GROWTH AND REPRODUCTION OF *STENELLA ATTENUATA* IN THE PACIFIC COAST OF JAPAN

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ABSTRACT

Data collected from 7 schools of *S. attenuata* were analyzed. Body length at birth is 89 cm. Sexual maturity is attained at 8.2 years in females and 10.3 years in males. Physical maturity is attained soon after the attainment of sexual maturity at a length of 194.9 cm (females) and 203.3 cm (males). The pigmentation and size of the animals slightly differ from the corresponding species in the eastern North Pacific. Mating seasons are in February and March, July, and November. Gestation lasts for 11.2 months, and lactation for 29 months on average. The mean length of reproductive cycle is about 50 months, but changes with the age of the animal. The annual mortality rate is 0.074 in the mature female and about half of it in immature animals. Some females live for more than 40 years, and have an average of 8.3 calves. The mortality is higher in males than in females. Schooling behavior is discussed.

INTRODUCTION

Stenella attenuata (Gray, 1846) is distributed widely in tropical and subtropical waters of the Indo-Pacific Ocean. In the eastern tropical Pacific the probably conspecific separate population (Perrin, 1973) *S. graffmani* is often caught by tuna seine, and its biology is being studied (Perrin, 1969, Perrin and Roberts, 1972). In the southern Pacific some biological study is reported by Dawbin (1966) based on animals caught at Malaita (Solomon Islands). Though this species is also caught at Taiwan by hand harpoons for human consumption (Kasuya, unpublished), it has not been studied biologically.

In Japanese coastal waters this species is common along the southern coast from Kyushu (Mizue and Yoshida, 1962) to Onahama (36°56′N, 139°55′E) (Kasuya, 1971), and has been caught sporadically by fishermen with hand harpoons or the driving method. On the east coast of Izu Peninsula *S. attenuata* is usually caught in October and early November slightly before the peak of the season of *S. coeruleoalba* (Tobayama, 1969), and on the west coast of Izu Peninsula (Nishiwaki, 1965) slightly after the spring season of *S. coeruleoalba*. However, on the coast of Kii Peninsula a few animals have been captured with hand harpoons in all seasons of the year, and recently fishermen have started to catch this species by the driving method in both winter and summer seasons. This suggests that *S. attenuata* lives in warmer waters than *S. coeruleoalba*, and in early autumn they move to the south along the Pacific coast of Japan. As they are found in waters at more than 16.8°C (Miyazaki *et al.*, 1974), they surely migrate up to 40°N but the information on northbound migration is scarce (Kasuya, 1971, Miyazaki *et al.* 1974). The distribution of this species in the Japan Sea is also unknown.

The biology of *S. attenuata* was partially studied by Nishiwaki *et al.* (1965). The present study is intended to clarify differences between the life history of this species from that of a similar species, *S. coeruleoalba*, and to provide some information on relationships between ecology, environment, and certain species of delphinidae.

MATERIALS AND METHODS

All the materials used in this report were obtained, with a few ancillary materials, from 7 schools caught by the driving method at Kawana or Futo on the east coast of Izu Peninsula, or at Taiji on the coast of Kii Peninsula (Fig. 1, Table 1). One 48 cm fetus was collected in February from a female caught by hand harpoon at Taiji, and 2 of the 4 sets of data on stomach contents of calves were obtained separately at Kawana.

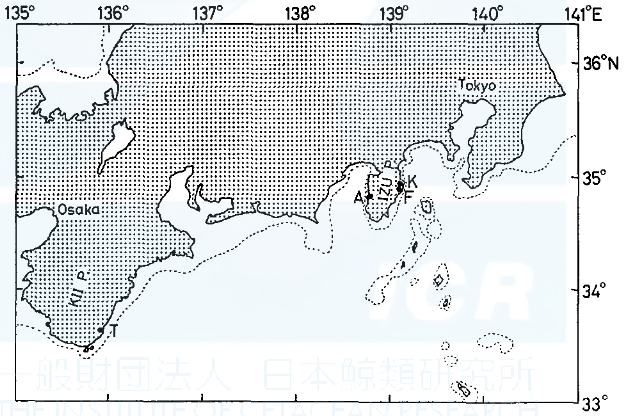

Fig. 1. Map showing the positions of sampling, A indicates Arari, K Kawana, F Futo, and T Taiji. Dotted lines indicate 200 m depth.

As shown in Fig. 2, school 1 was composed of adult males, females and newborn calves, but was lacking in calves of from 128 cm to 156 cm in body length. The pregnant females had small fetuses. The length frequencies of schools 2 to 5 are more or less similar with calves and adult dolphins of various length, but the fetuses were slightly bigger than those observed in school 1. School 6 was different from schools 2 to 5, in the larger size of fetuses. In school 7, full term fetuses and newborn calves were observed. It is difficult to know the exact composition of the larger individuals because of the limited material, but it may not be very different from that of school 3.

Body length was measured in 1 cm intervals in a straight line from the tip of the upper jaw to the bottom of the notch of the tail flukes. In some cases 4 length measurements shown by $4n \leqq L \leqq 4n+3$ were grouped, where n is an integer and L is body length in cm.

The mammary gland was observed in the field and classified into lactating and nonlactating. In some cases its thickness was measured in a longitudinal cut made by the fishermen, because they did not welcome transverse section of the mammary gland. These data were used for reference.

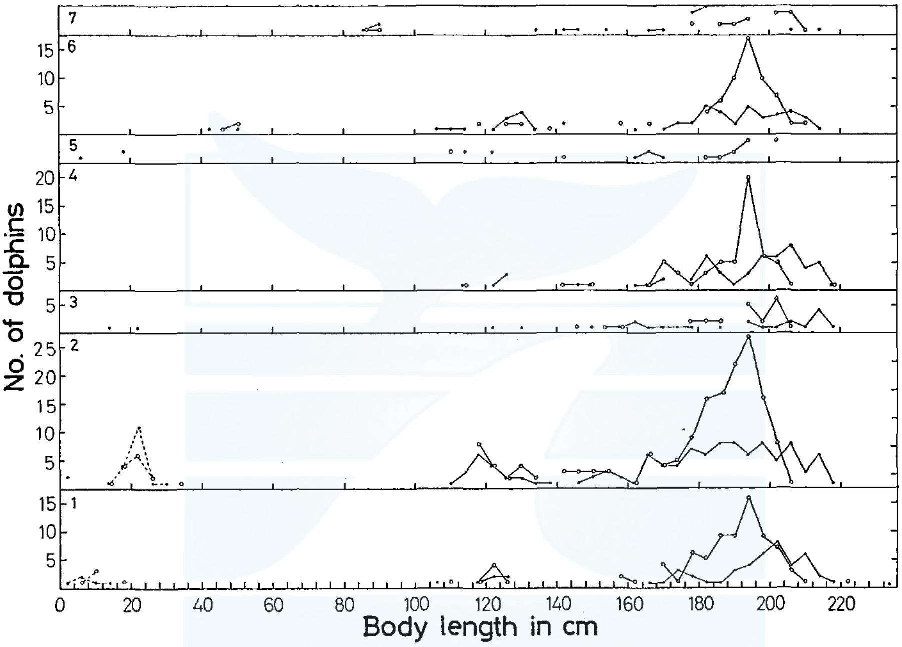

Fig. 2. Length frequencies of *S. attenuata* in the 7 schools studied. Numbers at the left indicate the school, open circles females, closed circles males, dotted lines fetuses, and solid lines postnatal animals. The full term fetuses and newborn calves in school 7 are not separated.

The ovaries were collected from most of the adult and immature females, and fixed with 10% formalin solution. The number of corpora albicantia and lutea was counted by Kasuya in the laboratory by slicing the ovary into about 1 to 2 mm thickness. The three diameters of all the corpora lutea and albicantia and those of the largest follicle were measured. The volume index of the corpora or follicle obtained by multiplying the three diameters was used in the analysis of ovarian activity. But in this report the mean diameter obtained as the cube root of the volume index has usually been used.

Both testes were collected from the males in schools 1 and 2, but only the left one in other schools. They were preserved in the same manner used for ovaries.

The weight was measured in the laboratory. As there is no significant difference expected in the weights of right and left testes, usually the left side was used for study and the right was used only when the left testis was not available.

Several maxillary teeth were collected from the center of the tooth row with a pair of gardening scissors. The tooth section for age determination was prepared after the method of Kasuya (1972) slightly modified to use a grinder. The growth layers in dentine were observed by Kasuya under transmitted light with a binocular microscope (×50).

TABLE 1. MATERIALS USED IN THIS REPORT.

School no.	Dates of		No. of dolphins*		Locality	Researcher
	catch	kill	caught	studied		
1	23, X, '70.	25, X.	264	131	Kawana	Kasuya and Miyazaki
2	10, XI, '70.	15, XI.	1381	273	„	„ „
3	4, XI, '72.	4, XI.	189	48	„	Miyazaki
4	13, XI, '72.	13, XI.	192	117	„	„
5	16, XI, '72.	18, XI.	67	23	Futo	„
6	12, II, '73.	12, II.	146	122	Taiji	„
7	2, VII, '73.	2, VII.	Ca. 60	36	„	Dawbin

*: Fetuses not included.

Some of the selected testes were studied histologically after staining with haematoxylin and eosin. In these cases samples were collected from the center of the cross section made at the midlength of a testis. In order to check the presence of spermatozoa in a wider range, smears were taken from most of the testes on the same cross section, and observed after staining with methylene blue. These testes observations were made by Miyazaki and Kasuya.

AGE DETERMINATION AND GROWTH

Age determination

The growth layers in dentine were used to determine the age characteristics as the cementum of *S. attenuata* is too thin to count the growth layers. The nature of the dentinal growth layers of this species does not differ much from that of *S. coeruleoalba* (Kasuya, 1972), but counting is slightly more difficult because of the irregularity of the layers. The poorly calcified secondary dentine is observed in teeth with about 12 or more layers. This may indicate that the growth of the dentine becomes slower in these ages, when physical maturity of the animal is attained.

To find the annual accumulation rate of dentinal growth layer, the condition of the last layer was checked on teeth which had 10 or less opaque bands and in which the thickness of the layer was not too thin to estimate the relative thickness. Though the relative thickness of the layer was estimated in comparison with the former layer taking into consideration the gradual decreasing size of the layer, this observation is less reliable than the identification of opaque or translucent layers. As shown in Fig. 3, most of the animals killed in July, October and November were forming opaque layers, but almost all the animals killed in February were accumulating translucent layers. In the present study it has been impossible to decide the date when the formation of the two kinds of layers alternate, but it seems probable that the alternations occur in December or January and in April or May, and that each opaque and translucent layer represent about 6 months respectively.

In this study the number of opaque layers in dentine, excluding the fetal layer, was counted together with observation of relative thickness and condition of the first and last layers. The layers were usually counted along the line set from the

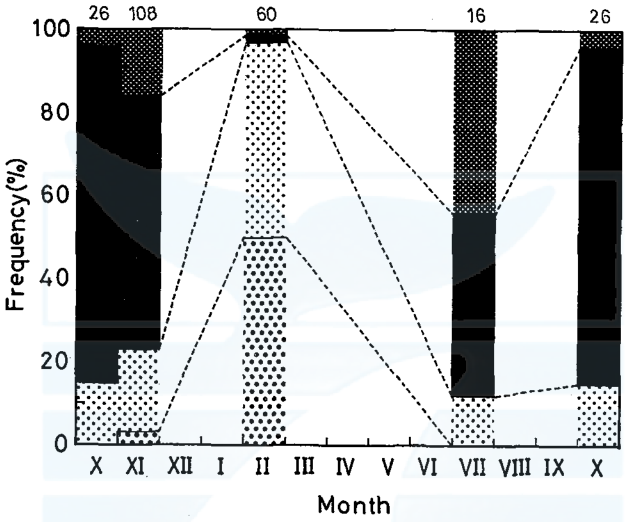

Fig. 3. Seasonal change of the formation of opaque and translucent dentine layers. Black with white spots indicates thin opaque layer, the black thick opaque layer, the white with small spots thin translucent layer, and the white with large spots thick translucent layer.

TABLE 2. CRITERION FOR CALCULATING THE AGE FROM THE NUMBER OF OPAQUE LAYERS (n).

First and last layers	Possible range of age	Approximate age (x)
tt-tt	$n+0.50\geqq x>n$	$x\fallingdotseq n+0.25$
tt- t	$n+0.25\geqq x>n-0.25$	$x\fallingdotseq n$
t- t oo-tt	$n\geqq x>n-0.50$	$x\fallingdotseq n-0.25$
oo- t o-tt	$n-0.25\geqq x>n-0.75$	$x\fallingdotseq n-0.50$
oo-oo o- t	$n-0.50\geqq x>n-1$	$x\fallingdotseq n-0.75$
oo- o	$n-0.75\geqq x>n-1.25$	$x\fallingdotseq n-1$
o- o	$n-1\geqq x>n-1.50$	$x\fallingdotseq n-1.25$

o: thin opaque, oo: thick opaque, t: thin translucent, tt: thick translucent middle of the neonatal line to the central portion of the pulp cavity, because the structure near the distal tip is sometimes discontinuous especially in the young layers. When the number of opaque bands (n) is counted the possible range of real age (x) is generally shown by the following formula.

$$n-1.5<x<n+0.5$$

In case of animals at 3.5 years or older, the approximate age was represented by the value at the center of both extremities, or

$$x \fallingdotseq n-0.5$$

However, in the case of the younger animals, it was calculated from the criterion shown in Table 2.

As indicated in the latter section the counting of the dentinal growth layers is not reliable after the accumulation of secondary dentine, but the age of animals obtained from dentinal growth layers by the above method has been used in this report without special comment.

Length frequencies

The length frequencies of fetuses and juveniles varies between schools. This reflects the special schooling behavior related to the maturity and reproductive cycle. These problems are dealt with separately. There is no significant difference observed between schools in the shape of the peaks for animals more than 184 cm in females or 196 cm in males. When all schools are combined, the highest frequency is found in the length group 192 cm to 195 cm in females, and 204 cm to 207 cm in males. The difference of the modal lengths is about 12 cm. Most females are shorter than 212 cm and males less than 220 cm, but exceptionally large records of a female and a male were 220 cm and 234 cm respectively.

The above modal lengths seem to be slightly bigger than that of *S. graffmani* reported by Perrin (1969).

Fetal growth and length of gestation

The mean body length at birth is estimated roughly from the 5 full term fetuses or newborn calves in school 7. In this school 85 cm female, 85 cm male, and 88 cm male were considered to be definitely prenatal because they were found with large umbilical cord attached, or taken out of the uterus by Dawbin. The 89.0 cm male was considered to be a newborn calf because it had no trace of umbilical cord, but the umbilicus was the shape of an oval hollow with thin epidermis and the size was larger than that of a fully healed umbilicus. Its stomach contained milk of about 13 g in weight. One 88 cm female animal was found in the pile of viscera with the thin fragment of the external layer of the umbilical cord. However, the size of the fragment was much smaller than that of the 3 specimens first mentioned. The dorsal fin was not bent completely to one side as in the case of the fetus, but stood obliquely. On the lateral side of the body of the animal there were observed several transverse shallow grooves which are often found on the fetus. It had no milk in the stomach. According to the observation of Nakajima *et al.* (1963) on a *Tursiops truncatus* born in an aquarium, it takes several hours for the dorsal fin to stand vertically. Our observation on a newborn *S. coeruleoalba*, 100 cm in body length, shows that it had plenty of milk in the stomach in spite of features quite similar to the above 88 cm *S. attenuata* in the umbilicus, dorsal fin, and grooves on the flank. This suggests that the 88 cm animal was postnatal. However, we have some query on the last specimen of *S. attenuata* as to whether it was delivered by the artificial action given to the mother in the period from the start of driving to the time of kill. However, the present best estimate of the mean body length of *S. attenuata* at birth comes between 88 cm and 89 cm. In this paper 89 cm has been used as the tentative mean length at birth. Even if it is 88 cm in reality, the length of gestation is changed by only 3 days, which is negligible in relation to our tentative estimate of the mean length of gestation obtained below.

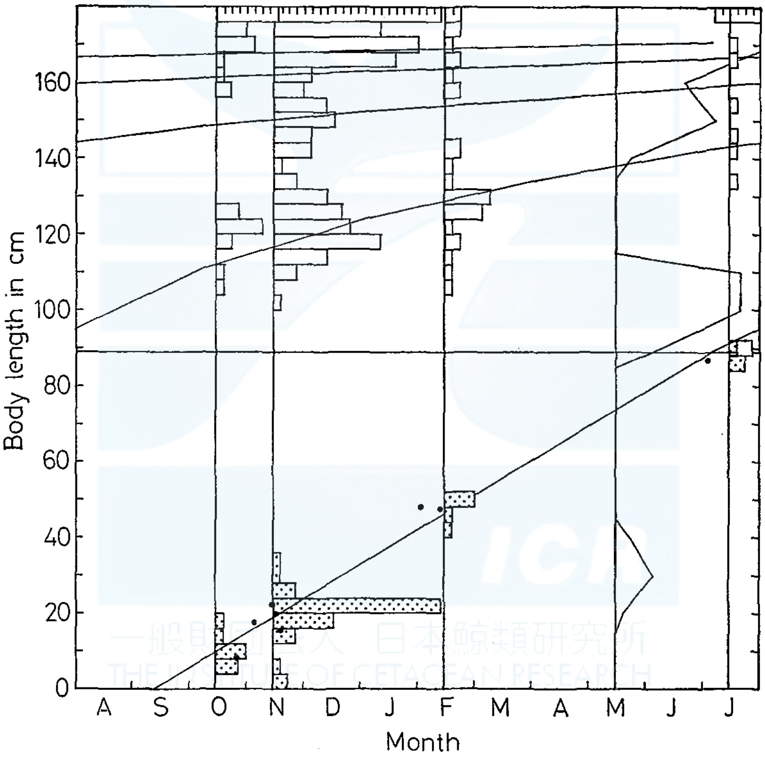

Fig. 4. Growth of fetus and juvenile calves. Length frequencies are grouped into months. The dotted area indicates fetuses, the white postnatal, and closed circles the mean body lengths of fetuses in each school. A school caught in May (Nishiwaki *et al*, 1965) is shown by solid line.

The length of gestation and fetal growth were calculated from the seasonal change of fetal length. In Fig. 4, the mean fetal length in each school was plotted against the date of kill. In school 2 the fetal length is bimodal, but it was not separated because the deviation from the main mode is not large. In other schools the fetal length is unimodal. In school 7 all the full term fetuses and newborn calves were combined in calculating the mean length. In addition to the 7 schools, one record of a fetus caught at Taiji in Feburary is also plotted in Fig. 4. All the above 8 points fall on a straight line, but the fetuses reported by Nishiwaki *et al.* (1965) come on quite a different position. The latter are considered to represent other mating seasons, and are dealt with separately. Laws (1959) showed in odontoceti that, except during the very early stage of growth, the relation between fetal length and the elapsed time after conception is shown by a single straight line. If a straight line is calculated by least squares for the above 8 points, the growth of the fetus is shown by the following formula,

$$y = 0.30094x - 76.74$$

where y is the length of the fetus in cm and x is the number of days counted from the last 1st of January. This formula shows that the daily increment of length at the straight part of the growth is 3.0 mm. The extended growth line cut the axis of time at day 255.01 or 12th of September, and attains the mean length at birth, 89 cm, on day 550.73 or 5th of July. Accordingly the length from the date when the extended straight line crosses the axis of time to the date of birth is 295.72 days.

If 0.135 × gestation period is tentatively used here for Lto of Laws (1959), which is the time from the start of gestation to the date when the extended straight line of the fetal growth cuts the axis of time, the length of gestation (L) is shown by the following formula

$$L - Lto = 295.72 \text{ days}$$
$$Lto = 0.135L$$

Then L is 341.87 days or 11.24 months and Lto is 46.15 days or 1.52 months. The date of conception of the growth line in Fig. 4 comes on 28th of July. The fetal growth rate of this species at the straight part of growth is close to that of *Tursiops* and *Phocoena* reported by Fraser and Huggett (1973).

Postnatal growth

The relation between body length and age of 195 males and 239 females is shown in the scatter diagram of Figs. 5 and 6.

The growth during the first three years is rapid. The mean growth curve of this part was drawn by eye based on the mean lengths in each 1/4 year interval and considering the distribution of each point in Figs. 5 and 6. As no sex difference in these age classes is observed, both sexes were combined.

The growth of males between the age of 3 years and 12 years, and of females between the age of 3 years and 7 years seems to be almost straight. The growth line of this age range was calculated by least squares based on the mean body lengths, weighted by the sample size. As the sample is small and no significant sex difference is observed in the age groups between 3 and 6 years, the data for females were included. Then, the the following relation is obtained between the year after birth (x) and the body length (y) in cm.

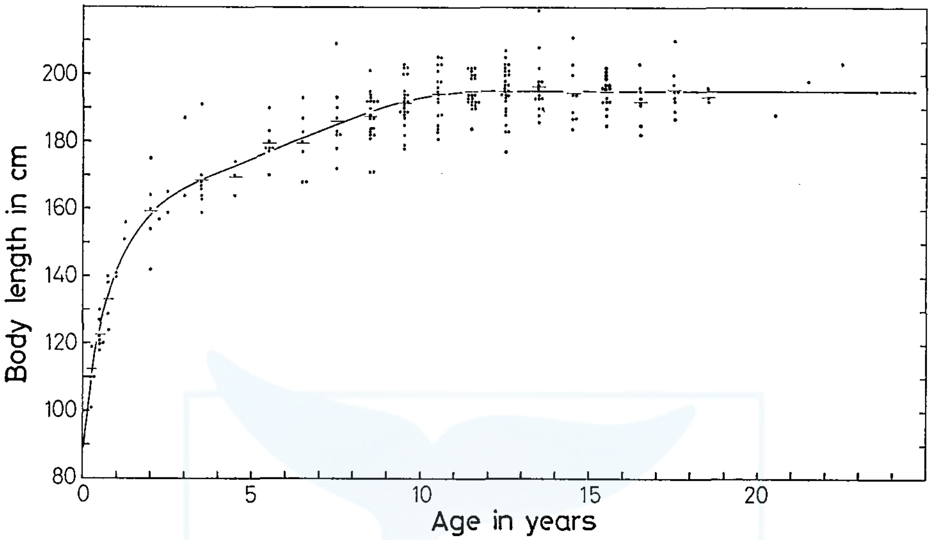

Fig. 5. Mean growth curve of female *S. attenuata*. Age was estimated from the dentine growth layers. Each spot indicates one animal and rod the mean body length.

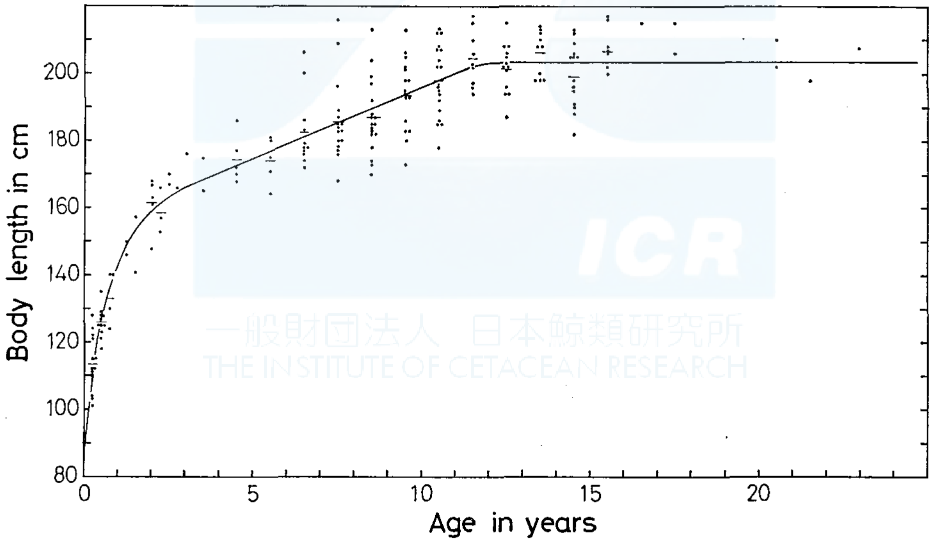

Fig. 6. Mean growth curve of male *S. attenuata*. For symbols see Fig. 5.

$$y = 4.20x + 153.8, \quad 3.5 \leqq x \leqq 11.5$$

This indicates that the mean annual increment of body length is 4.20 cm

The increase of the mean body length finishes in males at the age of 11.5 years. This is the age when most of the animals attain physical maturity. The asymptotic length of males at 203.3 cm is obtained as the mean of 49 males with ages of 12.5 years or more.

The mean growth of females becomes slower after 6.5 years of age and the differences of length between the sexes increases. The growth of females seems to stop at the 11th year. The mean asymptotic length of females obtained from 137 females which are at the age of 11.5 years or more, is 194.9 cm. This is 8.4 cm smaller than that of males. This difference results from the earlier slowing down of growth and the earlier attainment of physical maturity in females. Females seem to attain physical maturity soon after the attainment of sexual maturity as in the case of males. This is confirmed by the fact that the mean body length at the ovulation of 1, 2, 3, and 4 is 189.5, 191.4, 192.5, and 192.4 cm respectively, and attains at 5 ovulations 195.1 cm which is approximate to the asymptotic length 194.9 cm. Then the mean lengths do not show the increase but fluctuate in the range between 192 cm and 198 cm. The mean body length of the sample in each

TABLE 3. GROWTH OF *STENELLA ATTENUATA*.

Age (year)	Body Length (cm) mean of sample (sample size) ♂	 ♀	 on growth curve ♂	 ♀
0	89.0 (1)		89.0	
0.25	113.4 (17)		111.0	
0.50	124.6 (18)		124.6	
0.75	133.1 (8)		134.5	
1.00	140.5 (2)		142.7	
1.25	150.8 (4)		148.3	
1.50	149.0 (2)		152.3	
1.75	—		155.8	
2.00	160.2 (10)		158.9	
2.25	158.3 (4)		161.2	
2.50	165.3 (4)		163.1	
2.75	166.0 (1)		164.7	
3.00	175.7 (3)		166.0	
3.5	168.8 (10)		168.5	
4.5	172.6 (8)		172.7	
5.5	177.3 (13)		176.9	
6.5	182.6 (11)	179.4 (7)	181.1	181.1
7.5	185.7 (16)	186.2 (9)	185.3	185.0
8.5	186.8 (18)	187.6 (20)	189.5	188.3
9.5	193.3 (16)	191.5 (22)	193.7	191.5
10.5	198.1 (19)	194.0 (18)	197.9	194.0
11.5	204.4 (9)	194.9 (22)	202.1	194.9
12.5≦	203.3 (49)	194.9 (115)	203.3	194.9

age group and the corresponding body length on the growth curve obtained in the above are shown in Table 3.

Kasuya (1972) tried to adopt exponential formulae for the mean growth curve of *S. coeruleoalba*, but the fit was never good. In the present study we could not find a suitable formula to express the mean growth of the present species. For comparison, the mean growth curve of *S. coeruleoalba* is shown in Fig. 7. This was based on the 881 animals obtained by the end of 1972 including the data used by Kasuya (1972), in which age determination was made by the same author. The straight part of the male growth curve was calculated by least squares, but that of the female was drawn by eye. The feature of this part is its strong resemblance

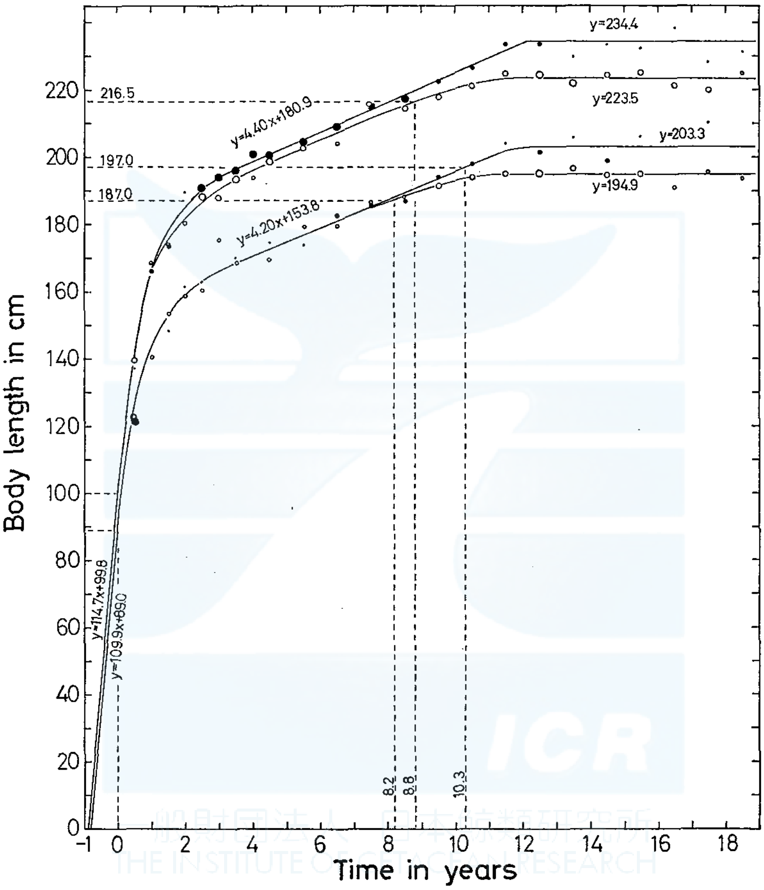

Fig. 7. Comparison of the mean growth curves of *Stenella coeruleoalba* (upper pair) and of *S. attenuata* (lower pair). The largest circles indicate the mean length represented by 25 or more animals, the intermediate from 11 to 24 animals, and the smallest 10 or less animals. In both species closed circles and the upper line indicate males and open circles and the lower line females. The age of female *S. coeruleoalba* at sexual maturity was cited from Kasuya (1972). The slow growth stage at early pregnancy is not shown.

to that of *S. attenuata,* except for the slight between sexes difference of length. If enough data is accumulated, a similar pattern of growth seems likely to be observed in *S. attenuata.* The age at physical maturity of *S. attenuata* seems to be about 1 year earlier than that of *S. coeruleoalba.* The difference of asymptotic lengths between two species is mainly affected by the difference of growth in young stage.

Weaning

Direct information on the start of the weaning is scanty (Table 4). Our data suggest that some animals start feeding on solid food at the length of 115 cm and the age of 1/4 year, but most of the animals start at about 130 cm, or about half a year after birth.

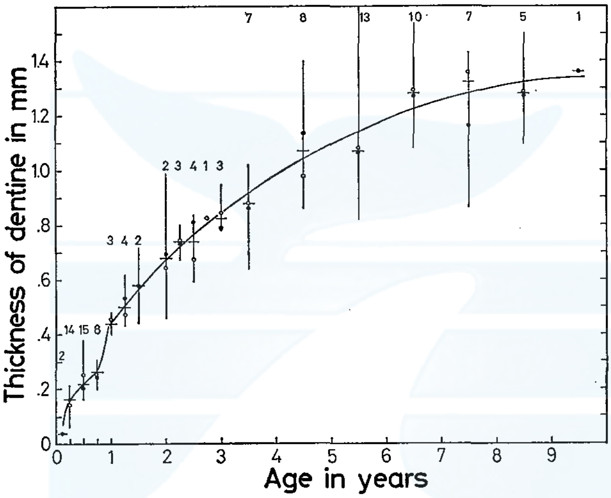

Fig. 8. Relation between age and the thickness of postnatal dentine of *S. attenuata.* Open circles indicate the mean of females, the closed males, and vertical and horizontal rods the range and mean for both sexes. Numbers at the top indicate sample size. The line was drawn by eye.

TABLE 4. STOMACH CONTENTS OF JUVENILE *STENELLA ATTENUATA.*

Body length	Age	Sex	Milk	Food remains	Nematoda
115 cm	—	♂		+	+
122 cm	1/4	♂		—	
128 cm	—	♂	+	—	—
129 cm	1/2	♂		+	
168 cm	—	♀		+	+

The thickness of postnatal dentine measured in cross section at the level of the proximal end of prenatal dentine was compared with the growth of the animal. As shown in Fig. 8, the increase of the thickness of dentine after 1 year of age shows a similar pattern to that of body length, but it shows a rapid increase at the age between 0.5 and 1.0 year. When it is compared with the body length (Fig. 9), the growth of dentine changes from a low rate to a higher rate at a body length of about 133 cm, which corresponds to the age of 0.7 year.

It is generally known that the baleen plates of mysticeti grow rapidly at the period of weaning. A similar feature is also expected in the growth of teeth, because teeth would start to have a mechanical function in catching food after the start of weaning. Probably the weaning of *S. attenuata* starts, in the average, at an age between 0.5 and 0.75 year or at the length of 130 cm. However, the weaning period seems to last long in the case of toothed whales, and the start of feeding on solid food does not necessarily mean the cessation of suckling. The duration of suckling is dealt with separately.

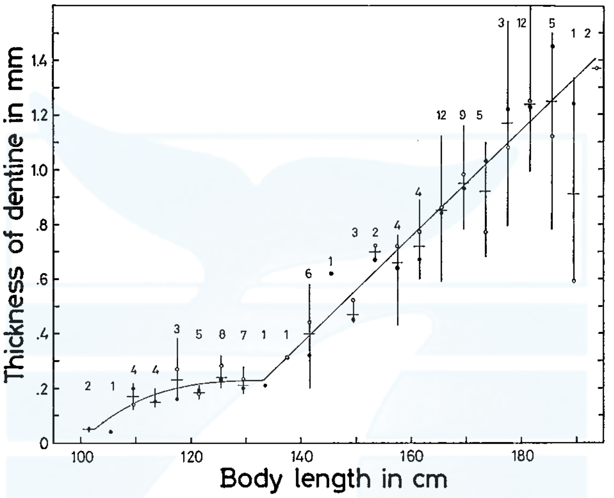

Fig. 9. Relation between the thickness of postnatal dentine and body length of *S. attenuata*. The line was drawn by eye. For other symbols see Fig. 8.

The calf of *Tursiops truncatus* starts to take solid food at an age of from 6.3 to 9 months, or 0.5 to 0.8 year (Tavolga and Essapian, 1957, Nakajima *et al*, 1963). This coincides well with the information obtained on *S. attenuata*.

Age at the attainment of sexual maturity of the female

As the left ovary of this species matures earlier than the right (Ohsumi, 1964), it is reasonable to expect earlier development of the left ovary even in immature animals.

Fig. 10 shows the difference of weight between the two ovaries of immature females of *S. attenuata*. In young animals the weight of the left ovary is nearly equal or slightly smaller than that of the right, but the growth of the left ovary starts to exceed that of the right at a body length of about 170 cm. The age corresponding to this length is about 4 years. This may indicate the approach of puberty even if development of the follicle has not started. This age is about one year later than the age of the male when the formation of spermatozoa in the testis starts.

Fig. 11 shows the relation between age and the diameter of the largest follicle of mature and immature females of *S. attenuata*. The observed largest diameter was between 10 and 11 mm. This size is considered to be close to the size at ovulation. The development of the follicle in immature females is observed only in animals at the ages of 6.5 years or more. This means that puberty of females starts at this age which is very close to the age at the attainment of sexual maturity, and that the growth of follicles is rapid to attain the size at ovulation.

The youngest mature female is found in the age class of 7.5 years and the oldest immature in that of 9.5 years. The percentage of newly mature females at

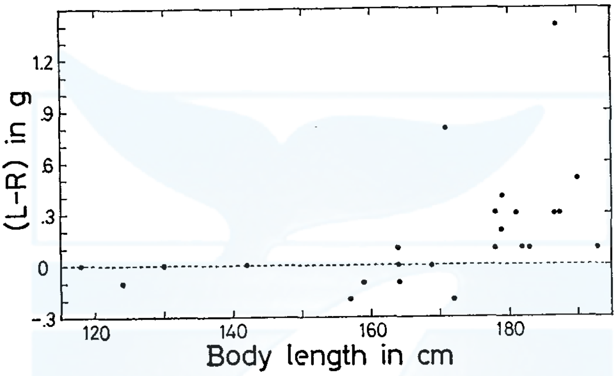

Fig. 10. Relation between the difference of the weights of both ovaries and body length in immature *S. attenuata*.

TABLE 5. MATURITY OF *S. ATTENUATA* BY AGE GROUPS.

Age	Male*				Female		
	immat.	pub.	mat.	mat. (%)	immat.	mat.	mat. (%)
<1	12	—	—	0	15	0	0
<2	2	—	—	0	4	0	0
≦3	2	3	—	0	10	0	0
3.5	—	1	—	0	8	0	0
4.5	—	2	—	0	3	0	0
5.5	—	3	—	0	7	0	0
6.5	—	9	1	10.0	7	0	0
7.5	—	12	—	0	6	2	25.0
8.5	—	13	2	13.3	7	12	63.2
9.5	—	9	3	25.0	2	18	90.0
10.5	—	7	11	61.2	0	18	100
11.5	—	2	6	75.0	0	21	100
12.5	—	3	8	72.8	0	27	100
13.5	—	1	8	88.9	0	15	100
14.5	—	—	10	100	0	11	100

* : Based on testis weight when other information was not available

the age of between 6.5 and 7.5 years, 7.5 and 8.5 years, 8.5 and 9.5 years, and 9.5 and 10.5 years are calculated from Table 5 as 25.0 %, 38.2 %, 26.8 % and 10.0 % respectively. This indicates that most of the animals attain maturity at an age between 7.5 and 8.5 years. But as there are observed some females which are considered to be in the second cycle of reproduction in the age classes of 7.5 and 8.5 years, a few females seem to attain sexual maturity at an age between 5.5 and 6.5 years (Table 19). The mean age of females at the attainment of sexual maturity was obtained after the method of Kasuya (1972) as the age where the cumulative frequency of immature animals in older age classes is equal to that of mature animals in younger age classes (Fig. 12). It gives the mean age of females at the

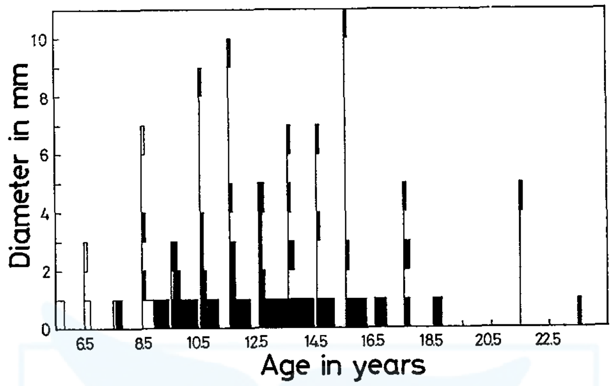

Fig. 11. Relation between the diameter of the largest follicle and age. White squares indicate immature females and black the mature.

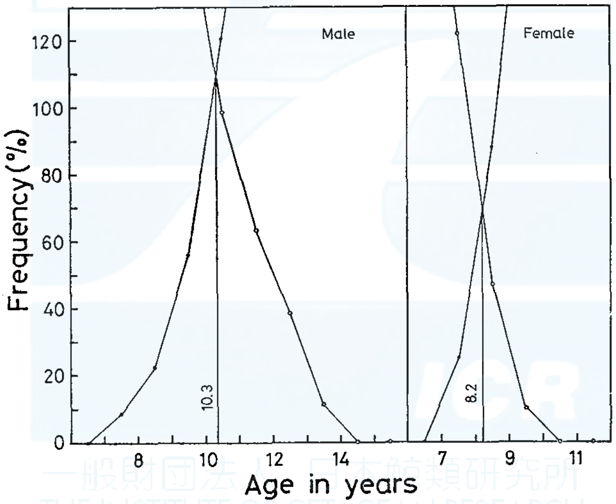

Fig. 12. Age at the attainment of sexual maturity in *S. attenuata*. Open circles indicate the cumulative frequency of immature animals, and closed circles that of mature animals. For explanation see text.

attainment of sexual maturity as 8.2 years. The body length at this age is 187 cm on the mean growth curve.

Age at the attainment of sexual maturity of males

The bilateral difference of testis weight was checked on 44 animals collected from schools 1 and 2.

If the mean of the left weight minus right weight is equal to zero it is concluded that there is no bilateral asymmetry. As shown in Table 6, the mean difference in mature animals is small enough to consider that there is no significant asymmetry of the testis weight. In testes with 68 g or less weight, the observed deviation of the mean from zero is large enough to be expected at the probability between 2 to5 %. But at present we consider that this does not prove asymmetry of testis weight, so the weight of the left testis was usually used in the following discussion.

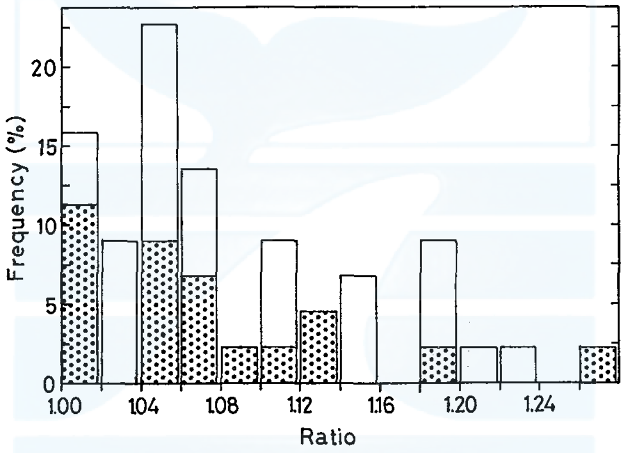

Fig. 13. Frequency distribution of the ratio of the weight of the heavier testis to the lighter. Dotted area indicates the pairs where the right testis is heavier or equal to the left.

TABLE 6. T-TEST OF THE SYMMETRY OF THE TESTES WEIGHT.

Weight (left, g)	Range (L.-R.)	Mean difference	Sample size	Standard error	Probability
68>	−10.9~ 1.4	−1.2720	25	0.5808	0.05>p>0.02
68≦	−30.0~30.0	+1.9053	19	3.6574	0.70>p>0.50
Total	−30.0~30.0	+0.1000	44	1.6075	p>0.90

The ratio of the heavier testis to the lighter comes between 1.00 and 1.28 (Fig. 13). However, about 93 % of all the pairs observed show a ratio of less than 1.20. This means that if the left testis is weighed, the weight of the right side is expected with a probability of more than 90 % to be between 1.20 and 1/1.20 (0.83) times that of the left.

The maturity of the testis was checked by two methods. One is histological examination of testis tissue taken from the center of the cross section at the midlength of the testis. When spermatozoa were observed in this part, the testis was considered to be in full maturity. The smallest testis in this condition was 66 g, and the largest immature testis was 71 g. Accordingly the mean weight of testis at the attainment of full sexual maturity is considered to be about 68 g, and any testis of this weight or heavier was classified as mature.

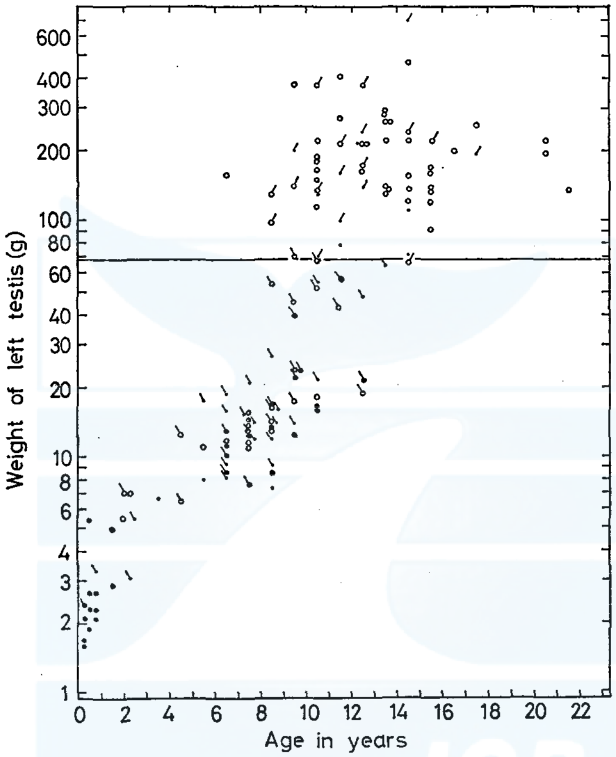

Fig. 14. Scatter diagram of the weight of testis and age. The weight of testis is plotted on logarithmic scale. Large closed circles indicate spermatozoa absent in the smear, open circles spermatozoa present in the smear, small closed circles no observation of the smear, rod at the upper left immaturity of the tissue at the center of testis, rod at the upper right the maturity, and solid line mean weight of testis at the attainment of sexual maturity.

Even if a testis is identified as immature by the above method, when the smear taken from the cross section at the midlength of the testis is observed some spermatozoa are usually found. This probably means that even when the core of the testis is not mature, some part, most likely the tissue at the periphery has already started the formation of spermatozoa. This phenomenon is the reverse of the observation on sperm whales reported by Best (1969), and will need further confirmation. An animal which has the testis at this stage is considered to be in puberty. This stage of testis was commonly found among those with weight between 6.0 g and 68 g, so any animal with a testis of between 6.0 g and 67.9 g was classified as puberal.

Among animals which have a testis weight corresponding to the criterion of puberty, there are some which have no spermatozoa in the smear. The ratio of these to all puberal animals varies between schools. This can be related to the reproductive season or the school structure and will be dealt with separately.

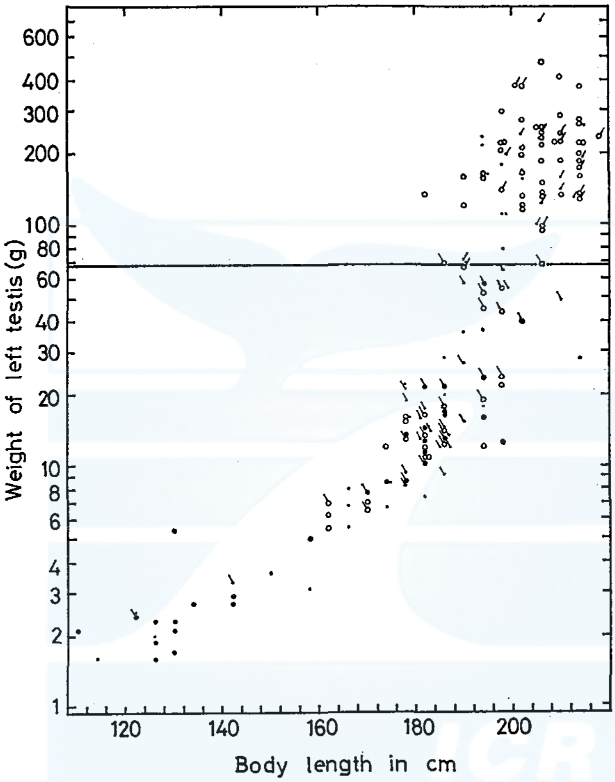

Fig. 15. Scatter diagram of the relation between weight of testis and body length. For symbols see Fig. 14.

As shown in Table 5 and Figs. 14 and 15, all males younger than 2.0 years or 160 cm in body length are immature. Puberal animals first appear in the age class 2.0 years and are observed until the age of 13.5 years. Most animals in age classes between 2 and 8 years or length between 160 cm and 187 cm belong to the puberal stage.

Fully mature animals start to appear at the age of 6.5 years and all animals attain sexual maturity by the age of 14 years. After this the weight of testis does not increase with age.

The mean age at the attainment of sexual maturity obtained by the same method used for females is 10.3 years. This is about one year higher than that of *S. coeruleoalba*, in spite of the larger weight of testis and smaller diameter of seminiferous tubules at sexual maturity of *S. attenuata*. The mean body length corresponding to this age, 197 cm, is obtained from the mean growth curve.

Fig. 16 shows the relation between mean diameter of seminiferous tubules and weight of testis. The histological samples were taken from the center of a section at midlength of the testis. The mean of the measurements of 15 tubules measured on a photograph was used as the mean diameter of tubules of the animal. The relationship between weight of testis and the mean diameter of tubules is shown by two lines as calculated below.

$$D=24.94\ W^{0.22528},\quad W<68$$

$$D=11.11\ W^{0.44692},\quad W\geqq 68$$

In the formulae, D is the mean diameter of tubules in μ, and W the weight of testis in g. The mean diameter of tubules at the attainment of sexual maturity is between 60 and 70 μ, which is smaller than that of *S. coeruleoalba* (Hirose and Nishiwak, 1971).

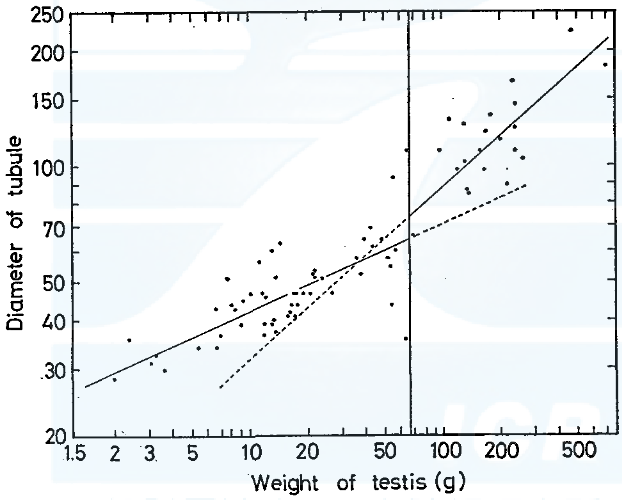

Fig. 16. Relation between the mean diameter of seminiferous tubules and the weight of testis, plotted on logarithmic scales. Lines are drawn by the least squares.

The weight is proportional to $D^{4.4}$ in immature animals but to $D^{2.2}$ in mature animals. This suggests that the fluctuation of the weight of testis of mature animals is affected by the change in diameter of seminiferous tubules.

The body length where half of the animals attain sexual maturity

This length is defined as that where the number of immature animals above this length is equal to that of mature animals below this length, and obtained by the same method used in the former section in calculating the mean age at the attainment of sexual maturity. It gives a length 181.9 cm for females and 194.3 cm for males (Fig. 17). These values are slightly shorter than the body lengths corresponding to the mean age at the attainment of sexual maturity. The difference is 5.1 cm in females and 2.7 cm in males. These discrepancies are reasonable, because the growth of the animal stops soon after the attainment of sexual maturity and the attainment of sexual maturity may be more dependent on age than on body length. However, the absolute values of the differences obtained here are not highly reliable. The body length where half of the animals are sexually mature is strongly affected by the age composition of the sample or of the population. If the ratio of sexually mature old animals decreases by the effect of exploitation, the value may become higher. This value is useful only when the maturity must be classified based on the body length frequency.

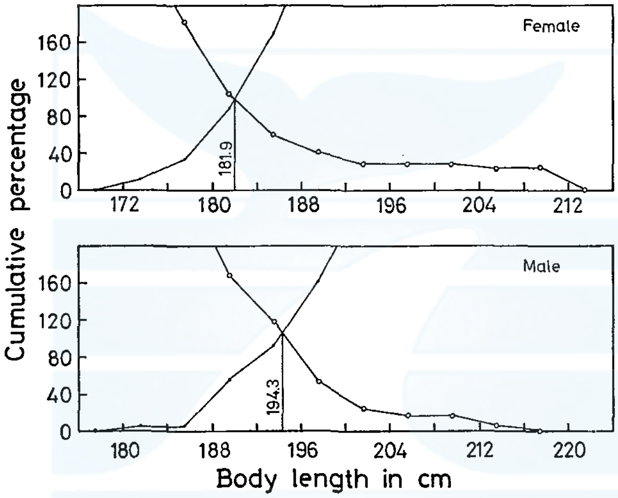

Fig. 17. Body length of *S. attenuata* where half of the animals attain sexual maturity. For explanation see text.

Body weight

Body weight of *S. atteuata* is known for 20 females and 14 males. These data are plotted on a logarithmic scale in Fig. 18. As the data are scarce a difference between the sexes was not demonstrated. The relation between body length (L, cm) and the weight (W, kg) seems to be expressed by two straight lines. If the formula $W=aL^b$ is calculated by least squares, the following constants are obtained. For the samples between 86 cm and 130 cm

$$a_1=0.0001901$$
$$b_1=2.3638$$

For the samples between 110 cm and 207 cm

$$a_2=0.00001876$$
$$b_2=2.8504$$

The two regression lines cross at the point L=116.6 cm. This means that the body weight of the newborn calf is heavier than the weight obtained by extrapolating the length-weight relationship of the older animals, and that after birth the calf grows more in length than in circumference and therefore becomes more slender. After the attainment of a length from 110 cm to 130 cm or an age of about 6 months, the circumference increases more closely in parallel with that of the body length than at the earlier stage. However, as b_2 is still less than 3, *S. attenuata* continues to become slender with increase of body length.

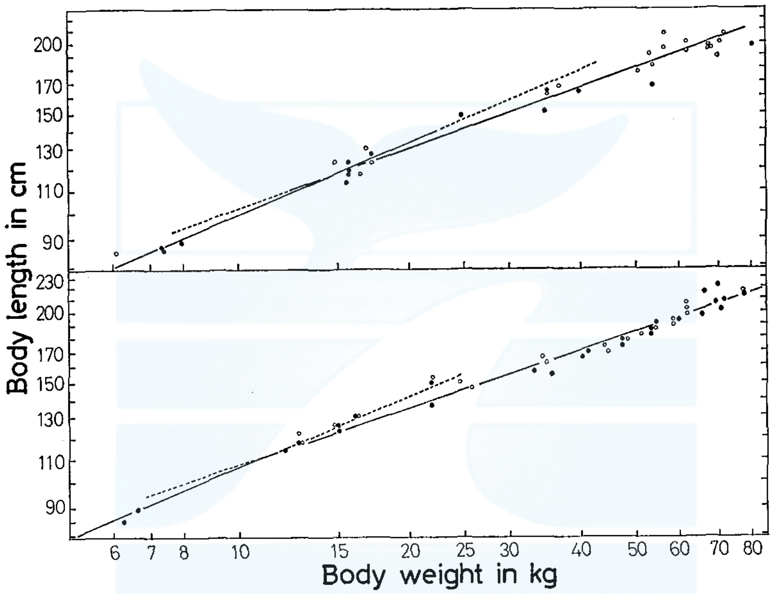

Fig. 18. Relation between body length and body weight (top), and weight without viscera (bottom). In the former each mark indicates one animal, and in the latter each mark the mean for each length group. Open circles indicate female and closed male. Weight and body length are plotted on logarithmic scale.

The weight of the animal without the viscera was measured by the fishermen. The mean weight in each length group calculated from 179 females and 148 males are shown in Fig. 18. The relation between body length and weight (w) without viscera in kg was obtained combining both sexes as follows:

For the data between 84 cm and 131 cm in body length

$$w=0.0001237L^{2.4217}$$

For the data between 112 cm and 220 cm in body length

$$w=0.000009887L^{2.9595}$$

These two lines cross at a body length of 109.8 cm

If the ratios of the visceral weight to the total weight is calculated from the data used in the top of Fig. 18, they are 17.5% (4 animals from 85 to 89 cm), 11.5% (10, 114–130 cm), 11.6% (9, 149–189 cm), and 9.9% (11, 190–207 cm). They seem to decrease with the growth of the animal, and the decrease is especially rapid at a body length between 89 cm and 114 cm. This feature is also presumed from the two sets of formulae in the above.

PIGMENTATION

The pigmentation of *S. attenuata* from the Pacific coast of Japan was studied on 100 animals in schools 1 and 2. The pigmentation was classified into 4 grades as explained below, and compared with the body length or with the age determination based on the dentinal growth layers. However, the latter was used only for reference, because age information is scanty. The body lengths were grouped into nearest 5 cm units.

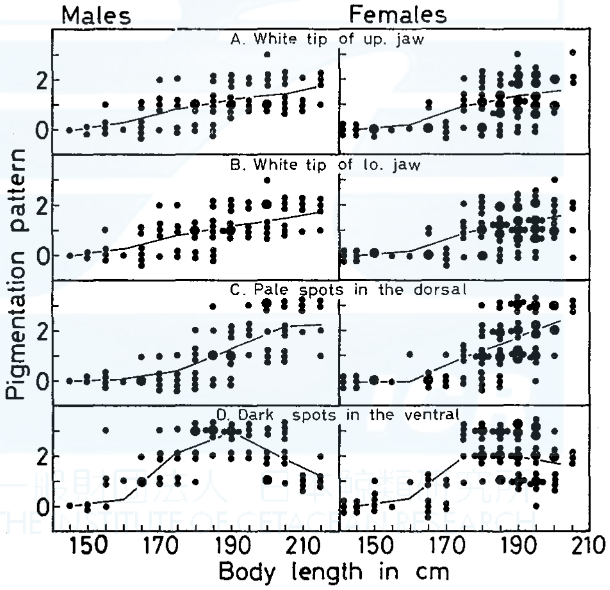

Fig. 19. Relation between body length and pigmentation of *S. attenuata*. Smaller circles represent one animal and the larger 5 animals. Body lengths are grouped into 5 cm intervals. Lines indicate the mathematical mean of the grades. For further explanation see text.

Pigmentation of newborn calf

The pigmentation of a newborn animal is pale and the pattern is quite different from that of an adult animal. The dorsal surface is bluish gray with a pale band extending postero-dorsally at the base of tail peduncle. Both jaws and the dorsal surface of the flipper is bluish gray. A dark band connects the eye and the base of the upper jaw, and a paler band connects the insertion of flipper and lower jaw. A very faint wide dark band extends from eye to the anal region. This band is covered, in the adult, by dark spots and becomes inconspicuous. Other parts of lateral and ventral regions are white. The border of the dorsal dark area and ventral white area is shaped like an arch at the part from the chest to the forehead. This pattern of pigmentation strongly resembles that of *Delphinus*.

White area at the tip of upper jaw

The white tip was classified into 4 patterns. Satage 0 represents no pure white area. In many animals classified into this stage, there is observed a small area of paler pigmentation at the tip of the jaw. Stage 1 is represented by the animal which has the white area but it does not extend posteriorly beyond the anterodorsal corner of the upper jaw, stage 2 by the animal of which the white area extends between the antero-dorsal corner and the midlength of the rostrum, and stage 3 by the animal of which the white area on the upper jaw extends beyond the midlength of the rostrum.

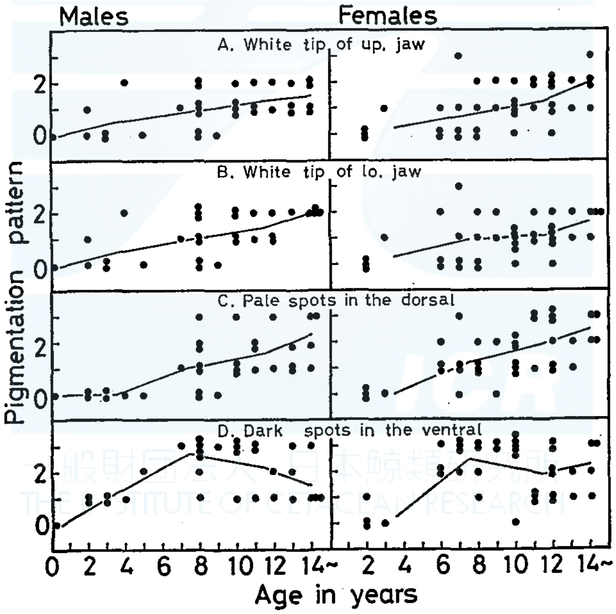

Fig. 20. Relation between the pigmentation of *S. attenuata* and the age of the animal. For symbols see Fig. 20.

The animal of stage 0, or the animal which has no white tip at the upper jaw is found only among animals smaller than 185 cm (male) or 195 cm (female) in body length. The white tip starts to develop at a body length of 155 cm and the ratio of animals with a white tip increases with age. The body length where half of the animals have a white tip is about 170 cm in both sexes. All animals have the white tip at a body length of 190 or 200 cm. The length 170 cm mentioned above corresponds to an age of about 3.5 years. According to age determination of a few animals, the white tip of the upper jaw is formed at an age between 2 and 12 years. As stage 2 is found in animals of slightly larger length, it is supposed that the extent of the white area increases in some degree with the growth of the animal.

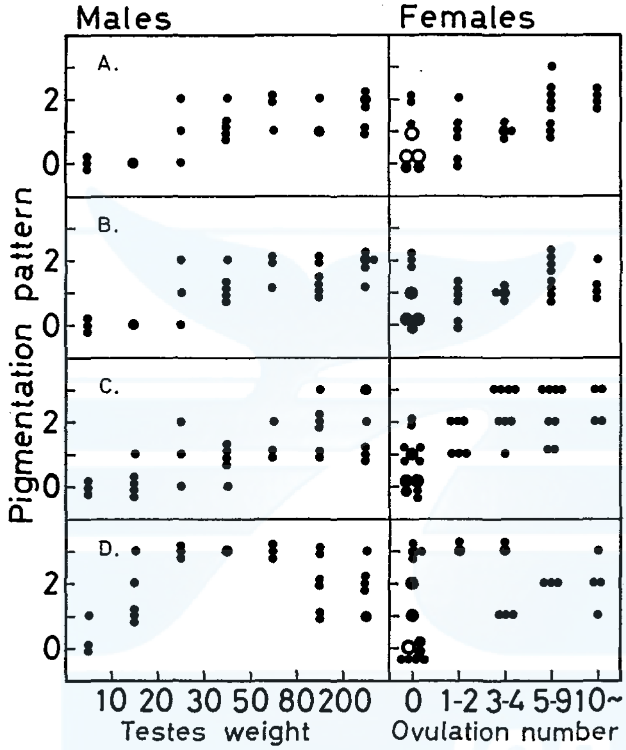

Fig. 21. Relation between the pigmentation of *S. attenuata* and gonadal condition. Open circles indicate 20 animals. For other symbols see Fig. 20.

White area at the tip of the lower jaw

The 4 stages of the development of the white area on the tip of the lower jaw were defined by the same method used above. The white areas on the tip of upper jaw and of lower jaw show good correlation, and both jaws showed the same stage in almost all the animals observed (Fig. 19). Accordingly, the mean body length where half of the animals have the white tip on the lower jaw is the same as the corresponding figure for that of the upper jaw.

White spots on the dorsal surface

The stage of this character was classified into 4 categories of stage 0 of no spot, of stage 3 of heaviest spot, and intermediate stages 1 and 2. The spot starts to appear in the earliest individuals at a length of 165 cm (male) or 170 cm (female), and all animals of more than 195 cm in body length have white spots on the dorsal surface. The body length where half of the animals have dorsal spots is about 180 cm in males and 170 cm in females. According to age determination all animals show the spots by the age of 9 years. The density of the spots increases with growth of the animal.

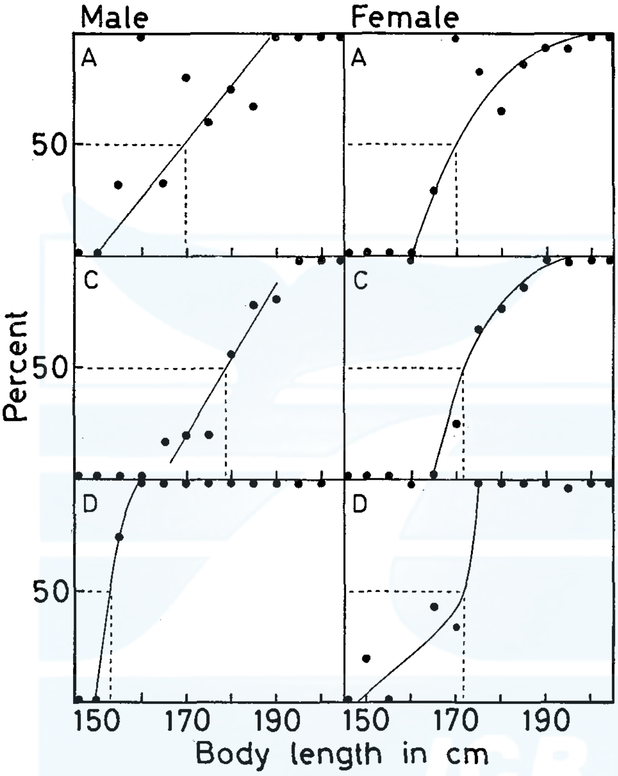

Fig. 22. Body lengths where half of the animals start to develop the pigmentation of the adult. Lines are drawn by eye.

Dark spots on the ventral surface.

The density of dark spots on the ventral surface was classified by the same method used for pale spots on the dorsal surface. The dark spots first appear on the lower jaw and on the band connecting the lower jaw and base of flipper, then on other parts of the ventral surface.

The age when dark spots start to develop shows a large sexual difference. In males it starts to develop between 150 cm and 160 cm in body length or between 1 $^{1}/_{4}$ and 2 years of age. However in females all the animals show the spots at 175 cm or 5 years of age. The body length where half of the animals have dark spots on the ventral surface is about 153 cm in males and about 170 cm in females. The former corresponds to an age of 1.5 years and the latter to an age of 3.5 years.

As shown in Fig. 19, the mathematical mean of the stages decreases after 190 cm in males and 180 cm in females. This does not mean the disappearance of the spots, but indicates that the spots are so numerous as to have contact with each other. In our method of classification this stage was not separated from the earlier stage because we checked mainly the density of independent spots. This stage seems to corresponds to the fused stage of Perrin (1969).

Discussion

The typical development of pigmentation is shown schematically in Fig. 23, and can be summarized as follows. The newborn male starts to develop dark spots in the ventral and throat region at the age of 1.5 years. The female does not have the spots at this age but show only slight darkening of the band connecting the base of flipper and lower jaw. At an age of about 3.5 years the white mark at the tip of both jaws of both sexes, and dorsal white spots and ventral dark spots of females start to develop. The white spots on the dorsal region start to develop in males at an age of about 6 years. Then both kinds of spots increase in density to fuse with each other, and attain the final adult form at the ages of 11 years in males and 9 years in females.

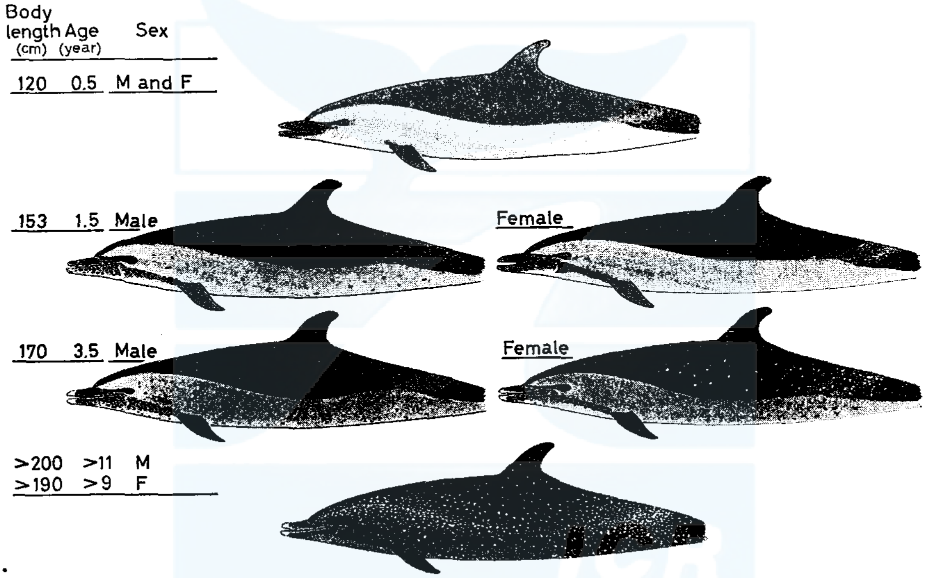

Fig. 23. Schematic figure of the pigmentation of *S. attenuata* at various growth stages.

The age when the animal attains the pigmentation of the adult coincides well with the age at the attainment of sexual maturity. The formation of the white tip on the jaws coincides with the age of the attainment of puberal stage, and with the time when the animals start to leave the breeding school and join the school of immature animals. This suggests that they may be formed by the influence of some kind of sex hormone. If there is any function in the white tips of jaws and in the mottled pattern, it seems to be a social and ecological function to help the visual identification of the species or of the growth stage of the same species as suggested by Yablokov (1963) and Evans and Bastian (1969). However, the probable effect as camouflage suggested for *S. plagiodon* (Caldwell and Caldwell, 1966) is not denied in *S. attenuata*.

The reasons for the delayed formation of dorsal white spots or of earlier formation of ventral dark spots observed in the male are not analyzed here. It may be related to the difference of endocrinological condition between the sexes.

Table 7 shows the frequency of the pigmentation patterns of females in various reproductive stages. Though other characteristics of pigmentation do not show any difference between the reproductive stages of mature females, the density of dark spots is slightly lower in lactating females. If these data really reflect the ratio in mature females, it is supposed that dark spots become less conspicuous in anoestrous females.

In the present data, 96.3 % of sexually mature females and 100 % of sexually mature males have the white part on the tip of the upper jaw. Animals with white tips are scarce in *S. attenuata* in the eastern Pacific (Perrin, 1969). This difference seems to indicate morphological differentiation between these two populations. In this respect the animals reported from Malaita (Dawbin, 1966) are closer to *S. attenuata* in the Pacific coast of Japan. If observations on pigmentation are

TABLE 7. PIGMENTATION OF FEMALE *S. ATTENUATA* BY REPRODUCTIVE CONDITION.

Character and stages[1]		Immature		Pregnant[2]		Lactating		Resting	
		no.	%	no.	%	no.	%	no.	%
A	0	22	57.9	0	0	3	6.5	0	0
	1	14	36.8	10	52.6	25	54.5	8	47.1
	2	2	5.3	9	47.4	18	39.0	8	47.1
	3	0	0	0	0	0	0	1	5.8
B	0	22	57.9	0	0	3	6.5	0	0
	1	13	34.2	13	68.4	30	65.2	10	58.8
	2	3	7.9	6	31.6	13	28.3	7	41.2
	3	0	0	0	0	0	0	0	0
C	0	20	60.6	1	5.3	1	2.2	5	31.3
	1	11	33.3	8	42.1	11	23.9	0	0
	2	2	6.1	5	26.3	18	39.1	5	31.3
	3	0	0	5	26.3	16	34.8	6	37.4
D	0	14	43.7	0	0	0	0	0	0
	1	3	9.4	3	15.8	19	41.3	3	17.6
	2	7	21.9	7	36.8	15	32.6	6	35.3
	3	8	25.0	9	47.4	12	26.1	8	47.1

[1] See Fig. 18. [2] Pregnant and simultaneously lactating females included.

made on many animals along the Malaita coast, it will give some information on the identification of populations.

The pigmentation of other spotted species *S. plagiodon* in the Atlantic (Caldwell and Caldwell, 1966) is distinguished from that of *S. attenuata* in the Pacific by the absence of the fusion of ventral dark spots and by the larger size of the spots.

FEMALE BREEDING CYCLE

Graafian follicle

The frequencies of the diameter of the follicle obtained as the cube root of the multiple of three dimensions are shown in Fig. 24. The ovaries of pregnant females are inactive having no large follicles in any school or in any season. The ovaries of all the lactating and the resting females in school 7, which was caught in July, show high activity. On the other hand in schools caught in November or in February, there were observed many lactating or resting females with inactive ovaries. As a result the mean diameter of the follicles of females in the two categories is smaller than that of the schooll killed in Juy. However, even in schools killed in February or in November the size of follicles of active females is not small. Accordingly it can not be concluded that all females in February and November are sexually inactive. It will need observations on more schools in various seasons to draw conclusions on the seasonal variation of the size of follicles.

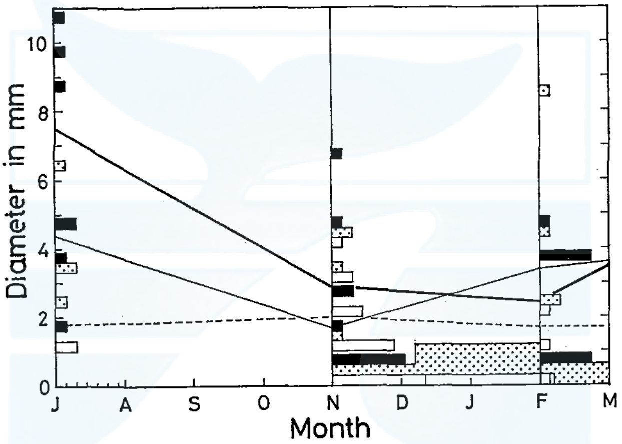

Fig. 24. Seasonal variation of the diameter of the largest follicle in mature females of *S. attenuata*. Black squares and thick solid lines indicate the resting females, dotted squares and thin solid lines the lactating, and white squres and dotted lines the pregnant or pregnant and simultaneously lactating.

Diameter of corpus luteum

Even when we got the ovaries of pregnant female it was not necessarily possible to obtain the fetus, because the fetus or fetus and part of uterus were sometimes removed by the fishermen and piled elsewhere. In these cases the pregnancy was checked by a fragment of uterus or by the condition of ovaries. Table 8 shows the relationship between the size of corpora lutea and the presence of a fetus. This table shows that if the corpus luteum is larger than 6000 mm^3 in volume index it may be correct to consider that the animal was pregnant. The scarcity of corpus luteum of the size between 4000 and 6000 mm^3 in volume index may indicate that when the ovulation is not successful even if the corupus luteum may grow to a size similar to that of corpus luteum of pregnancy, it may regress very rapidly. Accordingly, when other information is not available, we tentatively consisdered that a corpus luteum smaller than 4000 mm^3 in volume index or 15.87 mm in diameter as the corpus luteum of ovulation.

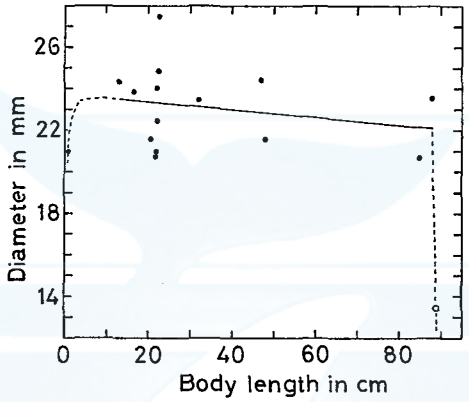

Fig. 25. Relation between the diameter of corpora lutea and body length of fetuses. Solid line is drawn by least squares, and dotted lines by eye. Open circle indicates a lactating female.

TABLE 8. SIZE OF LARGE CORPORA AND THE SEXUAL CONDITION OF FEMALE.

Range in volume index (mm^3)	Diameter (mm)	R	L	PL	P	PF	Total
1001– 2000	12.60	—	3	—	—	—	3
2001– 3000	14.42	1	1	—	—	—	2
3001– 4000	15.87	—	1	—	—	—	1
4001– 5000	17.10	—	—	—	—	—	—
5001– 6000	18.17	—	—	—	—	—	—
6001– 7000	19.13	1	—	1	1	—	3
7001– 8000	20.00	—	—	—	1	—	1
8001– 9000	20.80	—	—	—	1	1	2
9001–10000	21.54	—	—	—	2	4	6
10001–11000	22.24	—	—	—	—	2	2
11001–12000	22.89	—	—	—	1	1	2
12001–13000	23.51	—	—	—	1	—	1
13001–14000	24.10	—	—	—	—	2	2
15001–21000	30.00	—	—	—	—	5	6

R: resting. L: lactating. PL: pregnant and lactating, fetus not confirmed. P: pregnant, fetus not confirmed. PF: Pregnant, fetus confirmed.

The relation between diameter of corpus luteum of pregnancy and the body length of fetus is shown in Fig. 25. The diameter of a corpus luteum of a pregnant female with 1.0 cm fetus was so large as to be in the range of corpora with larger fetus. Though the diameter of corpus luteum does not show a large change related to the growth of the fetus, there seems to be a slight decreasing tendency. If the regression line is calculated by least squares for the 14 corpora corresponding to the medium and larger fetuses, it gives the relation $y=-0.01825x+23.700$, where y is the diameter in mm and x is the length of fetus in cm. The mean diameter at the time of parturition is 22.08 mm on the above formula.

Regression of corpus albicans

Fig. 26 shows the frequency of diameters of corpora albicantia in each age group. The modal diameter gradually decreases with the increase of the age of the animal until 14.5 years of age or the 7th year after the mean age at the attainment of sexual maturity. Then the highest peak of the mode stays between 2 and 3 mm in diameter, and the ratio of the corpora number constituting the mode increases with age. No corpora smaller than 1 mm in diameter were observed.

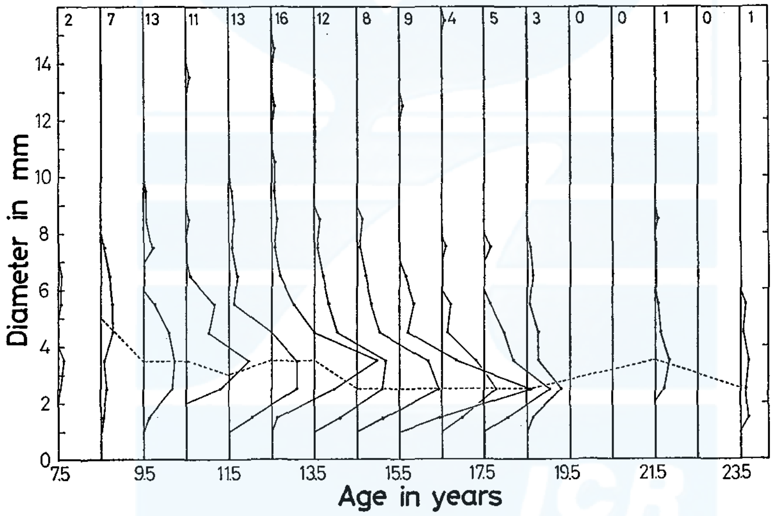

Fig. 26. Distribution of the diameter of corpora albicantia of *S. attenuata*. The numbers at the top indicate the number of animals, and the dotted line the position of the mode.

They indicates that the corpora albicantia attain a final size within several years after the start of regression and may stay in the ovary all the lifetime. The mean final diameter suggested by the shape of the mode is about 2.5 mm or slightly more.

It is easily supposed that the size of corpora albicantia decreases rapidly after the parturition. If the size of the largest corpora albicantia of lactating females in each school are arranged by size, some modes are observed. These modes may represent some parturition season. The mean growth curve and the mean modal length of calves caught in the same school give the time after parturiation. The length frequencies of juvenile calves and the size frequencies of the largest corpora albicantia of pregnancy of lactating female in corresponding schools are shown in Fig. 27. In this figure the few corpora albicantia of ovulation were omitted and

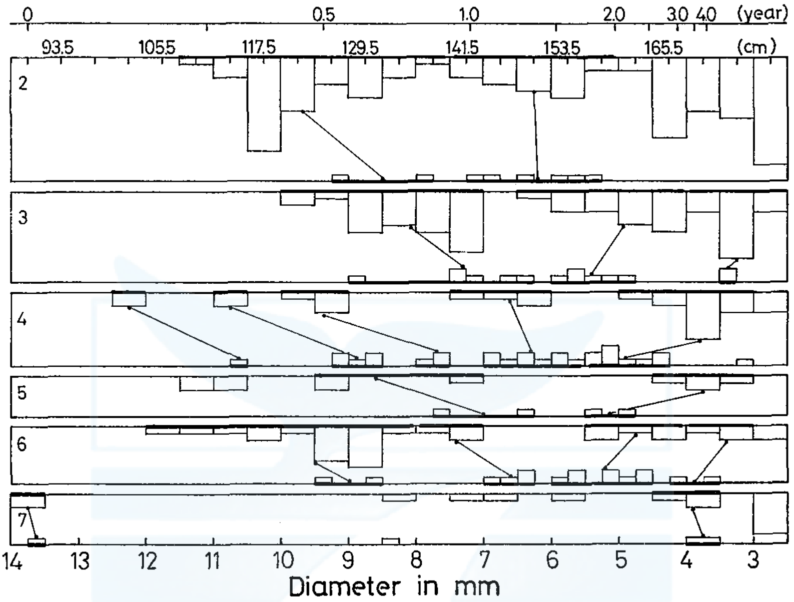

Fig. 27. Comparison of the frequency of the diameter of copora albicantia of the last parturiation of lactating females and the length frequency of juvenile calves. Scale in years was calculated from the growth curve. Numbers at the left indicate the school. The length frequency of school 3 was calculated from the weight data.

TABLE 9. LACTATING FEMALES WHICH OVULATED AFTER LAST PARTURITION.

Animal		Diameter of corpus (mm) of		No. of ovulation	
school	no.	largest	last parturition	postpartum	postlactum*
3	3	4.88	4.38	1	—
3	24	12.35	3.29	1	1
3	35	8.82	4.95	3	3
3	38	12.12	3.21	1	1
4	5	5.37	5.30	1	—
4	19	15.14	4.79	—	1
4	47	10.69	5.28	—	3
4	48	5.24	4.78	1	—
4	96	5.01	4.72	1	—
4	119	8.51	6.50	1	—
5	48	6.46	6.12	1	—
6	102	4.66	4.28	1	—

*: based on the criterion used in this study.

the probable corpus albicans of the last parturition was used. These exceptional individuals are shown in Table 9. The mean modal diameters of corpora albicantia of the last parturition of lactating females are plotted in Fig. 28 against the time after parturition. It shows that the regression of the size of corpora albicantia is so rapid that it regresses from the mean diameter of corpus luteum 22.08 mm to 13.6 mm within 0.2 months. Then the speed of regression gradually decreases, and after 16th month the diameter decrease is almost straight. If this line is extended, it reaches the mean final diameter of corpora albicantia at about 70 months. This coincides with the information described above.

The elapsed time after the start of regression of corpora lutea was calculated

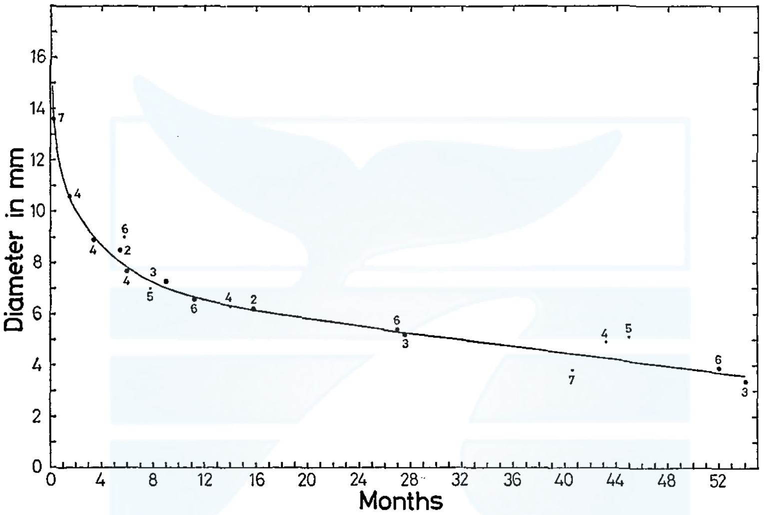

Fig. 28. Regression of the diameter of corpora albicantia obtained from the combinations in Fig. 27. Larger circles indicate reliable combinations, number by the each circle the school.

from the regression line of the corpora albicantia drawn for volume index and volume indices of the corpora, assuming that the size of corpus albicans of pregnancy and of ovulation is not significantly different. This assumption should not be unreasonable, because the corpus luteum of ovulation seems to attain a size near to that of pregnancy and the regression rate is rapid in the first month. The corpora albicantia of pregnancy were then identified based on the following assumptions and considering the reproductive conditions at the time of death.

1. During pregnancy the female does not ovulate.
2. There may be some postpartum ovulations or postlactum ovulations.
3. The time from a parturition to next conception is usually more than one year.

Thus the age of corpora albicantia which started the regression within recent 5 years were calculated and the corpora albicantia of pregnancy and those of ovulation were identified. The real date of ovulation of corpora albicantia of pregnancy is roughly estimated assuming that the length of gestation is 11.2 months. The date of ovulation of a corpus luteum of the pregenant female was calculated from the fetal growth curve and the fetal length. In a few cases where fetal length was not available the mean fetal length of the school was used.

Postpartum ovulations

The postpartum ovulations were analyzed in relation to the time from the preceding parturition based on the ovulation diagram prepared with regression curve of the corpora. The source of information was classified into two. The first (series A) is the ovarian activity after the last parturition ending at the death of the animal, which is more reliable because the time after the parturition is usually, but not necessarily, short and the reproductive condition of the female at the time of death was taken into consideration in assessing the corpora albicantia of the last pregnancy. The next (series B) is the ovarian activity from the parturition that occurred one cycle before the parturition used in series A and ends at the last conception. The date of parturition of series B is usually earlier than that of series A.

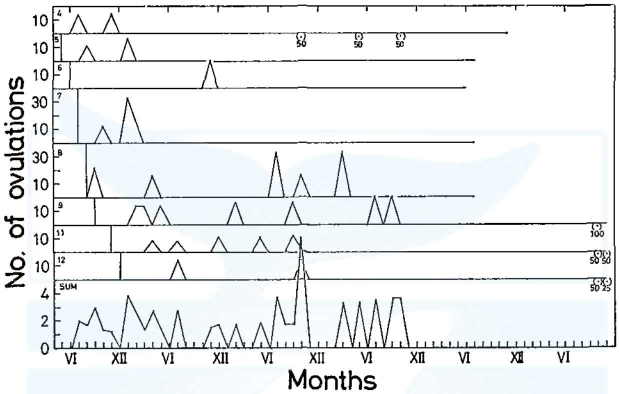

Fig. 29. Seasonal variation of ovulation shown in relation to the date of the last parturition. Females are grouped by the month of parturition (numerals at the left). The females that are grouped into Jan., Feb., March, and Oct., show no ovulation, but are included in the sum. Number of ovulations is shown per month per 100 animals. Based on series A.

TABLE 10. NUMBER OF POSTPARTUM AND POSTLACTUM OVULATIONS.

No.	Postpartum ovulations						Postlactum ov.		
	A		B		Total		No.	B	
0	60	82.2%	36	70.6%	96	77.4%	1	34	66.7%
1	10	13.7	6	11.8	16	12.9	2	14	27.5
2	2	2.7	9	17.6	11	8.9	3	2	3.9
3	1	1.4	0	0	1	0.8	4	1	2.0
Sum	73	100	51	100	124	100	Sum	51	100.1
Mean	0.234		0.471		0.331		mean	1.412	

At the first step the analysis was made on series A. The samples were grouped in accordance with the month of parturition, then the dates of ovulations were arranged chronologically and the frequency of ovulation per month per animal was calculated (Fig. 29). This only shows that the ovulations after the recent parturition had occured in various seasons of the year.

To know the range of the time when postpartum ovulations may occur, the relation between the time after the last parturition and the number of ovulations that occurred after the parturition was analyzed based on the materials of series A (Fig. 30). In some animals ovulation occurs soon after parturition and the number of ovulated females increases. As a result the percentage of unovulated females decreases untill the 12th month, then the percentage becomes rather stable during the next 12 months. After this the number of unovulated females again starts to decrease. We consider that the former period corresponds to the period of postpartum ovulations and the latter probably to postlactum ovulations.

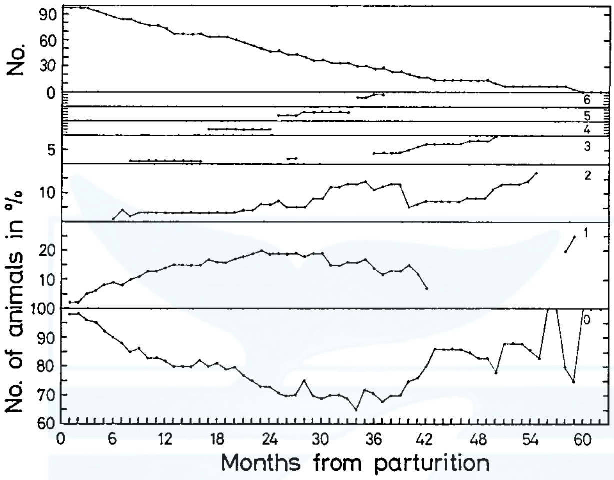

Fig. 30. Relation between the time from parturition and the number of ovulations undergone by each female (numbers at the right). Figure at the top indicates the number of females observed. Based on series A.

Thus defining postpartum ovulations, the time and frequency were obtained from series A and B (Tables 10 and 11). About 20% of the females have a post partum ovulation but they seems to be all infertile. The mean number of post partum ovulations is 0.331 per reproductive cycle.

As shown in Table 11 and Fig. 31 the time of the postpartum ovulation measured from the date of parturition shows some regularity. The first peak is in the 3rd month after parturition, then next peaks come with the interval of 4 months. These peaks may, as mentioned in a later section, correspond to the mating season of this species. But it must be noticed that some postpartum females do not ovulate in the first season but in the 2nd or 3rd seasons. The length of interval between two postpartum ovulations was studied on the few females which have experienced two or more postpartum ovulations. As shown in Fig. 31, if more than 1 ovulation are made in one breeding season the minimum of the interval is about 1 month. The longer intervals are approximately a multiple of 4 months.

Postlactum ovulation

The postlactum ovulation was tentatively defined as the ovulation occurring after 12 months or more from the last parturition, and analyzed only on the series B because series A does not end at conception. It was not confirmed here whether the animal has finished lactation by the first postlactum ovulation. However our data suggest that it is not necessarily so. As shown in Table 12 the interval between the last postpartum and the first postlactum ovulations, on animals where two or more postlactum ovulations exist, is usually 12 months or more. This means that the ovarian activity usually stops for a long period after the last postpartum ovulation. However only in 2 cases among 73 animals the interval was 4.0 or 8.8 months. In these cases the postpartum ovulation is almost continuous to postlactum ovulation. About 67 % of the females conceive by the first postlactum ovulation, and the remaining experience two or more postlactum ovulations. The mean number of postlactum ovulations is 1.412 per one reproductive cycle (Table 10).

The peak of postlactum ovulations is observed in the interval of 4 months (Table 11 and Fig. 31). There are some females which do not ovulate at the 4th month before conception but do it at the 8th or 12th. The information on postpartum and postlactum ovulations are shown in the diagram of Fig. 32.

The cycle of postlactum ovulation of females which have two or more postlac-

TABLE 11. TIME OF OVULATION MEASURED FROM THE DATE OF PARTURITION OR OF CONCEPTION.

Time in month (t)*	Postpartum ovulation				Postlactum ovulation			
	1st	2nd	3rd	Sum	2nd**	3rd	4th	Sum
n=1	3	—	—	3	3	—	—	3
2	4	1	—	5	—	—	—	—
3	5	1	—	6	—	—	—	—
4	2	1	—	3	4	—	—	4
5	2	1	—	3	3	—	—	3
6	4	2	—	6	—	1	—	1
7	4	3	—	7	1	—	—	1
8	2	2	1	5	2	—	—	2
9	1	1	—	2	1	—	—	1
10	—	—	—	—	—	—	—	—
11	—	—	—	—	—	—	—	—
12	—	—	—	—	—	1	1	2
13	—	—	—	—	3	—	—	3
14	—	—	—	—	—	—	—	—
18	—	—	—	—	—	1	—	1

*: Time range (t): $n-1 \leqq t < n$,

**: Nearest to postlactum ovulation of pregnancy or the first.

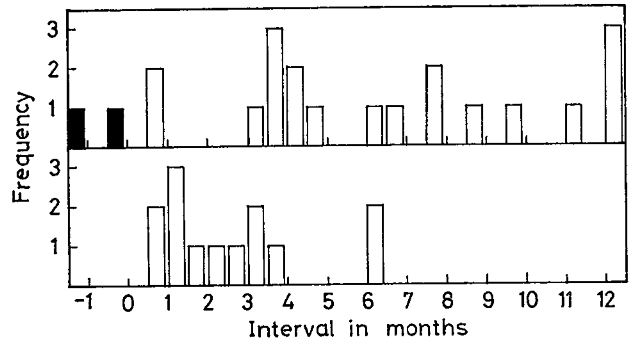

Fig. 31. Intervals of postlactum ovulations (top) and of postpartum ovulations (bottom), in the animals where several of them are observed. Black indicates unreasonable case, where the superficial date of ovulation comes after the date of conception.

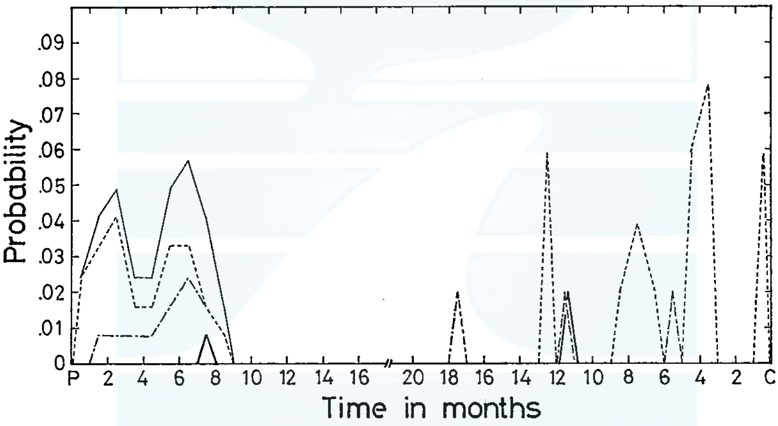

Fig. 32. Diagram of ovulation in one reproductive cycle. The postpartum ovulation is at the left and the postlactum ovulation at the right. P indicates parturition, C conception, dotted lines postpartum ovulation nearest to parturition or postlactum ovulation nearest to conception, chains the second, thick solid lines the third, and thin solid lines the total of postpartum ovulation. Probability of ovulation is shown by the number of ovulations per animal per cycle. The fertile postlactum ovulation, of which probability is 1, is not shown. The length of the reproductive cycle is set at 50.3 months, one of the estimate of mean reproductive cycle in *S. attenuata*.

TABLE 12. INTERVAL BETWEEN LAST POSTPARTUM OVULATION AND FIRST POSTLACTUM OVULATION.

Interval in month (n)*	4	9	11	12	13	17	20	24	29	31
Frequency	1	1	1	2	2	1	2	1	1	1

* : Interval is shown by month, n−1<month≦n

tum ovulations is classified into two types. One is the cycle of 4 months or a multiple of it. This may be the cycle related to the mating season. The other is short and is an ovulation cycle in one breeding season. This probable real oestrous cycle is of about 1 month. These features are quite similar to the cycle found in postpartum ovulations.

Accordingly it is concluded that *S. attenuata* is polyoestrous and the oestrous cycle is about 1 month, and this oestrous cycle occurs in some of the breeding seasons which have an interval of 4 months.

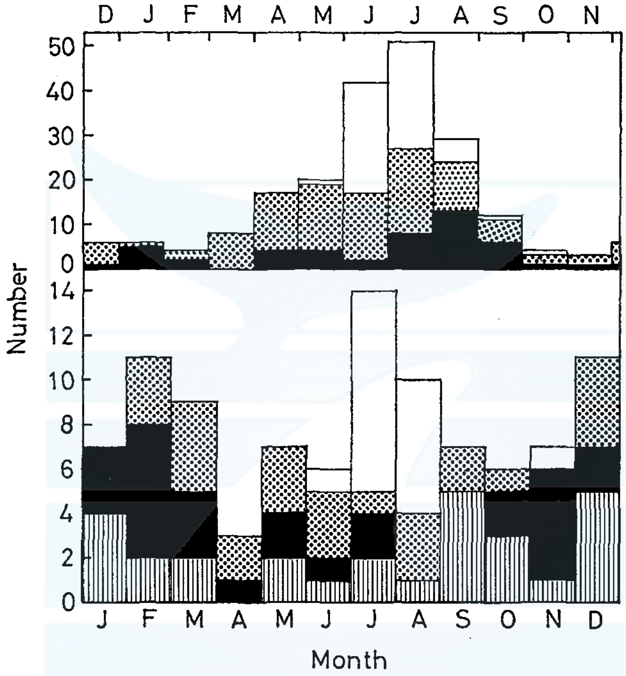

Fig. 33. Breeding season of *S. attenuata*. Top indicates the monthly frequency of parturition calculated from the length frequencies of fetuses and juvenile calves younger than 2 years of age. Bottom indicates the frequency of the date of conception calculated from the ovulation diagram. The scales of date of conception (bottom) and that of parturition (top) are moved apart for 11.2 months, the length of gestation. White areas indicate conception within 1 year before the death of the animal, the dotted that between 1 and 2 years, the black that between 2 and 3 years, and the shadowed that between 3 and 4 years.

Breeding season

The parturition seasons are calculated from the mean growth curve and length frequencies of juvenile calves and of fetuses (Fig. 33). As the apparent mating season differs between schools, it is necessary to observe many schools and a wide chronological range in obtaining the information on the mating season of the species.

However after the attainment of 2 years of age, it is impossible to estimate the date of birth because the growth of the calf becomes too slow compared with the range of individual variation of the body length. By this method the reproductive activity of the females in the most recent 3 years can be estimated. The date of conception was obtained by sliding the chronological scale of the parturition season for 11.2 months.

In all the 7 schools the peak of conception calculated from the fetal length is in July and August. This strongly suggests that one of the mating seasons of this species is in these months. The result calculated from animals born within one year is almost similar to that obtained from fetuses, but there appears another small peak of conception in January. Though the information obtained from the calves born between 1 and 2 years before death is inaccurate, there seems to be peaks of conception in February, in May and June, and in September. But when all are totaled there remain only two peaks of conception one in July and August, and the other in January and February.

The bottom of Fig. 33 indicates the frequency of conception in the past 4 years obtained from the size of the corpora albicantia of pregnancy. In this figure the date of conception corresponding with the corpora lutea of pregnancy was calculated from the length of fetus. There seems to be three peaks in the conception occurred between the past 1 and 4 years. However it is also possible to read in the total height two main peaks of mating between May and September, and between November and March, each of which having one accessory peak in it. This feature coincides with the seasonal change of the ratio of fertile ova to the total number of ovulations (Fig. 34). The ratio of fertile ova is higher in the two mating season. However the frequency of total ovulation shows another feature. As expected from the 4 months cycle of ovulation, there are observed three peaks in January to

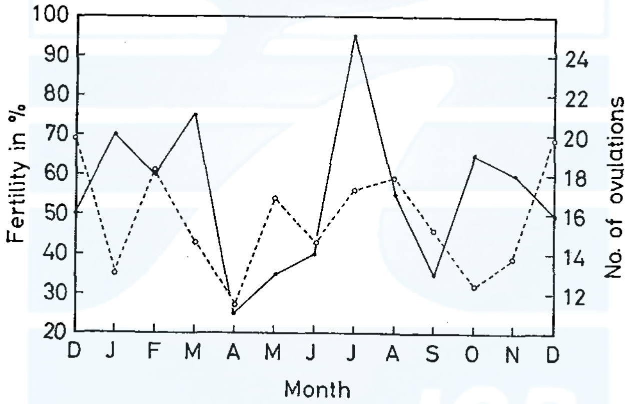

Fig. 34. Seasonal change of frequency of ovulations (solid line) and of the ratio of fertile ovulations (dotted line). Ovulations in the recent 4 years studied are combined.

March, July, and October and November.

The above three sets of data on mating seasons do not coincide well. Between the first two methods (Fig. 33), the peaks around February and that in July coincide. This first method is good in accuracy but covers too short period. On the other hand the second method covers a longer period and suggests the other peak in December, but the accuracy of dating is less reliable. The third method or the frequency of ovulation, which is similar to the second but includes all the ovulations, suggests a mating seasons of four months interval. To increase the accuracy of the second method, if the dates of the conception at each end of the series B or the selected reproductive cycles used in the former section is considered, there is observed three clear peaks of conception (Table. 13). Two of these mating seasons coincide well with those obtained from Fig. 33. The third peak in November coincides approximately with the corresponding peak in Fig. 33 (bottom) and frequency of ovulation in Fig. 34. Then the interval of the peaks are 4 months which is suggested by the postpartum and postlactum ovulations.

As a conclusion, though more confirmation is necessary, we are inclined to expect three mating seasons with the peaks in February and March, in July, and in November. The last two mating seasons coincide with the seasons of just after the north bound and south bound migrations, and the first just before the north bound migration. However it is probable that the migration is affected by the breeding cycle and there is a segregation of females in different reproductive conditions. The parturition seasons seems to be about one month ahead of the mating peak i.e. in Jannuary and February, in June, and in October.

TABLE 13. MONTHLY DISTRIBUTION OF DATE OF CONCEPTION OBTAINED FROM SERIES B.

Month	Jan.	Feb.	Mar.	Apr.	May	Jun.	July	Aug.	Sept.	Oct.	Nov.	Dec.
Frequency	1	7	4	1	1	5	14	5	1	4	4	4

Reproductive cycle

The mean length of reproductive cycle can be obtained from the ratio of various reproductive conditions assuming the 11.2 months for the approximate length of gestation. When the data of all the schools are combined the number of pregnant females is 64 or 25.6% of mature animals, including each half of the number of animals which are simultaneously lactating and pregnant into both categories (Table 27). The length of lactation $140 \div 64 \times 11.2 = 24.5$ months is calculated. By the same method the length of resting 8.1 months, and the length of one reproductive cycle of 43.8 months or 3.65 years are obtained.

If the samples are obtained evenly from various seasons in a year and covers schools of various reproductive stages, this method gives good information on the mean length of reproductive cycle. However, as can be seen in Table 27, the samples were collected mainly in October and November, and the frequency of mature females constituting the reproductive stages shows wide between school variation. In this condition we cannot expect the accuracy of the method. Another problem is the presence of females which are sexually mature but in which the reproductive stage was not identified. This kind of imperfect observation is usually made on animals whose reproductive organs have been removed by the fishermen and precise study was not made. On this case the identification of pregnant females is usually possible based on fragments of uterus. However it is very difficult to distinguish the resting animal from the very early stage of pregnancy. Accordingly the real ratio of resting animals, which represent the sexually mature females other

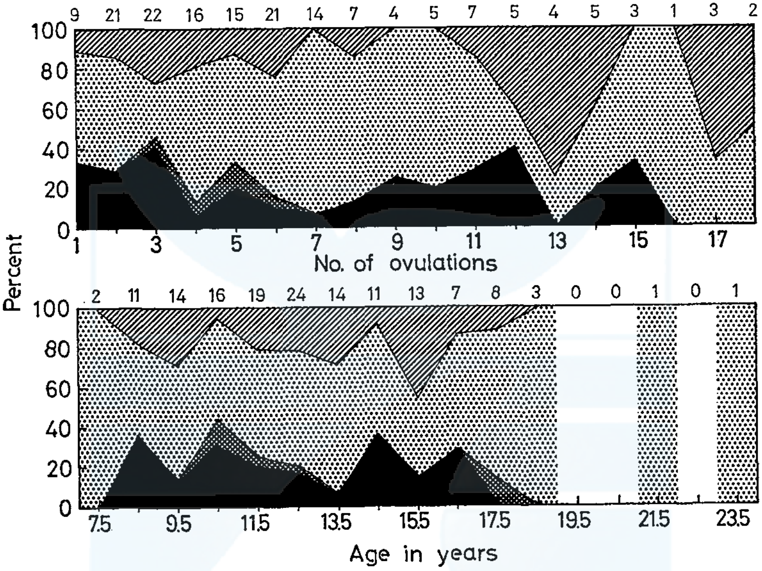

Fig. 35. Change of the ratio of sexual conditions by age in mature females of *S. attenuata*. Black indicates pregnant females, black with white spots those pregnant and simultaneously lactating, white with black spots those lactating, and lines those resting. The number at the top indicates sample size.

TABLE 14. RATIO OF REPRODUCTIVE CONDITIONS AT THE TIME OF DEATH AMONG MATURE FEMALES OF VARIOUS AGE GROUPS.

No. ovulations	Pregnant		Preg. & Lact.		Lactating		Resting		Total		Reproductive cycle (Months)
	no.	%	no.	%	no.	%	no.	%	no.	%	
1- 6	24	23.1	5	4.8	55	52.9	20	19.2	104	100	40.2
7-12	8	19.0	0	0	30	71.4	4	9.5	42	100	58.8
13-18	2	11.1	0	0	8	44.4	8	44.4	18	100	100.8
Total	34	20.7	5	3.1	93	56.7	32	19.5	164	100	50.3
Age (years)											
7.5-11.5	15	24.2	3	4.8	33	53.2	11	17.7	62	100	38.6
12.5-17.5	13	16.9	2	2.6	44	57.1	18	23.4	77	100	57.5
18.5-23.5	0	0	0	0	5	100	0	0	5	100	—
Total	28	19.4	5	3.5	82	56.9	29	20.1	144	100	52.9

than pregnant or lactating, may be higher than that observed. Accordingly the real mean reproductive cycle must be longer than 43.8 months.

Table 14 and Fig. 35 shows the change of the pregenant ratio accompanied with increase of age. They show that the ratio of pregnant females decreases and length of reproductive cycle increases in the older animals. The length of reproductive cycle calculated by adding all the ovulation classes or age classes are 50.3 and 52.9 months respectively. As these calculations are based on observation of reliable materials, the figures obtained are more reliable than the 43.8 months cycle obtained from Table 27. Furthermore as the ovulation data used in Table 14 represent 96.5 % of all the available ovulation data, the figures obtained from it seems to be the best estimate of the mean reproductive cycle of the present population of *Stenella attenuata* in Japanese coastal waters. It gives the length of gestation 11.2 months, lactation 29.3 months, resting 9.8 months, and total length of reproductive cycle 50.3 months or 4.19 years.

The mean length of reproductive cycle is obtained separately from the frequency of ovulations of conception. It is generally observed in the ovulation diagram that the presumed dates of ovulation are not very reliable in the case of 5 years or older corpora albicantia, and that it is almost impossible to distinguish the corpora of pregnancy and of ovulation on the diagram of that part. This is clearly shown in Table 15, where numbers of corpora albicanta of preganancy and of ovulation are shown together with the number of animals (no. × months). In this table the pregnant ratio and mean annual ovulation rate show smooth fluctuation until the 4th year from death, but they show higher fluctuation after the 5th years. The mean of the pregnant ratios in the recent 4 years in Table 15 is 0.2062, which gives the length of reproductive cycle as 54.3 months or 4.63 years. This figure is very close to the figure 50.3 or 52.9 months obtained from the ratio of various reproductive conditions of individuals of known age.

TABLE 15. REPRODUCTIVE PARAMETERS CALCULATED FROM OVULATION DIAGRAMS IN RELATION TO THE INTERVAL FROM THE DATE OF DEATH.

	Year	1st	2nd	3rd	4th	5th	6th
A.	Sample size (No. × Month)	1159	1464	1424	1312	1162	673
B.	Fertile ovulation	21	22	24	31	37	27
C.	Total ovulation	40	38	44	67	104	89
D.	Pregnant ratio (B×11.2÷A)	0.2029	0.1683	0.1888	0.2646	0.3566	0.4493
E.	Mean annual ovulation (C÷A×12)	0.4142	0.3115	0.3708	0.6128	1.0740	1.5869

The individual variation of the length of reproductive cycle is obtained, though it is unsatisfactory, from the ovulation diagram. Fig. 36 shows the relation between the time after the last partutition and reproductive stage at the time of death. It shows that some individuals finish lactation at about the 17th month after parturition but some animals continue lactation for about 60 months or 5 years after parturition. If the length of lactation means the length of the suckling period, the calf may continue to take both milk and solid food until the age of 17 months in the shortest case or of 60 months in the longest case after starting to feed on solid food at the age of about 9 months. It is highly probable that the lactation is finished in the usual shortly before the conception, and that the lactation lasts longer on an animal of which interval between conceptions is long.

The length of lactation can be presumed from a direct comparison of the number of juvenile calves and that of lactating females caught together (Kasuya 1972). This method does not give the mean length of lactation but the longest range. At first step, the body length where the cumulative length frequency of juvenile animals coincides with the number of lactating females (Table 27) was obtained as shown on Fig. 37. Schools 5 and 7 were excluded here because the number of investigated lactating female was too few. On Fig. 35 the results obtained from schools 2 and 6 give a very small length (correspond to 1.0 and 1.75 years respectively), so they will not give the real length of lactation but will show only that there were no large suckling calf in the school. Accordingly the informations obtained from schools 1, 3 and 4, or the length 169 cm, 178 cm and 175 cm respectively, were used here. Then the modal lengths of the peak which includes the above body lengths were obtained on Fig. 2. They are shown in parentheses in Fig. 35. The ages corresponding to these modal lengths read on the mean growth curve are 4.0, 5 1/4 and 4.0 years respectively. For the comparison, same method was applied for the age frequencies of the schools 3 and 6. In these schools the ages of all the

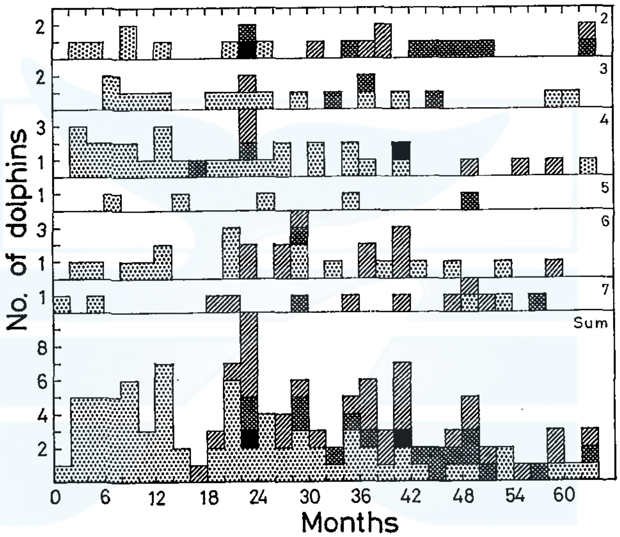

Fig. 36. Relation between the sexual condition at the time of death and the length of time after last parturition, obtained from the ovulation diagram series A. Black dots indicate lactating females, lines the resting, white dots the pregnant, and black the females lactating and simultaneously pregnant. Numbers at the right show the school.

young animals of known length were determined. The length of lactation obtained by it was 5.5 years (school 3) or 1.5 years (school 6), showing a good coincidence with that obtained from the body length frequencies. These result indicates that in some animals the lactation lasts for 4 or 5 years, even if there are many females which finish the lactation within a shorter period.

The date when the female starts the next pregnancy, or that enter into the next cycle after weaning the calf, is calculated by estimating the date of conception from the length of fetus. Fig. 38 indicates that some females enter into the next pregnancy at about 18 months after the last parturition. After this date, the number of females which enter into the next pregnancy increases rapidly. At 28th month after parturition there begins to appear the females which give birth to the next calf and complete one reproductive cycle. The time when all animals complete the reproductive cycle is about 68 months. This information on the length of reproductive cycle coincides approximately with that obtained by other methods. In this method, as the abundance of lactating female is underestimated compared with that of pregnant females, it is incorrect to presume the mean length of reproductive cycle as the time when 50 % of females finish the cycle.

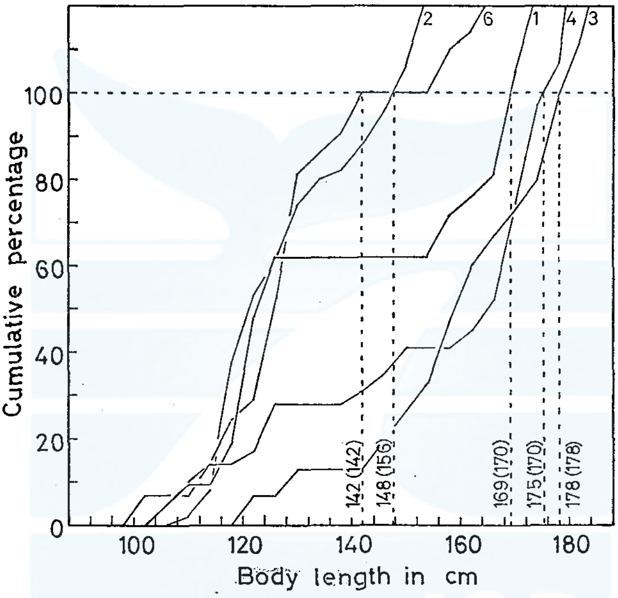

Fig. 37. To ascertain the maximum length of lactation, the cumulative frequency of calves is compared with the number of lactating females. Numbers at the top indicate schools. For further explanation see text.

Fig. 39 shows the length frequency of reproductive cycles based on 67 cycles of 64 animals obtained from the series B. As the ovulation diagram covers only about 65 months, the frequency of long reproductive cycles is underestimated and the cycles longer than 60 months are entirely neglected. However this can give a

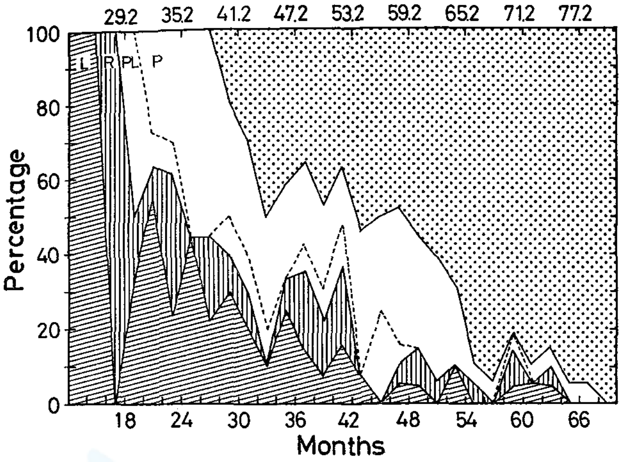

Fig. 38. Length of reproductive cycle calculated from the data in Fig. 36 and length of fetuses. The dotted area indicates the females which have finished the cycle after giving birth to the calf. Scale at the top indicates the number of months from last conception, and that at the bottom months from last parturition. L, lactating. R, resting. P, pregnant. PL, pregnant and lactating.

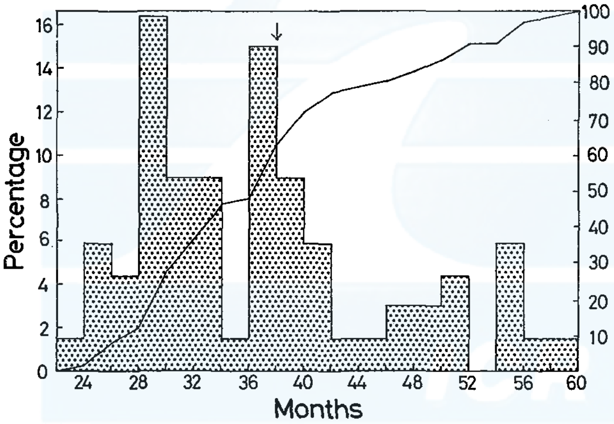

Fig. 39. Frequency of the length of reproductive cycle in months obtained as the interval between the dates of two ovulations of pregnancy (left scale), and its cumulative frequency (solid line and right scale). Arrow indicates the position of mean length of the cycle.

rough idea on the range of the length of reproductive cycle. An exceptionally short reproductive cycle is about 23 months, but most of the cycles are more than 29 months. This means some few females start the next pregnancy at the 12th month after the former parturition but more usually at the 18th or later months as indicated in Fig. 38.

As the length of reproductive cycle changes with age, the reproductive parameters must be obtained in relation to the age of the animal. At first step the number of animals, number of fertile ovulations, and total number of ovulations in the recent 4 years were calculated on the ovulation diagram for each group of females classified by the number of ovulations at the time of death. Then the mean values of various parameters in the past 4 years were calculated (Table 16). The constants of the regression lines calculated by least squares are shown in the same table, and by the lines in Fig. 40. It shows that the mean length of a reproductive cycle increases rapidly from 3.6 years of the young animal to 6.5 years for the old animal. This prolongation of reproductive cycle in old females is not produced by the cessation of ovulation, but by the increase of unsuccessful ovulations. The fertility ratio of ova decreases from 64 % of young animals to 32 % of old animals. On the other hand the number of annual ovulation shows a very slight increase with age. Anyway such a long mean reproductive cycle of old females suggests

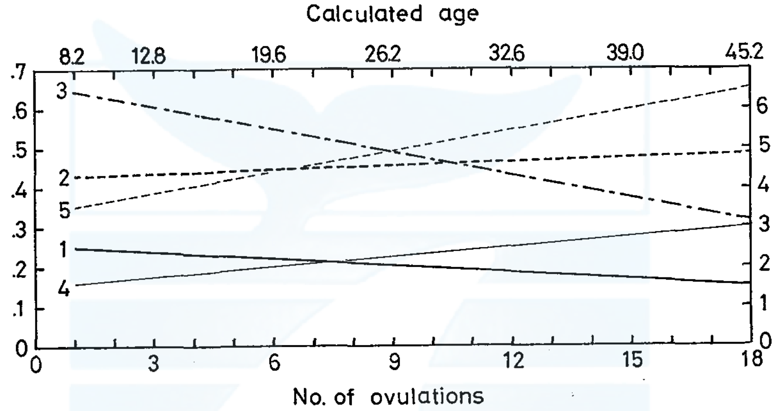

Fig. 40. Relation between age and reproductive parameters obtained from the ovulation diagram. 1 indicates pregnant ratio (left scale), 2 annual ovulation rate (left scale), 3 fertility ratio of ovum (left scale), 4 number of ovulations in a reproductive cycle (right scale), and 5 length of reproductive cycle in years (right scale).

TABLE 16. REPRODUCTIVE PARAMETERS CALCULATED FROM OVULATION DIAGRAMS OF THE PAST 48 MONTHS IN RELATION TO THE NUMBER OF OVULATIONS AT DEATH.

Number of ovulations at death	1–3	4–6	7–9	10–12	13–15	16–18	a*	b*
A. Sample size, No.×Month	1474	1606	959	733	565	288	—	—
B. Fertile ovulation	36	23	21	12	12	3	—	—
C. Total ovulation	50	67	33	26	28	10	—	—
D. Pregnant ratio	0.2735	0.1604	0.2453	0.1834	0.2379	0.1167	−0.00584	0.2584
E. Mean annual ovulation	0.4071	0.5006	0.4129	0.4256	0.5947	0.4167	0.00327	0.4286
F. Ovulation per reproductive cycle	1.389	2.913	1.571	2.167	2.333	0.333	0.0817	1.518
G. Length of reproductive cycle, Month	40.94	69.83	45.67	61.08	47.08	96.00	2.119	39.97
H. Fertility of ovum	0.7200	0.3433	0.6364	0.6415	0.4286	0.3000	−0.01923	0.6643

* $y=ax+b$. $D=B\times 11.2\div A$, $E=C\div A\times 12$, $F=C\div B$, $G=A\div B$, $H=B\div C$.

that their participation in reproduction is almost negligible.

Accumulation rate of corpora albicantia

The corpora albicantia with clear yellow or yellow brown colour and have no internal structure typical of usual corpora albicantia nor typical external scar were considered to have been derived from atretic lutealized follicles (Harrison and Ridgway, 1971), and were not included in the number or corpora albicantia. The number of corpora atretica was counted, if found, when the number of corpora albicantia and lutea was counted. The relation between number of ovulations and of corpora atretica is shown in Table 17. However if they had been searched for more intensively, the number might have been more than that shown here.

No corpora atretica are observed in immature animals. However, in the mature animals, corpora atretica ranging from 0 to 13 in number were observed. It does not seem to increase with the age of animals. This may be because the size of corpora atretica decreases rapidly and many of them have been overlooked. But at present the possibilities are not denied that corpora atretica are formed frequently in young animals or that very few corpora atretica are erroneously included as corpora albicantia.

Ohsumi (1964) showed on *S. attenuata* that the left ovary is precocious and the number of ovulations in the left ovary usually predominates that in the right. Among the present 171 pairs of mature ovaries, 162 pairs or 95.7 % of the total females had the higher number of corpora in the left ovary. This supports his result.

TABLE 17. RELATION BETWEEN NO. OF OVULATIONS AND NO. OF CORPORA ATRETICA OBSERVED.

No. of ovulations	0	1	2	3	4	5	6	7	8	9	10	13	mean
0	126	—	—	—	—	—	—	—	—	—	—	—	0
1	10	1	—	—	—	—	—	—	—	—	—	—	0.09
2	18	2	1	—	—	—	—	—	—	—	—	1	0.77
3	18	3	—	—	—	—	1	—	1	—	—	—	0.74
4	16	—	—	—	—	—	—	—	—	—	—	—	0
5	13	1	—	—	—	—	1	—	—	—	—	—	0.47
6	18	2	1	—	—	1	—	—	—	—	—	—	0.41
7	10	3	2	—	—	—	—	—	—	—	—	—	0.47
8	6	—	—	—	1	—	—	—	—	—	—	—	0.57
9	4	—	—	—	—	—	—	—	—	—	—	—	0
10	2	2	—	—	—	—	—	—	1	—	—	—	2.00
11	6	1	—	—	—	—	—	—	—	—	—	—	0.14
12	4	1	—	—	—	—	—	—	—	—	—	—	0.20
13	1	1	1	—	—	—	—	1	—	—	—	—	2.50
14	3	1	1	—	—	—	—	—	—	—	—	—	0.60
15	2	1	—	—	—	—	—	—	—	—	—	—	0.33
16	—	—	—	—	—	—	1	—	—	—	—	—	6.00
17	2	—	—	—	1	—	—	—	—	—	—	—	1.33
18	1	1	—	—	—	—	—	—	—	—	—	—	0.50
Total	260	20	6	0	2	1	3	1	2	0	0	1	0.33

However, the presence of 8 pairs (4.7 %) of ovaries, in which the number of corpora in right ovary exceeds that in the left, indicates that there may be few females which do not show the precocity of left ovary. The same number of corpora in each ovary was observed only in one (0.6 %) female. These few females should be dealt with separately in analyzing the ovulation activity of the females with precocious left ovary.

Fig. 41 shows the mean number of ovulations in one ovary plotted against the number of ovulations in both ovaries. It is considered from this figure that the right ovary of some of the females with a precocious left ovary starts to ovulate at the age of 6 to 10 ovulations. But most of the left ovaries cease the ovulation at 13 or 14 ovulations when the right ovary take the place of left ovary. The mean number of ovulations at this stage calculated from 13 females with 13 or more corpora is 13.5. The thick solid and dotted lines in Fig. 41 indicate the mean ovulation activity of the female with a precocious left ovary. On the other hand the bilateral asymmetry is not clear in females in which the corpora number in the left ovary does not exceed that in right ovary. This may mean that the right ovary of these individuals starts to ovulate at a younger age, or that both ovaries ovulate equally. Possibly both cases occur in these individuals.

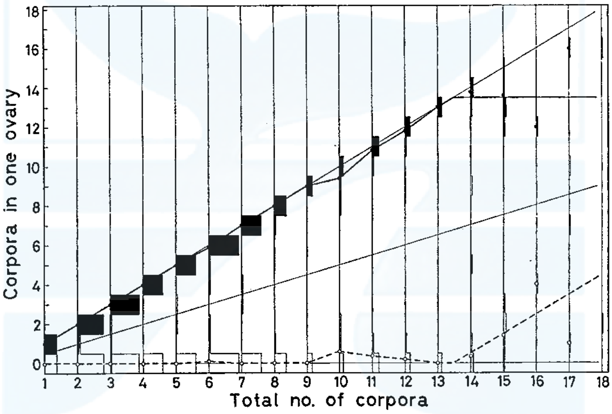

Fig. 41. The asymmetry of corpora number in the ovaries of *S. attenuata*. Black squares indicates the frequency of corpora in left ovary, the white that in right ovary, closed circles and thick solid line the mean number of corpora in the left ovary of the female with precocious left ovary, and open circles and dotted line that in right ovary in the same animal. Three thin solid lines indicate the case where all the corpora are in the left ovary or in the right ovary, and the cases where both ovaries have the same number of corpora.

The accumulation rate of corpora albicantia in one reproductive cycle was shown to change from 1.6 of youngest animals to 3.0 of oldest animals (Fig. 40). The mean accumulation rate of corpora in all the age groups is obtained by totalling the mean number of postpartum ovulations and that of postlactum ovulations (Table 10). This method gives the value 1.743 for the mean number of ovulations in one reproductive cycle. This value corresponds in Fig. 40 to the value at the age of 3 ovulations or 12.8 years of age calculated by the method mentioned in a later section.

The number of ovulations experienced before the first pregnancy is obtained by two methods. One is to use the ovulation diagram. In some recently matured females the number of ovulations undergone before the first pregnancy is directly counted on the ovulation diagram (Table 18). The mean of these ovulations is 1.784, which is fairly close to the number of ovulations per one reproductive cycle obtained as above and to the value obtained on *Globicephala melaena* (Sergeant, 1962). The second is the method of Sergenat (1962). If the female attains the sexual maturity at age between 5.5 and 10.5 years of age and minimum length of reproductive cycle is 2 years, most of the young pregnant or lactating females may be in the first cycle of reproduction (Table 19). In this table the animals shown by italics were excluded from the calculation because they are considered to be in the second cycle. Then the mean number of ovulation 2.08 was obtained from 13 animals, which is too high compared with the values obtained by the above two methods. This is possibly because some postpartum ovulations, or females in the second cycle are included.

Accordingly we conclude that, though it may change with the age of the animal, the mean number of ovulations in one reproductive cycle is between 1.7 and 1.8, and that it will not be very different from the number of ovulations undergone before the first pregnancy.

The relation between the number of ovulations and the age determined by the dentinal growth layers is shown in Fig. 42. The highest annual accumulation

TABLE 18. NUMBER OF OVULATIONS UNDERGONE BEFORE THE FIRST PREGNANCY (FROM OVULATION DIAGRAM).

No. of ovulations	Frequency	
	no.	%
1	19	51.4
2	9	24.3
3	7	18.9
4	2	5.4

TABLE 19. NUMBER OF OVULATIONS IN RECENTLY MATURED PREGNANT OR LACTATING FEMALES.

Age	No. of ovulations									
	1	2	3	4	5	6	7	8	9	10
7.5	1			*1*						
8.5		3	2			*1*				
9.5	3	2	1	1		*1*		*1*		*1*
Total	4	5	3	1+*1*		*2*		*1*		*1*

rate of the corpora is 3.0 on the figure and the lowest 0.50. The relation between the number of ovulations (y) and the age (x) of the mature females, $y=0.821x-3.967$, was obtained by least squares. If this annual accumulation rate 0.821 is applied to the mean length of the reproductive cycle 4.19 years, the number of ovulations in one reproductive cycle must be 3.44. Even if the shorter and less reasonable estimate of reproductive cycle 3.65 years is adopted the ovulation in one cycle is 3.00. These values are higher than any other values obtained in this section, and considered to be unreasonable.

The open circles and dotted line in Fig. 42 indicate the mean age corresponding to each number of ovulations. This dotted line is almost vertical after the attainment of 12.5 years of age. As the annual ovulation rate does not change much with the age of animal (see Fig. 40), this tendency must indicate that the age of the animals older than that point is underestimated. This age corresponds roughly to the time when the poorly calcified secondary dentine starts to be accumulated in the pulp cavity and age determination becomes difficult. As physical maturity of this species is attained by the age of 11.5 years, it will be concluded that after the attainment of physical maturity the secondary dentine is accumulated and reliable age determination becomes impossible by the present technique.

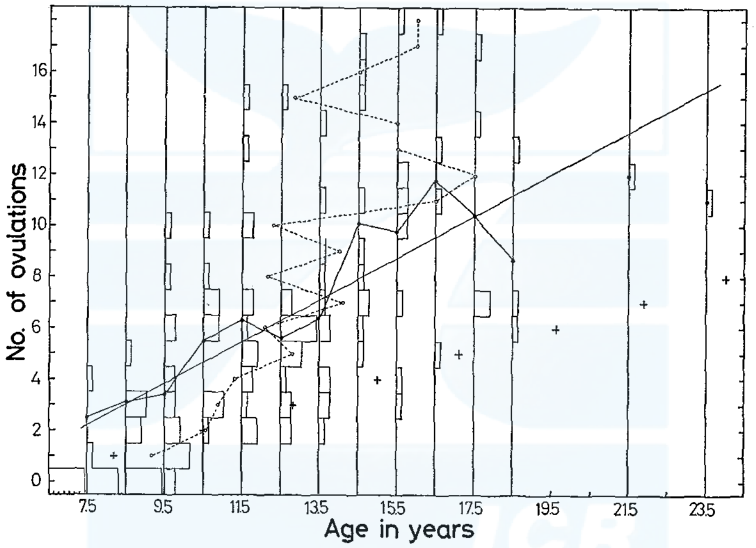

Fig. 42. Relation between number of ovulations and age of *S. attenuata* estimated from the dentinal layers. Open circles and the dotted line indicate the mean age in each ovulation number, closed circles and thick solid line the mean number of ovulations in each age class, thin solid line the relation between ovulation and age calculated by least squares, and cross marks the number of ovulations estimated from the ovulation diagram.

A similar feature is expected even in *Stenella coeruleoalba*. Though Kasuya (1972) obtained the number of ovulation-age relationship $y=0.69x-5.16$, the fitness is poor in younger animals. And the relationship between mean ages and number of ovulations is almost vertical after the age of 14 years. This is an indication of underestimation of the age. If 13 years of age or younger 15 females selected from his data (Kasuya 1972, Fig. 14), excuding one 10 years old female which shows too high count of the corpora, are used, 0.325 is obtained as the annual ovulation rate. This value is less than the half of the annual ovulation rate estimated by Kasuya (1972).

It is impossible to use a similar method to estimate the real ovulation rate of *S. attenuata*, because reliable age determination is possible only for a shorter period. The real annual ovulation rate of *S. attenuata* was calculated from the relation between the annual ovulation rate and the number of ovulations (Table 16).

$$Y_t = 0.00327x_t + 0.4286$$

where y_t is the mean annual ovulation rate between the age t and t−4 years and x_t is the number of ovulations at the age of t years. This formula means that the annual ovulation rate is approximately 0.432 at the first year after the attainment of sexual maturity and 0.487 at the age of 18 ovulations which is the oldest animal observed. These values are higher than the corresponding value obtained in *S. coeruleoalba*, but coincides with our observation that simultaneous ovulation is rare in *S. coeruleoalba*. A *Tursiops truncatus* matured and died in captivity had undergone 7 ovulations in 15 years (Sergeant *et al*, 1973) showing an ovulation rate, 0.465/year, similar to that of *S. attenuata*.

The number of corpora albicantia and lutea at age t is obtained from the above formula. If the constants of the above formula are shown by a and b, it is rewritten as follows.

$$x_{t+1} - x_t = ax_{t+1} + b$$

or

$$x_{t+1} = \frac{1}{1-a}x_t + \frac{b}{1-a}$$

Here, if the age at sexual maturity is shown by m, the number of ovulations at n years after sexual maturity is shown by the following equations,

$$x_m = 1$$

$$x_{m+n} = r^n + b\sum_{n=1}^{n} r^n$$

where n is interger and r is $(1-a)^{-1}$.

As a and b are obtained from Table 16, the number of ovulations at age m+n is calculated from this formula. The age corresponding to each ovulation number was obtained on the graph and shown in Table 24. The oldest animal observed had undergone 18 ovulations corresponds the age of 45.2 years. However as an animal with many corpora may have undergone an annual ovulation higher than the average, the observed real maximum age is considered to be less than 45 years.

LIFE TABLE

Litter size

Among 59 confirmed pregnancies, twins were observed only in two females in school 1., the other 57 pregnancies were single. Accordingly the ratio of twins in total pregnancy is 3.39 %, and the mean litter size is 1.034.

Sex ratio

The sex ratio is shown in this paper by the number of males per one female. It is shown in Tables 20 and 21, and Fig. 43 that the number of males exceeds that of females in the fetus and newborn animals. Then the ratio of male constantly decreases to attain the sex ratio of 0.579 in the age groups of more than 10 years of age where animals of both sexes have attained sexual maturity. As males attain sexual maturity 2 years later than females, the sex ratio of mature animals is very low. When calculated from length frequency it is 0.380, and when calculated from 10 years or older males and 8 years or older females it is 0.440. Probably the former figure is close to the truth because it is based on much more data. A similar ten-

TABLE 20. SEX RATIO OF *S. ATTENUATA* BY SCHOOLS AND LENGTH RANGES.

School	Sex	Fetus	Juvenile[1]	Puberal[2]	Mature[3]	Total
1	♀	5	10	13	58	86
	♂	3	7	14	29	53
		0.600	0.700	1.077	0.500	0.616
2	♀	14	38	22	105	179
	♂	19	33	44	31	127
		1.357	0.868	2.000	0.295	0.709
3	♀	0	3	2	18	23
	♂	2	7	5	11	25
			2.333	2.500	0.611	1.087
4	♀	0	3	11	45	59
	♂	2	10	16	32	60
			3.333	1.455	0.711	1.017
5	♀	0	3	1	11	15
	♂	3	4	4	0	11
			1.333	4.000	0	0.733
6	♀	3	12	1	59	75
	♂	2	14	21	15	52
		0.667	1.167	2.100	0.254	0.693
7	♀	2	0	2	17	21
	♂	2	5	11	1	19
		1.000		2.200	0.059	0.905
Total	♀	24	69	52	313	458
	♂	33	80	115	119	347
		1.357	1.159	2.212	0.380	0.758

[1] up to 165 cm, [2] 166 cm to 181 cm (♀), or 194 cm (♂), [3] more than 182 cm (♀), or 195 cm (♂).

dency of the ratio in relation to the age of animal is also found in *Globicephala melaena* (Sergeant, 1962).

There are three possible reasons for the fluctuation of sex ratio. One possibility is the segregation of adult males. Though it may exist in the puberal stage, there is observed no rapid change of sex ratio at the ages corresponding to the sexual maturity of the animal. Accordingly this possibility cannot explain all the phenomena. The other possibility is the difference of catchability between sexes. As males are always single, they might find more chances to escape from the chasing boats. However, the fact that the sex ratio continuously decreases with age even before the attainment of sexual maturity denies this hypothesis.

The only certain reason is the higher mortality of the male. As physical maturity is attained slightly earlier in females and age determination by the dentine

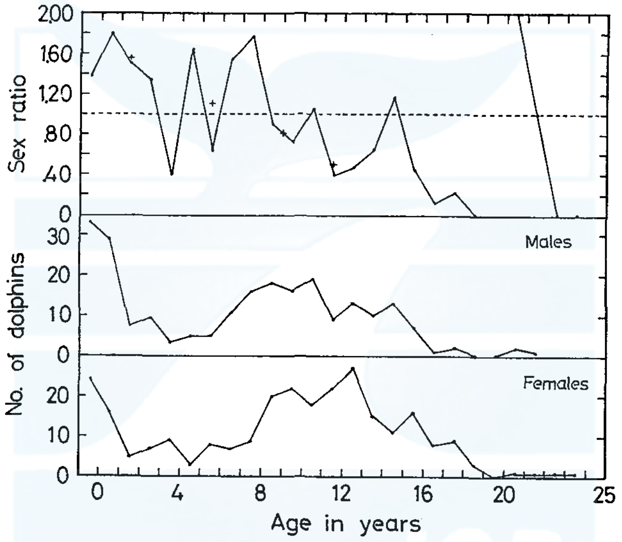

Fig. 43. Relation between sex ratio and age of the animal presumed from the dentine layers. Crosses indicate the mean sex ratio in Table 21.

TABLE 21. SEX RATIO OF *S. ATTENUATA* BY AGE DETERMINED BY DENTINE LAYERS.

Age		Female no.	Male no.	Sex ratio
range	mode			
0>	−0.5	24	33	1.375
3≧, > 0	1.5	29	45	1.552
8>, > 3	5.5	35	39	1.114
10>, > 8	9.0	42	34	0.810
13>, >10	11.5	60	31	0.517
>13		73	46	0.630
Total		239	195	0.816

layer becomes difficult, if the mortality rate of both sexes is equal there must be observed more old males than the females. However as shown in Fig. 43, the number of males of the age more than 16 years is only 6, whereas the corresponding number of females is 34. This indicates that the mortality of the male is much higher than that of the female.

If the mortality of the male can be higher than that of female in any stage of the life, it is reasonable to expect that the sex ratio may change even in the fetal stage. But this problem was not analysed in this paper. When the mortality coefficient of male is shown by m, that of female by μ, and the sex ratio at birth by a, the sex ratio at the age of t years can be shown by the formula in the below.

$$\text{Sex ratio} = a \cdot e^{-(m-\mu)t}$$

The a and $m-\mu$ are obtained from the 5 mean sex ratios in Table 21. The data on animals older than 12.5 years were not included because age determination by dentine growth layer is in some case unreliable. The a and $m-\mu$ calculated by the least squares are 1.568 and 0.08348 respectively. This indicates that 38.94% of total number of newborn calves is female. The age when the both sexes are equal in number is 5.4 years of age. In other species of mammals such a high sex ratio at birth is observed in red deer (Asdel, 1964).

Mortality and recruitment

Fig. 44 shows the age frequencies of the 239 females and 195 males based on the age determined by the dentine growth layers. The age is grouped into nearest n+0.5 years, where n is an integer. Each half of animals at the age of 1.0, 2.0, and 3.0 years were divided into age groups of younger or older animals.

The number of animals between 3 and 8 years of age is small. This category of animals may have left the breeding schools which we had the chance to study. The highest frequency of females is in the age group of 12.5 years and that of males 10.5. If the mortality is constant after this year and the age determination is correct, there is expected to be the following equation,

$$l_t = l_0 e^{-\mu t}$$

where t is the age of animal in years, l_t the number of animals at age t, and μ the mortality coefficient. The mortality coefficient of the animals of both sexes more than 12.5 years old were calculated by the least squares. It gives the mortality coefficient,

$$\mu = 0.3545$$

or the annual mortality rate,

$$M = 1 - e^{-\mu} = 0.2985$$

The mortality coefficient of mature females can be calculateed by another method, based on the annual ovulation rate. The age frequency calculated with the Number of ovulation-Age relationship is shown in Table 22 and Fig. 45. The mortality coefficient and mortality rate of mature female, μ and M, calculated for

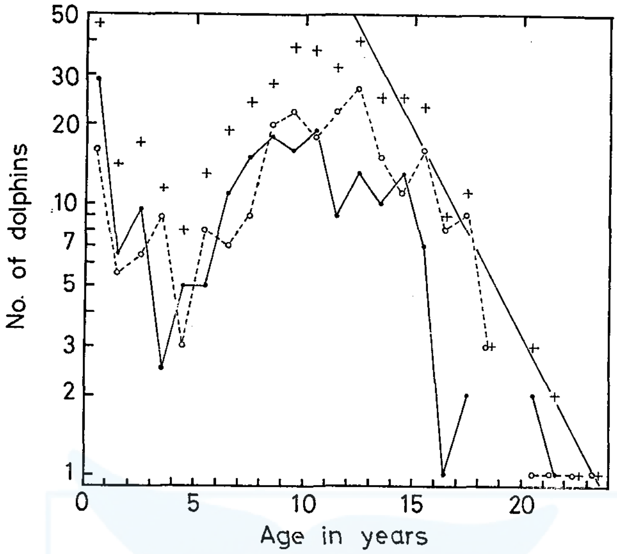

Fig. 44. Age frequency of *S. attenuata* based on the dentine layers. Open circles and dotted line indicate females, and closed circles and solid line males. Crosses show the total of both sexes including animals of unknown sex. Straight line was calculated by least squares for all animals of more than 12.5 years of age.

TABLE 22. FREQUENCIES OF NO. OF OVULATIONS AND OF AGE CALCULATED FROM NO. OF OVULATIONS.

No. of ovulations	Calculated age	School no.							Total
		1	2	3	4	5	6	7	
0	—	22	64	5	15	5	13	—	124
1	8.2	1	4	2	3	—	1	—	11
2	10.5	9	2	—	2	1	5	3	22
3	12.8	4	5	2	4	—	5	3	23
4	15.0	4	5	1	3	—	3	—	16
5	17.3	5	2	1	5	—	—	2	15
6	19.6	6	3	4	3	1	5	—	22
7	21.8	3	1	4	2	2	2	1	15
8	24.0	1	1	—	1	1	2	1	7
9	26.2	1	1	—	1	1	—	—	4
10	28.4	—	—	2	1	—	2	—	5
11	30.5	1	—	1	5	—	—	—	7
12	32.6	—	1	—	2	—	1	1	5
13	34.8	—	2	—	—	—	1	1	4
14	36.9	—	1	2	1	—	1	—	5
15	39.0	—	1	—	1	—	1	—	3
16	41.1	—	—	1	—	—	—	—	1
17	43.1	—	—	—	—	—	2	1	3
18	45.2	—	—	—	2	—	—	—	2
No. of the mature	—	35	29	20	36	6	31	13	170

the ages corresponding to 2 or more ovulations are shown below.

$$\mu = 0.07705$$
$$M = 0.07416$$

The catch of *S. attenuata* by means of the driving method is, on the coast of Izu Peninsula, sporadic and small in number (Table 23). The catch of school no. 7 at Taiji by the same method was the second case at least in recent several years. Though the tuna seine is operated in the western North Pacific, as schools of tuna are usually found by the floating wood or flocks of birds in these waters, the catch of *S. attenuata* by tuna boats seems to be negligible (Ohsumi, 1972, Dr. Suda, personal communication). Catch by means of hand harpoon is operated off Taiji on the coast of Kii peninsula. But the number caught is small.

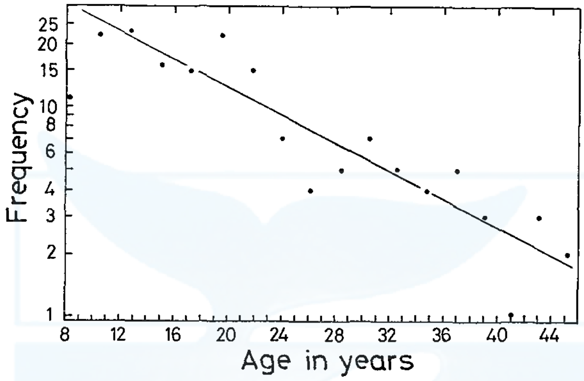

Fig. 45. Age frequency of female *S. attenuata* calculated from the number of ovulations and estimated accumulation rate of corpora. Line was calculated by least squares excluding a point of the youngest animal.

TABLE 23. NUMBERS OF *S. ATTENUATA* CAUGHT AT IZU AND KII PENINSULA.

Year Driving	1963	'64	'65	'66	'67	'68	'69	'70	'71	'72	'73[1]
no. of school	1	1	0	2	2	0	1	7	0	4	5+
no. of dolphin	37	470	0	322	373	0	437	2907	0	660	1366+
Harpoon[2]	—	—	—	—	—	—	—	14	37	12	17+

1963–1968: Tobayama (1969), [1]: Includes 206 animals in two schools caught at Taiji. [2]: Taiji.

Accordingly, the population of *S. attenuata* in the western North Pacific is considered to be close to virgin stock. In the stationary virgin stock, there must be an equation shown below.

$$S \cdot r^{-1} \cdot f \cdot l \cdot e^{-\mu' t} = S \cdot (1 - e^{-\mu})$$

where S is the number of sexually mature females, r length of reproductive cycle in year, f ratio of females at birth, l the mean litter size, t the age at the attainment of sexuall maturity, μ' the mean mortality coefficient before the attainment of sexual maturity, and μ the mean mortality coefficient of sexually mature females. Assuming t=8, r=50.3 months (=4.19 years), 1=1.034, and f=0.3894, the following values are obtained.

$$\mu' = -0.14312, \text{ and } M' = -0.13335, \text{ when } \mu = 0.3545$$
$$\mu' = 0.03240, \text{ and } M' = 0.03188, \text{ when } \mu = 0.07705\,.$$

The values at the top are unreasonalbe, indicating that the mortality coefficient, μ=0.3545, obtained from the age frequency based on the dentine growth layer is too high. This is easily expected because the age of physically matured animal is often underestimated by this method. Accordingly, one of the estimates of the mean mortality coefficient of immature females is 0.03240 when that of mature females is 0.07705. The mean length of reproductive cycle 50.3 months used here is the best estimate. Even when the less reasonable under- or over- estimates 43.8 months or 54.3 months are applied, the mean mortality coefficients of immature females are 0.04964 or 0.02264 respectively and still certainly lower than that of mature females. Possibly the best estimate of the mean mortality coefficients of immature females seems to be between the above two estimates or 0.023 and 0.049. This is about half of the value for mature females.

The rough estimate of the morality of the male is calculated from the mortality of female and the sex ratio at the age t. As $m-\mu$=0.08348 was obtained in page 209, the mean mortality coefficient of the male at the age between 0 and 8 years is

$$m = 0.08348+0.03240 = 0.12588$$

and that at the age over 8 years is

$$m = 0.08348+0.07705 = 0.16053$$

The corresponding annual mortality rates are 0.118 and 0.148 respectivelty.

The present result shows that the mortality of immature animals is lower than that of sexually matured animals. Brodie (1969) suggested that the long lactation of toothed whales will be effective as the period of education. This seems to be true in *S. attenuata.* This species starts feeding on solid food at the age of about 3/4 years, but it continues to take both solid food and milk at least by the age of 1.5 years. This weaning period seems to work as the education or training period of the calf, and work to lower the mortality of the young calf. The immature animals of both sexes aggregate after weaning, to have probable cooperative life. Of course other than these special mode of life, the life of immature female free from the reproductive activity must keep the mortality lower than that of sexually mature females.

The probability of survival in Fig. 46 and Table 24 is drawn based on the lowest mortality coefficients in the above and assuming 8 years as the age at the attainment of sexual maturity. It indicates that the number of females at attainment of the maturity is 83.4% of that at the birth. The mean life expectancy of newborn females is 14.6 years, and that of sexually mature females is 17.0 years.

The probable number of gestations experienced by a female is obtained by integrating the relation between fertility rate of ova and number of ovulations (x) in Table 16.

$$\int_1^n (-0.01923x+0.6643)dx$$

The known highest number of ovulations, 18, suggests 8.3 gestations in the past. The number of gestations, corresponding to the mean number of ovulations of adult females, 6.16, is 3.2.

The number of female calves (R_t) produced annually by the mature females (S_t) of the age t is shown by the following formula, assuming the start of conception at the beginning of the year.

$$R_t = S_t \cdot r_t^{-1} \cdot l \cdot f \cdot \rho^{11.2/12}$$

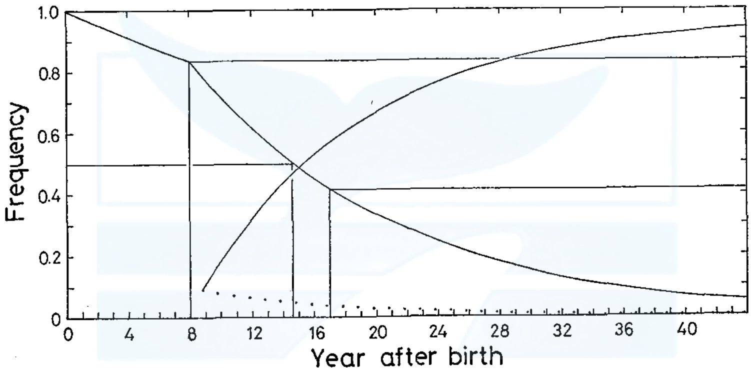

Fig. 46. Calculated survival and reproduction in the female of *S. attenuata*. Small dots at the bottom indicate the annual recruitment.

TABLE 24. LIFE TABLE OF FEMALE *S. ATTENUATA* AT SELECTED AGES.

Year after birth	Probability of survival[1]	Total ouvlation	Annual ovulation rate	Fertility ratio of ovum	Ratio of pregnant female	Reproductive cycle, year	Annual reproductive rate[2]	Total reproduction
0	1.0000	0	0	—	0	—	0	0
4	0.9134	0	0	—	0	—	0	0
8	0.8343	1	0.432	0.645	0.253	3.51	0.1068	0.089
12	0.6130	2.7	0.437	0.612	0.243	3.81	0.0984	0.370
16	0.4504	4.5	0.443	0.578	0.232	4.13	0.0908	0.560
17	0.4170	4.9	0.445	0.570	0.230	4.20	0.0893	0.597
20	0.3310	6.3	0.449	0.543	0.222	4.44	0.0843	0.690
24	0.2432	8.1	0.455	0.509	0.211	4.76	0.0787	0.778
28	0.1787	9.9	0.461	0.474	0.201	5.08	0.0738	0.839
32	0.1313	11.8	0.467	0.437	0.189	5.41	0.0692	0.881
36	0.0965	13.7	0.473	0.401	0.178	5.75	0.0652	0.910
40	0.0709	15.6	0.480	0.364	0.167	6.09	0.0616	0.930
44	0.0521	17.5	0.486	0.332	0.156	6.42	0.0584	0.944
48	0.0383	19.5	0.492	0.290	0.145	6.77	0.0553	0.954

[1] $lt=e^{-0.02264t}$, $1 \leqq t \leqq 8$. $lt=0.834335e^{-0.07705(t-8)}$, $t \geqq 8$. [2] R_t/S_t.

where ρ is the annual survival rate, r_t the length of reproductive cycle in year at age t, and 11.2/12 is the length of gestation in year. Other symbols are same with the formula in page 211. r_t is calculated from the relation between the number of ovulations and age (page 206), and that between length of reproductive cycle and number of ovulations (Table 16).

The annual recruitment thus calculated, and the total recruitment are shown in Fig. 46. Though the total recruitment must be 1 when the probability of survival is 0, l_t of the formula of survival, $l_t = l_0 e^{-\mu t}$, can be 0 only when t is infinite. In Fig. 46 the probability of survival at the age 48 is 3.83 %, but the probability of total recruitment is 95.40 %, and the recruitment seems to be slightly lower to keep the population stable. But as this model is based on several assumptions, the above defect is considered to be negligible at present.

If the population is depleted as the result of exploitation, the total reproductive rate $\Sigma R_t / \Sigma S_t$ will increase as the results of the increase of the ratio of young mature female with high reproductive potential, and of the shortening of reproductive cycle of each age classes. The increase of the ratio of the female in the newborn animals is also expected. This change of sex ratio works to increase the reproductive rate.

SCHOOLING BEHAVIOR

School size

The information of the number of dolphins constituting one school of *S. attenuata* was obtained from the records of the catch by the driving method in the fishermen's cooperative unions at Arari, Futo, Kawana, and Taiji. The records cover the years from 1963 to 1973. As fishermen hope to catch all the animals they find, they may sometimes drive to combine schools found at close distance. However, it is also probable for them to lose a part of the school. However these problems are not discussed here, because the information at the time of driving is insufficient and the definition of a school is also unsatisfactory.

Table 25 shows the frequency of the size of the school. The smallest school was composed of 37 animals, and the largest, 1,381 animals. The mean school size is 281.0 animals. There are 4 modes observed in the frequency, or from 37 to 98, from 120 to 437, from 509 to 617, and 1,381. The modal means are shown in the table and they suggest that the basic unit of the school is less than 100 animals, and that larger schools might be formed as the result of annexation of the smaller schools.

Immature animals

The age frequency of 7 shcools shows that the number of juvenile animals of the age between 2 and 7 years is few (Figs. 44 and 47). It is lowest at the age of 3.5 years (male) or 4.5 years (female). Though we had no chance to confirm it, it is suggested that the calves of the above age classes may have left the school of the mother as in the case of *S. coeruleoalba* (Kasuya, 1972). The age when they leave the

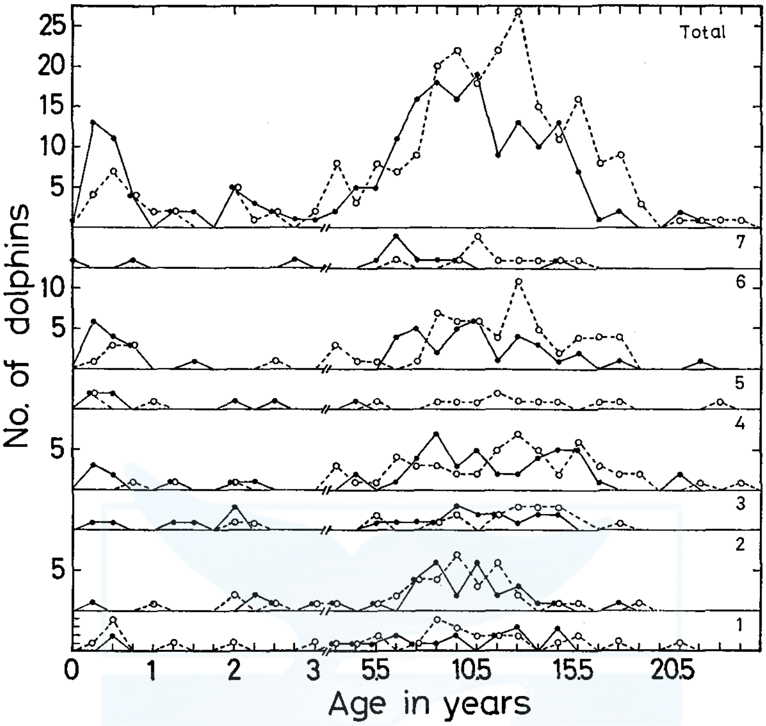

Fig. 47. Age frequency of *S. attenuata* by schools and sexes based on dentine growth layers. Open circles and dotted lines indicate females, and closed circles and solid lines males.

TABLE 25. SCHOOL SIZE FREQUENCY OF *S. ATTENUATA* CAUGHT BY DRIVING METHOD[1].

School size	No. of schools	Percent	Mean
1- 24	0	0	65.5
25- 49	1	4.8	
50- 74	2	9.5	
75- 99	1	4.8	
100- 124	1	4.8	235.9
125- 149	1	4.8	
150- 199	5	23.8	
200- 299	4	19.0	
300- 399	2	9.5	
400- 499	1	4.8	
500- 599	1	4.8	563.0
600- 699	1	4.8	
1300-1399	1	4.8	1381.0
Total	21	100	

[1] 4 schools reported by Tobayama (1969) and Nishiwaki (1965) included.

mother's school is not directly known, but it may be soon after the weaning. It was indicated from the length of lactation that calves of *S. attenuata* are weaned at the age between 17 and 60 months with an average of 29.3 months (2.44 years). As the latter age is slighly before the age of lowest frequency, the above supposition is supported. The age when the calf leaves the mother's school might be slightly earlier in males than the female.

After the age of 3 or 4 years, the number of immature animals in the breeding school increases. In females, the age of 4 years corresponds to the time when the weight of left ovary start to exceeds that of the right indicating the approach of the puberty. And in males the age of 3 years is the time when the production of spermatozoa, an indication of the arrival of puberty, is started in many animals. Accodingly it is highly probable that the calves of both sexes which have left the mother's school gradually return to the school of mature animals after reaching puberty, and all the animals will return by the attainment of sexual maturity. However some of the few calves which are accompanied by the lactating female for more than 4 years might attain puberty or sexual maturity in the same school.

The school of immature animals of *S. coeruleoalba* reported by Kasuya (1972) was composed of the males between 1.50 years and 12.5 years of age (228 samples), and of the females between 2.75 years and 7.75 years of age (62 samples). The modal age of that school was 4.5 years in males and 3.5 years in females. This feature strongly resembles the schooling behavior of juvenile animals of *S. attenuata* presumed here.

The school of mature females usually contains puberal animals in it. The only exception among 7 schools is school 5. In this school the animals of the age corresponding to the puberal stage are only 2 animals. As the age determination was made on only one third of the total number of the animals in the school, it is not

TABLE 26. PRESENCE OF SPERMATOZOA IN TESTIS SMEAR.

School no.	Spermatozoa	Testis weight (g)		
		0–5.9	6–67.9	68≦
3	none	3	1	—
	few	1	6	1
	medium	—	1	5
	many	—	—	3
	mean weight (g)	4.8	23.4	281.9
4	none	—	—	—
	few	—	8	2
	medium	—	7	9
	many	—	—	17
	mean weight (g)	—	17.3	195.6
6	none	10	17	—
	few	—	1	7
	medium	—	—	6
	many	—	—	2
	mean weight (g)	2.2	18.1	158.6

conclusive at present as to whether there is a school of mature females which does not contain puberal animals. However it is highly probable that the connection between puberal animals and mature females is less strong and the former form smaller groups when the school is dispersed or leave the latter school to join with a school of immature animals.

If the sexual activity of the puberal males, or males from 6 g to 67.9 g in testis weight, is shown by the density of spermatozoa in the testis smear, the activity is high in schools 2, 3 and 4 (Table 26). And a parallel relationship is observed between the sexual activity of puberal males and that of mature males indicated by smears or by the mean weight of testes. However it was not conclusive as to whether it is related with the reproductive cycle of the male or with the schooling behavior.

Mature female

The age frequency of mature females in each school does not show the predominance of a particular age class, but seems to be evenly distributed and affected only by the mortality (Fig. 47).

As shown in Table 27, the breeding school of *S. attenuata* always contains both pregnant females and lactating females. But the ratio of the latter to the former varies widely between schools. The lowest ratio about 1.0 is found in the schools 1 and 5, and the highest ratio 6.4 in the school 4. Most of the mature females in school 4 were in lactating or resting stage. The abundance of resting females is more variable from 0 in schools 1 and 5 to 3.5 times of the pregnant females in school 7.

The history of the reproductive activity of the females in each school is known from the length frequency of the juvenile calves and of fetuses (Fig. 48). The simplest example is in school 6, where the mating peaks in the past are in March, January, and August (from left to right in Fig. 48). The intervals between the peaks are 17 months and 12 months respectively. The feature of school 1 are very similar to that of school 6, except for a small peak in October. The intervals between the peaks in the school 1 are 16, 4.0, and 10.5 months.

School 2 shows complicated features. The peaks of conception are in February, late May, October, January, May, August, July, and October. The intervals are 3.5, 4.0, 3.5, 4.0, 3.0, 11.0, and 3.0 months. Possibly the schools 4 and 5 belong to a similar pattern with the approximate interval of the peaks of 4.0, 4.5, 4.0, and 9.0 months for school 4, and 4.5, 3.5, and 11.0 months for school 5. School 7 has no small fetus, but the arrangement of mating peaks in schools 3 and 7 is not largely different from that of school 2.

It is already suggested that *S. attenuata* in the Japanese coastal waters has 3 mating seasons. If all the mature females stay in the same school for their life time, there should be observed the peaks of 3 mating seasons in one school because the length of reproductive cycle is highly variable between animals and it is difficult for all the females to conceive synchronously in only one of the 3 mating seasons. No such case was observed in any of 8 schools studied by us or by Nishiwaki *et al*, (1965). This strongly suggests that the member of mature females in any shcool is

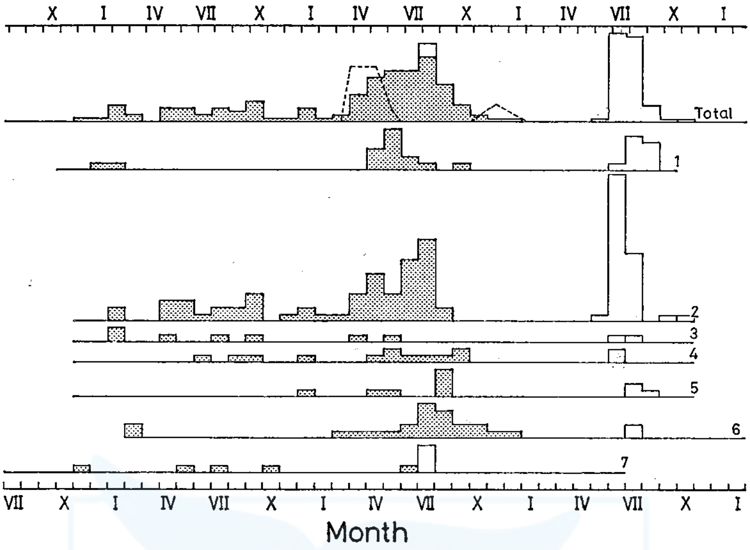

Fig. 48. Frequency of date of conception (scale at the top) and of parturition (scale at the bottom). Dotted areas indicate the frequency obtained from the body length of postnatal animals, white from that of fetuses, and dotted lines cited from Nishiwaki *et al* (1965). Numbers indicate the school.

TABLE 27. RATIO OF REPRODUCTIVE CONDITIONS OF FEMALE *S. ATTENUATA.*

School	Date killed	Imma-ture**	Mature						Total***
			un-known	preg-nant	p. & l.	lacta-ting	resting	total*	
1	25, Oct.	24	12	15	3	18	0	36	72
		33.3%		41.7	8.3	50.0	0	100	
2	15, Nov.	67	4	19	2	47	18	86	157
		42.7%		22.1	2.3	54.7	20.9	100	
3	4, Nov.	5	0	4	0	15	1	20	25
		20.0%		20.0	0	75.0	5.0	100	
4	13, Nov.	15	3	3	1	28	7	39	57
		26.3%		7.7	2.6	71.8	17.9	100	
5	18, Nov.	5	2	4	0	4	0	8	15
		33.3%		50.0	0	50.0	0	100	
6	12, Feb.	13	8	14	0	21	13	48	69
		18.8	%	29.2	0	43.8	27.1	100.1	
7	2, Jul.	3	2	2	0	4	7	13	18
		16.7%		15.4	0	30.8	53.8	100	
Total		132	31	61	6	137	46	250	413
		32.0%		24.4	2.4	54.8	18.4	100	

*: Excluding the unknown.
**: Percentage of total.
***: Excluding the maturity unknown.

not fixed but some of them can be exchanged between schools.

The interval between two recent mating peaks is usually long, but the intervals obtained from length frequencies of postnatal individual is often appears short. This seems to indicate that the oestrous females assemble together to conceive as suggested in *S. coeruleoalba* (Kasuya, 1972), and this connection is retained during the period of gestation. However after parturition the connection becomes weaker with the elapse of the time, and some of the lactating females may move to another school accompanying the calf in some case. Possibly the shift of the lactating females between schools is related to the cycle of postpartum or postlactum ovulations. The schooling behavior of resting females is probably similar to the late lactating females, but the ratio of the between school movement will be much higher.

The frequency of interval between the two mating peaks in the present 7 schools has 4 modes with the modal means of 3.8 month (13 examples), 8.1 months (4), 11.2 months (4), and 16.5 months (2). These modal means are a multiple of 4 months which is the interval of mating season of this species. If the combination of the peaks of conception observed in the present schools are formed through the random combination of each peaks, the frequency of each mode are expected to lie on the straight line shown in Fig. 49. However, the above data shows a higher frequency of the 4 months interval. This means that the neighbouring two mating peaks are not completely independent. Probably the females which failed to conceive in a mating season may often stay in the same school to conceive in the next mating season. This case is represented by a smaller peak next to the main peak

TABLE 28. MATURITY FREQUENCIES AND SEX RATIO OF MALE *S. ATTENUATA*.

School no.	Date killed	Testis weight in g						Total	Sex ratio of the mature
		imm.*	mat.*	5.9≧	6.0~67.9	68≦	unknown		
1	25, Oct.	16	21	0	2	8	3	50	0.605
		34.0%	44.7	0	4.3	17.0			
2	15, Nov.	49	17	4	20	11	7	108	0.311
		48.5%	16.8	4.0	19.8	10.9			
3	4, Nov.	1	0	4	9	9	0	23	0.450
		4.3%	0	17.4	39.1	39.1			
4	13, Nov.	11	2	0	15	30	0	58	0.762
		19.0%	3.4	0	25.9	51.7			
5	18, Nov.	8	0	0	0	0	0	8	0
		100 %	0	0	0	0			
6	12, Feb.	2	1	12	20	15	0	50	0.286
		4.0%	2.0	24.0	40.0	30.0			
7	2, Jul.	7	0	1	8	1	0	17	0.067
		41.2%	0	5.9	47.1	5.9			
Total		94	41	21	74	74	10	314	0.409
		30.9%	13.5	6.9	24.3	24.3			

* : Maturity of testis was identified by eye on the beach.

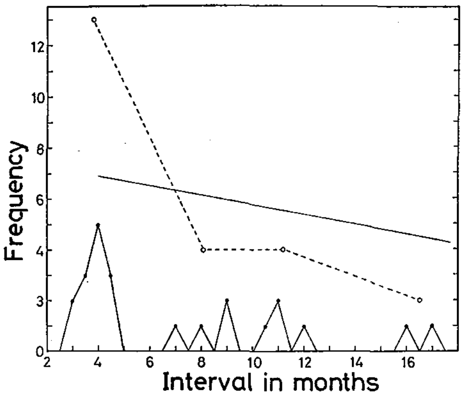

Fig. 49. Frequency of the interval of mating peaks in the 7 schools. Open circles and dotted line indicate the total frequency in each mode plotted against the modal mean of the interval. Straight solid line shows the frequency expected when mating peaks are independent.

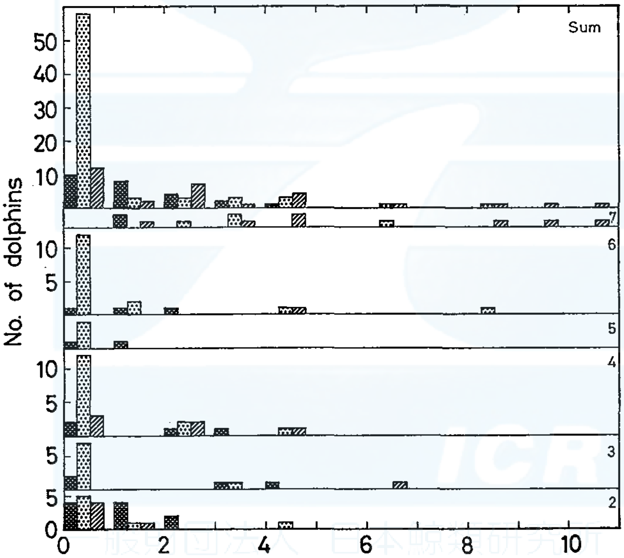

Fig. 50. Diameter of the largest Graafian follicle. White spots indicate pregnant females, black spots the lactating, and lines the resting. Schools are shown by the number at right.

observed in schools 2 and 1. In some cases, oestrous females from other schools exceeding in number the oestrous females in the original school, may join to this school. This is suggested by the 6th peak (from the left) of school 2, where the preceeding 5th peak is smaller. Of course there can be the case where all females which should have constituted the subsidiary peak shift to another school as suggested by the long intervals of peaks.

The origin of other peaks of short interval or of peaks of long interval might be the result of the annexation of schools or random exchange of members between two or more schools. The relative abundance of the 8, 12, and 16 months interval of peaks of conception decreases at the rate expected in random combination.

Mature males

As the diameter of seminiferous tubules and the weight of testis show a linear relationship, the weight of testis of mature male can be used as an indicator of reproductive activity. The mean weight of testis of mature male was compared with the mean diameter of the largest follicle of the mature females caught in the same

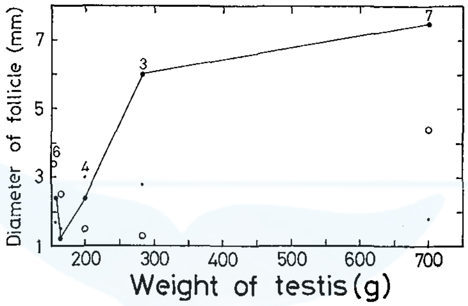

Fig. 51. Relation between the mean weight of testis of mature animal and mean diameter of Graafian follicle of the female in a same school. Large closed circle indicates the follicle diameter of resting female, open circle that of lactating female, and small closed circle that of pregnant female. Schools are shown by the numbers.

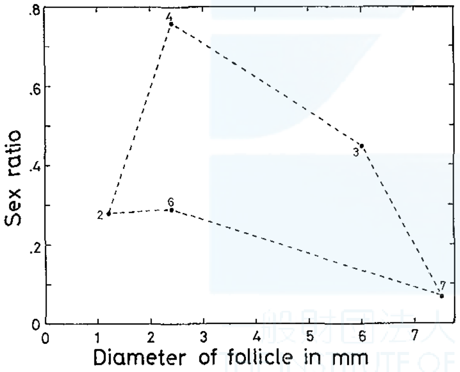

Fig. 52. Relation between the mean diameter of Graafian follicles of resting females and the sex ratio of mature individuals in the same school. Schools are shown by the number. The dotted line indicates the highest and lowest range.

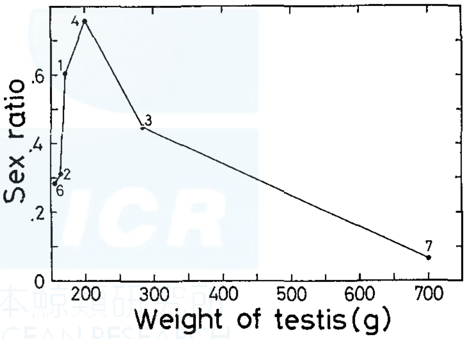

Fig. 53. Relation between sex ratio of mature animals and mean weight of testis of mature males in the corresponding school. Schools are shown by the number.

school (Fig. 51). The mean weight of testis shows a positive correlation with the diameter of the follicle of resting females. As resting females with large follicles are ready to ovulate, it is reasonable to expect males of high activity in the same school.

The sex ratio of mature individuals is small in schools containing resting females with large follicles (Fig. 52). A similar but clearer tendency is observed when it is compared with the mean weight of testis of mature males (Fig. 53). Though it is not shown in Figs. 51, 52 and 53, school 5, which does not contain resting females nor lactating females with follicles larger than 1.0 mm in diameter and is considered to be in low mating activity, it has no sexually mature male.

These results suggest that in schools at the beginning of the approach of heat many mature males may assemble in the same school, but at the peak of the heat most of them except a few males of high activity leave the school. It is highly possible that there is intrasexual aggression between the males of *S. attenuata* as in the case of another delphinidae species *Globicephala melaena* suggested by Sergeant (1962).

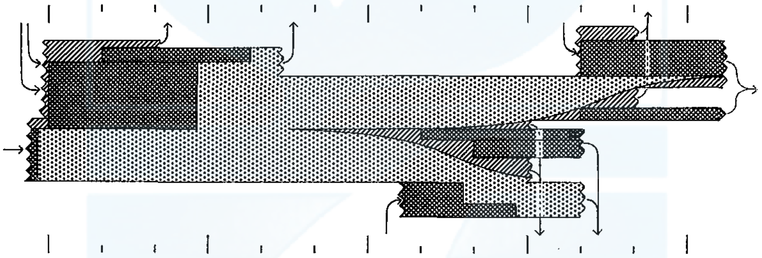

Fig. 54. Schematic figure showing one of the possible between school exchange of mature females. Arrows indicate the annexation or the split of the school. White spots indicate pregnant females, black spots the lactating, lines the resting. Mating seasons in each 4 months inteval are shown by vertical rods.

Discussion

It is well reported in several species of delphinidae that their school is compact in some cases, but in other cases it is composed of many smaller schools dispersed in a wide area. Sergeant (1962) and Saayman and Tayler (1973) suggested that it will be related to feeding or sexual behavior of the animal. Our observation on a large school of *S. coeruleoalba*, found in the evening of 24, Oct. 1972 at 34°52′ N, 141°05′ E, showed that it covered a wide area of about 21 km in one diameter and composed of numerous small groups of dolphins. This smaller groups had a distance of about 3 km to 15 km from each other, and were composed of 10 to 200 individuals. Some of them contained calves accompanied by the mother and several were composed mostly of smaller animals. This suggests that the larger schools of *S. coeruleoalba* contains smaller units.

It is probable that several small units leave the main larger school after which a larger dispersed school again forms a compact school, or that the smaller units move to an other school when the two groups come to a close distance. Fig. 54 was drawn on the assumption that the exchange or shift of the members between schools can occur through the procedure mentioned in the above. In this figure, though the composition of the reproductive condition at both ends of the diagram is similar, the members are largely different. The immature animals are not shown because their behavior is simple, the mature male was also excluded as its behavior is not well understood.

ACKNOWLEDGMENTS

The collection of data and samples were made through the cooperation of the fishermen's cooperative unions at Kawana, Futo, and Taiji. We had the help of Dr. T. Kajihara of the Ocean Research Institute and of Mr. J. H. Perano in collecting smaples. Dr. W. F. Perrin of the National Marine Fisheries Service kindly read the draft. Dr. K. Tatsukawa of the Ocean Research Institute, and Dr. A. Ohsumi and Dr. A. Suda of the Far Seas Fisheries Research Laboratory gave us valuable suggestions. This study was technically assisted by Miss. S. Wada and Miss. K. Nagayama and Mr. K. Kureha. These persons are deeply acknowledged.

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EXPLANATION OF PLATES

PLATE I

Fig. 1. *S. attenuata*, female, 118 cm in body length. Pigmentation of newborn stage.

Fig. 2. *S. attenuata*, female, 178 cm in body length. Dark spots have started to appear only on the lower jaw, and the white area on the tip of jaws is also started. The both characters are classified into stage 1.

Fig. 3. *S. attenuata*, data unknown. The white tips of jaws are classified into stage 2, and the dark and white spots into stage 3.

Fig. 4. *S. attenuata*, male, 209 cm in body length, same animal with Fig. 4 in Plate II. The white tip of jaws are classified into stage 2, white dorsal spots into stage 2, and dark ventral spots into stage 3.

Fig. 5. *S. attenuata*, adult male. The white tip of upper jaw is classified into stage 3, that of lower jaw into stage 2, white dorsal spots into stage 2, and ventral dark spots into stage 3.

Fig. 6. *S. attenuata*, dorsal view of left flipper of juvenile animal, showing the dark spots on the surface.

PLATE II

Fig. 1. *S. attenuata*, female, 117 cm in body length. Showing the pigmentation of newborn animal. An animal in the other side is also newborn calf.

Fig. 2. *S. attenuata*, female, 189 cm in body length (center). The conditions of two kinds of spots are classified into stage 3, and the white areas at the tip of jaws into stage 1. An animal at this side is a juvenile male.

Fig. 3. *S. attenuata*, male, 181 cm in body length. Ventral white spots are classified into stage 3, and other characters into stage 1.

Fig. 4. *S. attenuata*, male, 209 cm in body length, ventral view. Same animal with Fig. 4 in Plate I.

Fig. 5. *S. attenuata*, ventral wiew of an adult male.

PLATE III

Fig. 1 (top). Underwater photograph of a group of adult or subadult *S. attenuata* in the school 5 enclosed in the harbor, showing the conspicuous white tip of beak. (Photographed by N. Miyazaki)

Fig. 2 (bottom). Mother and suckling calf in the same school, showing the difference of the pigmentation of ventral region. (Photographed by N. Miyazaki)

PLATE IV

Tooth section of *S. attenuata.* photographed under transmitted light.

Fig. 1. 104 cm, male, killed on 12th, Feb. A thin translucent layer is accumulated. Less than 1/4 year.

Fig. 2. 112 cm, male, killed on 18th, Nov. A thick opaque layer is accumulated. About 1/4 year old.

Fig. 3. 135 cm, male, killed on 12th, Feb. A thin opaque layer and a thick translucent layer of full thickness are accumulated. About 3/4 year old.

Fig. 4. 175 cm, female, killed on 13th, Nov. A thin opaque layer and 2 opaque layers of full thickness are accumulated. About 2 1/4 years old.

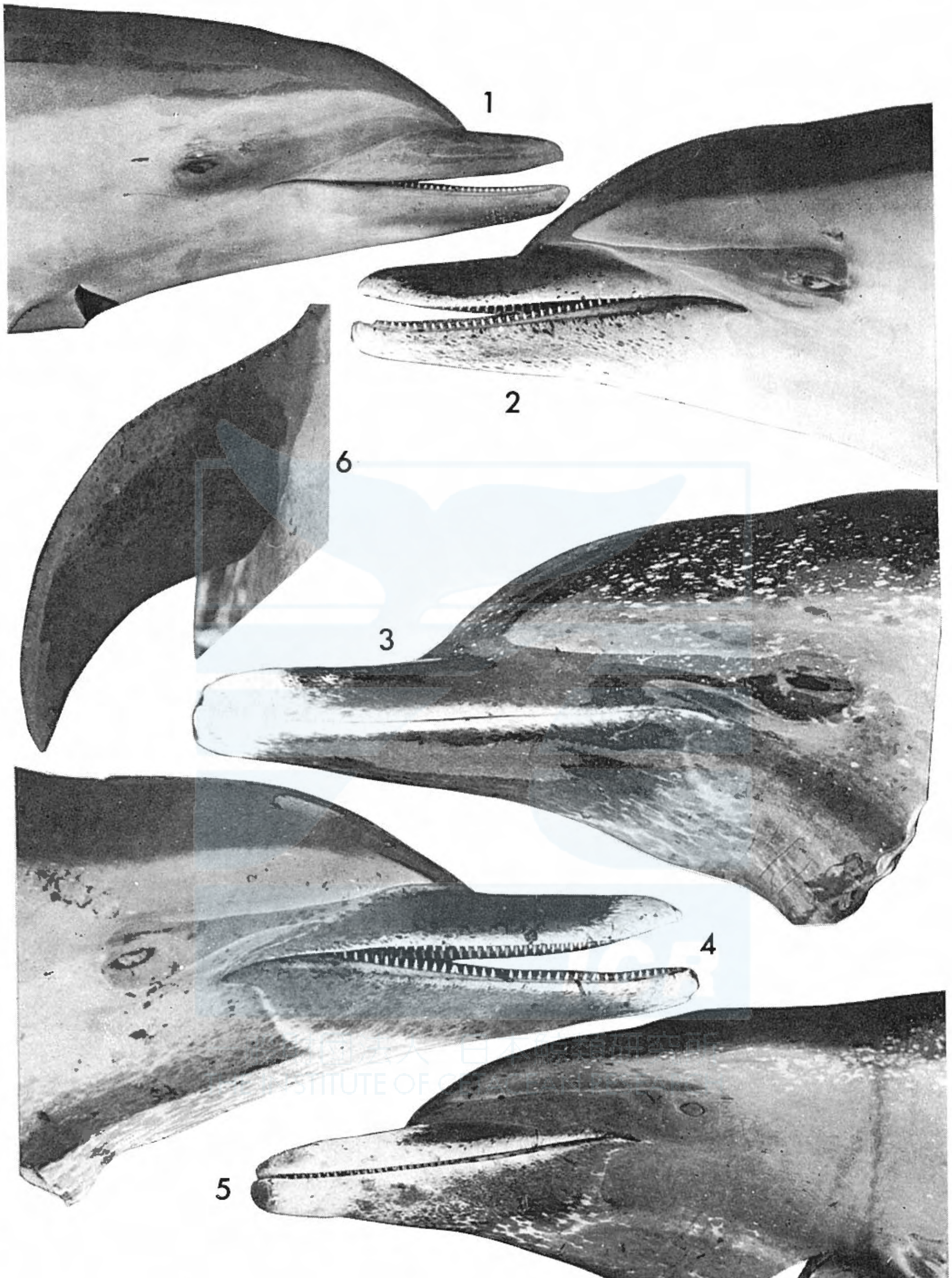
PLATE V

Fig. 1. 166 cm, male, killed on 2nd July. 3 opaque layers are accumulated. The both first and last layers are thin translucent layer. About 2 3/4 years old.

Fig. 2. 177 cm, female, immature, killed on 2nd, July. 6 opaque layers are accumulated. The first and the last layers are the thick opaque layer. About 5.5 years old.

Fig. 3. 205 cm, female, two corpora in the ovaries, killed on 2nd, July. 11 opaque layers are accumulated and the pulp cavity is still wide. About 10.5 years old.

Fig. 4. 195 cm, female, 11 corpora in the ovaries, killed on 13th Nov. 24 opaque layers are observed, and pulp cavity is filled with secondary dentine. Real age will be more than the number of the opaque layers.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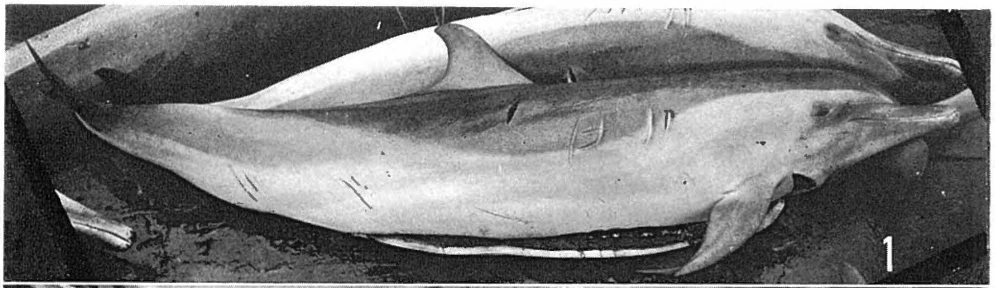

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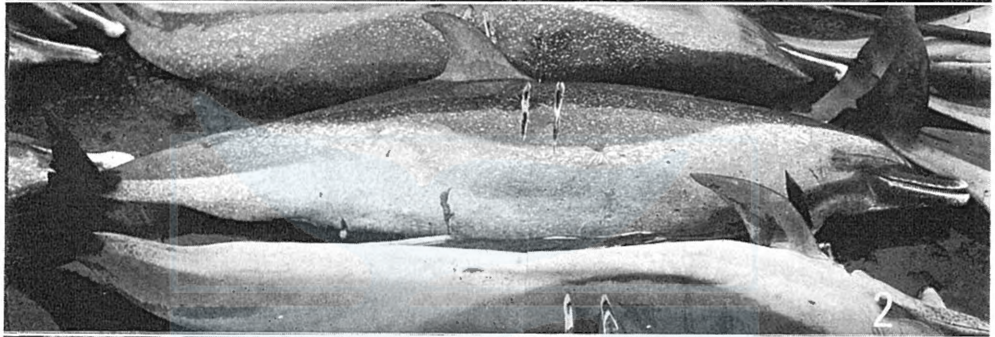

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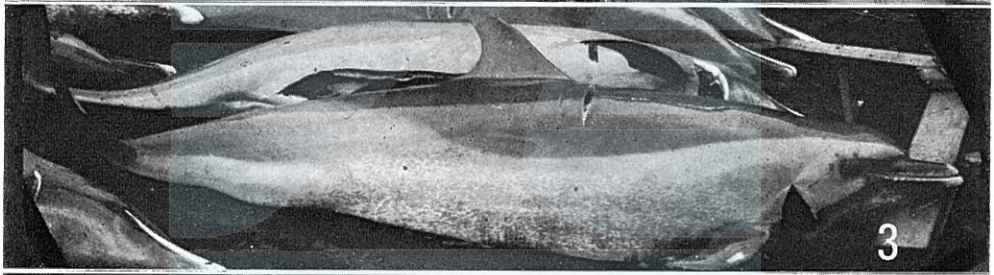

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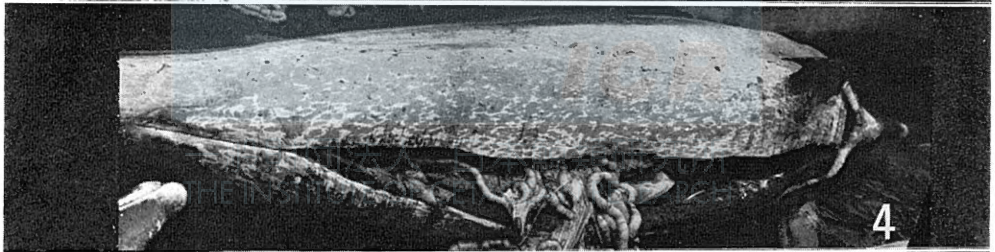

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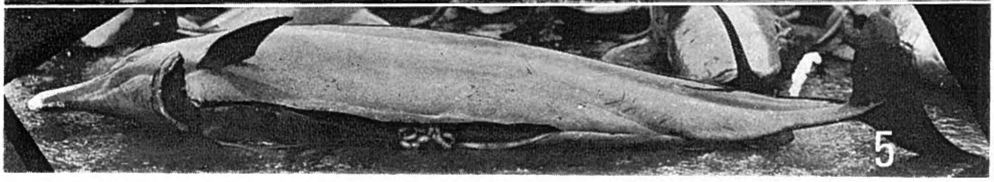

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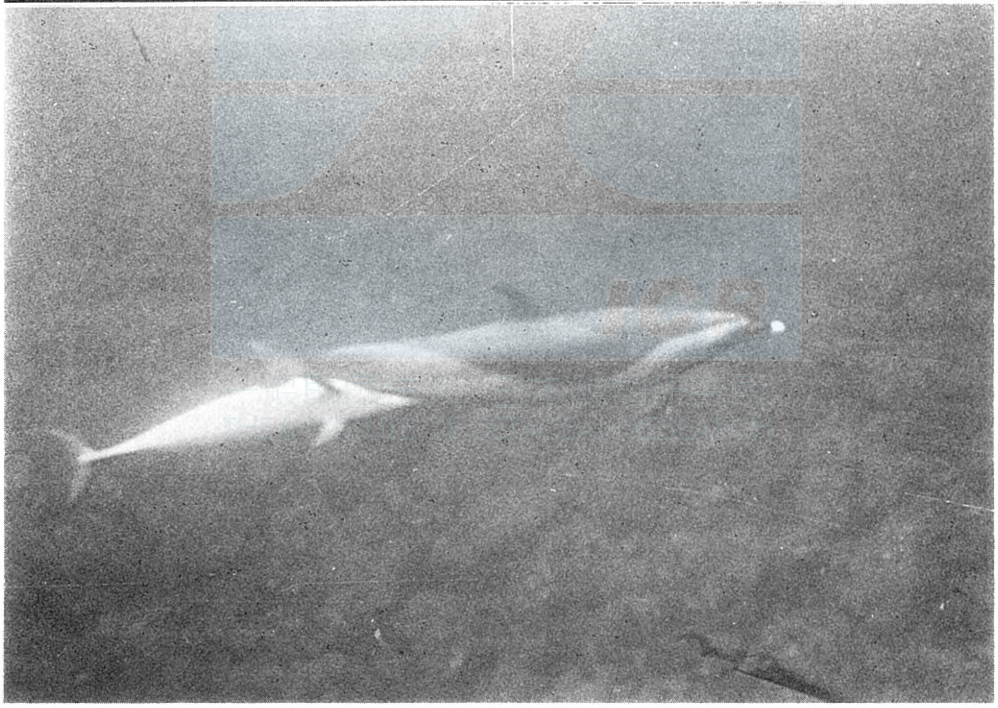

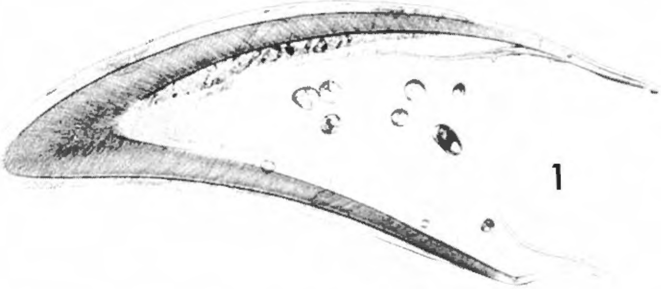
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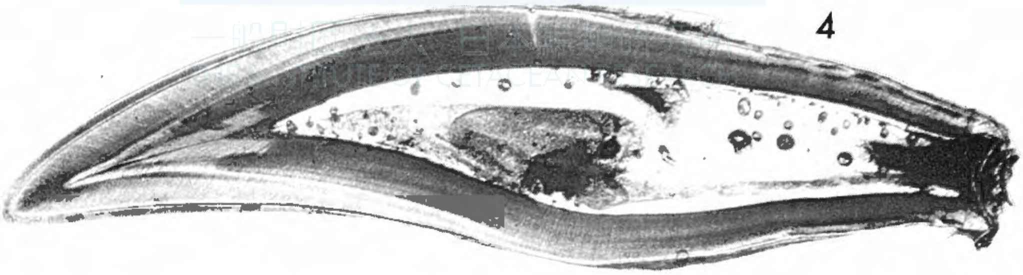
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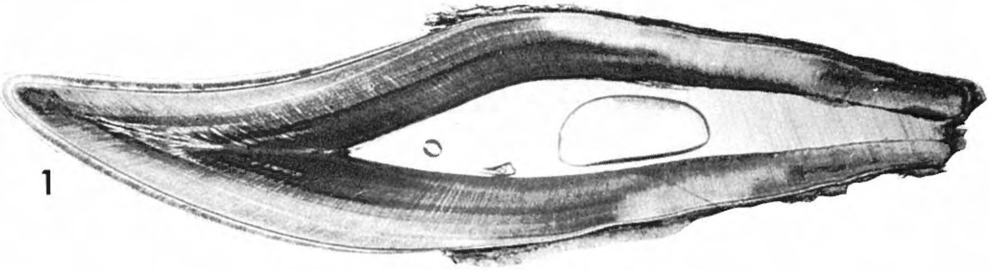

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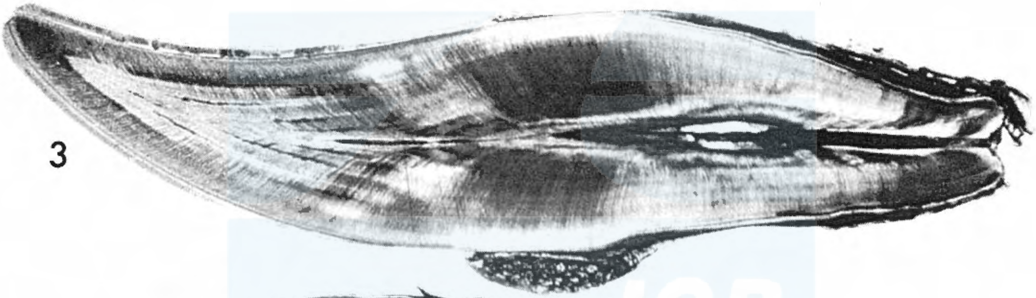

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