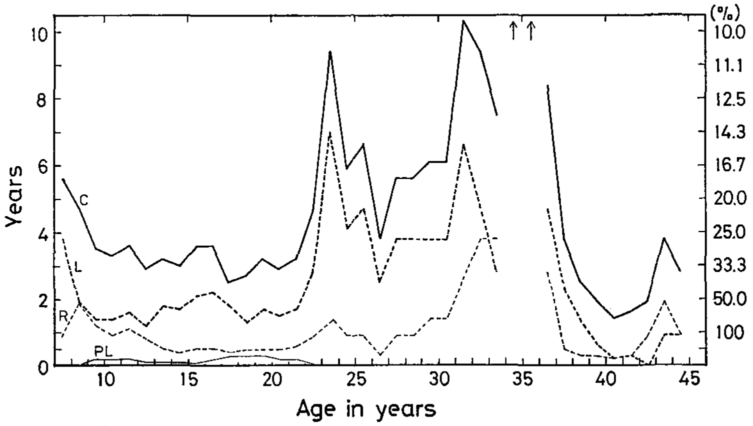


Fig. 12. *S. attenuata*, relationship between age and the mean reproductive parameters estimated from the ratio of reproductive stages. C: calving interval (left scale) and annual pregnancy rate calculated from it (right scale), L: length of lactation, R: length of resting period, PL: length of the period lactating and simultaneously pregnant. Each value is calculated combining the data of nearest 5 age classes. The age classes indicated by arrow containe no pregnant female.

TABLE 5. DIFFERENCE OF REPRODUCTIVE PARAMETERS OF ADULT FEMALES BETWEEN AGE CLASSES

Species	*S. attenuata*				
Age class (year)	7—15	15—25	25—35	35—46	Total[1]
No. animals	31	64	22	13	130 (164)
Pregnancy (years)	0.83	0.72	0.94	0.94	0.79 (0.82)
PL (years)	0.10	0.22	0	0	0.14 (0.12)
Lactation (years)	1.46	2.04	4.06	1.40	1.99 (2.23)
Resting (years)	0.83	0.55	1.87	0.70	0.77 (0.77)
Calving interval (years)	3.23	3.53	6.87	3.04	3.69 (3.94)
Annual pregnancy rate (%)	31.0	21.7	14.6	28.8	27.1 (25.4)
Species	*S. coeruleoalba*				
Age class (year)	5—15	15—25	25—35	35—49	Total
No. animals	72	63	22	8	165
Pregnancy (years)	0.95	0.73	0.94	0.75	0.86
PL (years)	0.05	0.27	0.06	0.25	0.14
Lactation (years)	0.24	0.46	0.24	0.75	0.33
Resting (years)	0.07	0.07	0.06	0.25	0.08
Calving interval (years)	1.31	1.54	1.29	2.00	1.41
Annual pregnancy rate (%)	76.4	65.1	77.3	50.0	70.9

[1] In parenthesis includes age unknown animals cited from Kasuya *et al.* 1974, Table 14.

$$\text{Annual pregnancy rate} = (\text{Calving interval})^{-1} = \frac{P+PL}{G}$$

Then mean length of each reproductive stage is estimated by the formula

$$\frac{X}{P+PL} \cdot G$$

where X indicates the ratio of females at one of the above 4 stages. This method gives correct estimates only when the samples are not seasonally biased. As the present data, especially those of *S. coeruleoalba*, were collected in the limited season, there might occur some bias of this kind. However, since the mating of both species of *Stenella* occurs in wide range of the seasons and there exist probable three mating peaks in *S. attenuata* (Kasuya *et al.* 1974) and two (Kasuya 1972) or three (Miyazaki 1975) peaks in *S. coeruleoalba*, such kind of bias can be small enough compared with the bias caused by the inclination of the dolphins to form separate schools by the sex, growth and reproductive stages suggested by Kasuya (1972), Kasuya *et al.* (1974), and Miyazaki (1975).

The length of gestation of *S. attenuata* was estimated by Kasuya *et al* (1974) to be 11.24 months or 0.94 years. If this gestation length is used for the above calculation, the mean length of calving intervals is estimated to be 3.94 years, mean length of lactation (L+PL) 2.35 years, and mean length of resting period 0.77 years (Table 5). Though the data used here are same with those in Kasuya *et al* (1974), as the treatment of the females pregnant and simultaneously lactating is different the figures are slightly changed. The analyses of the parameters in relation to the age of the female reveals that the mean calving interval is shorter in the females below the age of 23 years and only in those age classes the pregnant and simultaneously lactating females are observed. After this age the length of calving interval increases, which at first step accompanies the increase of the length of lactation and then the increase of resting period. This phenomenon can be interpreted that, in the younger females, the lactation ceases at about 2 years after the former parturition almost synchronizing with the start of the next conception, and in the older females as the start of the next conception delays the period of lactation is extended up to about 4 years in the average when the calf stops suckling affected by the change of the behavior. This age of the calf is the time when the calves are expected to leave the school of their mothers (Kasuya *et al* 1974). If, then, the next gestation does not start for more than 4 years, there can occur the increase of resting females. The extremely rapid increase of the mean calving interval after the age of 30 years seems to suggest the presence of the females that ceases the ovulatory activity. The decline of the length of calving interval or the increase of annual pregnancy rate after the age of 37 years is the reverse of the former trend, but the similar phenomenon is found also in *S. coeruleoalba*. One possible explanation for it might be that the old females which ceases the ovulatory activity die, by the age between 35 and 40 years, earlier than the still active females which is fewer in number, and even the latter females they often die at the last parturition without followed by the lactation.

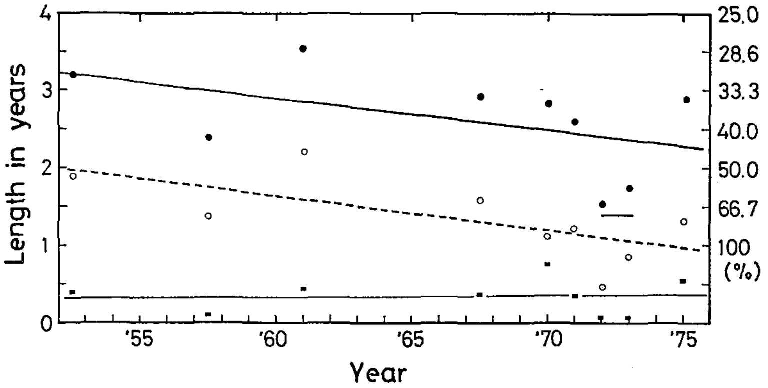


Fig. 13. *S. coeruleoalba*, annual fluctuation of the mean reproductive parameters estimated from the ratio of the reproductive stages. Closed circle and solid line indicate the length of calving interval (left scale) and the annual pregnancy rate (right scale), open circle and dotted line length of lactation (L+PL, left scale), and square and thin solid line length of resting period (left scale). For further explanation see text.

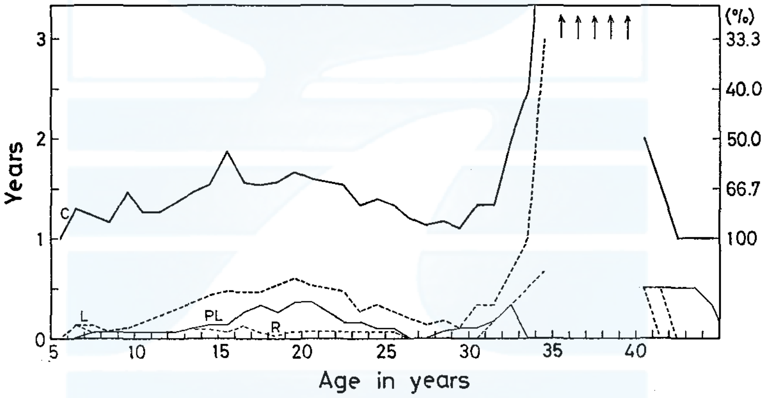


Fig. 14. *S. coeruleoalba*, relationship between age and the mean reproductive parameters. For further explanation see Fig. 12.

For *S. coeruleoalba*, there is no reliable estimation of the gestation length, however it was roughly suspected by Kasuya (1972) to be about 12 months. In the present study this estimation is used without further confirmation. Kasuya and Miyazaki (1976) indicated that the mean calving interval in the population of *S. coeruleoalba* off the Pacific coast of Japan is decreasing accompanied with a decrease in the population level. If the data of 33 pregnant, 44 lactating, and 18 resting females obtained from the two schools caught in 1975 (see Table 1) are added to the data reported by Kasuya and Miyazaki (1976), the following trend is estimated by the least squares (see also Fig. 13).

$$\text{Calving interval} = -0.040838x + 82.944$$

$$\text{Length of lactation} = -0.044982x + 89.811$$

$$\text{Resting period} = 0.001951x - 3.485$$

where x indicates the calender year, and length of each stage is indicated by year. The length of lactation includes both the period of lactation and that of lactating and simultaneously pregnant. The above formula gives the estimation of the mean calving interval of 2.39 years in between 1972 and 1973 when the present materials were collected. This is slightly longer than the calving interval estimated from the regression in Kasuya and Miyazaki (1976). As shown in Fig. 13, the catch in these two seasons is strongly biased by the high ratio of pregnant females, and the mean calving interval estimated from the materials used in this study is only 1.41 years (see the short bar in Fig. 13), which is only 59.0% of the unbiased estimate calculated from the above regression. Accordingly only a general trend of the change of reproductive parameters related with the age of the female can be discussed in this study, and if necessary the above bias must be corrected.

In *S. coeruleoalba*, the period of shorter calving interval lasts about 10 years longer than *S. attenuata* until about 32 years of age, and the period when the lactating and simultaneously pregnant females occur also last longer. After this period, the pregnancy rate declines rapidly and then increases as observed in *S. attenuata*. Though the reason of the difference of the period of the high reproductive activity between the two species of *Stenella* is not conslusive, it seems to be possible to attribute it to the difference of the population level because the Japanese coastal population of *S. attenuata* is close to the unexploited level (Kasuya *et al.* 1974) and that of *S. coeruleoalba* has been exploited since before 1897 and the decline of the population is indicated (Kasuya and Miyazaki 1976).

Sex ratio

The sex ratio of *S. attenuata* was already analysed by Kasuya *et al.* (1974) and the predominance of the male in fetal and juvenile stages was indicated. Table 6 shows the sex ratio of fetus and of the juvenile animals not exceeding 142 cm in body length which corresponds to the age of one year on the mean growth curve. As the sex ratio of the species at the time of birth will be between those of the above two growth stages, the ratio of females at the instance of birth, 41.6%, was obtained by combining the data of the two categories.

The ratio of females at the instance of birth in the population of *S. coeruleoalba* was estimated by Kasuya and Miyazaki (1976) to be 47.6% based on large number of samples (Table 6). Though they included the animals corresponding, on the mean growth curve, to the age up to 1.25 years, it will not give significant bias.

Fig. 15 shows the change of the sex ratio related with the age of the dolphins. The extraordinaly high ratio of the males at the age between 5 and 11 years in *S. attenuata* or between 2 and 15 years in *S. coeruleoalba* is considered to be the result of the sexual segregation in the period between weaning and the attainment of full sexual maturity. Possibly the ages when the young dolphins move from the nursery school to the school of immature animals and

TABLE 6. SEX RATIO OF THE DOLPHINS AT BIRTH

Species	*S. attenuata*			*S. coeruleoalba*[1]		
Stage	fetus	juvenile[2]	Total	fetus	juvenile[3]	Total
No. males	39	79	118	351	385	736
No. females	31	53	84	310	359	669
Female, %	44.3	41.4	41.6	46.9	48.3	47.6
Male/Female	1.26	1.49	1.40	1.13	1.07	1.10

1) Data cited from Kasuya and Miyazaki 1976.
2) Not exceeding 142 cm.
3) Not exceeding 172 cm.

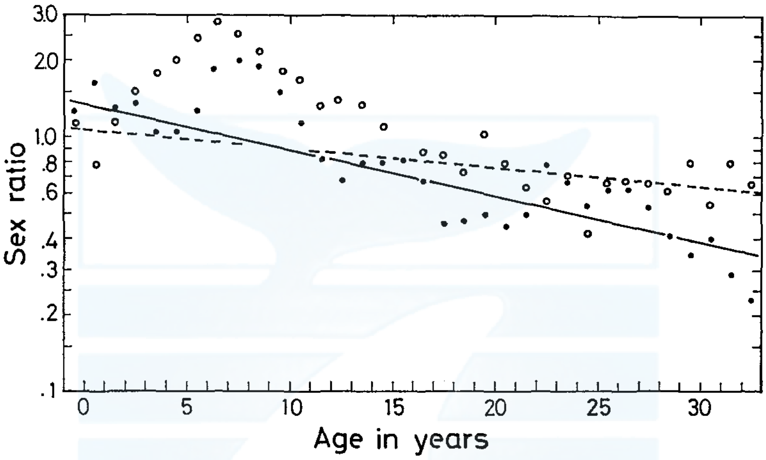


Fig. 15. Relationship between sex ratio (male/female) and the age of *S. attenuata* (closed circle and solid line) and of *S. coeruleoalba* (open circle and dotted line). The ratio for the age more than one year is calculated combining the data of the nearest 5 age classes. For other explanation see text.

then to the school of adult dolphins will be different between the sexes, and this in combination with the kinds of schools studied by me will give such a bias in the sex ratio. If these age classes are excluded there is observed a decline of the ratio with the progress of the age of the animals, which will indicate the sexual difference of the mortality rate. When μ and μ' indicate the annual natural mortality coefficient of male and female respectively, and R_x the sex ratio (male/female) at the age of x years, there is expected the following relationship.

$$R_x = R_0 e^{-(\mu-\mu')x}.$$

The regression lines in Fig. 15 and the following figures are calculated by the least squares based on the sex ratio at birth obtained above and the points in Fig. 15 corresponding to the ages above 11 years (*S. attenuata*) or 15 years (*S. coeruleoalba*). In case of *S. coeruleoalba* the mortality is affected by natural mortality and fishing mortality. However, as the fishing mortality rate of the species is not expected to be different between sexes, it can be neglected in the calculation.

	$\mu-\mu'$	R_0
S. attenuata	0.0412	1.32
S. coeruleoalba	0.0171	1.06

These figures indicate that the difference of the natural mortality coefficient between the sexes is higher in *S. attenuata*, and that it is partially compensated by the higher ratio of the male at birth.

Age composition and mortality

The age composition of *S. attenuata* obtained from 158 males and 200 females are shown in Figs. 16 and 17. The age composition suggests the presence of segregation related with the age and the sexual maturity of the animals below the 13 years of age as already mentioned in the former sections. The slope of the age frequency at the right side of this point indicates the natural mortality, as the fishing mortality is negligible in this population. Though the mortality seems to be slightly higher in the females above 31 years, the least squares calculated ignorering this minor change gives the following annual mortality rate for *S. attenuata*.

Sex	Coefficient	Rate in %	Age in years
Female	0.0779	7.49	14≦
Male	0.1135	10.73	14≦

The difference of the annual mortality coefficient between sexes is 0.356 and coincides well with the corresponding figure estimated from the sex ratio.

Since the above rates can be considered to represent the mean annual mortality rate of the adult animals, the mean mortality of the immature stage is estimated as follows. When the following abreviations are used

A: Number of mature females
l_x: Number of females at the age of x years
C: Calving interval in years
L: Litter size
m: Mean age at the onset of sexual maturity
s: Ratio of females at birth
μ_1: Mean annual mortality coefficient of immature females
μ_2: Mean annual mortality coefficient of mature females

there must be the next relations in an unexploited stationary population.

$$l_0=\frac{A\cdot L\cdot s}{C}$$

$$l_m=l_0e^{-\mu_1 m}$$

$$A=l_m\int_m^\infty e^{-\mu_2(x-m)}dx$$

As C=3.94, s=0.416, m=9.0, and μ_2=0.0779 are obtained in this study, and the

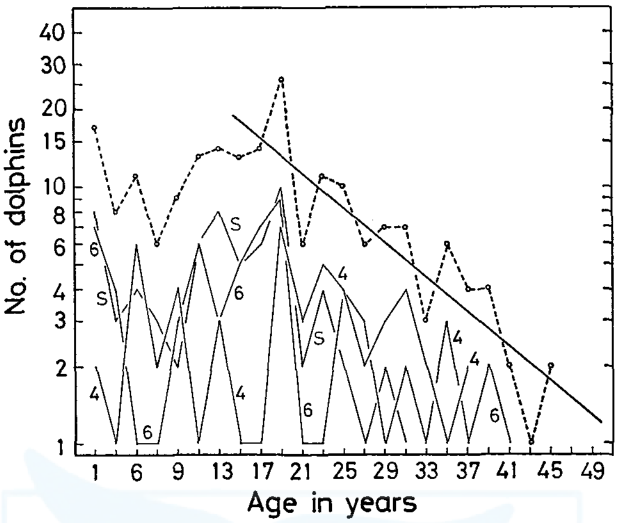


Fig. 16. *S. attenuata*, age composition of the 200 females based on cemental layers. 4 indicate School no. 4, 6 school no. 6, S sum of the school nos. 1, 2, 3, 5 and 7, and the open circle and dotted line the total of the seven schools. Each two age groups are combined.

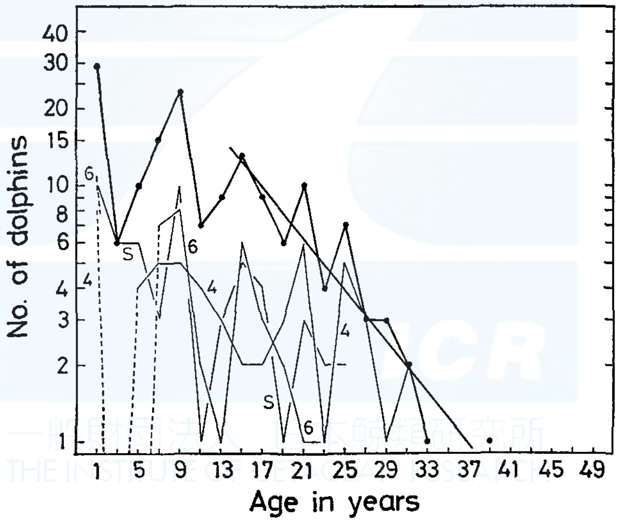


Fig. 17. *S. attenuata*, age composition of the 158 males. Closed circle and thick solid line indicate the total of seven schools. For other explanation see Fig. 16.

litter size is 1.0 (Kasuya *et al.* 1974), the following estimate of the mean annual natural mortality rate of immature female of *S. attenuata* is obtained from the above formulae.

Sex	Coefficient	Rate in %	Age in years
Female	0.0338	3.32	≦9.0

As the difference of the mortality coefficient between the sexes is between 0.0412 and 0.0356 or approximately 0.038, the rough estimate of the mean annual natural mortality of the immature male is as follows.

Sex	Coefficient	Rate in %	Age in years
Male	0.072	6.9	≦9.0

The natural mortality rates of the immature dolphins estimated here are the mean of the mortality of all the age classes from 0 year to the age at the attainment of sexual maturity, and the possible higher mortality expected for the suckling calves is not separated. It was already indicated by Kasuya *et al.* (1974) on *S. attenuata* that the mean natural mortality rate in the immature period must be lower than that in the adult stage. The present study gives results similar to those obtained in the previous study.

The age compositions of 341 females and of 488 males of *S. coeruleoalba* are shown in Figs. 18 and 19. In these age data, the age of 62 females and 217 males of the school no. 22 was determined by counting the dentinal layers by ordinary method. Because of the segregation of the immature individuals (Kasuya 1972, Miyazaki 1975) as in the case of *S. attenuata*, only the slope above the age of 12 years in females or that above 14 years in males can indicate the mortality under certain assumption mentioned below. They are as follows.

Sex	Coefficient	Rate in %	Age in years
Female	0.0919	8.78	12≦
Male	0.1143	10.80	14≦

Above values can indicate the mean annual total mortality during the period from 1920's to 1959's only when the population is assumed to be stationary. However, as the exploitation of this population became higher near the end of the last war as in the case of *Phocoenoides* (Kasuya 1976 a and b) and the population has been decreasing (Kasuya and Miyazaki 1976), the estimation is not fully accurate. The total mortality rate in the postwar period must be estimated separately. This can be made using the frequency of corpora number, because the method can afford more abundant data. Fig. 20 shows the age composition of sexually mature females calculated from the frequency of corpora number cited from Kasuya and Miyazaki (1976) and the accumulation rate of corpora (0.414/year) estimated in this study. There is observed two slopes in the age frequency. The first is from 15.9 (4 corpora) to 28.4 years (9 corpora) of age and the second slope is from 30.9 years (10 corpora) and above. If the mortality is calculated separately, the following figures are obtained as the estimates of the total annual mortality rate of mature females.

Sex	Coefficient	Rate in %	Age in years
Female	0.1258	11.82	15.9–28.4
Female	0.0951	9.07	30.9–51.1
Female	0.0896	8.57	15.9–51.1

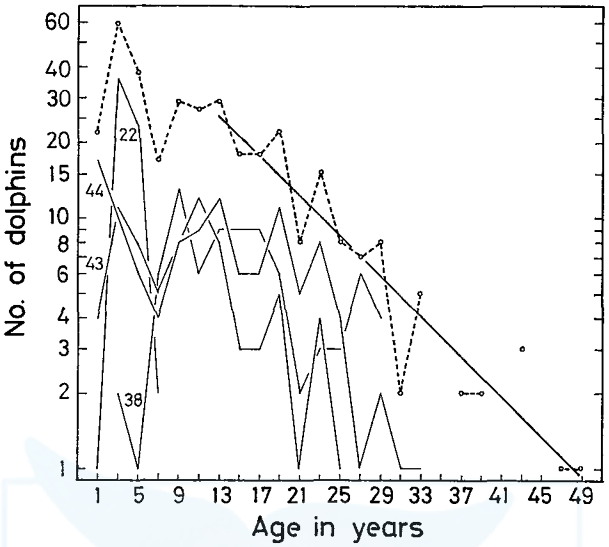


Fig. 18. *S. coeruleoalba*, age composition of the 341 females. Numerals indicate the school number. The age composition of school no. 22 was based on the ordinary method of reading of dentinal layers. For other marks see Fig. 16.

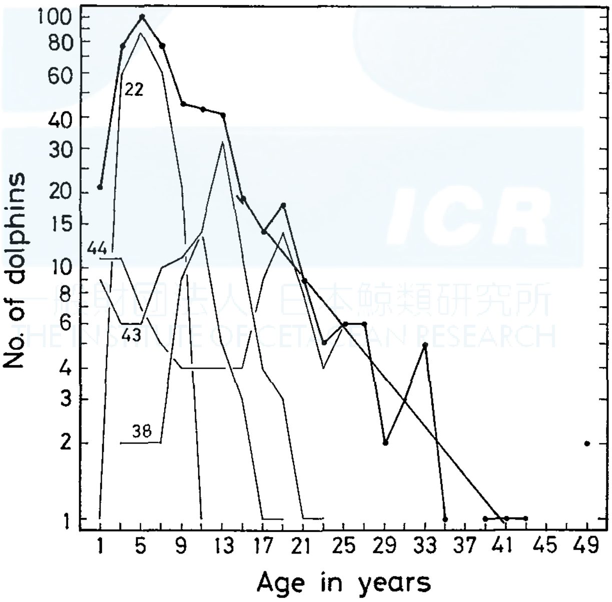


Fig. 19. *S. coeruleoalba*, age composition of the 488 males. For marks see Figs. 17 and 18.

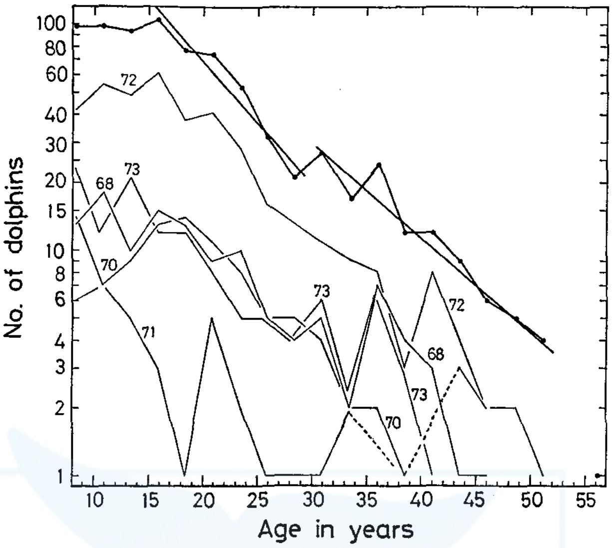


Fig. 20. *S. coeruleoalba*, age composition of the 772 adult females based on the number of corpora in the ovaries. Number indicate the sampling year, and closed circle and thick line the total. For further explanations see text.

The mortality rate calculated from all the age classes above 15.9 years coincides well with the figure obtained above based on the cemental layers. This may indicate the correctness of the above calculation. Furthermore, since the date of birth of dolphins at the boundary of the two slopes, 28 to 30 years before 1972 when most of the samples were collected, approximately coincides with the end of the last war in 1945, the annual mortality rate of 11.8% seems to indicate the rough estimation of the mean total mortality rate of the females in the years near the end of the war to late 1950's. As the difference of the annual mortality coefficient between sexes is in between 0.0171 and 0.0224 or about 0.020, the total mortality coefficient of the adult male in the corresponding years might be 0.126+0.020=0.146 or 13.6% per year. Though the mean mortality rate in the immature stage is expected to be lower than that of adult dolphins as in the case of *S. attenuata*, it is not possible to estimate it at present. The natural mortality rate is also unknown.

DISCUSSION

Age determination method

When the layers in dentine and cementum are compared, the higher number is almost always found in the latter in case of the dolphins older than 9 (*S. attenuata*) or 11 (*S. coeruleoalba*) years of age. If, after these ages, the number of dentinal layers plotted against the number of cemental layers showed an increase slower than that in younger stage, it would be possible to interpret that the accumulation rate of cemental layers increases after these ages and that of dentinal layers stays constant. However, as the number of dentinal layers of older age groups is constant without showing any correlation with that of cemental layers, it is concluded that the accumulation of the dentinal layers stops at various ages between 9 or 11 years and about 25 years, or that the dentinal layers become too thin to be distinguished by the present method. Recently same phenomenon was confirmed by Dr. P. B. Best (person. comm.) on *Lagenorhynchus obscurus* through tetracyclin marking. He considers that "dentinal layers accumulate annually in young dolphins, but deposition of dentine slows down in older animals and may cease altogether". As the tooth at this stage is hardly distinguishable from that at preceeding stage through the observation of the pulp cavity, it seems to be safe to use the cemental layers for the age determination of the dolphins with more than 9 (*S. attenuata*) or 11 (*S. coeruleoalba*) dentinal layers. However it must be noted for the practical use of the cemental layer that the counting of the layers is more difficult and unreliable than that of dentinal layers, and that it is necessary to confirm the coincidence of the counts of the two kinds of layers on the decalcified and stained preparation of the tooth of young dolphin.

Furthermore, it should be remembered that the suitable way of preparing the tooth for age determination can be different between species of dolphins. If the present method of preparation is applied on *Phocoenoides* or *Lagenorhynchus* tooth, it gives good result for reading the cemental layers. However, in cases of *Globicephala macrorhynchus* and *Pontoporia blainvillei* the decalcification and staining are not necessary if the tooth is ground thinly enough, and the thick and irregular cemental layers in *Platanista gangetica* seems difficult to use for age determination.

Life history parameters

From the above reasons, the life history parameters estimated previously by reading dentinal layers and concerning the sexually mature dolphins are now unreliable. They are the accumulation rate of the corpora, mortality rate, and the age at the attainment of asymptotic length. In case of *S. attenuata*, the mean age at the onset of sexual maturity must also be corrected. However, as the accumulation rate of the corpora of this species was estimated from the comparison of corpora diameter and the growth of suckling calves, and the mortality rate from the corpora number and the accumulation rate (Kasuya *et al.* 1974), they are not much affected by the present study (Table 7). It is also confirmed that the ovulation rate and the calving interval estimated in the present study give the mean number of ovulations in one reproductive cycle 1.62 which is close to the estimation of 1.7 to 1.8 made by Kasuya *et al.* (1974).

Miyazaki (1675) estimated, for *S. coeruleoalba*, the annual ovulation rate of 0.59 based on the age-number of corpora relationship of the animals between the age of 11 and 15 dentinal layers, and this result was used by Kasuya and Miyazaki (1976) for the estimation of the mortality rate and the population.

TABLE 7. COMPARISON OF LIFE HISTORY PARAMETERS OF THE TWO SPECIES OF *STENELLA* OFF THE PACIFIC COAST OF JAPAN

Species Parameters	*S. attenuata* Previous study[1]	*S. attenuata* Present study	*S. coeruleoalba* Previous studies	*S. coeruleoalba* Present study
1. Gestation (months)	11.24	—	12	—
2. Length at birth (cm)	89	—	99.8[1]	—
3. Length at 1 year of age (cm)	142.7	142.5	164.5	164.0
4. Length at 3 years of age (cm)				
male	166.0	163.0	194.0	193.0
female		161.5	191.0	189.0
5. Length at 9 years of age (cm)				
male	191.5	186.0	220.5	222.0
female	190.0	187.5	217.0	218.0
6. Length at 50% maturity (cm)				
male	194.3	—	218.3[3]	—
female	181.9	—	211.5	—
7. Asymptotic length (em)				
male	203.3	207.1	234.4[1]	236.0
female	194.9	193.9	223.5	225.3
8. Age at asymptotic length (years)				
male	12	22	12	21
female	11	12	11	17
9. Age at 50% maturity				
male	10.3	11.8	9.2[2]	9.0
female	8.2	9.0	8.8	(8.5)
10. Maximum age (years)				
male	24	40	25[1]	50
female	24	46	26	49
11. Calving interval (years)	4.19	3.94	2.20('73)[3]	2.37('73)
12. Length of lactation (years)	2.44	2.35	0.89('73)[3]	1.06('73)
13. Annual pregnancy rate (%)	23.8	25.4	45.5 ('73)[3]	42.2 ('73)
14. Annual ovulation rate	0.43-0.49	0.412	0.590[4]	0.414
15. Annual mortality rate (%)				
adult female	7.4	7.5	12.8[3]	11.8
immature female	3.2	3.3	—	—
adult male	14.8	10.7	—	13.6
immature male	11.8	6.9	—	—
16. Ratio of female at birth (%)	38.9	41.6	47.6[3]	—
17. Maximum no. of calves produced by one female	8.3	9	—	16
18. Mean no. of calves produced by one female	—	2.40[5]	—	0.96[5,6]

1) Kasuya *et al.* 1974, 2) Kasuya 1972, 3) Kasuya and Miyazaki 1976, 4) Miyazaki 1975, 5) $e^{-9\mu_1}\int_0^\infty e^{-\mu_2 x}dx$/calving interval, 6) $\mu_2=0.07$, fishing mortality coefficient 0.0558, and calving interval 2.90 years in 1960 are assumed.

However, in view of the result of the present study, it seems to be improbale that the age-number of corpora relationship can fit such a linear line as indicated by Miyazaki (1975, and see Kasuya and Miyazaki 1976). Actually, any data possessed by myself or by Dr. Miyazaki, both of which were used in Miyazaki (1975), failed to reproduce the graph cited in Kasuya and Miyazaki (1976). Possibly many individuals younger than 16 dentinal layers and with high corpora count might have been arbitrarily excluded from his calculation. Accordingly, the accumulation rate of corpora estimated in this study, 0.414 per annum, is considered to be more reasonable.

However, as this ovulation rate is estimated from the gradient of age-number of corpora relationship, it gives only the ovulation rate in the year when the dolphin attained the sexual maturity. Even if the ovulation rate is changing in recent years, it will not be detected by this method until the recently matured females attain a certain age and the change of the gradient is detected. As the ovulation rate of *S. coeruleoalba* estimated in this study is not different from that of *S. attenuata* at initial population level, and is close even with 0.38 to 0.45 the rate of the *P. catodon* estimated by dentinal layers (Bannister 1969 cited in Gambell 1972, Best 1970, Gambell 1972), 0.5 of *H. ampullatus* (Christensen 1973), and 0.39 to 0.51 of *G. melaena* estimated by indirect method (Sergeant 1962), it is suspected that the annual ovulation rate of toothed whales at their initial population level will not be much different between the species, and that the annual ovulation rate of two kinds of *Stenella* estimated in this study must be that at initial population level.

The population of *S. coeruleoalba* off the Pacific coast of Japan has been depleted in recent years to about half of the initial level, and the mean calving interval is changing shorter (Kasuya and Miyazaki 1976, and see Table 8 and Fig. 14 of this study). If the mean calving interval of this population in between 1972 and 1973 is 2.39 years as calculated from the regression line (see page 89) and the mean annual ovulation rate is 0.414, the mean number of ovulations in one reproductive cycle is only 0.989. This is not significantly different from one ovulation per cycle, or the rate only theoretically possible when all the ovulations are followed by the conception and seems to be actually impossible. This problem can be explained by one or two of the following assumptions.

1. Annual ovulation rate has started to increase in recent years, when the calving interval is so shortened that the further shortening can not be achieved by the improvement of the ratio of successfull ovulation.
2. Length of calving interval is underestimated.

Though it is sure that the estimation of the mean calving interval is liable to alteration when better estimation of gestation length is obtained or when the data of the ratio of females at various reproductive stages covering wider seasons are obtained, the bias of the present estimation was expected not to be large (page 88). And I suspect that the first assumption is more probable.

It has been generally supposed that when the population is depleted by the exploitation, the pregnancy rate or the calving interval of the cetaceans will change in order to result in the increase of recruitment (Laws 1961). This phenomenon seems to have been detected with insufficient accuracy in the population of *S. coeruleoalba* off the Pacific coast of Japan (Kasuya and Miyazaki 1976). The difference of pregnancy rate between *S. coeruleoalba* and *S. attenuata* indicated in the present study can be the reflection of different strength of exploitation. If the relationships between pregnancy rate and age of the animals of the two species of *Stenella* are compared (Figs. 12 and 14) in view of the above hypothesis, there are expected several factors influencing the change of mean pregnancy rate in a population. The first and the most direct is the shortening of calving interval in all the age classes. This is expected from the fact that the mean calving interval of the unexploited *S. attenuata* is about 3.4 years in the age classes of high reproductive activity, and the corresponding figures of exploited *S. coeruleoalba* is about 1.4/0.590=2.4 years when the bias of the data is corrected (see page 90). The second factor is the extension of the period of high reproductive activity from up to 22 years of age as observed in *S. attenuata* to up to 32 years of age in *S. coeruleoalba.* These two factors will result in the decrease of the mean length of lactation, which is suggested from the facts that the shortening of mean calving interval of *S. coeruleoalba* in recent years is achieved by the shortening of the period of lactation (Kasuya and Miyazaki 1976, page 89 of this study) and that the length of lactation in the ages of high reproductive activity is generally shorter than that in older age classes (page 88). The third and the most indirect factor will be the increase of the ratio of young and reproductively active females, which is the result of the high recruitment rate brought by the former two factors and of higher fishing mortality rate. Though the attainment of sexual maturity at younger age is expected when the population decreases as already observed in fin whale (Lockyer 1972), it ts not clear if the difference of the mean age at the onset of sexual maturity between the two species of *Stenella* observed in this study is due to it. It seems to be probable in the delphinids that the length of nursing period is more variable than the age at the onset of sexual maturity. So, when the population is depleted by the exploitation, the shortening of the calving interval directly related with that of nursing period as indicated in this study will occur before the change in the age at the attainment of sexual maturity does.

Kasuya *et al.* (1974) estimated from the analysis of the size distribution of the corpora in the ovaries that the maximum number of calves produced by one female is 8.3 in *S. attenuata.* It was shown in the present study that the age of the oldest female of the species is about 46 years, mean calving interval 3.94 years and the mean age at the start of the sexual maturity 9 years. These figures give the estimation of the maximum number of calves that can be produced by a female, or (46–9)/3.94=9 calves. This figure coincides extremely well with the estimate made by Kasuya *et al.* (1974) through the analysis of corpora. If the similar calculation is made for *S. coeruleoalba* in the early 1970's, it gives approximate figure (49–9)/2.4=16 calves. The extremely higher number of production of calves in the latter species must be the sum of the above mentioned reaction of the population to the exploitation.

Estimation of the population of S. coeruleoalba

In view of the present study indicating the minor change of the parameters, the population analysis made by Kasuya and Miyazaki (1976) shall be reconsidered based on the improved parameters concerning total mortality rate of post-war period, annual change of mean calving interval, and calving interval at initial population level taken from that of *S. attenuata*. Furthermore, the catch statistics at Taiji in 1973 and the total catch of the same year shall be corrected to 1,000 and 8,200 dolphins respectively instead of 7,500 and 14,700 used by Kasuya and Miyazaki (1976), and the total catch of the species in 1974, 13,000 animals, was added.

If the analyses of the population is made by the same principle as used by Kasuya and Miyazaki (1976), the relationship between net annual recruitment rate (R in %) and the population (P in thousands) estimated for each year between 1960 and 1975 based on the recruitment and catch is shown by the following least squares regressions.

$$R=-0.01190P+4.437, \quad \text{when } \mu_2=0.07$$
$$R=-0.01598P+6.462, \quad \text{when } \mu_2=0.08\,.$$

TABLE 8. COMPARISON OF POPULATION ANALYSIS OF *S. COERULEOALBA* BETWEEN PREVIOUS AND PRESENT ESTIMATES

	Kasuya and Miyazaki[1]		Present estimation	
Assumption, μ_2 [2]	0.07	0.08	0.07	0.08
Presumed μ_1 [3]	0.05354	0.03870	0.0606	0.0458
Mean annual catch around 1960	14,000	14,000	14,000	14,000
Total mortality coefficient	0.1365	0.1365	0.1258	0.1258
Fishing mortality coefficient	0.0665	0.0565	0.0558	0.0458
Fishing mortality rate	0.0643	0.0549	0.0543	0.0448
Population around 1960	218,000	255,000	258,000	313,000
Population at 1974	129,000	186,000	176,000	252,000
R[4] at 1974 level	3.09%	3.21%	2.34%	2.44%
SY[5] at 1974 level	3,980	5,960	4,120	6,140
Initial population	≧321,000	≧340,000	≧373,000	≧404,000
Population, MSY[6] level	161,000	170,000	186,000	202,000
R at MSY[6] level	2.57%	3.53%	2.22%	3.23%
MSY	4,130	6,010	4,140	6,530

1) Kasuya and Miyazaki 1976, 2) Annual natural mortality coefficient of adult female, 3) Mean annual natural mortality coefficient of immature female calculated from μ_2, sex ratio 0.476, and calving interval of *S. attenuata* at initial level, 4) Net annual recruitment rate, estimated from the relationship between P and R in the above, 5) Sustainable yield, 6) Maximum sustainable yield.

These equations give reproductive rate slightly lower than that in Kasuya and Miyazaki (1976). The minimum initial population is estimated as the value of P corresponding to $R=0$. Other revised population parameters based on the above equations are shown in Table 8. Though, the population is suspected to be continuously decreasing since 1970 at an mean rate of 2,700 ($\mu_1=0.08$) or 4,800 ($\mu_2=0.07$) dolphins per year, it is unnecessary to alter their conclusion saying that the present status of the population is " close to the level producing the maximum sustainable yield of 4,000 to 6,000 dolphins per annum ". This is the result of the interference of the higher population estimate lead from the lower fishing mortality rate in the post-war period and the lower recruitment rate calculated from the new estimate of mean calving interval. However it is also important to note that the population parameters lead from the assumption of the natural mortality coefficient $\mu_2=0.07$ might be closer to the truth. The reason is that, if we consider that the length of lifetime of *S. coeruleoalba* is probably longer than that of *S. attenuata* by about 10% (see Table 7), the natural mortality coefficient of adult female of the former species is suspected to be about 10% lower than that of the latter species $\mu_2=0.0779$.

The annual net recruitment rate at the instance of extinction is extraporated from the above equations as 0.04437 (when the natural mortality coefficient of adult female $\mu_2=0.07$) or 0.06462 ($\mu_2=0.08$). The mean calving interval giving these recruitment rates, under the assumption that other parameters stays unchanged, are calculated with the following equations modified from those in page 92 of this study (Kasuya and Miyazaki 1976),

$$l_0 = A \cdot L \cdot s/C$$

$$A = l_0 e^{-(\mu_1+f)m}/(\mu_2+f)$$

$$R = 1-e^{-f}$$

where f indicates sustainable fishing mortality coefficient. They are 1.59 (when $\mu_2=0.07$) or 1.18 ($\mu_2=0.08$) years. If the ratio of females which start the next conception increase linearly after the preceding parturition and the length of gestation of this species is about 12 months (Kasuya 1972), all the females must start the conception within 1.2 or 0.36 years respectively after the last parturition. Though they are not impossible, the latter seems to be difficult to be accomplished if the mating peaks of two (Kasuya 1972) or three (Miyazaki 1975) times in a year are retained unchanged. However, it is possible to expect at the lower population level, the non linear change of recruitment rate affected by the change of other reproductive parameters (age at the attainment of sexual maturity, sex ratio, or mortality rate of weaning calves) which are not detected at present.

ACKNOWLEDGMENTS

I am greatly indebted to Mr. S. Matsui of the Taiji Whale Museum and to Dr. N. Miyazaki of the Ocean Research Institute, University of Tokyo, for collecting the data and samples. Dr. R. L. Brownell of the Smithsonian Institution kindly read the manuscript and criticized. The preparation of tooth sections and the analysis of the data were made with the assistance of Miss S. Wada and Miss M. Oya of the Ocean Research Institute. These persons are deeply acknowledged.

REFERENCES

BEST, P.B., 1970. The sperm whale (*Physter catodon*) off the west coast of South Africa. 5. Age, growth and mortality. *Investl. Rep. Div. Sea Fish. S. Africa*, 79: 1-27.

CHRISTENSEN, I., 1973. Age determination, age distribution and growth of bottlenose whale, *Hyperoodon ampullatus* (Forster) in the Labrador Sea. *Norwegian J. Zool.*, 21(4) : 33-340.

GAMBELL, R., 1972. Sperm whales off Durban. *Discovery Rep.*, 35: 199-358.

HIROSE, K., T. KASUYA, T. KAZIHARA and M. NISHIWAKI, 1970. Biological study of the corpus luteum and the corpus albicans of blue white dolphin (*Stenella caeruleoalba*). *J. Mamm. Soc. Japan*, 5(1) : 33-39.

KASUYA, T., 1972. Growth and reproduction of *Stenella caeruleoalba* based on the age determination by means of dentinal growth layers. *Sci. Rep. Whales Res. Inst.*, 24: 57-79.

KASUYA, T., 1976a. The stock of striped dolphin, part 1 and 2. *Geiken Tsushin*, 295: 19-23, 296: 29-35. (In Japanese)

KASUYA, T., 1976b. Preliminary report of the biology, catch and populations of *Phocoenoides* in the western North Pacific. ACMRR/MM/SC 21, 20p.

KASUYA, T. and N. MIYAZAKI, 1976. The stock of *Stenella coeruleoalba* off the Pacific coast of Japan. ACMRR/MM/SC 25, 37p.

KASUYA, T., N. MIYAZAKI and W.H. DAWBIN, 1974. Growth and reproduction of *Stenella attenuata* in the Pacific coast of Japan. *Sci. Rep. Whales Res. Inst.*, 26: 157-226.

LAWS, R.M., 1961. Reproduction, growth and age of southern fin whale. *Discovery Rep.*, 31: 327-486.

LOCKYER, C., 1972. The age at sexual maturity of the southern fin whale (*Balaenoptera physalus*) using annual layer counts in the year plug. *J. Cons. Inst. Explor. Mer.*, 34(2) : 276-294.

MITCHELL, E. and V.M. KOZICKI, 1975. Autum stranding of a northern bottlenose whale (*Hyperoodon ampullatus*) in the Bay of Fundy, Nova Scotia. *J. Fish. Res. Board Canada*, 32: 1019-1040.

MIYAZAKI, N., 1975. School structure of *Stenella coeruleoalba*. *Doctoral thesis, Faculty of Agriculture Univ. Tokyo* (Manuscript, in Japanese).

OHSUMI, S., T. KASUYA and M. NISHIWAKI, 1963. Accumulation rate of dentinal growth layers in the maxillary tooth of the sperm whale. *Sci. Rep. Whales Res. Inst.*, 17: 15-35.

OHSUMI, S., 1965. Reproduction of the sperm whale in the North-West Pacific. *Sci. Rep. Whales Res. Inst.*, 20: 1-16.

SERGEANT, D.E., 1959. Age determination of odontocete whales from dentinal growth layers. *Norw. Whaling Gaz.*, 48(6) : 273-288.

SERGEANT, D.E., 1962. The biology of the pilot or pothead whale, *Globicephala melaena* (Traill) in Newfoundland waters. *Bull. Fish. Res. Bd. Canada.*, 132: 1-84.

SERGEANT, D.E., D.K. CALDWELL and M.C. CALDWELL, 1973. Age, growth, and maturity of bottlenosed dolphin (*Turiops truncatus*) from Northeast Florida. *J. Fish. Res. Board Canada*, 30: 1009-1011.

EXPLANATION OF PLATES

PLATE I

Fig. 1. Decalcified and stained tooth section of *S. attenuata*, 167 cm male (school 5, no. 54), pulp cavity at the right. White spots indicate 3 stainable cemental layers, and numerals stainable postnatal dentinal layers. Scale indicates 0.1 mm.

Fig. 2. Another part of the same tooth section in Fig. 1, cusp at the left and pulp cavity at the bottom. 0 indicates prenatal dentine. For other marks see Fig. 1.

Fig. 3. Cemental part of a decalcified and stained tooth section of *S. attenuata*, 195 cm female (school 3, no. 35), dentine at the right. 46 cemental layers are counted. Scale indicates 0.1 mm.

PLATE II

Fig. 1. Decalcified and stained tooth section of *S. coeruleoalba*, 232 cm male (school 44, no. 337), cusp at the lower left and pulp cavity at the lower right. 28 dentinal layers are counted. Scale indicates 0.1 mm.

Fig. 2. Cemental part of the same tooth section in Fig. 1, dentine at the bottom. 28 cemental layers are counted. Scale indicates 0.1 mm.

Fig. 3. Cemental part of a decalcified and stained tooth section of *S. coeruleoalba*, 227 cm male (school 44, no. 166), dentine at the right. 40 cemental layers are counted. Scale indicates 0.1 mm.

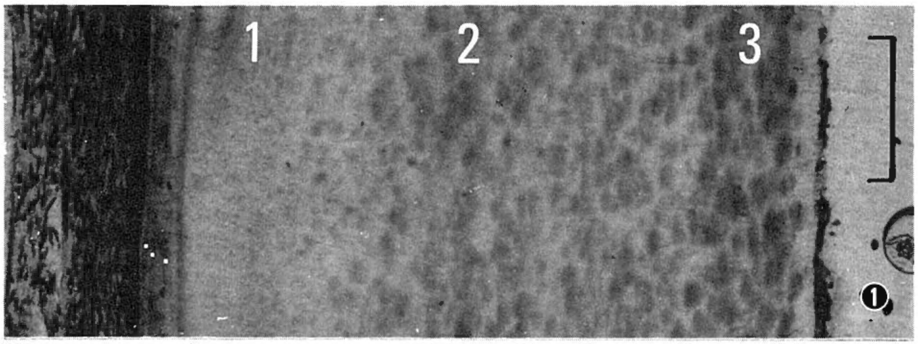
PLATE III

Fig. 1. Cemental part of a decalcified and stained tooth section of *S. coeruleoalba*, 241 cm male (school 44, no. 295), dentine at the lower left. 49 cemental layers are counted. Scale indicates 0.1 mm.

Fig. 2. Comparison of a tooth section before and after the decalcification and staining. *S. coeruleoalba*, 161 cm male (school 38, no. 161), pulp cavity at the right. Scale indicates 0.1 mm. Top: After decalcification and staining. Bars indicate stainable dentinal layers. Bottom: Before decalcification. Bars indicate opaque dentinal layers.

PLATE IV

Decalcified and stained tooth of *S. attenuata*, 183 cm male (school 7, no. 27). 10 stainable layers are counted in both cementum and dentine. Numerals indicate prenatal dentin (0) and postnatal dentinal layers (1-10). Pulp cavity at the lower right. Scale indicate 0.1 mm.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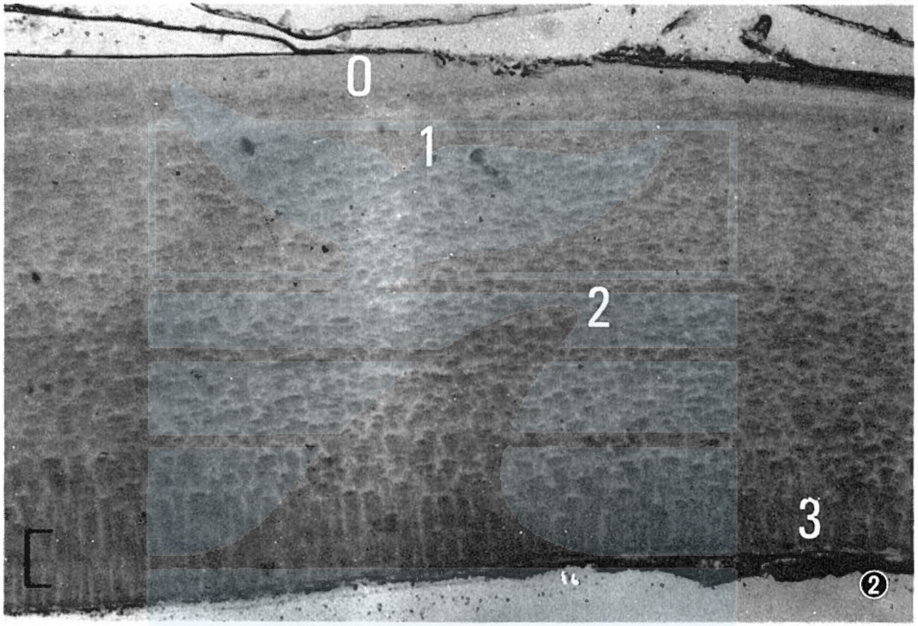
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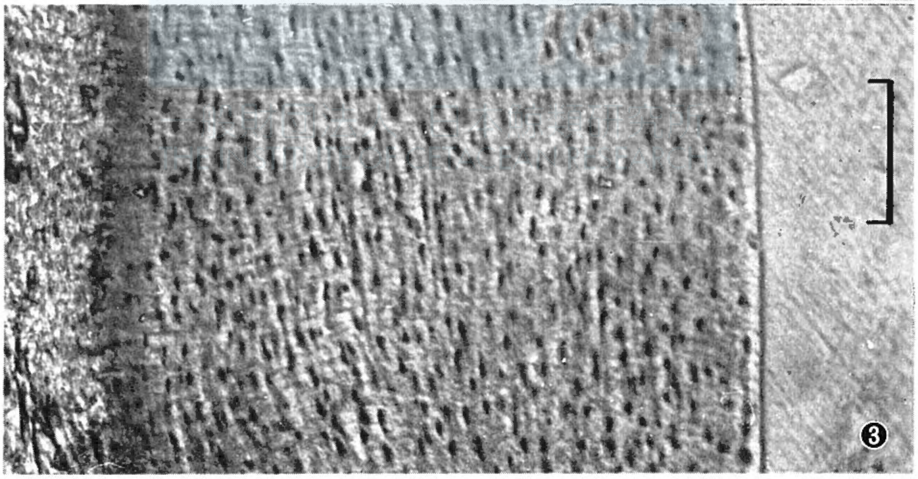
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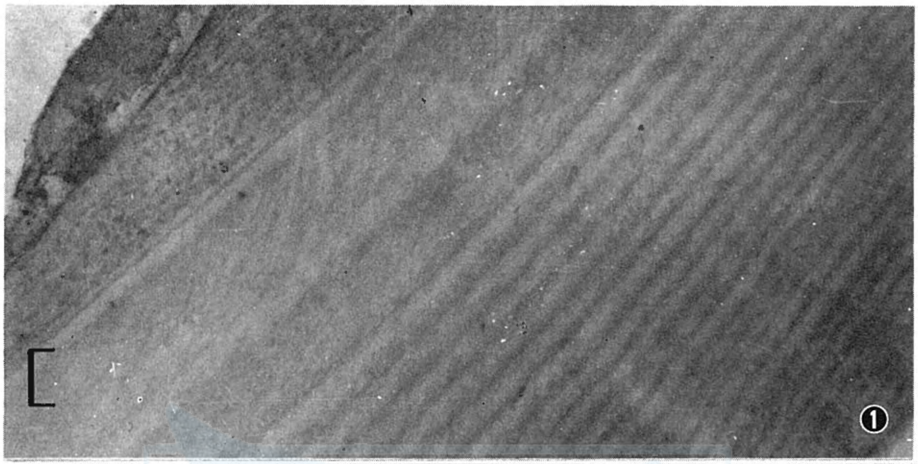
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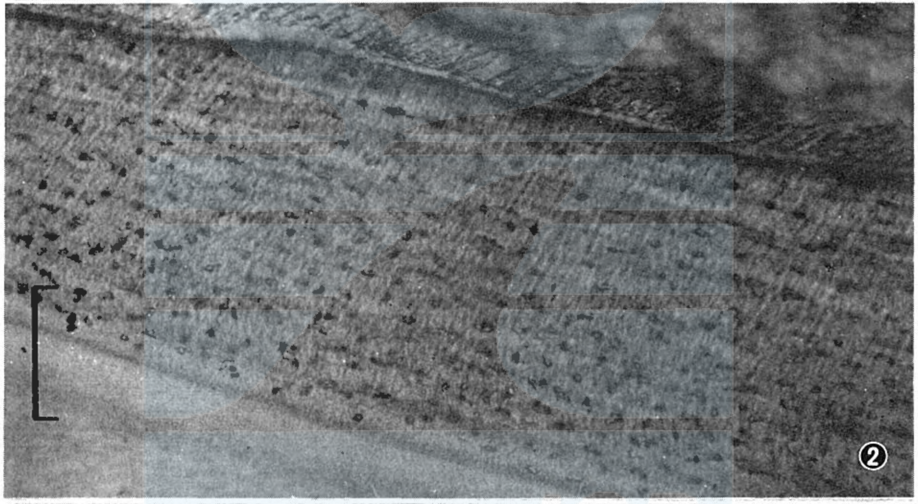
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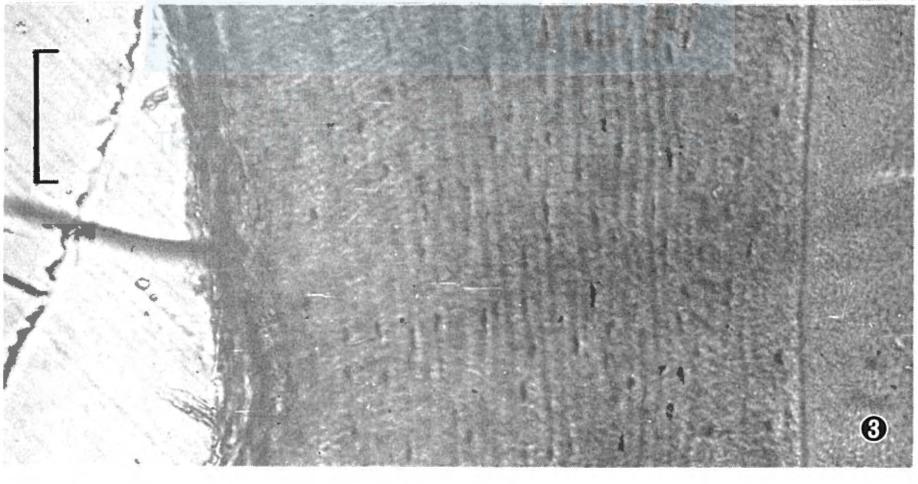
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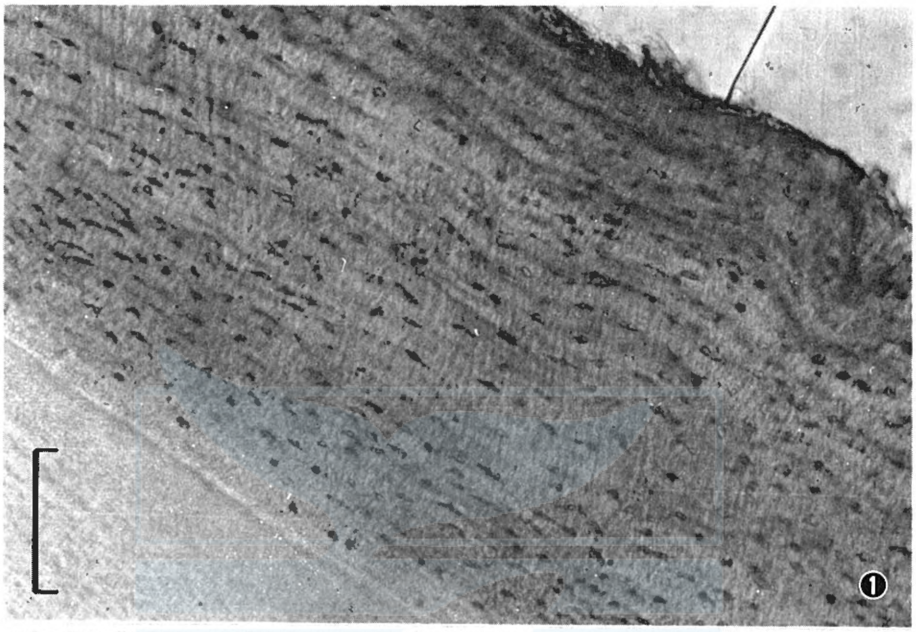
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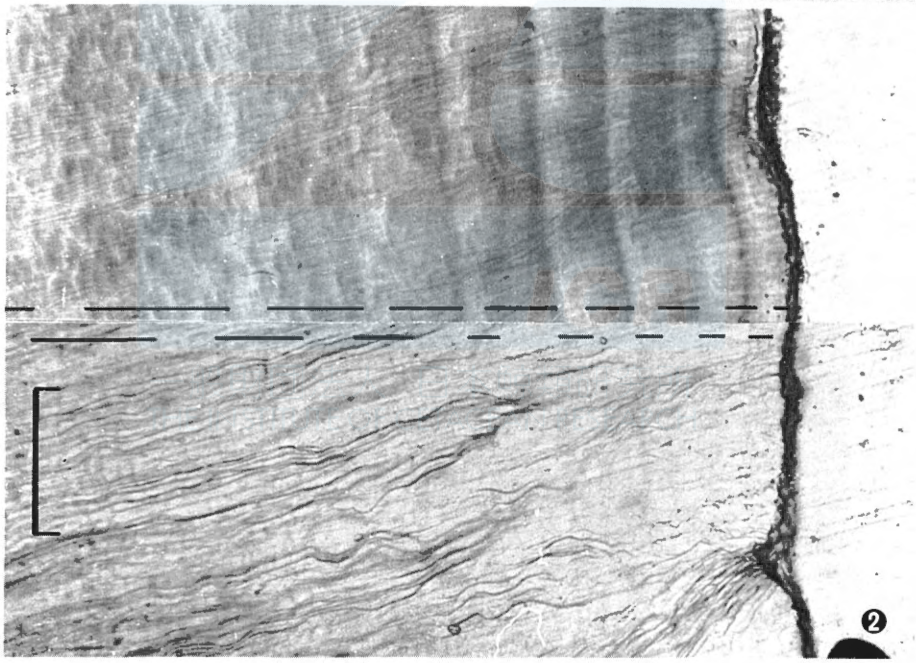
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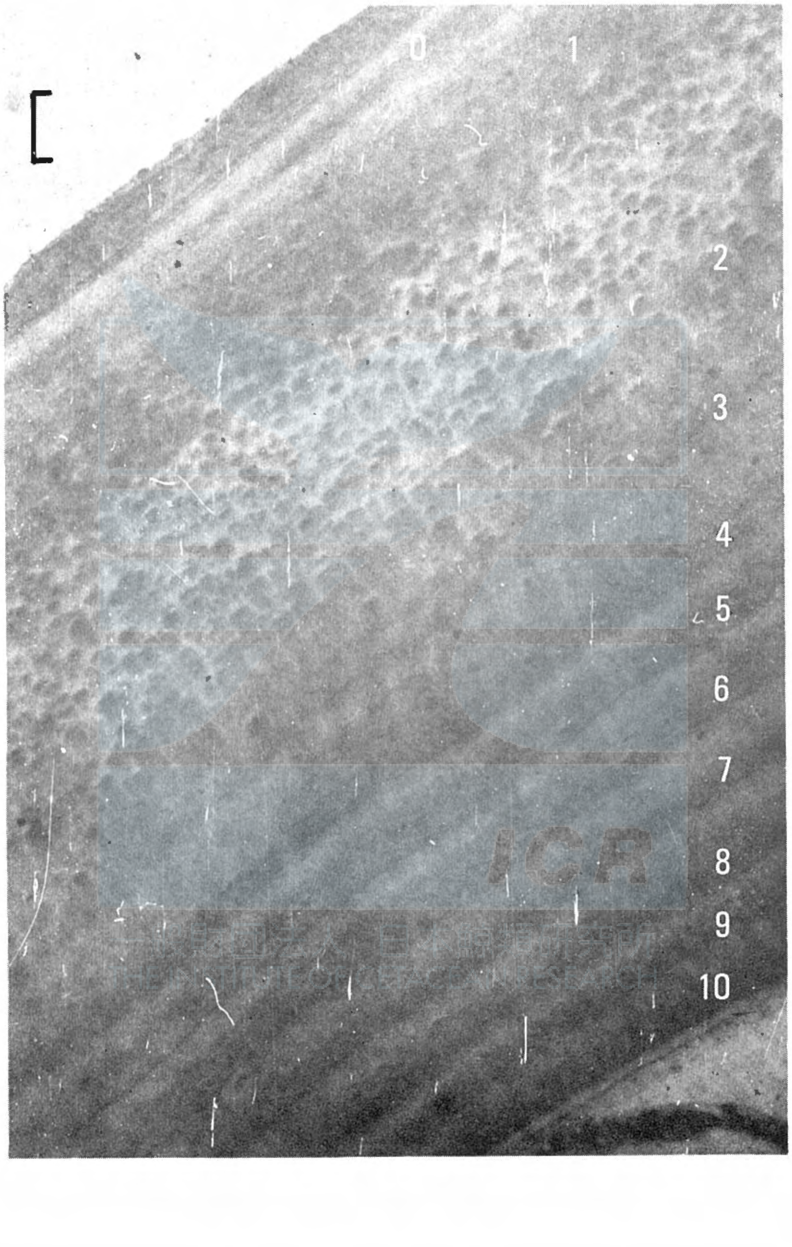
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