

GROWTH AND REPRODUCTION OF *STENELLA CAERULEOALBA* BASED ON THE AGE DETERMINATION BY MEANS OF DENTINAL GROWTH LAYERS

TOSHIO KASUYA*

ABSTRACT

Growth and reproduction of *Stenella caeruleoalba* caught on the Pacific coast of Japan in October to January were studied based on the annual growth layers in dentine. The mating seasons are in May and June, and in November and December. Calves are born after 12 months gestation at 100 cm in body length. They attain sexual maturity at 9 years at the lengths 212 cm in females and 220 cm in males, and physical maturity at 14 to 15 years at the lengths 222 cm in females and 236 cm in males. Lactation lasts about 1.5 years. Mean reproductive cycle is about 3 years or slightly less. Oestrous females assemble to form a school, which is retained at least for one reproductive cycle but can join with the schools in other growth and reproductive stages of both sexes.

INTRODUCTION

The dolphin fishing was formerly operated in the several villages along the coast of the Izu Peninsula, which situates in the Pacific coast of Japan (Japanese Fisheries Bureau 1900). But in most of these places this fishing was abolished before the world war II.

Though, until few years ago Arari on the west coast of the Izu Peninsula operated this fishing for *Stenella caeruleoalba* (Meyen, 1833) and other delphinids in spring season (Nishiwaki and Yagi 1953, Nishiwaki *et al.* 1965), the operation have recently ceased. At present, only Futo and Kawana on the east coast are cooperatively operating this fishing with several speed boats.

The fishing season for these two villages usually starts in the middle of October and closes in December, but few catches have been made in January and early October. The catches are mostly *Stenella caeruleoalba* with occasional catch of *Stenella attenuata* and other delphinids (Tobayama 1969). According to the private communication of Mr. N. Miyazaki, the mean annual catch of *Stenella caeruleoalba* in the both villages is about 4980 individuals in recent 3 seasons from 1968-'69 to 1970-'71, when the catch was regulated by the fishermen to control the market price.

The schools of *Stenella caeruleoalba* are found mostly in the waters off the south east to north coast of Oshima Island, and then chased into the Kawana harbor or the Futo harbor (Tobayama 1969). There are few catches in the west coast of the

* Ocean Research Institute, University of Tokyo, Tokyo.

island. As shown in Fig. 1, there is a strong inflow of warm water in the south east entrance of the Sagami Bay. The migration of this species in the Sagami Bay and its south east entrance seems to be related with this current.

This study was intended to obtain some informations on the growth and reproduction of *Stenella caeruleoalba* as a base of the population study.

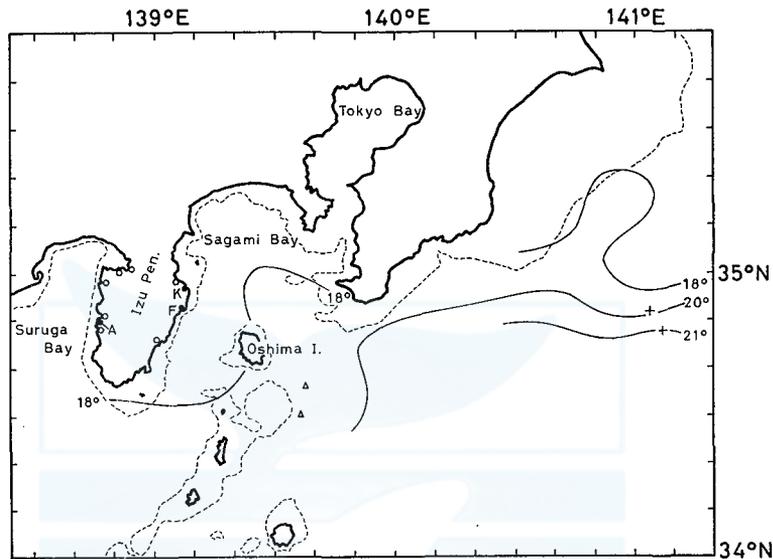


Fig. 1. Map showing the geography around Sagami Bay with the position of sighting of this species in Nov. 1971 (cross) and in Nov. 1970 (triangle). The surface isothermal line is based on the observation in November 1971. Dotted line indicates 200 m line of the depth. A indicates Arari, F Futo, K Kawana, and other white circles the position where dolphin fishing was formerly operated.

MATERIALS AND METHOD

Most of the materials used in this report were obtained from the 4 schools, schools A, B, F, and G in Table 1, processed at Kawana or Futo in 1967, '68, and '70.

School A, captured on 15 Nov. 1968 and processed at Futo, contained 1680 individuals, and 406 individuals were studied randomly. They were composed of newborn calves, juvenile, and mature individuals of both sexes, but lacking in the calves from 110 cm to 140 cm in body length. Fetuses from 5 cm to 105 cm in body length were observed.

School B was caught on 16 Nov. 1968 and processed at Kawana. Among 319 dolphins constituted this school, 318 were studied. This school was composed of juvenile and mature individuals of both sexes ranging from 160 cm to 255 cm in body length, with an exception of a calf of 100 cm. No pregnant female was observed.

School F, caught on 26 Nov. 1967 and processed on 28 Nov. at Kawana, was composed of about 3,300 individuals, among which only 146 were studied randomly. They were composed of newborn calves, juvenile and adult individuals ranging in

TABLE 1. SOME INFORMATIONS ON THE SCHOOL COMPOSITION OF *STENELLA CAERULEOALBA*

School no.	No. caught	No. ¹⁾ studied	Sex ratio (male, %)	Ratio in mature female (%)				Immaturity in females (%)	Date killed
				p	l	p&l	r		
A	1,680	406	31.3	41.1 ²⁾	47.7	0.5	10.7	18.1	16, 18, 22 Nov. '68
B	319	318	56.0	0	89.5	0	10.5	86.2	17 Nov. '68
C	330	38	—	—	—	—	—	—	21 Oct. '70
D	256	256	—	—	—	—	—	—	2 Dec. '70
E	2,000	125	—	—	—	—	—	—	22 Nov. '70
F	3,300	150	34.0	2.0	80.4	0	17.6	47.4	28 Nov. '67
G	330	84	41.7	23.3	63.3	0	13.3	31.3	14 Oct. '70
H	101	58	—	—	—	—	—	—	4 Oct. '71
I	—	22	—	—	—	—	—	—	19 Nov. '69

¹⁾ Fetus not included. ²⁾ 3 recently ovulated nonpregnant females included. P pregnant. L lactating. R resting. P&L pregnant and simultaneously lactating.

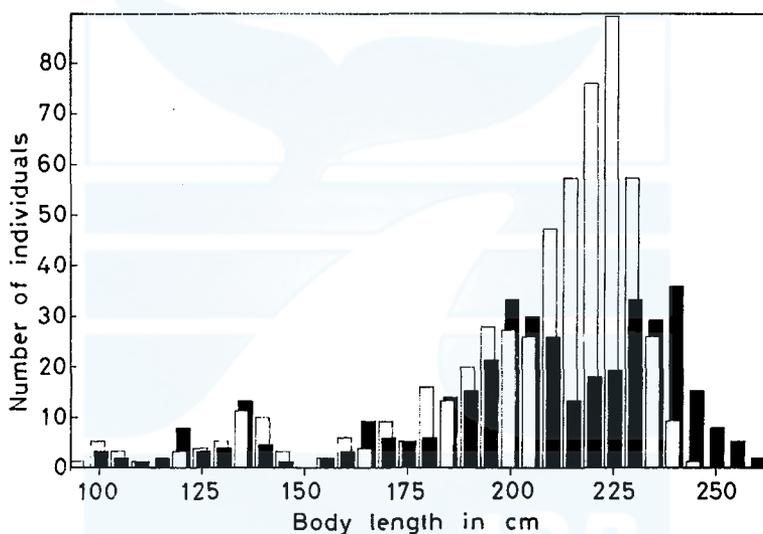


Fig. 2. Body length frequency of the materials used in this study, schools A, B, F and G are combined. Black indicates male and white female.

body length from 95 cm to 255 cm. But the dolphins of 150 cm to 195 cm were scarce. Only three fetuses were observed.

School G was captured on 12 Oct. 1970, and processed and studied on 14 Oct. Among 330 individuals constituted this school 84 individuals were studied randomly. They were composed of juvenile calves ranging from 100 cm to 130 cm and from 165 cm to 200 cm, and adult individuals of both sexes ranging from 210 cm to 260 cm in body length. Few fetuses were observed.

The body length was measured in each 1 cm interval in a straight line from the tip of upper jaw to the bottom of the notch of the tail flukes by two persons with a tape measure. When the length was analyzed, each body lengths were grouped into

the nearest 5 cm.

The mammary gland was observed in the field and classified into lactating and non-lactating. Ovaries were collected from all the adult females and from most of the immature females, and fixed with 10% formalin solution. The number of corpora albicantia and lutea was counted in the laboratory slicing the ovary into about 1 to 2 mm thickness. The both testis were collected from all the males and preserved with same manner as used for ovaries. The weight was measured in the laboratory. When a corpus luteum was observed in the ovary, the uterus was carefully searched for small embryo.

Several teeth were collected with a hammer and a chisel usually from the central part of the upper tooth row, and fixed with 10% formalin solution.

For preparing the tooth for age determination, at first the connective tissue was removed with nife, then its half side was ground off perpendiculary with stones of various granule. The polished surface was glued on a plastic board with synthetic resin, then the other side was polished with the same manner to a thickness from 50 to 70 μ . The growth layers in dentine were observed under transmitted light with binocular microscope ($\times 20$ — $\times 50$).

Other than the materials obtained from the schools A, B, F, and G, some tooth samples and biological data collected at Kawana, Futo, and Taiji ($33^{\circ}35'N$, $135^{\circ}55'E$) were presented by Dr. S. Ohsumi and Dr. K. Hirose. They are used in analyzing the growth curve. The informations on the body lengths of the fetuses and juvenile calves of the schools C, D, E, and H were offered by Mr. N. Miyazaki, and those of school I by Dr. K. Hirose. These body length frequencies are used in analyzing the reproduction of this species.

AGE DETERMINATION

The dentinal growth layers are used in this study as the age characteristics of *Stenella caeruleoalba*. In the dentine of this species, as shown in Pls. I and II, there are observed the layers of opaque and translucent dentine arranged alternately. Though, the thickness of the layer varies at the positions on a tooth, the thickest is the layer formed in the fetal stage. This fetal layer is usually composed of a opaque dentine. But sometimes there are observed one or two faint laminated structure, on which no study was conducted. Probably this will be a reflection of the physiological conditions of the mother which have affected the formation of the laminated dentine of the mother. Though there is a neonatal line between the fetal dentine and the postnatal dentine, this structure is inconspicuous in this species than in the sperm whale (Ohsumi *et al* 1963).

The structure, the thickness and translucency, of the postnatal dentine bounded on the neonatal line is variable between the animals. This will be related with the date of birth and the season when the alternation of the opaque and translucent layers occurs. There are usually observed one or two faint translucent layers in the thick opaque layer accumulated just after the birth. But this fine structure was not used for age determination, because it was not expected to show the annual accumula-

tion cycle.

The thickness of the postnatal layers decreases with the age of accumulation, especially the 7th or 8th and the latter layers are thinner. The dentine of about 15th or latter layers is composed of poorly calcified secondary dentine as in the case of *Globicephala melaena* (Sergeant 1962). It is possible to read the laminations in this secondary dentine with slight difficulty.

Though the boundary of opaque and translucent layers is usually not clear, there is no indication to consider that there is significant difference of the thickness between two layers.

Fig. 3 shows the seasonal change of the conditions of the newest dentinal growth layer in the tooth with 13 or less layers, in which the layer is not too thin to make the accurate observation. It is expected, from Fig. 3, that the alternation of dentinal layer from the opaque to the translucent occurs in from November to December.

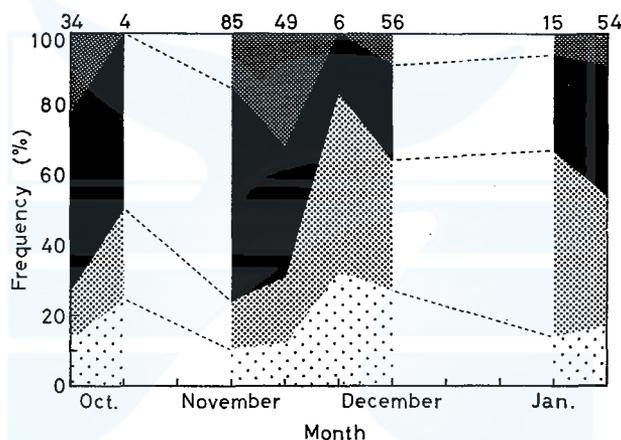


Fig. 3. The condition of the newest dentinal layers. The marks indicate thin opaque layer, thick opaque layer, thin translucent layer, and thick translucent layer (from top to bottom). The numbers at the top indicate the sample size. The dates of the kill are grouped into the 1st, 2nd, and 3rd decade of month.

In this study it is presumed that the opaque layer is accumulated in summer and the translucent in winter as in the case of *Physeter catodon* (Ohsumi *et al* 1963), *Tursiops truncatus* (Sergeant 1959), and *Globicephala melaena* (Sergeant 1962).

For determining the age of the dolphins, it was tentatively assumed that the opaque and translucent layers indicate the growth in 6 months respectively. And in the animals with the number of opaque layers 5 or less, the age was determined to each nearest 1/4 years considering the conditions and thickness of the oldest (formed just after birth) and the newest layer, in the animals with between 6 and 10 layers to nearest 1/2 years, and in the animals with more than 10 layers the number of the opaque layers was used as the approximate age of the animal.

GROWTH

Lengths and length frequencies

The length frequencies show characteristic features in each schools. This is considered to be resulted from the schooling behavior related with the maturity and reproductive cycle. Descriptions of the length frequencies of each schools are roughly made in the chapter of Materials and Method, and some discussions in the chapter of Reproduction.

When schools A, B, F, and G are combined, the smallest individual is found in the length group of 95 cm, the largest female in 245, and the largest male in 260 (Fig. 2). The highest frequency of the adult female is in the length group of 225 cm, and that of male probably in 240 cm. The length of the adult male seems to exceeds that of the female about 15 cm (see *Growth curve*).

No significant difference of length frequency between both sexes is observed in the animal smaller than 175 cm.

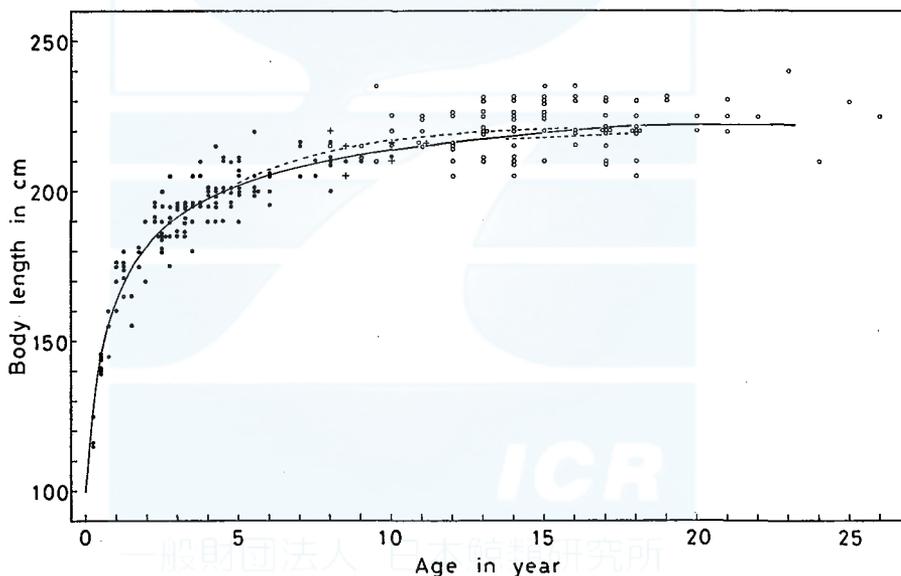


Fig. 4. The mean growth curve of the female. One dentinal layer corresponds to one year. Closed circle indicates immature female, open circle mature, and cross unknown. For explanation see text.

Growth curve

The relation between body length and the age in 218 females is shown in Fig. 4. The growth is characteristic in the rapid increase of the length in the first 2 years. The increase of the body length seems to stop at the age of 14 or 15 years. This age is considered to mean the time when most of the female individuals attain the physical maturity. As the mean body length of the 36 females at the age of 16 years or more is

222.4 cm, it is considered that the mean maximum body length attained by the female is approximately 222 cm. The age of oldest female was 26 years.

The mean growth curve shown by a solid line in Fig. 4 was drawn by eye, considering the mean body lengths in each ages. Based on this growth curve and the mean body length at birth obtained separately, it was tried to adapt the Bertalanffy's growth formula, $L(t) = a(1 - e^{-\beta t})$, using Walford's finite differences diagram. But it was impossible to adapt single growth formula for the mean growth curve of the female. For the growth of the first 2.5 years, the formula with the constances $a = 192.2$, $\alpha = -0.7350$, and $\beta = 1.1384$ fits perfectly. The growth curve at the age of 2.5 years or more can be calculated from the above diagram, the mean final length 222.4 cm, and $L(2.5) = 186.8$ of the former formula. This gives the constances $a = 222.4$, $\alpha = -1.1813$, and $\beta = 0.2601$, which is shown by the dotted line at the top in Fig. 4. These two formulae can be considered to represent approximately the mean growth curve of the female *Stenella caeruleoalba*. But the fitness of the latter formula is not good for the ages between 6 and 12 years. Another formula which fits better only to those ages is shown by the constances $a = 219.1$, $\alpha = -1.3026$, $\beta = 0.2445$, and shown by the dotted line at the bottom in Fig. 4.

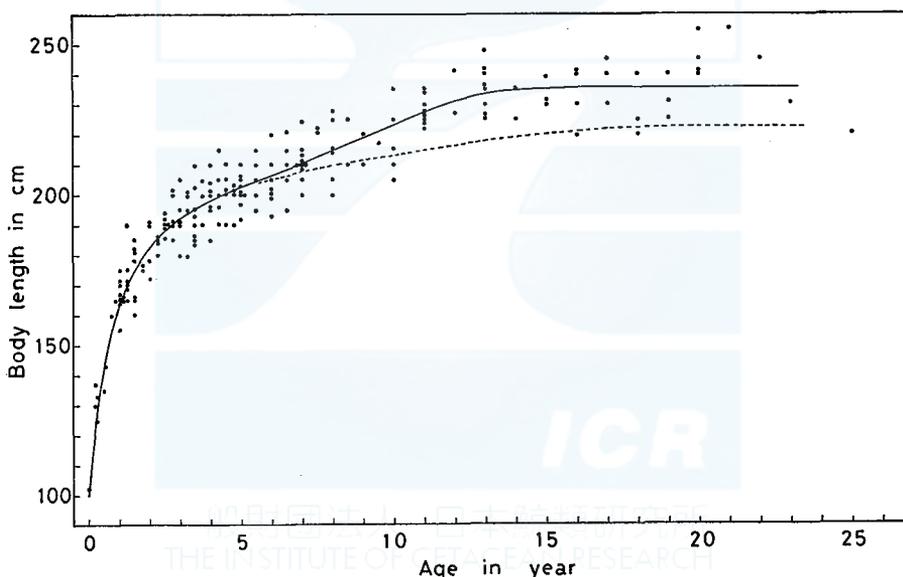


Fig. 5. The mean growth curve of the male. Solid line is drawn for male by eye. Dotted line is the female growth curve shown by the solid line in Fig. 4.

The relation between body length and age in 191 males is shown in Fig. 5. The line was drawn by eye. In the younger individuals the growth of the male is same with that of the female. The difference of the body length between both sexes appears at about 6th year. After this age the growth is rapid and attains the approximate length 230 cm at the age of 13 years. This rapid growth will probably related with the attainment of the sexual maturity, and resembles with that of the

male *Physeter catodon* (Nishiwaki *et al* 1958). But the growth does not continue so long period as the sperm whale. The physical maturity is considered from the growth curve to be attained at 14 or 15th year as in the case of the female. The mean body length of the males of 16 or more years old is 235.9 cm or approximately 236 cm, which is considered to be the mean maximum body length attained by the male. This length is 14 cm larger than that of the female, which coincides with the value expected from the body length frequency.

The age of the oldest male was 25 years.

Mean body length at birth

Because of the scarcity of the samples, the body length at birth was obtained combining the both sexes. This will not give erroneous result because there is observed no sexual dimorphism in the body length of the younger individuals.

The mean body length at birth was calculated from the body length frequencies of the large fetus and newborn calf. The data from the 4 schools, A, B, F and G were used for this purpose. The body lengths were grouped into each nearest 5 cm units. The largest fetus and the smallest calf were found in the length groups of 105 cm and 95 cm respectively. So the length frequencies in the length groups between 90 cm and 110 cm are considered here.

The numbers of calves and fetuses in the above range are 17 and 73 respectively, and the frequencies of both categories are equal in the length group 105 cm (Table 2). But there is a wide discrepancy between the total numbers of fetus and calf. As the cause of this phenomenon, it is possible to expect two reasons. One is related with the method of fishing in which a school of dolphins is chased for several hours to be driven into the harbor, during this chase some of newborn calves may be lost. The other less probable cause is the difference of the schooling behavior or segregation of the newborn calf and the mother.

TABLE 2. BODY LENGTH FREQUENCIES OF FETUSES AND CALVES

Body length (cm)	Fetus (no.)	Calf (no.)	Fetus (%)	Calf (%)	% of calf (corrected)
90	15	0	20.50	0	0
95	27	1	36.99	5.88	13.72
100	27	8	36.99	47.06	55.99
105	4	5	5.48	29.41	84.29
110	0	3	0	17.65	100
Total	73	17	100	100	50.00

Though the correctness of these possible presumptions are not proved in this study, the length frequencies were corrected to equalize the total numbers of fetus and calf. Then the ratios of the calf and the fetus were calculated in each length groups (Table 2). From this corrected percentage of the calf, the regression line $y = 5.411x - 490.3$ is obtained by the method of least squares, where y is the frequency of the calf in percentage and x is the body length in cm. The mean body length at birth, 99.8 cm, is obtained from this formula as the body length corresponding to the

frequency of 50% (Fig. 6). But when the accuracy of the measurement is considered, it is better to say that the mean body length at birth is 100 cm.

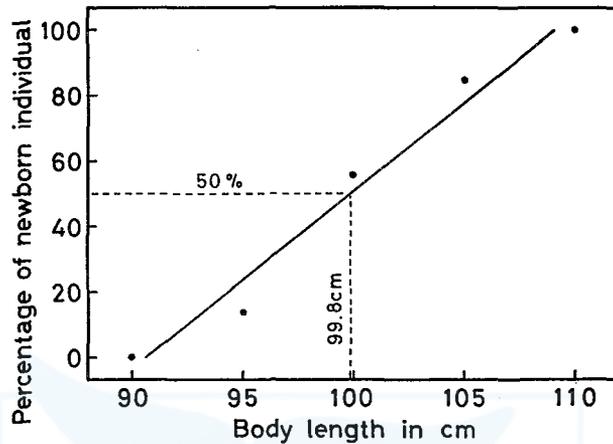


Fig. 6. Mean body length at birth, for explanation see text.

Age at the attainment of sexual maturity

In Table 3 the females with corpus luteum or albicans were identified as attained sexual maturity, and the animals of the age of 6.5, 7.5, 8.5, and 9.5 years were included into the age groups of 6, 7, 8, and 9 years respectively (see Materials and Method). The oldest immature female and the youngest mature female were found in the age groups of 10 years and 8 years respectively. As the materials are very few, and the ratio of the mature individual fluctuates too wide to obtain the regression line, another method was used to estimate the mean age at the attainment of sexual maturity.

At first step, the percentages of mature and immature animals were calculated in each age groups, then those of the immature animals were added from the older age groups to the younger, and those of the mature from the younger to the older. These accumulated percentages are shown in Fig. 7. The mean age of the female at the

TABLE 3. AGE FREQUENCIES OF IMMATURE AND MATURE ANIMALS OF BOTH SEXES

Age	No. of females		No. of males	
	immature	mature	immature	mature
6	2	0	8	0
7	2	0	8	1
8	8	1	4	0
9	1	4	1	2
10	1	2	1	2
11	0	3	2	5
12	0	7	0	1
Total	14	17	24	11

attainment of the sexual maturity is obtained in the figure as the point where two lines cross. This gives the age 8.8 years.

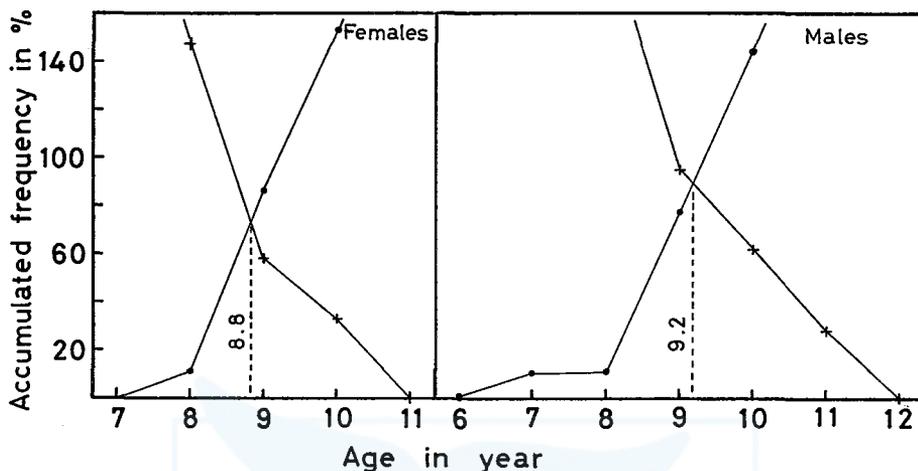


Fig. 7. Mean age at the attainment of sexual maturity. Circle indicates the frequency of mature individual, and cross the immature.

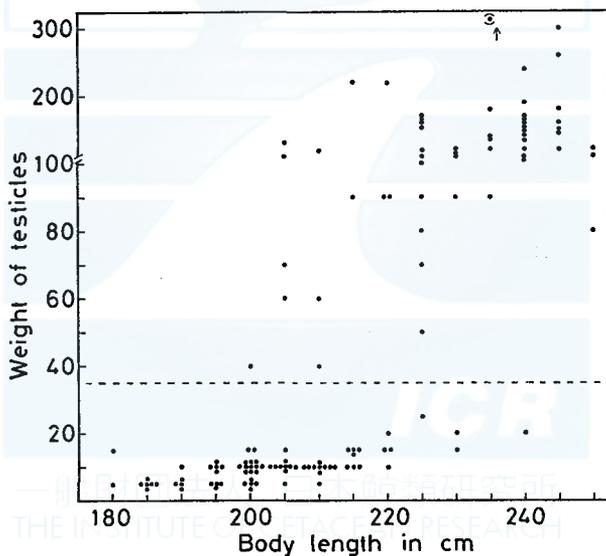


Fig. 8. Relation between body length and the weight of both testis. Dotted line indicates the mean weight at the attainment of sexual maturity used in this study.

Another estimation can be obtained from the relation between age and number of ovulations (Fig. 14), as the age when the number of ovulation is 1.0. The mean age of the female at the attainment of sexual maturity obtained by this method is 8.9 years. These two figures coincide well.

Fig. 8 shows the relation between body length and the combined weight of both testes. Hirose and Nishiwaki (1971) showed with similar materials used in this study

that the testes of more than 40 g are mature. Though they did not give the mean weight of testis at the attainment of sexual maturity, it is considered to be between 30 g and 40 g. In the present study the testis with 35 g or more in combined weight were considered to be sexually mature.

In the males, the oldest immature animal and the youngest mature were found in the age of 11 and 7 years respectively. The mean age of the male at the attainment of sexual maturity, obtained by the same procedure used in the female, is 9.2 years (Fig. 7).

At present there is no reason to consider that the difference of the ages of the both sexes at the attainment of sexual maturity is significant. And the best estimation for both sexes seems to be the age of 9 years.

The mean body lengths at the age of 9 years obtained on the mean growth curve are 212 cm for female, and 219 cm for male.

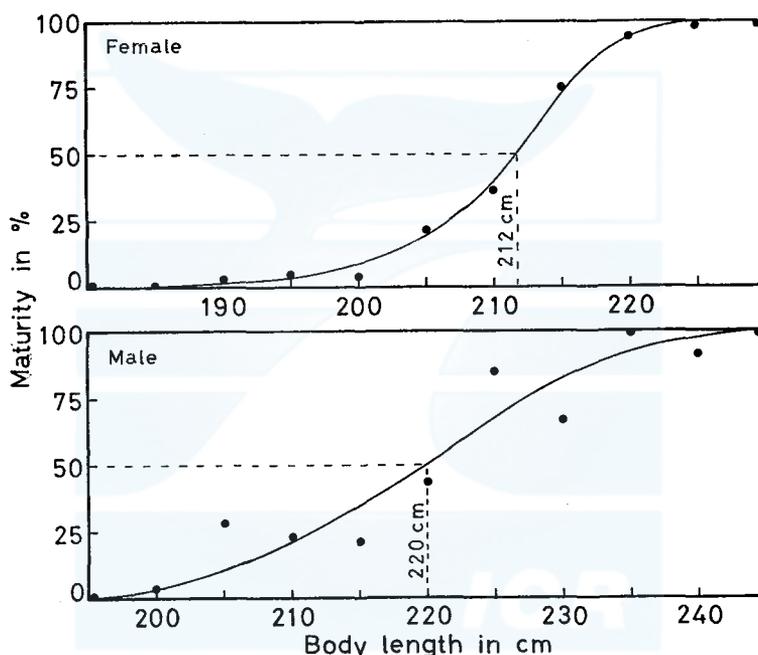


Fig. 9. The body lengths where 50% of individuals are sexually mature. Lines are drawn by eye.

Body length at the attainment of sexual maturity

The ranges between the largest immature individual and the smallest mature are from 190 cm to 220 cm for females, and from 200 cm to 240 cm for males.

The mean body length at the attainment of the sexual maturity was obtained directly from the ratio of the matured individuals in each length groups.

Fig. 9 is based on the 640 immature females and 604 mature females, and 53 immature males and 46 mature males. On the regression lines in Fig. 9, the length where 50% of individuals are sexually mature is 212 cm for females, and 220 cm for

males. These figures coincide well with those obtained from the mean age at the attainment of sexual maturity and the mean growth curve.

REPRODUCTION

Sex ratio

Table 4 shows the sex ratios in 4 schools caught at Kawana or Futo, and that of

TABLE 4. SEX RATIO IN PRENATAL AND POSTNATAL INDIVIDUALS, SHOWN BY THE NUMBER OF FEMALES PER 100 MALES

School	Prenatal		Postnatal			
	male	female	male	female	total	sex ratio
A	53	53	127	279	406	219.6
B	0	0	178	140	319	78.6
F	1	1	51	99	150	194.1
G	4	3	35	48	83	172.9
Taiji specimens	0	0	51	40	91	78.4
Total no.	58	57	442	606	1,048	137.1
Sex ratio	100	98.2	100	137.1	—	—

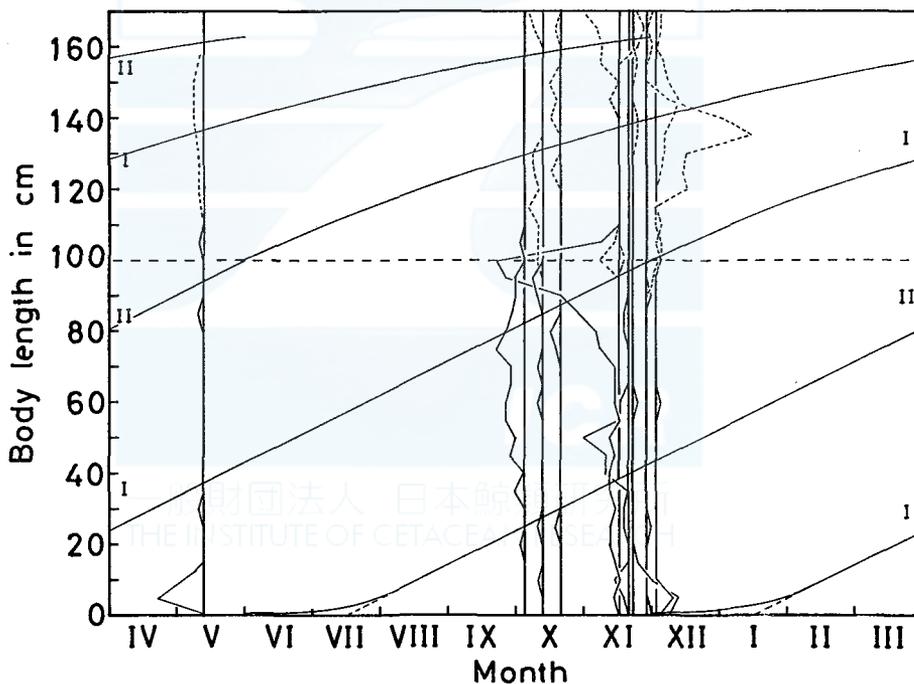


Fig. 10. Body length frequency of the fetus (solid line) and juvenile calf (dotted line). One month interval means 15 individuals. The growth curve of the fetus was drawn presuming 12 month of gestation, and that of calf is based on the growth formula. I is started on the 1st of June and II on the 1st of December. The school D, F, E, I, B (right side, no fetus) and A (left side), C, G, and H are plotted against the date of the catch (from right to left). A school in May is cited from Nishiwaki and Yagi (1953).

the catch off Taiji in January 1969. The ratio is shown by the number of females per 100 males. The Taiji specimens were caught with hand harpoons from various schools and studied by Dr. K. Hirose.

These data show that the sex ratio of the postnatal individuals varies in each schools. This will probably be related with the characteristic schooling behavior concerning the sexual conditions of the animal, and will not show the real sex ratio in the population. The number of both sexes in fetuses is considered to be nearly equal, and no uneven sex ratio is suggested.

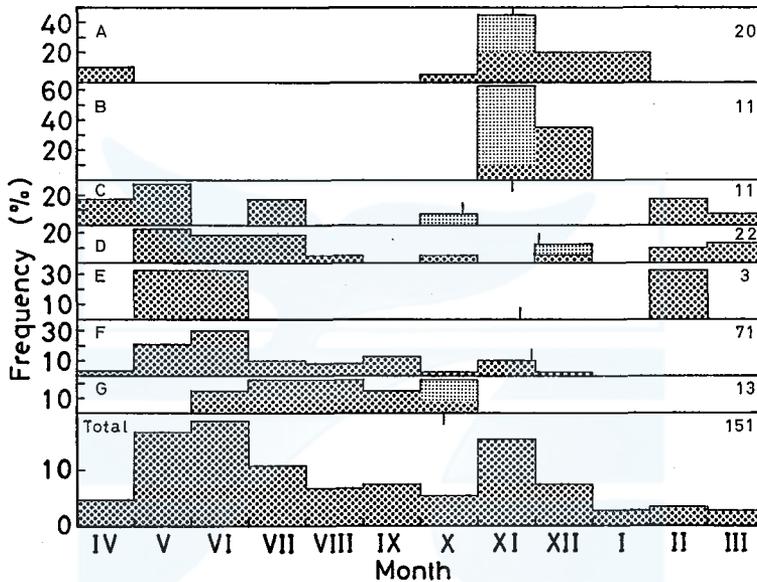


Fig. 11. Frequency of the date of birth of the one year or younger individuals of both sexes calculated with the growth formula. Square with smaller dots indicates the individuals born 12 months prior to the date of catch. The numbers in the right indicate the sample size, and the vertical rod the date of catch.

Parturition season

As there are observed many full termed fetuses and newborn calves in the schools caught in November and December (Fig. 10), this season seems to be at least a part of one of the parturition seasons of *Stenella caeruleoalba*.

Fig. 11 shows the frequency of the parturition inferred with the growth formula, the date of catch, and the body length of juvenile calf of 165 cm or less which is considered to contain one year old calves and all the younger individuals. It is seen in this figure that, though some parturitions may occur in any season of the year, this species have two peaks of parturition one in May and June, and the other in November and December. In this figure, the autumn peaks is smaller than the spring peak. But it will not be necessary to think that the autumn peak is smaller than the other, because the frequency of the date of birth inferred from the length

and date of kill with fetal growth curve shows the reversal pattern (Fig. 12).

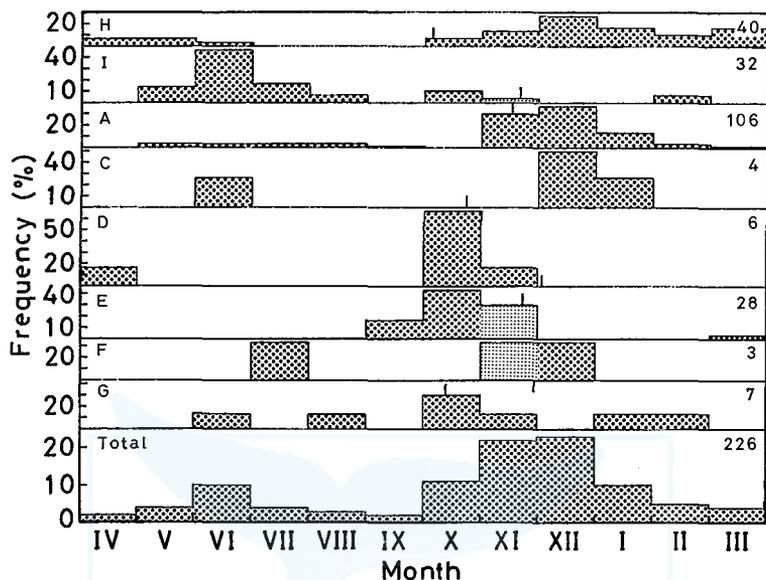


Fig. 12. Frequency of the expected date of birth calculated with the growth curve of fetus. Square with smaller dots indicates the fetuses expected to have been born 12 month after the date of catch. The numbers at the right indicate the sample size, and the vertical rod date of catch.

Mating season

Many small embryos are observed in the females caught in November and December (Figs. 10 and 13). In these figures the smallest length group includes the embryos smaller than 2.5 cm, which range is a half of the width of the length range of 5 cm applied to larger fetuses. Accordingly the height of the frequency of the smallest group must be doubled to compare the relative abundance with that of the larger length groups. Then it reveals that the relative abundance of the fetuses of 2.5 cm or less in body length is higher than that of the next length group.

This will indicate that the beginning of the mating season is at slightly prior to November, and the newly impregnated females are still increasing in November and December. Accordingly it is reasonable to consider that one of the mating seasons is in November and December. As this season coincides with the autumn parturition season, another mating season in May and June is expected. This is supported by the existence of small embryos, 10 fetuses under 10 cm, in a school caught in May at Arari (Nishiwaki and Yagi 1953, referred in Fig. 10 of this report).

Length of gestation

As the sampling period is restricted to October, November, and early December, it is impossible to follow the seasonal increase of the body length of the fetuses to pre-

sume the gestation period and the growth of fetus.

But it can be presumed from the seasons of mating and parturition, and body length frequency of the fetus. As mentioned above, both peaks of mating and parturition are in spring and autumn with the interval of 6 months, then the approximate length of gestation must be a multiple of 6 months. On the other hand, there are observed three peaks in the fetal length frequency in autumn season (Fig. 13).

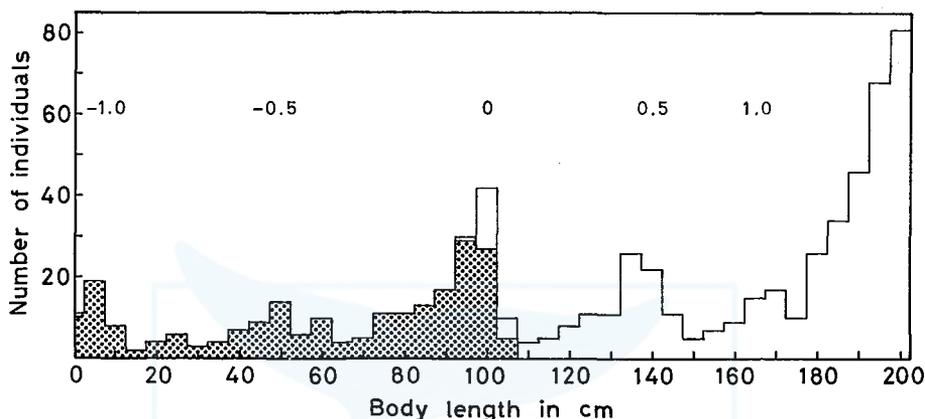


Fig. 13. Body length frequency of the fetus (dotted area) and juvenile calf (white area) in the catch of October to December. Figures at the top indicate approximate age shown by the year from the birth. Schools A to I are combined.

The smallest peak is composed of the newly impregnated fetuses, the largest of the full termed fetuses, and the median of the fetuses impregnated in the preceding season. If the length of gestation period is 18 months or more, there must be observed 4 or more peaks, which is inconsistent with the above observation. Accordingly the gestation period of *Stenella caeruleoalba* is presumed to be about 12 months.

The mean fetal growth curve in Fig. 10 is drawn based on the above gestation period using the method of Laws (1959). $0.13 \times$ Gestation period is tentatively used here for Lt_0 of Laws (1959), which is the time when the extended straight line of the fetal growth cuts the axis of time. The starts of gestation are put at the 1st of December (growth curve I) and at the 1st of June (growth curve II). The growth curve of the calf is based on the growth formula.

Fig. 12 shows the frequency of the date of birth inferred with the fetal growth curve, from the length frequency of the fetus and the date of kill. There are two parturition seasons one in June and the other in November and December. This result coincides well with the parturition frequency obtained independently (Fig. 11). It is interesting that the shapes of the autumn parturition peak in Fig. 12 and that of spring parturition peak in Fig. 11 are similar and the highest peaks are in December and June respectively. This will indicate that the frequency of parturition is slightly higher in December and June than in the preceding months, and will support the correctness of the presumed gestation period of 12 months.

For the comparison, the frequency of parturition was calculated on the as-

sumption of the gestation of 11 months and that of 13 months. When 11 months gestation and $0.18 \times \text{Gestation period for } Lt_0$ are assumed, the spring parturition peak is in April. And when gestation of 13 months and $0.13 \times \text{Gestation period for } Lt_0$ are assumed, the spring peak is in the range from April to June with the highest in May. These results do not fit to that obtained from the length frequencies of the juvenile calves.

Length of lactation

In this study the direct information indicating the length of suckling period was not obtained, because no stomach content was studied. But it is expected that the calf starts feeding on food before the age of 0.5 year, because most of the teeth except those in the anterior and posterior regions of the tooth row have erupted in all the individuals of that age.

The length of lactation was estimated from the number of lactating females and that of juvenile individuals caught together. There are observed several peaks in the body length frequencies of each schools. The peaks of the younger individuals are considered to represent the individuals born in some particular parturition seasons, and their approximate age can be presumed from the body length at the mode of frequency. The peak at 100 cm (schools A, B, and F) is considered to be composed of individuals born in the autumn season when they were caught, and that at 165 cm (schools A and B) is of the dolphins about 1 year old. The peaks at 120 cm (school F) and at 115 cm (school G) will have been born about 1/4 year before the catch, and that at 140 cm about 1/2 year before, and that at 170 cm about 1 1/4 years before the catch.

TABLE 5. LENGTH FREQUENCIES OF THE JUVENILE INDIVIDUALS, THEIR APPROXIMATE AGE, AND NUMBER OF LACTATING FEMALES.

School	Length frequency (cm)				Number of lactating females
	Range	Mode	Age	Number	
A	100-105	100	0	5	94
	145-170	165	1	23	
	175-190	185	2	7	
	200-		7+	244	
B	100	100	0	1	17
	160-170	165	1	14	
	175-215	200	2, 2+	245	
	220-			60	
F	95-110	105	0	9	41
	115-125	120	1/4	15	
	130-145	140	1/2	46	
	160-175	170	1 1/4	3	
	185-		4+	77	
G	100-130	115	1/4	11	19
	165-180	170	1 1/4	7	
	195-		4+	54	

The number of the lactating females nearly coincides with that of calves younger than 1 1/4 years old (schools B and G). The number of 2 years and older calves caught together with the lactating females is very few comparing with that of the younger individuals.

The school A was caught on 15 Nov. 1968, and the members were killed on 16, 18, and 22 Nov. when I had a chance to study some of them, but I had no chance to study many dead individuals picked up daily from the harbor and sold. The ratio of the suckling calf may have been higher in these dead individuals which I missed to study. This will be the reason of the low frequency of the juvenile calves in the sample compared with the lactating females. The quite reverse case is found in the school F. This school was caught on 26 Nov. 1967, and I studied on 28 Nov. only the carcasses of the dolphins which had died in the water and picked up. In this school, the number of juvenile calves is higher than that of the lactating females. But even in these schools, A and F, it can be suggested that the 2 years old calves are rarely accompanied by the lactating mother.

The lactating females are divided into two groups by the size of the largest corpus albicans (Hirose *et al* 1970). The Futo school and Kawana school in Hirose *et al* (1970) correspond to the school A and B of Table 1 respectively. Probably the lactating females with larger corpus albicans, which is few in number, will be the mothers of newborn calves, and those with the smaller the mothers of the calves of the ages from 1.0 to 1 1/4 years old.

As the conclusion of above discussions, it can be said that lactation lasts at least for 1 1/4 years, and probably for about 1.5 years as in the case of *Tursiops truncatus* (Tabolga and Essapian 1957, Nakajima *et al* 1963), but rarely for 2.0 years. The calves which have started feeding on food by the age of about 0.5 year, will continue to take both food and milk until the age of about 1.5 years.

Female reproductive cycle

As the females lactating and simultaneously pregnant are very rare in the catch and the recently ovulated nonpregnant 3 females were not lactating (Table 1), most of the female seems not to ovulate in the period of lactation.

Between schools, there is wide variation of the ratio of the resting females, in which all the mature females other than the pregnant or lactating are included. But it may be approximately between 10.5 and 17.6% of the total number of the mature females (Table 1). If this ratio is compared with the total of the length of gestation (1 year) and length of lactation (about 1.5 years and surely more than 1 1/4 years), the average resting period of between 0.29 and 0.53 year (in case of 1.5 years lactation), or between 0.26 and 0.48 years (in case of less probable 1 1/4 years lactation) is obtained.

Accordingly the probable mean reproductive cycle of the female is presumed to be about 3 years or slightly less (gestation 1, lactation 1.5, resting from 0.3 to 0.5 year). This means that some females are impregnated in the same mating season when they have weaned the calves, and most of the females in the next mating season.

In this species the corpus albicans probably remain in the ovary all through its life (Fig. 14). The mean annual accumulation rate of the corpus albicans and luteum

is 0.69, and the lowest and the highest accumulation rates are 0.25 and 1.6 respectively. To explain the mean accumulation rate and the mean reproductive cycle, there must be expected about two ovulations in one reproductive cycle (Table 6). But as indicated by the lowest accumulation rate, there must be few females which stay anoestrus for 3 years after giving birth to the calves and show the reproductive cycle of 4 years.

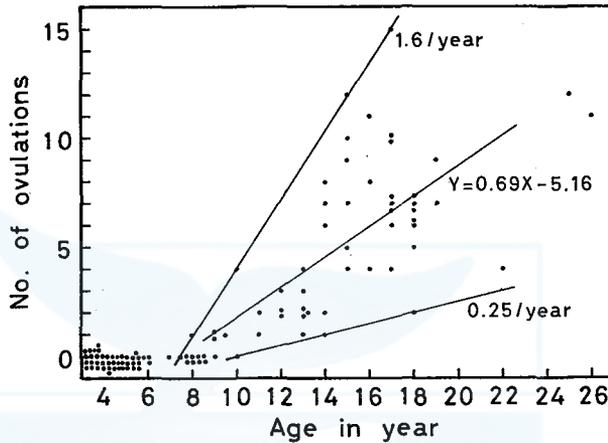


Fig. 14. Relation between age and the number of corpora albicantia and luteum. The regression line is calculated by the method of least squares, and the highest and lowest ranges are drawn by eye.

TABLE 6. MEAN ANNUAL OVULATION RATE CALCULATED FROM THE ASSUMED REPRODUCTIVE CYCLE AND NUMBER OF OVULATIONS IN A CYCLE.

Preg- nant (year)	Lactat- ing (year)	Rest- ing (year)	Reproductive cycle (year)	Number of ovulations					
				1	2	3	4	5	6
1	1.25	0	2.25	0.44	0.89	1.33	—	—	—
1	1.25	0.26	2.51	0.40	0.80	1.20	1.59	—	—
1	1.25	0.48	2.73	0.37	0.73	1.10	1.47	—	—
1	1.25	1.75	4.00	0.25	0.50	0.75	1.00	1.25	1.50
1	1.50	0	2.50	0.40	0.80	1.20	1.60	—	—
1	1.50	0.29	2.79	0.36	0.72	1.08	1.43	—	—
1	1.50	0.53	3.03	0.33	0.66	0.99	1.32	—	—
1	1.50	1.50	4.00	0.25	0.50	0.75	1.00	1.25	1.50

Reproductive cycle and school

Fig. 15 shows the frequencies of the date of conception inferred with the mean growth curves of fetus and juvenile individual. The materials include all the fetus and the calves smaller than 165 cm in body length. It is sure in the preceding discussion that these calves are still accompanied by the mother. The frequencies of conception calculated from the calves are shown by white area, and those calculated

from the fetuses are shown by dotted area. The height of the highest peaks of the both frequencies in each schools are modified to be equal.

When schools are seen from the date of the conception of the fetus, the schools are grouped into two patterns. One includes the schools in which the fetuses are mostly composed of the autumn fetus (fertilized in autumn mating season), and the other the schools in which the fetuses are mostly composed of the spring fetus. The schools A, C, D, E, G, and H belong to the former, and school I to the latter. Because of the scarcity of materials it is impossible to classify the school F. The school B did not contain the pregnant female.

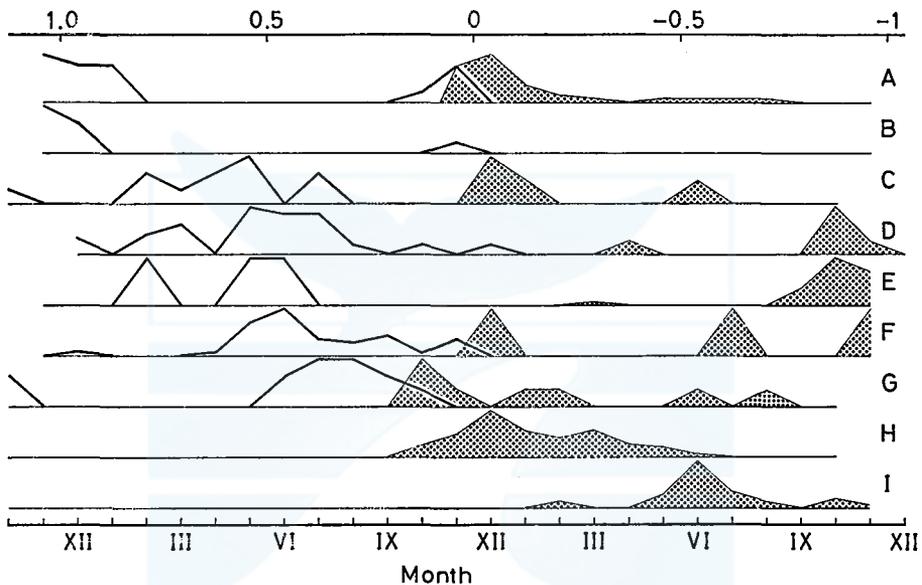


Fig. 15. Frequency of the date of conception of the fetus and calf smaller than 165 cm in body length, calculated by the growth curve. Figures at the top indicate the approximate age of samples at the time of catch. Dotted area indicates the fetuses and the white area calves. For further explanation see text.

Similar classification is possible by the date of conception of the juvenile calves. The calves in schools A and B are mostly composed of the autumn calf (fertilized and born in the autumn season), and those of the schools C, D, E, and F are mostly composed of spring calf. The school G shows the intermediate pattern.

There is observed various combinations between the fertilized date of calves and that of fetuses in the same school. In the school B only calves are observed, in the school A autumn calves and autumn fetuses are observed in one year interval, in the school C mostly spring calves and autumn fetuses in half year interval, in the schools D and E spring calves and autumn fetuses with about 1.5 year interval. In the school F the sample of fetus is too few to conclude, but probably it belongs to the same type with the school D. In the school G the larger fetuses and smaller calves seems to belong to one continuous mating season which slightly deviates from the

typical mating season, and there is also observed few fertilizations in half year intervals at both sides of the main peak. In the schools H and I, there is observed no calves smaller than 190 cm and 205 cm respectively. These observation lead me to the following hypothesis on the behavior of the mature female.

The oestrous females may assemble together in a mating season, and will be impregnated. This stage is observed in the schools H and I. The school thus formed is expected to be the base of other complicated schools, when seen only from the side of mature females. This connection of the females will be retained through the period of lactation and at least until the next oestrous cycle. This stage is seen in the school B. Then the females will reconstruct the school in accordance with the stage of the reproductive cycle. This is the reason why there is observed a peculiarity of the season of the conception of calf or fetus in each schools. All the other schools may have been formed as the result of sporadic annexation of the schools of pregnant females and that of lactating females in various stage of reproductive cycle. No special affinity between the original schools related with the size of calf and that of fetus is expected. The annexation between the lactating schools, or between the pregnant schools is not denied.

The schooling behaviors of the immature individuals of both sexes and of mature males are not well studied. If the males of 220 cm or more in body length are tentatively classified into mature, the numbers of mature males in the schools A, B, F, and G are 93, 41, 11, and 18, or 64.1%, 24.2%, 21.6%, and 54.6% of mature females (212 cm or more in length) respectively. It is considered that numerous mature males are found together with the mature females. There is an example of the school composed of immature individuals. This school, composed of about 600 individuals, was caught on 14 Dec. 1971, and random investigation was made on 303 animals by me and Mr. N. Miyazaki. Among these dolphins, all the 66 females were sexually immature and only 6 males in 237 males had testes weighed more than mean testes weight at the attainment of sexual maturity applied in this study.

Though there are observed many spring calves and autumn fetuses, the number of spring fetus is scarce in the present materials (Fig. 13). This may suggest the presence of the segregation of females related with the reproductive cycle. But further confirmation is needed on this problem.

DISCUSSION

There have been published two contrary opinions on the accumulation rate of the dentinal growth layers. Sergeant (1959, 1962) showed on *Tursiops truncatus* and *Globicephala melaena* that one opaque and one clear (translucent) layer are accumulated annually, and that the former in summer and the latter in winter. Similar conclusion was obtained on *Physeter catodon* by Ohsumi *et al* (1963), But Gambell and Grzegorzewska (1967) on *Physeter catodon*, Brodie (1969, 1971) on *Delphinapterus leucas*, and Kleinenberg and Klevezal (1962, cited in Brodie 1969) on *Delphinus delphis* considered that two layers are accumulated annually.

However, as indicated by Sergeant (1962), Ohsumi *et al* (1963), and Brodie

(1969) there are observed several fine layers in one dentinal growth layer. Especially in case of the young sperm whale, one growth layer of Ohsumi *et al* (1963) is usually composed of two parallel layers. Similar one or two vague layers are also observed in the 1st layer of *Stenella caeruleoalba*.

I consider that the above mentioned contravention on the accumulation rate of dentinal layers may be mostly caused by the different interpretation of the fine structure of the layer. It will be most necessary, at present, to establish the standards suited for each species, and then define the accumulation rates in each species.

According to the observation on the several western Pacific *Tursiops truncatus* born in an aquarium, the body lengths at the ages of 0.5, 1.0, and 2.0 years are 133 %, 155 %, and 185 % of the length at birth respectively (Nakajima *et al* 1963). In the Atlantic *T. truncatus*, the similar figure at the age of 7 or 8 months is 160 % (Essapian 1953). These figures coincide well with the growth of *Stenella caeruleoalba* presumed in this study, and suggest the correctness of my interpretation of the dentinal growth layers.

In *Stenella caeruleoalba*, the sexual maturity is attained in the 9th year in both sexes as in the case of *Physeter catodon* (Nishiwaki *et al* 1958, Ohsumi *et al* 1963). But in *Globicephala melaena* (Sergeant 1962) and *Delphinapterus leucas* (Brodie 1971), the mean age of the female at the attainment of sexual maturity is from 4 to 6 years, which is about half of that of the male. Further study is desired to have a conclusion if this result reflects the real growth of these species, or simply resulted from the different interpretation of the dentinal layers.

The mating season of *Stenella caeruleoalba* is peculiar in the possession of bimodal peaks. In the northern species, *Physeter catodon* has a mating season in April (Ohsumi 1965), *Delphinapterus leucas* in April and May (Laws 1959, Brodie 1971), *Globicephala melaena* in April and May (Sergeant 1962), *Phocoena phocoena* in from July to August (Laws 1959, Fisher 1970, Møhl-Hansen 1954). The mating seasons of the former 3 species nearly coincides with the spring peak of *Stenella caeruleoalba*, but the mating season of *Phocoena phocoena* situates in the summer, or at the intermediate season of the spring and autumn peaks of *Stenella caeruleoalba*.

With the relation of the various lengths of gestation period, the parturition seasons are in August in northern *Physeter catodon* (Ohsumi 1965), in June (Laws 1959) or in July and August (Brodie 1971) in *Delphinapterus leucas*, in August in *Globicephala melaena* (Sergeant 1962), and in July (Laws 1959) or in June and July (Fisher 1970) in *Phocoena phocoena*.

These informations are obtained, with one exception of *Physeter catodon*, from the species in colder waters. In these species the mating season and the length of gestation will have been adapted to put the parturition season in the northern summer or late spring, when the environment is better for newborn calves. However, *Stenella caeruleoalba* is considered to distribute, in the western Pacific, in warmer waters (Kasuya 1971, Kasuya and Oguro 1972), and not to migrate north of the northern boundary of the Japan current. Therefore it will not be an important factor for this species to give birth to the calves in summer season. This will have a relation with the existence of the two parturition season in *Stenella caeruleoalba*.

Tursiops truncatus in captivity had the gestation period of about 12 months and nursing period of 18 months (Tavolga and Essapian 1957), or nursing period of 16 months (Nakajima *et al* 1963). These figures show good coincidence with that obtained in *Stenella caeruleoalba*.

Ohsumi (1971) reported a hypothesis on the structure of the school of *Physeter catodon*. There are several structural differences between the school of *Stenella caeruleoalba* and that of *P. catodon*. One is the continuity of the members in the school of mature female of *Physeter catodon*. If this exists in the school of *Stenella caeruleoalba*, it is reasonable to expect the spring fetus and autumn fetus in same frequency in one school. This was not observed in the present study and the continuity, in the strict sense, of the members in nursing school can not be expected in *Stenella caeruleoalba*. Other characteristic features of the school of *Stenella caeruleoalba* are the larger size of the school and the larger number of the mature males found together with the mature females. The juvenile school is observed in *Stenella caeruleoalba* as in the cases of *Physeter catodon* (Ohsumi 1971) and *Globicephala melaena* (Sergeant 1962).

Perrin (1969) considered the between-school differences in coloration detected in *Stenella graffmani* to suggest the generic entities of the school of this species. This is inconsistent with the informations on the schooling behavior of *Stenella caeruleoalba* obtained in this study.

ACKNOWLEDGMENTS

Sincere thanks are due to Dr. S. Ohsumi of The Far Seas Fisheries Research Laboratory, Dr. K. Hirose and Mr. N. Miyazaki of The Ocean Research Institute, University of Tokyo, who offered the tooth samples and many biological informations.

Dr. T. Kajihara and Dr. M. Nishiwaki of The Ocean Research Institute are acknowledged for their cooperation and the valuable suggestions.

REFERENCES

- BRODIE, P. F., 1969. Mandibular layering in *Delphinapterus leucas* and age determination. *Nature*, 221: 956-958.
- BRODIE, P. F., 1971. A reconsideration of aspect of growth, reproduction, and behavior of the white whale (*Delphinapterus leucas*), with reference to the Cumberland Sound, Baffin Island, population. *J. Fish. Res. Board of Canada*, 28(9): 1309-1318.
- ESSAPIAN, F. S., 1953. The birth and growth of a porpoise. *Natural History*, 62(9): 392-399.
- FISHER, H. D., 1970. Reproduction in the common porpoise (*Phocoena phocoena*) of the North Atlantic. *J. Zool.*, 161: 471-486.
- GAMBELL, R., and C. GRZEGORZEWSKA, 1967. The rate of lamina formation in sperm whale teeth. *Norsk Hvalfangst-tid.*, 56(6): 117-121.
- HIROSE, K., T. KASUYA, T. KAZIHARA, and M. NISHIWAKI, 1970. Biological study of the corpus luteum and the corpus albicans of blue white dolphin (*Stenella caeruleoalba*). *J. Mamm. Soc. Japan*, 5(1): 33-39.
- HIROSE, K., and M. NISHIWAKI, 1971. Biological study on the testis of blue white dolphin, *Stenella caeruleoalba*. *J. Mamm. Soc. Japan*, 5(3): 91-98.
- JAPANESE FISHERIES BUREAU, 1900. *Nihon suisan hosaishi (Fishing in Japan)*. Suisan Shoin, Tokyo. vol. 1, pp. 424. (in Japanese).
- KASUYA, T., and N. OGURO, 1972. A new tagging method of dolphins. *Sci. Rep. Whales Res. Inst.*, 23: 81-85.

- LAWSON, R. M., 1959. The foetal growth of whales with special reference to the fin whale *Balaenoptera physalus* L. *Discovery Rep.*, 29 : 281-308.
- MØHL-HANSEN, U., 1954. Investigations on reproduction and growth of the porpoise (*Phocoena phocoena* L.) from the Baltic. *Vidensk. Medd. fra Dansk naturh. Foren.*, 116 : 369-396.
- NAKAJIMA, M., K. TAKAHASHI, M. OGURA, and K. SAWAURA, 1963. On the growth of infants of the small size toothed whales. *J. Jap. Ass. Zool. Gardens and Aquarium*, 5(1) : 16-22. (in Japanese).
- NISHIWAKI, M., T. HIBIYA, and S. OHSUMI (KIMURA), 1958. Age study of sperm whale based on reading of tooth laminations. *Sci. Rep. Whales Res. Inst.*, 13 : 135-153.
- NISHIWAKI, M., M. NAKAJIMA, and T. KAMIYA, 1965. A rare species of dolphin (*Stenella attenuata*) from Arari, Japan. *Sci. Rep. Whales Res. Inst.*, 19 : 53-64.
- NISHIWAKI, M., and T. YAGI, 1953. On the growth of teeth in a dolphin (*Prodelphinus caeruleoalba*) (I). *Sci. Rep. Whales Res. Inst.*, 8 : 133-146.
- OHSUMI, S., 1965. Reproduction of the sperm whale in the northwest Pacific. *Sci. Rep. Whales Res. Inst.*, 19 : 1-35.
- OHSUMI, S., 1971. Some investigations on the school structure of sperm whale. *Sci. Rep. Whales Res. Inst.*, 23 : 1-25.
- OHSUMI, S., T. KASUYA, and M. NISHIWAKI, 1963. The accumulation rate of dentinal growth layers in the maxillary tooth of the sperm whale. *Sci. Rep. Whales Res. Inst.*, 17 : 15-35.
- PERRIN, W. F., 1969. Color pattern of the eastern Pacific spotted porpoise *Stenella graffmani* Lönnberg (Cetacea, Delphinidae). *Zoologica*, 54(4) : 135-151.
- SERGEANT, D. E., 1959. Age determination in odontoceti whales from dentinal growth layers. *Norsk Hvalfangst-tid.*, 48(6) : 273-288.
- SERGEANT, D. E., 1962. The biology of the pilot or pothead whale *Globicephala melaena* (Trail) in Newfoundland waters. *Bull. Fisheries Res. Board of Canada*, 132 : 1-84.
- TABOLGA, M. C., and F. S. ESSAPIAN, 1957. The behavior of the bottle-nosed dolphin (*Tursiops truncatus*) : mating, pregnancy, parturition, and mother-infant behavior. *Zoologica*, 42(1) : 11-31.
- TOBAYAMA, T., 1969. School size and its fluctuation in the catch of *Stenella caeruleoalba* in Sagami Bay. *Geiken Tsushin*, 217 : 109-119. (in Japanese).

EXPLANATION OF PLATES

In all the figures the contrast is reversed, or translucent layer is seen dark and opaque layer light.

PLATE I

- Fig. 1. Thin ground section of tooth of 92 cm fetus.
- Fig. 2. Thin ground section of tooth of a female, 116 cm, 1/4 year.
- Fig. 3. Thin ground section of tooth of a female, 173 cm, 1 year.

PLATE II

- Fig. 1. Thin ground section of tooth of a female, 193 cm, 4 1/4 year.
- Fig. 2. Thin ground section of tooth of a male, 216 cm, 13 year.
- Fig. 3. Thin ground section of tooth of a male, 221 cm, 25 year.



一般財団法人 日本鯨類研究所
THE INSTITUTE OF CETACEAN RESEARCH

