EFFECT OF EXPLOITATION ON REPRODUCTIVE PARAMETERS OF THE SPOTTED AND STRIPED DOLPHINS OFF THE PACIFIC COAST OF JAPAN*

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ABSTRACT

Age composition and reproductive status of samples from two species of dolphins taken in the Japanese drive fishery are analyzed. A slight decline in the minimum age at attainment of sexual maturity was noted in females of the lightly exploited spotted dolphin. Females of the more intensely exploited striped dolphin underwent a decline in the mean age at sexual maturation from 9.7 years (1956 cohort) to 7.2 years (1970 cohort), accompanied by a decline of the minimum age at maturity. A more tentative finding on the species is the shortening of the mean reproductive cycle from 4.00 years (1955) to 2.76 years (1977). This is a direct result primarily of the probable change in the lactation period but also of the change in the resting period and in the proportion of lactating females simultaneously pregnant. Exploitation and response of the population has probably changed the age composition in the striped dolphin more than that of the spotted dolphin.

INTRODUCTION

The Japanese dolphin fishery was widely distributed along the coast of Japan in the last century but has been limited in recent years to Taiji (driving), Izu coast (driving, Fig. 1), Choshi in Chiba Prefecture (hand harpoon), Okinawa (driving and hand harpoon), Tsushima and Goto Islands off northern Kyushu (driving) and Sanriku coast (hand harpoon) (Bureau of Fisheries, 1911; Wilke, Taniwaki and Kuroda, 1953; Ohsumi, 1972; Miyazaki, Kasuya and Nishiwaki, 1974; Kasuya, 1978; 1982; in press; Miyazaki, 1980; 1983). Although the hand harpoon fisheries can take dolphins of most species, large catches of *Stenella* are limited to the first two locations. Details of the recent geographical distribution of the catch were reviewed by Miyazaki (1983).

Driving or netting of the striped dolphin, *Stenella coeruleoalba* (Meyen,

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1833), has been carried out along the Izu coast since the late 19th century (Fig. 1) and at Taiji (33°36′N, 135°56′E) on the Kii Peninsula only in recent years. The stock of the species has declined since World War II (Kasuya, 1976a; Kasuya and Miyazaki, 1982).

The drive fishery for spotted dolphins, *S. attenuata* (Gray, 1846), was started at Arari on the Izu coast in 1959 (Nishiwaki, Nakajima and Kamiya, 1965). Although small number of this species must have been taken with hand harpoon elsewhere (e.g. Taiji), the catches have been relatively small compared with that of the striped dolphin (Miyazaki *et al.*, 1974; Miyazaki, 1983) (Catch of this species at Arari given by Miyazaki *et al.* (1974) erroneously included "Hasunaga" which is now known to be the bottlenose dolphin, *Tursiops truncatus* (Kasuya, 1976b).)

This study analyzes recent changes in life history parameters of the striped dolphin off the Pacific coast of Japan in comparison with those of the less intensely exploited population of spotted dolphins in the same area.

MATERIALS AND METHODS

Materials

The data are based on schools driven at Kawana and Futo on the Izu coast and Taiji on the Kii Peninsula in the period 1952 to 1980 inclusive. Until recently all the dolphin schools driven by the fishery and examined by any biologist were numbered serially by species. Among these schools only those listed in Table 2 were examined by myself; these constituted the main body of the present material (other schools were not directly accessible to me). These were 13 schools of striped dolphins driven on the Izu coast and 13 schools of

TABLE 1. MATERIALS USED IN THIS STUDY

	Species	Striped dolphin	Spotted dolphin
A.	Main data, school analyses	3,000 individuals in 13 schools caught in 1967-1980	1,319 individuals in 13 schools caught in 1970-1980
B.	Ancillary age data	110 individuals in 6 schools caught in 1960-1967	
C.	Ancillary data on neonatal sex ratio (not included in item A)	287 individuals in 16 schools caught in 1952-1970	22 individuals in a school caught in 1975 (school no. 8)
D.	Published data (Kasuya and Miyazaki, 1982, some included in item A)	Data on pregnancy rates 1952 to 1972	

spotted dolphins driven on the Izu coast or at Taiji (A in Table 1; Table 2). With the exceptions of the schools examined by Dr N. Miyazaki in the 1970 to 1973 seasons (included in D in Table 1, used in analysis of annual change of pregnancy rate), schools examined by biologists tended to be relatively larger schools for which processing started or continued on the day following the drive. The processing and examination of dolphins in these schools were done as follows. In the fishing harbour, a group of fishermen netted a part of the dolphin school and landed them (10 to 30 individuals at one time, alive or

TABLE 2. DETAILS OF SCHOOL CLASSIFIED IN ITEM A IN TABLE 1

School no.	Place of driving	Date of driving	Date of data collection	Number of individuals caught	examined	aged	Remarks
	Striped dolphin						
7	Kawana	26, Nov., '67	28, Nov.	3300	150	0[1]	
8	Futo	15, Nov., '68	17-18, Nov.	1680	372	24[1]	
9	Kawana	16, Nov., '68	16-17, Nov.	322	322	104[1]	
10	Kawana	18, Nov., '68	18, Nov.	600	21	0	Item C in Table 1
12	Futo	12, Oct., '70	14, Oct.	330	84	4[1]	
22	Kawana	14, Dec., '71	15, Dec.	903	306	280[1]	
38	Kawana	17, Nov., '72	20, Nov.	411	201	153	
43	Kawana	15, Nov., '73	19, Nov.	414	249	225	
44	Kawana	20, Nov., '73	22, Nov.	1724	466	222	
45	Kawana	22, Nov., '75	24-25, Nov.	1000	399	362	Two schools mixed after driving
46	Kawana	23, Nov., '75	24-25, Nov.				
47	Futo	3, Nov., '76	4, Nov.	735	161	147	
48	Kawana	24, Nov., '77	25, Nov.	795	250	248	
49	Kawana	27, Nov., '80	28, Nov.	431	140	0[2]	Half of the school was driven.
	Spotted dolphin						
1	Kawana	23, Oct., '70	25, Oct.	264	131	52	
2	Kawana	10, Nov., '70	15, Nov.	1381	272	52	
3	Kawana	4, Nov., '72	4, Nov.	189	46	38	
4	Kawana	13, Nov., '72	13, Nov.	192	117	109	
5	Futo	16, Nov., '72	18, Nov.	67	23	23	
6	Taiji	12, Feb., '73	12, Feb.	146	122	115	
7	Taiji	2, Jul., '73	2, Jul.	60	35	21	
8	Taiji	24, Jan., '75	24-25, Jan.	102	102	0	Item C in Table 1
9	Taiji	16, Jan., '76	17, Jan.	91	43	6	
10	Kawana	19, Oct., '76	19, Oct.	377	45	44	
12	Futo	25, Nov., '77	26-27, Oct.	344	119	118	
13	Futo	13, Dec., '78	14-15, Dec.	756	166	151	
14	Kawana	18, Nov., '80	18, Nov.	308	100	0[2]	
15	Kawana	20, Nov., '80	21, Nov.	750	100	0[2]	

1) Aged using dentine layers: individuals over 11 layers excluded.

2) Age determination not completed.

dead). Another group of fishermen killed the landed animals if necessary and removed the viscera. Biologists (usually a group of three or four persons) working among the latter group of fishermen collected the required data and samples. As soon as that group of dolphins was handled, the next group was landed. From 500 to 1,000 individuals were processed in a day. We tried not to bias our sample by choosing animals of any particular growth or reproductive stages; this was helped by the need to process animals very quickly. The dolphins in the harbour were completely mixed by the repeated operation, and no difference of composition was detected between landings from one school (confirmed in two days of operations on School no. 8). Therefore I believe that the sample was representative of the schools examined.

Another small body of data on the striped dolphin was collected on the Izu coast by other biologists in the period not covered by the above data; these were aged by myself and used in an analysis of recent change in age at attainment of sexual maturity (B in Table 1).

The estimation of neonatal sex ratio is based on 287 striped and 22 spotted dolphins (juveniles) examined on the Izu coast by various biologists in 1952 to 1975 (C in Table 1) in addition to those mentioned above (A in Table 1). Pregnancy rate data on the striped dolphin in Table 3 of Kasuya and Miyazaki (1982) were combined with those collected more recently and used for the analysis of year-to-year change in pregnancy rate.

Methods

Age was determined by myself using growth layers in dentine and/or cementum. Cemental counts were used only for individuals with closed pulp cavities. The method of preparation and reading is described in Kasuya (1976a) and Perrin and Myrick (1980). The deposition rate of these layers was shown to be annual for spotted dolphin and assumed to be annual for the striped dolphin based on the similarity of life history in the two species (Kasuya, 1976a). Ages betwen n and n+1 years are represented by n+0.5 years (n being an integer).

Sexual maturity of females was determined by the presence of a corpus luteum or albicans in the ovaries.

Reproductive status of female dolphins was classified into four stages: resting, pregnant, pregnant and simultaneously lactating, and lactating. The mean length of the reproductive cycle was calculated from the proportion of females at each stage, with necessary corrections for sample bias (see REPRODUCTIVE CYCLE) and assuming a gestation time of 12 months for the striped dolphin (Kasuya, 1972. Although Miyazaki (1984) gave estimation of 13.4 months, the difference is not important because the present study analyzes the trend rather than the absolute values of the reproductive cycle) and 11.24 months for the spotted dolphin (Kasuya, Miyazaki and Dawbin, 1974). The simultaneously pregnant and lactating class was treated as representing an independent phase, and its mean period was estimated as for the other phases.

Pregnancy was determined in 10 schools (nos 7, 8, 9, 43 through 49) by the presence of fetus. However, nonpregnant females of the striped dolphin having a corpus luteum were recorded as pregnant in other schools, for which ovaries were not examined by myself. This overestimates the pregnancy rate. Therefore these data were adjusted, using the proportion of non-pregnant females having a corpus luteum of ovulation in the former schools. Females having more than one corpus luteum of ovulation were rare, and they were dealt as those having one.

Change of fishing operation and scope of samples

Kasuya and Miyazaki (1982) briefly described historical changes in the dolphin fishery along the Izu coast, where most of the present samples were obtained.

Enoshima was once known by the dolphin product (Matsuse, ca 1645, cited by Hawley, 1960, p.181). This is the oldest record of the possible dolphin fishery on the coast of Sagami Bay available to me (Fig. 1).

Kawana village, one of the two places now operating a dolphin fishery on the Izu coast, is known to have established a hunting team in 1888 (recorded on a stone monument at Kawana built in 1922). Another record (Bureau of Fisheries, 1911) shows, however, that the fishery was common in the area in those days and the dolphin species hunted were the Pacific white-sided dolphin, *Lagenorhynchus obliquidens* Gill, 1865, (which is not now hunted because of difficulties in driving it), the short-finned pilot whale, *Globicephala macrorhynchus* Gray, 1846, and the striped dolphin. The main changes in the fisheries have been expansion of the maximum operational distance, through improvement of fishing vessels, from coastal waters (a few nautical miles offshore), to Oshima Island (20 nm), and then to occasional searching up to 50 nm offshore, and a decrease in the number of driving groups (teams of fishermen) on the coast (Table 3). The effect of such changes in the operation on the present study was ignored, because (1) the operation had expanded to the waters adjacent to Oshima Island (20 nm) before the collection of the present materials started in 1952, (2) drives from such a far distance as 50 nm seemed have not been recorded, and (3) all the present samples were obtained from schools taken in Sagami Bay or within a few nautical miles of Oshima Island (25 nm from port, Fig. 1).

At Taiji, the catch of these species was usually below 1,000 individuals per year (Miyazaki *et al.*, 1974). It increased after the establishment of a driveing team in 1973 (Miyazaki, 1980; 1983) and a second team in 1980. Only four schools of spotted dolphins were examined at Taiji for the present study (Table 2). Although there is no direct evidence, the spotted dolphins caught in the two locations are assumed to belong to one population, following the conclusion of Miyazaki *et al.* (1974), deduced from comparison of seasonal changes in oceanographical conditions and the distribution of the dolphins.

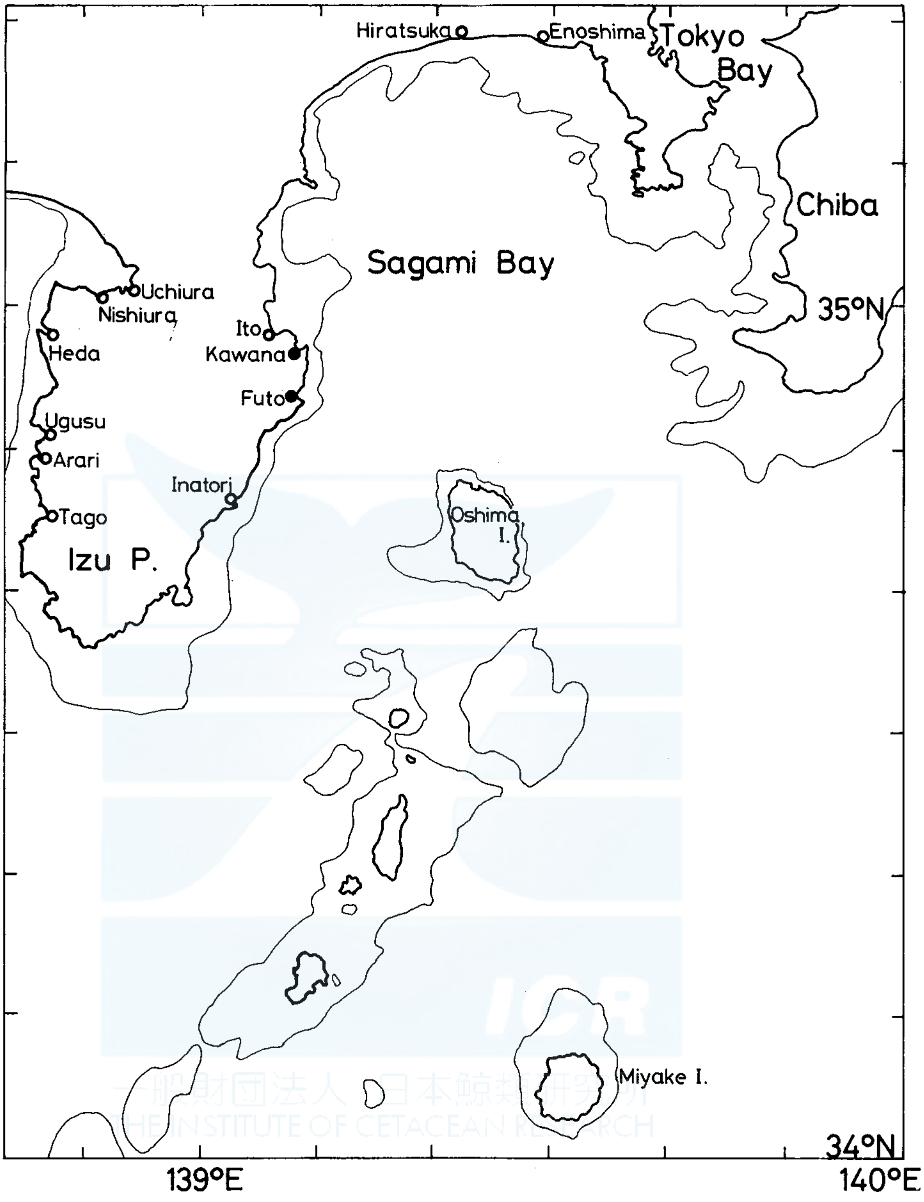

Fig. 1. Map of the area for the dolphin fishery off Izu coast and adjacent area. Thick solid line indicates coastline, and thin solid line the 200 m depth. Ten locations of previous operation (open circle) and two places of present operation (closed circle) are indicated. Types of the fishery were driving (Arari, Futo, Heda, Inatori, Ito, Kawana, Nishiura, Uchiura, Ugusu and Tago), dragnet (Hiratsuka), and unrecorded (Enoshima). (Bureau of Fish., 1911; Hawley, 1960; Kasuya, unpub.)

TABLE 3. CHRONOLOGY OF THE BIOLOGICAL DATA AND DETAILS OF THE FISHERIES FOR STRIPED AND SPOTTED DOLPHINS IN JAPANESE WATERS

year	Dolphin fishery	Biological data
1911	Common on the Izu coast.	
1920's	Expansion of fishing ground to Oshima I. (20 nm) with introduction of motor vessels.	Births of oldest dolphins in the present sample.
1945-'50	Postwar expansion of catch at Arari, Futo, Inatori* and Kawana.	
1952		Start of monitoring of pregnancy rate, striped dolphin.
1956		First cohort examined for annual change of maturation age.
1959	First driving of spotted dolphin.	
1961	Last significant catch (> 100/yr) at Arari on Izu coast. Fishery continues at Kawana and Futo.	
1962	Expansion of searching area close to Miyake I. (50 nm) with the introduction of high-speed boats.	
1968	Last two driving teams on Izu coast joined in operation.	
1970		Last cohort examined for annual change of maturation age.
1973	Start of driving fishery for *Stenella* at Taiji.	Start of monitoring of pregnancy rate, spotted dolphin.
1980	Establish of 2nd driving team at Taiji.	Last data of present study.
1982	Two teams at Taiji joined and set catch limits by species, which were not reached by following operations.	

* Inatori ceased operation between 1945 and 1961.

SCHOOL VARIATION

Fig. 2 shows the age frequency distribution for the eight striped dolphin schools analyzed in this study. Four schools (nos 7, 8, 9 and 12) were excluded from Fig. 2. These were breeding schools containing old individuals, but age for these was determined using only dentinal layers and individual ages over 11 growth layers (presumably years) are often unreliable (Kasuya, 1976a). Data from School no. 22 were for 62 immature females below eight years and 218 males below 13 years (mostly immature); this is considered to be an immature school as described by Miyazaki and Nishiwaki (1978), who listed more examples of this types of school. Six other schools contained immature

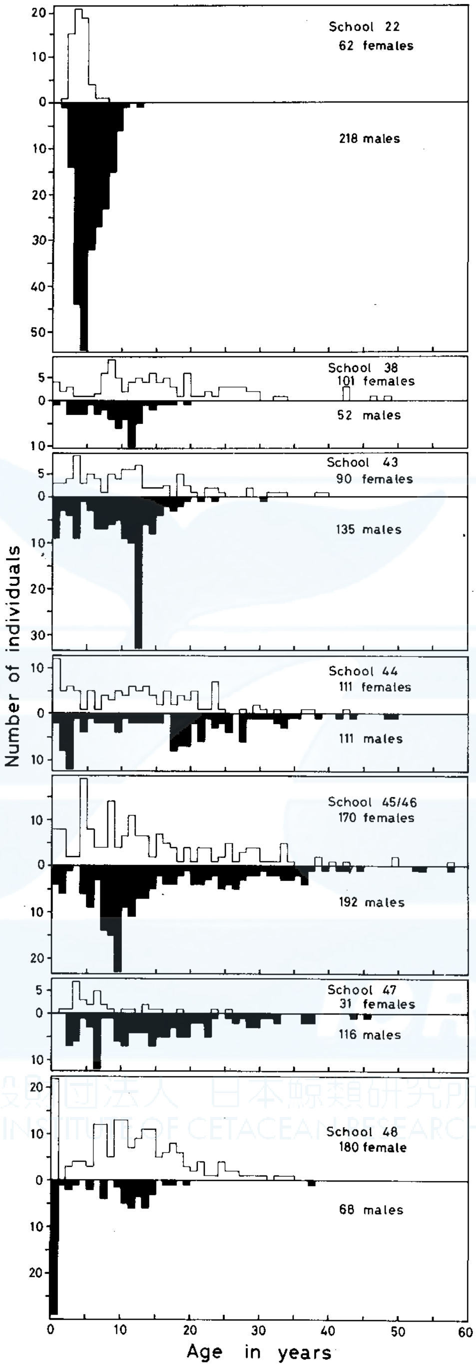

Fig. 2. Age composition of some of the striped dolphin schools used in this study. Only schools with large sample size and listed in item A in Table 1 are indicated.

and mature individuals of both sexes and were considered to be breeding schools. These latter schools show peaks and troughs at various ages below 10 years. This, together with the presence of immature schools, suggests that a group of immature individuals in a breeding school may occasionally segregate to form an immature school (Kasuya, 1972; Miyazaki and Nishiwaki, 1978). This can cause an important bias in the estimates of age frequency and sex ratio of immature individuals.

Fig. 3 shows the age composition of 10 spotted dolphin schools (excluding School 6 that is represented by a small sample). Although they do not include immature schools as observed in the striped dolphin, the presence of troughs at ages below 10 years and the lack of dolphins at around five years of age (ages between weaning and attainment of sexual maturity, see AGE AT SEXUAL MATURITY) in the total age frequency (Fig. 9) suggest the possibility that juveniles of both sexes are segregating from these breeding schools (Kasuya *et al.*, 1974).

Postnatal sex ratios in the schools of striped and spotted dolphins are shown in Table 4. The percentage of females in the sample varies from 22 to 73% (x̄ = 50.5%, SD = 16.4) in the striped dolphin, and from 44 to 66% (x̄ = 57.5%, SD = 6.9) in the spotted dolphin, with smaller between-school variation in the latter species.

Similar analyses were carried out on proportions of sexually mature

TABLE 4. SCHOOL VARIATION IN POSTNATAL SEX RATIO

Striped dolphin (1967-'80)				Spotted dolphin (1970-'80)			
School no.	Males no.	Females no.	Females %	School no.	Males no.	Females no.	Females %
7	51	99	66.0	1	50	81	61.8
8	134	238	63.9	2	108	164	60.2
9	182	140	43.4	3	23	23	50.0
12	35	49	58.3	4	58	59	50.4
22	235	71	23.2	5	8	15	65.2
38	73	128	63.7	6	50	72	59.0
43	146	103	41.3	7	17	18	51.4
44	256	210	45.0	9	15	28	65.1
45/46	206	193	48.3	10	19	26	57.7
47	126	35	21.7	12	40	79	66.3
48	68	182	72.8	13	63	103	62.0
49	57	83	59.2	14	45	55	55.0
				15	56	44	44.0
Total	1,569	1,531	49.4	Total	552	767	58.2
Mean			50.5	Mean			57.5
SD			16.4	SD			6.9
CV			0.3	CV			0.1

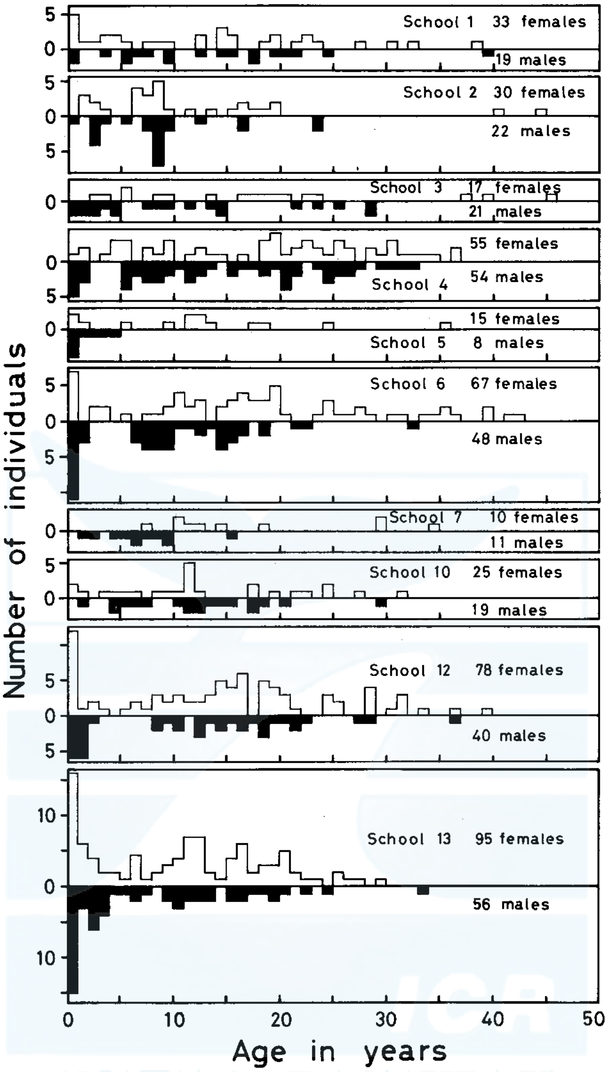

Fig. 3. Age compositions of some of the spotted dolphin schools used in this study. Only schools with large sample size and listed in item A in Table 1 are indicated.

females and reproductive status of adult females (Tables 5 and 6). The between-school variation of these parameters was consistently greater in the striped dolphin, even accounting for differences in school-size frequencies. This means that the between-school variation of these parameters is greater in the striped dolphin schools and suggests that larger sample size may be required for the striped dolphins in order to estimate structure of the population migrating to the fishing ground.

TABLE 5. SCHOOL VARIATION IN FEMALE MATURITY RATE

Striped dolphin (1967-'80)				Spotted dolphin (1970-'80)			
School no.	Immature no.	Mature no.	Mature %	School no.	Immature no.	Mature no.	Mature %
7	46	51	52.5	1	24	48	66.6
8	41	195	82.6	2	67	87	56.4
9	113	20	15.0	3	5	18	78.2
12	15	33	68.7	4	15	42	73.6
22	71	0	0.0	5	5	10	66.6
38	23	103	81.7	6	13	56	81.1
43	38	63	62.3	7	3	15	83.3
44	66	143	68.4	9	10	18	64.2
45/46	69	115	62.5	10	8	18	69.2
47	22	10	31.2	12	22	56	71.7
48	53	129	70.8	13	40	62	60.7
49	31	52	62.6	14	21	31	59.6
				15	13	30	69.7
Total	588	914	60.8	Total	246	491	66.6
Mean			54.8	Mean			69.3
SD			26.0	SD			8.2
CV			0.5	CV			0.1

TABLE 6. SCHOOL VARIATION IN FEMALE REPRODUCTIVE STATUS

Striped dolphin (1967-'80)					Spotted dolphin (1970-'80)				
School no.	Preg	PL	Lact	Rest	School no.	Preg	PL	Lact	Rest
7	2	0	40	9	1	15	3	18	0
8	78	2	86	22	2	17	2	47	17
9	0	0	18	2	3	2	0	15	1
12	7	0	20	4	4	3	1	28	7
22	0	0	0	0	5	4	0	4	0
38	79	1	7	2	6	4	0	21	13
43	20	0	22	5	7	2	0	4	7
44	58	21	47	6	9	1	0	15	1
45/46	34	0	45	19	10	3	1	13	1
47	2	2	1	4	12	11	1	39	5
48	29	9	81	6	13	13	5	36	5
49	19	12	15	5	14	9	2	16	4
					15	1	1	21	6
Total, no.	328	47	382	84	Total, no.	85	16	277	67
Total, %	39.0	5.6	45.4	10.0	Total, %	19.1	3.6	62.2	15.1
Mean, %	32.8	6.5	47.3	13.4	Mean, %	19.5	3.0	62.5	15.0
SD, %	23.8	9.5	25.9	11.5	SD, %	13.7	3.2	15.6	15.1
CV, %	0.7	1.5	0.5	0.9	CV, %	0.7	1.1	0.2	1.0

Preg: pregnant, PL: pregnant and simultaneously lactating, Lact: lactating, Rest: resting

SEX RATIO

Neonatal sex ratio

Neonatal sex ratio was estimated from the sex ratio of fetuses and postnatal individuals below one year of age. Fetuses below 5 cm were excluded, because sex identification is unreliable. All other postnatal individuals below 164 cm (striped dolphin) or below 142 cm (spotted dolphin) were included. These correspond to the age of one year on the respective mean growth curves (Kasuya *et al.*, 1974; Kasuya, 1976a). One of the reasons for the inclusion of calves is to increase the sample size (for further discussions see Kasuya and Marsh, 1984). The results are shown in Table 7.

In the striped dolphin, the sex ratio was not significantly different from 1 : 1 in all years, in both fetuses and calves (Chi-square test, $p > 0.9$). The 841 sexed fetuses and calves yield an estimation of proportion of neonate females of 50.4%.

TABLE 7. NEONATAL SEX RATIO

Species and Season	Fetuses	Calves	Total	
	no.	no.	no.	%
Striped dolphin				
1950-1959 females	5	57	62	51.66
males	6	52	58	
1960-1969 females	55	120	175	49.71
males	53	124	177	
1970-1980 females	103	84	187	50.67
males	93	89	182	
Total females	163	261	424	50.41
males	152	265	417	
Spotted dolphin				
1970-1980 females	48	83	131	44.86
males	62	99	161	

In the sample of spotted dolphins, there were fewer females than males in both fetal and postnatal stages below one year. The neonatal sex ratio estimated from 292 fetuses and calves is 44.9% (females). This is not significantly different from parity ($0.05 < p < 0.1$).

No change in neonatal sex ratio was detected in either species during the study period.

Postnatal sex ratio

Fig. 4 shows age-related changes in the postnatal sex ratio expressed by the proportion of females. In the striped dolphin, the ratio was low between 2 and 10 years of age. This is an effect of the data from an immature school (no. 22), where males predominated. After this age, change in the sex ratio is slight, the ratio being approximately 1 : 1.

The spotted dolphin showed different changes. The proportion of females steadily increased till the age of 40 years. This reflects either a higher mortality rate or segregation of adult males (see AGE COMPOSITION AND MORTALITY).

No temporal trend in the postnatal sex ratio was detected in either of the two species.

AGE AT SEXUAL MATURITY

Method

Female age at the attainment of sexual maturity was analyzed for each cohort (defined as the individuals born in the same year, determined from date of death and age at death).

The process is explained below using the following hypothetical age-maturity composition of three years' samples.

Age at death (yr)		0.5	1.5	2.5	3.5	Total
1980 catch,	immature	50	30	10	0	90
	mature	0	10	15	20	45
1981 catch,	immature	100	60	20	0	180
	mature	0	20	30	40	90
1982 catch,	immature	200	120	40	0	360
	mature	0	40	60	80	180

The above data yield the ratios of immature : mature individuals in each cohort at various ages as follows (catch year in parentheses):

Age at death (yr)	0.5	1.5	2.5	3.5
1979 cohort	–	30 : 10 ('80)	20 : 30 ('81)	0 : 80 ('82)
1980 cohort	50 : 0 ('80)	60 : 20 ('81)	40 : 60 ('82)	–

Then the proportion of sexually mature individuals of a cohort at different ages are calculated from these figures. This method assumes that there is no selection in the fishery between mature and immature individuals of the same age caught in a given fishing season. This is certainly not the case for the striped dolphin and possibly also the spotted dolphin (see SCHOOL VARIATION).

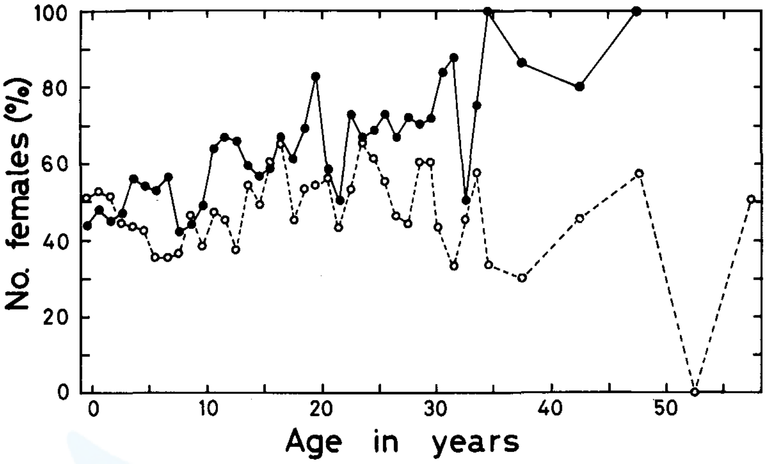

Fig. 4. Age specific sex ratio of striped (open circle and dotted line) and spotted dolphin (closed circle and solid line). Eight striped dolphin schools (nos. 22, 38 and 43 through 48) and 11 spotted dolphin schools (nos. 1 through 13, excluding 8 and 11) are used.

However, the method has the advantage of being free from the sort of bias that occurs, for example, when mean age at sexual maturation is estimated from the transition phase in the earplug of baleen whales (Lockyer, 1972; Cook and de la Mare, 1983; Kato, 1983; Sakuramoto, Kato and Tanaka, 1984).

The age ranges in samples for the earliest cohort and latest cohort were over four years (1950 cohort) and under eight years (1970 cohort), respectively, in the striped dolphin, and over nine years (1961 cohort) and under seven years (1972 cohort) in the spotted dolphin. These earliest and latest cohorts were specified so as to include both mature and immature individuals.

I analyze below the relationships between year of birth and the average age at the attainment of sexual maturity, age of the youngest sexually mature female in the sample, and age of the oldest immature female in the sample. These indices (especially minimum age at the attainment of sexual maturity) seem to be sensitive in some mammals to environmental changes (Laws, Parker and Johnstone, 1975; Ohsumi, in press).

There are several methods for calculating "average" age at attainment of sexual maturity; each can yield different results (DeMaster, 1984). In the present study, it was estimated as the age at 50%-mature on a linear regression weighted by sample size. Even though the proportion of sexually mature individuals may not increase strictly linearly with increasing age, the error can be minimized by using in the regression only the points in the 50%-mature region. Because of the limitation of samples, the analysis was done combining

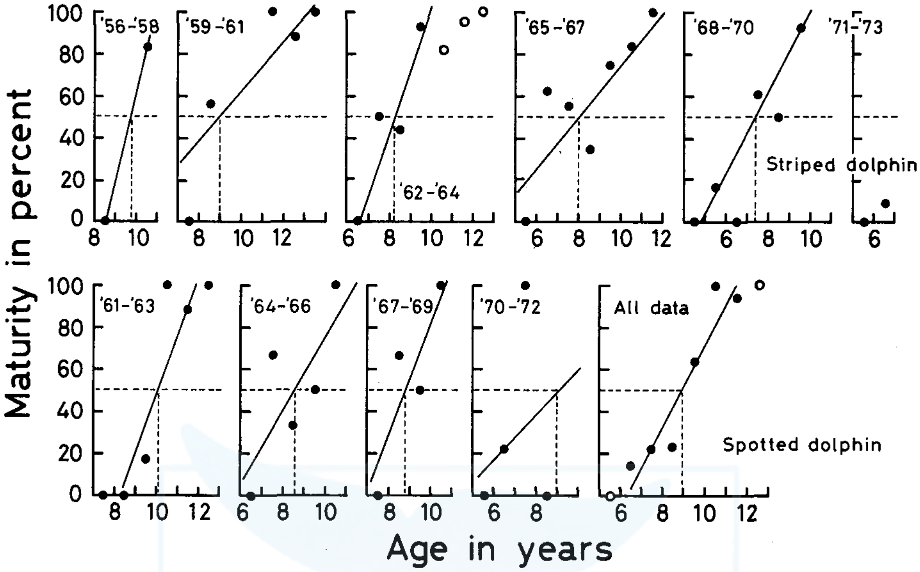

Fig. 5. Estimation of age when half of the females are sexually mature. Cohorts of three successive birth years are grouped. The least-squares regressions are calculated for points indicated by closed circle and weighted by sample size.

data for three contiguous cohorts, yielding five estimates for the striped dolphin and four for the spotted dolphin (Fig. 5).

Striped dolphin, age at sexual maturity

The average age at sexual maturation was estimated at 9.7 years for the 1956-'58 cohorts. It steadily declined to 7.4 years for the 1968-'70 cohorts (Fig. 6). The least-squares regression between the mean age at attainment of sexual maturity (Y, year) and the calendar year of birth (X, using the central year for each cohort group) is expressed by

$$Y = -0.183X + 367.70, \qquad 1957 \leq x \leq 1969, \; r = 0.99$$

Equation 1

The slope is significantly different from zero (t-test, $0.001 < p < 0.01$).

In any of the cohorts before 1962, the observed minimum age of mature females and the maximum age of immature females do not overlap. This is a result of small sample size, as is the apparent increase in maximum age of immature females.

However, in the recent cohorts where sample is large, the age of the youngest mature female seems to be declining (Fig. 6). It was between seven and eight years in the cohorts of 1963 to 1966, but in the more recent cohorts some females matured before six years of age. Also, the age of the oldest im-

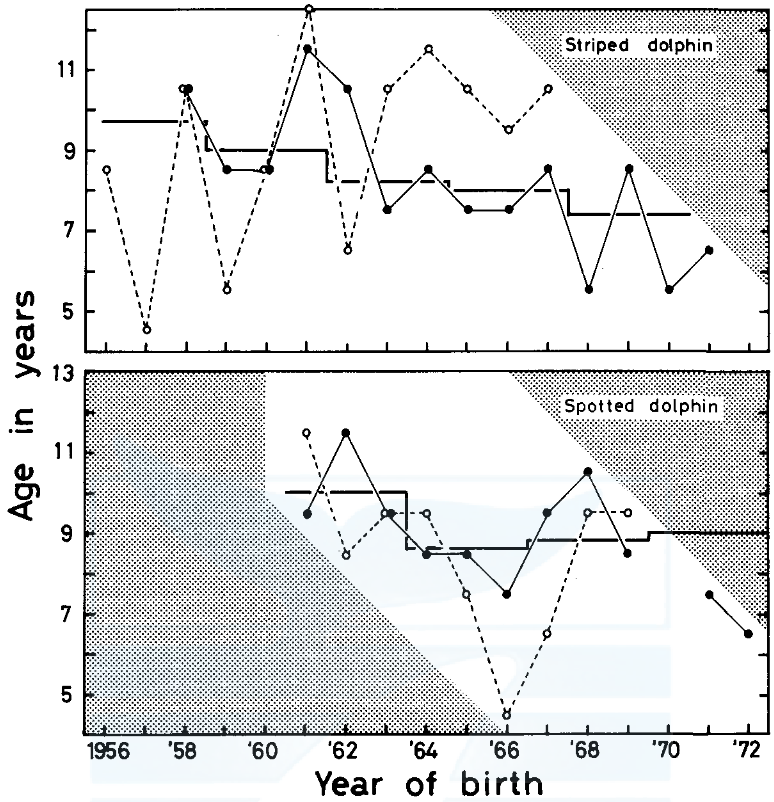

Fig. 6. Annual changes of the age where 50% of females are sexually mature (thick solid line), of the age of the youngest mature female (closed circle and solid line), and of the age of the oldest immature female (open circle and dotted line). Shaded area indicate the ages not included in the analysis.

mature female appears to have declined after the 1963 cohort, but the change is less clear than that of the maturation age.

Spotted dolphin, age at sexual maturity

The average age at sexual maturity for females ranged between 8.6 years (1964-'66 cohorts) and 10.1 years (1961-'63 cohorts) (Fig. 5). The regression coefficient of average age at sexual maturity on year of birth was not significantly different from zero ($p>0.1$) (Fig. 6.)

A least-squares regression between age of females (X, year) and maturity (Y, %) for all data from 1961 to 1972 yields

$$Y = 27.455X - 194.70, \qquad 6.5 \leq X \leq 11.5, \ r=0.95$$

Equation 2

Y = 50 when X = 8.9 (Fig. 5). This is not different from the value of 9.0 years obtained in earlier analyses (Kasuya, 1976a).

The age of the youngest mature female was over eight years for the cohorts before 1965, but in more recent cohorts there were some females that matured at an age below seven years

REPRODUCTIVE CYCLE

Mean reproductive cycle

Two kinds of corrections were made before estimating the length of the average reproductive cycle. The first was to separate true pregnant females from nonpregnant females having corpus luteum of ovulation.

For the striped dolphin, only the data for 10 schools (nos 7, 8, 9 and 43 through 49) distinguish between the two cases. The numbers of pregnant, pregnant & lactating, lactating and resting females in these schools were 242, 47, 354 and 78, respectively. Among these, the individuals with corpus luteum of ovulation but no fetus number 15 (14 resting and one lactating). I therefore estimate that (242+47)/(242+47+15) or 0.951 of the "pregnant females" from other schools were probably actually pregnant.

For the spotted dolphin, all the pregnant females were distinguished from nonpregnant females having a corpus luteum of ovulation. The true pregnancies were 0.971 of the number with corpus luteum, close to the result for the striped dolphin.

The second correction is for possible bias in the apparent pregnancy rate. Table 8 shows the number of pregnant females in the sample (corrected as explained above) and the number of calves below a body length corresponding to the age of one year. Since the length of gestation is about one year, the nursing period lasts more than one year, and breeding in these species is seasonally diffuse (Kasuya, 1972; Kasuya *et al.*, 1974; Miyazaki, 1977; 1984), the relative abundances of these two states are expected to be similar (juvenile mortality is ignored). However, they are rather dissimilar, and the differences are opposite in the two species, i.e. pregnant females exceed calves in the striped dolphin sample, but calves exceed pregnant females in the spotted dolphin sample.

I consider the main cause of this discrepancy to be sample bias resulting from the difference in catchability of schools at the two reproductive states (i.e. difference in timing of migration to the fishing ground, geographical segregation, or timing of the breeding peaks). The small number of schools examined could also be a problem. Inaccurate ageing of juvenile is not a likely cause, because the ageing techniques are the same for the two species (for discussion of juvenile growth rates in these species, see Kasuya, 1972; Kasuya *et al.*, 1974; Perrin, Coe and Zweifell, 1976). A similar, but more pronounced, discrepancy was found in a sample of the short-finned pilot whale, *Globicephala macrorhynchus*, caught by the drive fishery (Kasuya and Marsh, 1984).

TABLE 8. COMPARISON OF NUMBER OF PREGNANT FEMALES AND CALVES BELOW AGE OF ONE YEAR, FOR SCHOOLS IN TABLE 2

	Confirmed	Extrapolated*	Total
Striped dolphin (1967-'80)			
Number of pregnant females**	328	34.8	412.6
Females pregnant and lactating**	47	2.8	
Calves at or below 164 cm	262		262.0
Difference			+150.6
Spotted dolphin (1970-'80)			
Number of pregnant females**	85	10.0	112.5
Females pregnant and lactating**	16	1.5	
Calves at or below 142 cm	172		172.0
Difference			−59.5

*: Extrapolated for the mature females examined but without record of reproductive status.
**: Nonpregnant females having corpus luteum of ovulation excluded.

TABLE 9. ESTIMATION OF TRUE REPRODUCTIVE CYCLE, FOR SCHOOLS IN TABLE 2.

	No. individuals		Proportion (%)		Length (year)	
	apparent*	corrected	apparent*	corrected	apparent*	corrected
Striped dolphin (1967-'80)						
Pregnant	362.8	212.2- 362.8	39.0	29.8- 34.1	0.87	0.82-0.88
Preg. and lactating	49.8	49.8- 49.8	5.6	6.5- 4.7	0.13	0.18-0.12
Lactating	409.8	409.8- 560.4	45.6	53.7- 52.6	1.02	1.48-1.36
Resting	91.6	91.6- 91.6	10.0	12.0- 8.6	0.22	0.33-0.22
Total	914.0	763.4-1064.6	100.0	100.0-100.0	2.24	2.81-2.58
Spotted dolphin (1970-'80)						
Pregnant	95.0	95.0- 154.5	19.1	22.0- 28.1	0.79	0.79-0.84
Preg. and lactating	17.5	17.5- 17.5	3.6	4.1- 3.2	0.15	0.15-0.09
Lactating	302.3	242.8- 302.3	62.2	56.3- 54.9	2.57	2.02-1.65
Resting	76.2	76.2- 76.2	15.1	17.6- 13.8	0.62	0.63-0.42
Total	491.0	431.5- 550.5	100.0	100.0-100.0	4.13	3.59-3.00

*Corrected for small number of mature females of unknown reproductive status.

The proportions of the reproductive states were adjusted for the striped dolphin in two alternative ways to yield a range of estimates: by assuming that pregnant females were overrepresented or that calves (i.e. number of lactating females) were underrepresented (Table 9). For example, the corrected number of the pregnant striped dolphins in Table 9 was obtained using figures in Table 8 as 362.8-150.6=212.2 (assuming overrepresentation of pregnant females), and the lactaing females as 49.8+150.6=560.4 (assuming the underrepresentation of lactating females). The latter assumes that females which have been lactating less than one year and those lactating for more than one year are biased in the same way in the present sample. The reverse was assumed for the spotted dolphin. The resting females are thus assumed to be schooling with lactating females or with pregnant females. This may cover the probable range of bias. Table 9 also shows the mean length of each reproductive stage.

With the above correction, the length of lactation (including lactation accompanied by pregnancy) in the striped dolphin increases about 29 to 44% over the uncorrected value, and the resting period is also slightly extended. On the other hand, in the spotted dolphin, the length of lactation is shortened by about 20 to 36% from the uncorrected figure, and the resting period is slightly shortened.

Thus the mean breeding cycle is extended in the striped dolphin from 2.24 years (uncorrected) to 2.58 or 2.81 years. Since there is no reason to prefer one of these two figures, I tentatively consider that the true calving interval will be between the two, or close to their mean (2.70 years). This is 20.3% longer than the uncorrected figure. The corrected calving interval for the spotted dolphin is about 3.30 years, which is about 20.2% less than the uncorrected figure.

This correction for sample bias in apparent pregnancy rate should be considered rather tentative because it does not take into account uncertainties about mortality and growth of juveniles.

Age-specific reproductive cycle

Fig. 7 shows the age specific reproductive cycles for female striped and spotted dolphins. The mean length of each reporoductive stage was claculated using the above described method, but no correction of sample bias in reproductive states rate was done. Five or more year-classes were grouped for each estimate.

Striped dolphin. The oldest female was 57.5 years old and was resting. The two next oldest females were 49.5 years old (one lactating and the other resting), and the oldest (confirmed) pregnant female was 48.5 years old. The oldest simultaneously pregnant and lactating (PL) female was 42.5 years old, but the next oldest female of this status was only 30.5 years old.

The correlation between the length of lactation (Y, year) and age (X, year) is not high, but the data for animals less than 45 years old give the following least-squares regression,

$$Y = 0.0328X + 0.40, \quad X<45, \quad r=0.76, \qquad \text{Equation 3}$$

and the slope is significantly different from zero (t-test, $0.02<p<0.05$).

The resting period (Y, year) is very short in young females being less than 0.2 years, but increases after 30 years of age. The correlation is shown by

$$Y = 0.0293X - 0.49, \quad X>30, \quad r=0.91 \qquad \text{Equation 4}$$

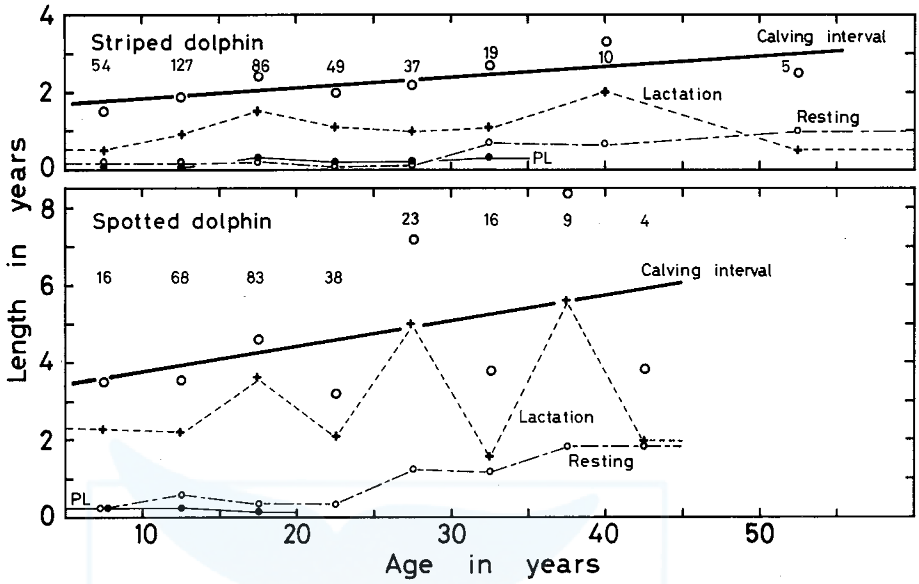

Fig. 7. Age specific reproductive cycle of female striped and spotted dolphins. Contiguous 5, 10 or 15 age classes are grouped for the analysis. Data used are from eight striped dolphin schools (nos 22, 38 and 43 through 48), and 11 spotted dolphin schools (nos 1 to 13, excluding 8 and 11). Figures are calculated from the ratio to pregnant females and are not corrected for sample bias of reproductive stages. Females with corpus luteum of ovulation are not dealt as pregnant. Numerals at the top indicate sample size.

and the regression coefficient is significantly different from zero ($0.02 < p < 0.05$).

The mean length of calving interval (Y, year) shows high correlation for all age range (X, year), giving a least-squares regression,

$$Y = 0.0273X + 1.60, \quad 5 < X < 55, \quad r = 0.73, \qquad \text{Equation 5}$$

and the slope is significantly different from zero ($0.02 < p < 0.05$).

The age above which there are no pregnant and simultaneously lactating females coincides with an increase of the resting period from below 0.2 year to about one year. This is an indication that the reproductive potential of female striped dolphins declines after about 30 years.

Spotted dolphin. The oldest female spotted dolphin was 45.5 years old and was lactating. The next oldest female (44.5 years) was resting, and the oldest pregnant female was 40.5 years old. PL females were 20.5 years old or less.

Although the length of lactation seems to be positively correlated with age, the slope of a least-squares regression is not significantly different from zero ($0.8 < p < 0.9$).

The resting stage (Y, year) is short (<0.6 year) below the age (X, year) of 25 years, after which it increases considerably with age. The least-squares regression fitted for points above 20 years is expressed by

$$Y = 0.886X - 13.18, \quad X>20, \quad r=0.92, \qquad \text{Equation 6}$$

and the slope is significantly different from zero (t-test, $0.02<p<0.05$).

The mean calving interval also appears to show positive correlation with age but the linear-regression is insignificant ($0.3<p<0.5$).

As described above, the only significant age-related changes in reproductive parameters in female spotted dolphins are in the abundance of PL females and resting females. These two parameters show a negative correlation with each other, as observed in the striped dolphin. Therefore, it is reasonable to conclude that reproductive potential in the species declines with age. The absence of significant correlation between age and calving interval or lactation length may be an artifact of small sample size.

Conclusion. The longevity of the female striped dolphin is probably about 10 years greater than that in the spotted dolphin, and the stage of low reproductive potential (indicated by rapid increase of resting females and disappearance of PL females) starts later in the striped dolphin. The absolute value of reproductive potential of the striped dolphin remain higher even with great age (indicated by the shorter lengths of resting period and calving interval). These differences are at odds with general tendency in mammals for a longer-lived species to have lower annual productivity. Thus I suspect that the difference in the reproductive parameters between the two species may not be entirely due to species-specific differences but relate in some degree to differences in history of exploitation.

Historical change in reproductive cycle

Fig. 8 shows the relationship between mean length of calving cycle (and its components) and the date of capture. Because variation among schools in the proportions for the reproductive stages was large, as mentioned above, years represented by only one school were combined with successive seasons in most cases to reduce year-to-year fluctuation. No correction for sample bias in reproductive states was made.

Striped dolphin. As mentioned above (see MATERIALS AND METHODS), most of the data for the striped dolphin do not distinguish pregnant females from nonpregnant females with corpus luteum of ovulation. Therefore in all the analyses of the striped dolphin in this section all females having corpus luteum are dealt as pregnant. The true number of pregnant females is about 0.951 of the females having a corpus luteum (see Mean reproductive cycle of this section).

Although there is an apparent downward trend for the striped dolphin, only one component of the cycle, proportion of PL females, exhibits a statistically significant increasing trend, and that only in recent years. Correlation of

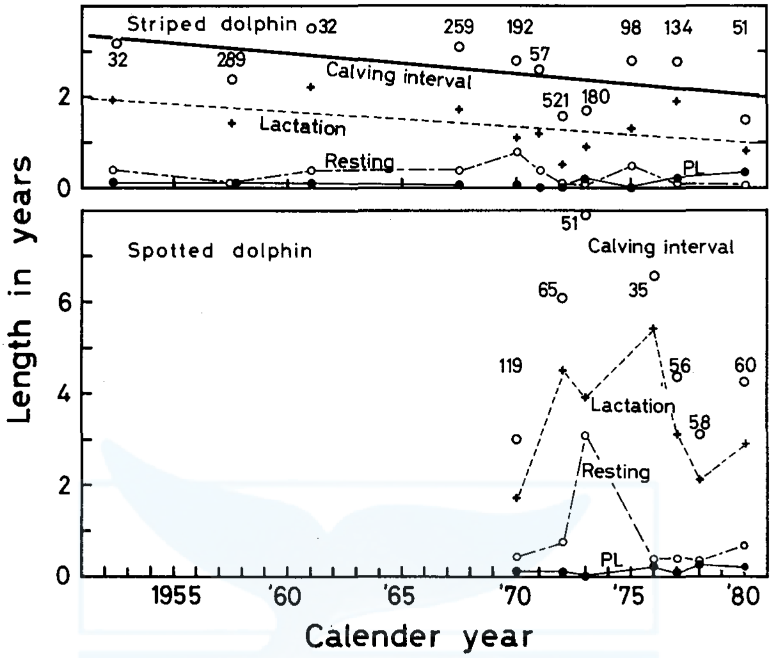

Fig. 8. Annual change in length of reproductive cycle of female striped and spotted dolphins. The data for striped dolphins in the years 1952, '53, '57, '58, '61, '70, '71 and '72 are based on Kasuya and Miyazaki (1982). Figures are calculated from the proportion of pregnant females and are not corrected for sample bias of proportion of reproductive stages. For the striped dolphin, all the females having a corpus luteum of ovulation are dealt as pregnant. Numerals at the top indicate sample size.

the mean length of the PL stage (Y in years, uncorrected for the bias due to segregation) with year (X) for the eight seasons after 1966) is expressed by

$$Y = 2.7590X - 50.25, \quad X \geq 1967, \quad r=0.75, \qquad \text{Equation 7}$$

and the slope is significantly different from zero (t-test, $0.02 < p < 0.05$). This result should be confirmed by collecting more data, because it is not based on a very long period of time.

The mean length of the resting period seems to have a downward trend in recent years, but the regression coefficient is not significantly different from zero ($0.1 < p < 0.2$).

The mean length of lactation also shows an apparent downward trend, but the slope is not significantly different from zero ($0.1 < p < 0.2$).

The mean calving interval (Y in year, uncorrected for bias of corpus luteum of ovulation and segregation) in relation to season (X, after 1952) is shown by the least-squares regression

$$Y = -0.04440X + 89.97, \quad X \geq 1952, \quad r=0.55, \qquad \text{Equation 8}$$

Although the regression coefficient is not significantly different from zero ($0.05 < p < 0.1$), the general downward trend in many of the reproductive parameters mentioned above suggest that more data will prove it significant. This equation and the correction factors for the underrepresentation of lactating female (1.203) and for nonpregnant females having a corpus luteum of ovulation (0.951) give the following estimates of the possible calving interval for the species.

1955 season: $3.160 \cdot 1.203 / 0.951 = 4.00$ years
1960 season: $2.938 \cdot 1.203 / 0.951 = 3.72$ years
1977 season: $2.183 \cdot 1.203 / 0.951 = 2.76$ years

The mean calving interval could have decreased about 1.24 years in the past 22 years between 1955 and 1977.

Spotted dolphin. There are no statistically significant trends over the period sampled.

AGE COMPOSITION AND MORTALITY

Catch data can be used for estimation of mortality rates only when a fishery does not select certain age classes and when the annual recruitment and population size are constant (Caughley, 1966). These conditions are not met for the striped and spotted dolphins. Therefore, the present effort was directed to comparing the age composition of the striped dolphin with that of the less intensively exploited spotted dolphin to attempt to elucidate the possible effect of the longer-term fishery on the age composition of the striped dolphin.

Spotted dolphin

The frequency of juveniles in the present sample is unreasonably low (Fig. 9). This is presumably due to segregation of weaned juveniles from the breeding schools that formed the present sample. Males of adult age classes are consistently fewer than the females of the same age. This could be due to segregation and/or higher mortality rates in males. The two oldest females were aged at 45.5 and 44.5 years, respectively, and the oldest male at 42.5 years. This suggests a slight longer longevity in females.

Caughley (1966; 1977) reviewed the age composition of wild-mammal populations and concluded that mortality rate is dependent on age, i.e., a high juvenile mortality rate that decreases with age, and a lower adult mortality rate followed by a higher rate in older age classes. Males of some polygynous species have a W-shaped mortality curve (Ralls, Brownell and Ballou, 1980).

The age composition of spotted dolphin shows the pattern indicated by Caughly (1966; 1977), except for the juvenile bias, but the data are insufficient to allow detection of details of age-related changes. However the least-

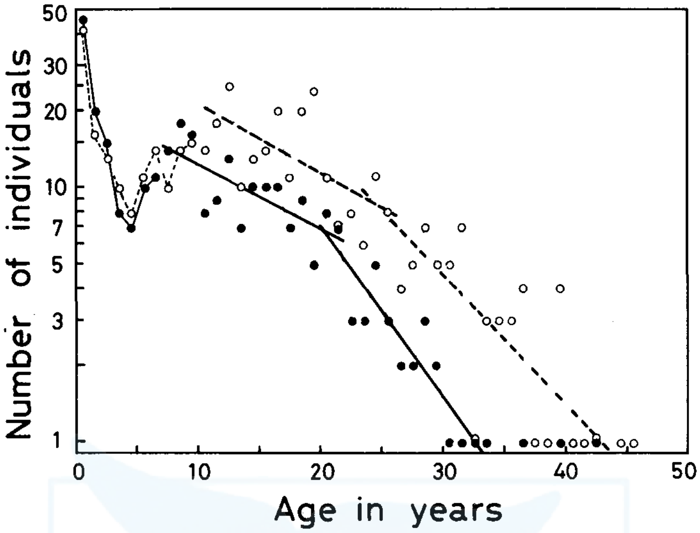

Fig. 9. Age composition of the spotted dolphin. Open circle and dotted line indicate females, and closed circle and solid line males. The thick straight lines (dotted and solid) are least-squares regressions for the indicated age ranges. Eleven schools (nos 1 to 13, except 8 and 11) are included.

squares regressions fitted to the intermediate and older age classes (Fig. 9) suggest higher apparent mortality rate for the older age class (Table 10). The calculations include only data below the age where zero frequency starts to appear in order to avoid bias due to ignoring zero frequency in the calculation. These results are similar to the estimation using the geometric method of Robson and Chapman (1961) (Table 10).

The difference of the apparent mortality rate between medium (approximately from 10 to 22 years of age) and the older age classes is significant (t-test, $p<0.01$). Although the male mortality appeared slightly higher than that of the females of the same age, as suggested by the female sex ratio increasing with age, this difference is not significant in the present small sample.

Assuming a stationary population, a rough estimation of juvenile mortality rate was done as follows. First, the annual production of 43.49 female calves was calculated by (Number of aged females, 431 individuals) × (Proportion of adult females, 0.666) × (Neonatal sex ratio, 0.5) / (Average calving interval, 3.30 years). This annual production is close to the observed frequency of 42 females between 0 and 1 year of age. Then a hypothetical uniform mortality rate was calculated for ages between year 0 (43.49 females) and year 11 (20.01 females calculated from the regression in Fig. 9). This gives 6.9% as the mean annual mortality rate of females between 0 and 11 years of age.

TABLE 10. APPARENT ANNUAL MORTALITY RATE CALCULATED FROM AGE COMPOSITION OF SPOTTED AND STRIPED DOLPHINS

Method	A	B
Spotted dolphin		
Female, 11-26 yr	0.0609	0.0563 ±0.0310
24-43 yr	0.1104	0.1026 ±0.0418
>24 yr	–	0.1348 ±0.0282
Male, 7-22 yr	0.0555	0.0590 ±0.0361
20-34 yr	0.1437	0.1494 ±0.0734
>20 yr	–	0.1618 ±0.0439
Striped dolphin		
Female, 11-22 yr	0.1141	0.1074 ±0.0376
20-34 yr	0.0773	0.0622 ±0.0442
32-41 yr	0.0192	0.2132 ±0.1453
>32 yr	–	0.1408 ±0.0468
Male, 11-22 yr	0.1340	0.1486 ±0.0366
20-34 yr	0.0536	0.0534 ±0.0471
32-46 yr	0.1328	0.1489 ±0.0771
>32 yr	–	0.1419 ±0.0398

A: From least-squares regression in Figs. 9 and 10.
B: After Robson and Chapman (1961), best point estimate with 95% confidence interval.

Striped dolphin

The age frequency below 10 years is largely dependent on the catch of the uncommon immature schools and is not reliable. The oldest individuals were aged at 57.5 years (one male and one female) and the next oldest at 53.5 years. Five males and five females were older than the oldest spotted dolphin (45.5 years old), suggesting a greater longevity in striped dolphins. A sexes difference in longevity is not suggested by the present sample.

The apparent mortality rate was calculated in the same way as for the spotted dolphin (Table 10). Since the population has been exploited probably for more than one century and there are symptoms suggesting decline of the population size (see DISCUSSION), it is not possible to estimate the true mortality rate from these figures. However the general pattern of the steeper slope of the oldest age class (Fig. 10) is similar to that of the spotted dolphin. This will reflect the age specific change of the natural mortality rate.

The slope of the age frequency below 33 years is less steep, but it seems to change at an age of about 21 years (slightly steeper in the younger age). Kasuya and Miyazaki (1982) found a similar change in age frequency data calculated from the ovarian corpora frequency. Although the present sample was insufficient for further analysis, it is probable that it reflects one or both of "the fishing mortality increase" and "increase in the annual recruitment" that might have occurred about 20 years before the commencement of sampl-

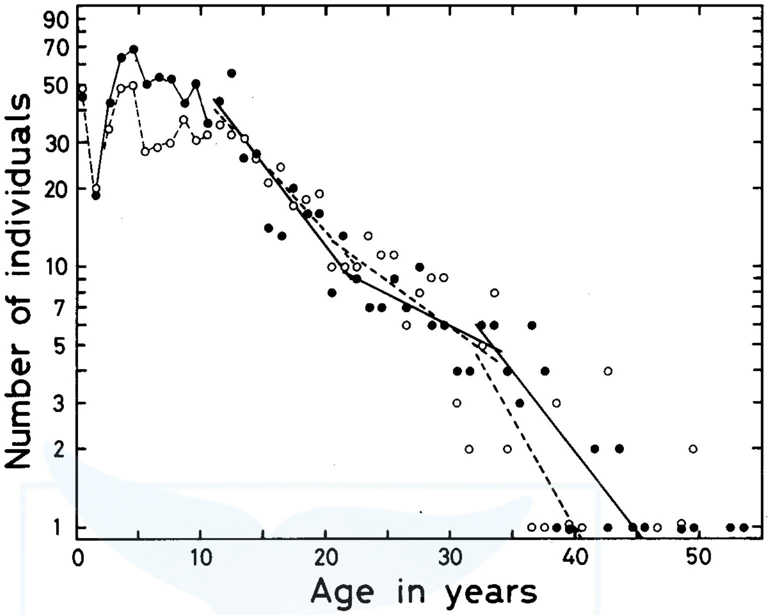

Fig. 10. Age composition of the striped dolphin. Closed circle and solid line indicate males, and open circle and dotted line females. The thick straight lines (dotted and solid) are least-squares regressions for the indicated age ranges. Eight schools (nos 22, 38 and 43 through 48) are included.

ing in 1972 to 1977 as the result of high catches after World War II (Kasuya and Miyazaki, 1982; Miyazaki, 1983).

DISCUSSION

Kasuya and Miyazaki (1982) suggested for the striped dolphin population off the Pacific coast of Japan that the population could not sustain the catch level of the early 1970's, because it exceeded the maximum sustainable yield. Their conclusion was based on the catch curve and changes in the operation pattern such as the number and quality of vessels used, expansion of the fishing ground, and an increased proportion of other delphinids in the catch (their analysis of catch curve was later refined by Kasuya (1976a) using improved age determination, but the conclusion remained unchanged). Although these catch curve analyses may need further examination (Anon., 1981), the changes in the fishing operation will still remain valid as an indication of change of the population level.

Later, Miyazaki (1983) analyzed the catch per unit of effort (CPUE) in the fishery, expressed by the number of captured individuals or the number of schools caught per searching day. Although he was not certain if the

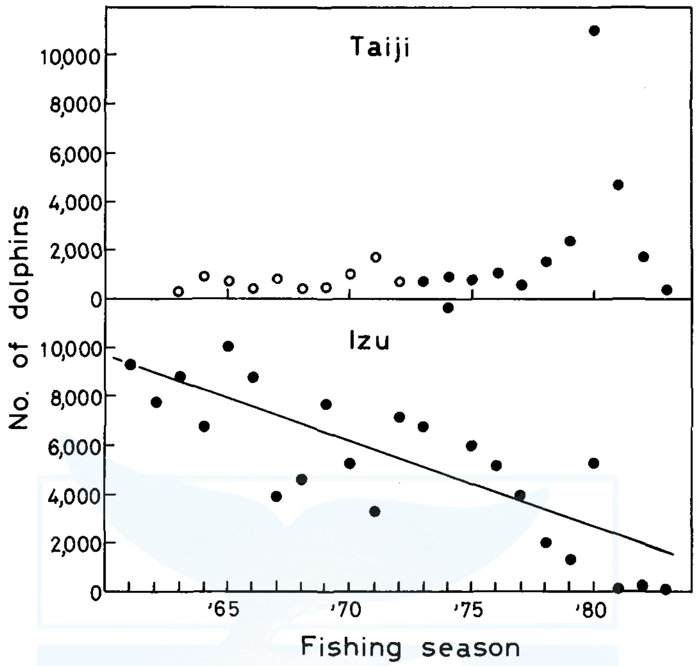

Fig. 11. Landing of the striped dolphin at Taiji and off Izu peninsula (Kawana and Futo) by hand-held harpoon (open circle) and drive fishery (closed circle) for the period where a complete statistics are available. Both equipment and number of hunting teams remained unchanged at Izu coast for the period indicated, but they had changed considerably at Taiji. Straight line represent a linear regression of the annual catch on the fishing season Y = −348.0X + 691,800). The fishing season off Izu coast is indicated by the starting date of the season. The shot-and-lost individuals in the hand-held harpoon fishery at Taiji are not included (see text).

population was stational (Miyazaki, pers. comm.) he could not find a significant decline in the annual catch or in the CPUE serieses.

However, in fisheries such as the drive fishery, where the scouting vessels stop their searching operation for the day and start driving as soon as they find a dolphin school, the change in CPUE underrepresents that of the stock level (Cook, in press). Furthermore, the recent catch of the striped dolphin off the Izu coast has further declined without any change in the equipment used (246 individuals in 1982 and 40 in 1983. Anon., 1984; 1985). The decline of catch after 1961, where complete statistics are available for the two villages (Futo and Kawana) and the equipment remained the same, is significant ($p<0.001$, t-test of the gradient of the regression coefficient of annual catch on fishing season, see Fig. 11). Using only data from the period of the cooperative operation by the two teams (since 1968) gives the same result

$(0.005 < p < 0.01)$. The decline of dolphin meat demand was not indicated, because the catch of the Dall's porpoise in the northern Japan increased in recent years (Anon., 1983; 1984).

The fishing season off Izu coast, where they drive southbound schools, has also changed over the period sampled, from October-January (1960's), to October-December (1969 to 1979), to September-December (1980), and finally to September-November since 1981 (most of these data are available in Miyazaki, 1983), although the higher demand for dolphin meat in colder months remained the same.

These changes as well as those pointed out by Kasuya and Miyazaki (1982), suggest the decline of the stock level. However, the catch of the species off Taiji has not shown a significant decline since the start of the drive fishery in 1973. This could be explained if the density change occurred earlier at the periphery of the population's distribution (off the Izu coast) before it happened near the core area (Taiji) (Cook, in press). This could also explain the change in the fishing season off the Izu coast mentioned above.

The possible density dependent changes in the life history parameters of the striped dolphin population may appear too small to account for drastic decline in the catch off the Izu coast. This could be due to either the incomplete mixing of population members or a population decline accompanied by reduction of the range size. The first explanation assumes that the population declined only in the area close to the fishing ground and that the fishery continued to take schools migrating in from the surrounding area that was damaged less by the fishery. The second assumes that, due to the reduction of population range, even with rapid mixing, the density of the remaining stock changed less than would be expected from the apparent decline of the population level in the fishing ground. In both cases, the apparent decline of the population size may result in neither a parallel change of density in the remaining population nor in the expected improvement of its reproductive capacity. It is also true in these cases that the decline of the population level in the periphery of the range may exaggerate the decline of the entire population.

The above discussion, suggesting the decline of the striped dolphin population, is consistent with the density dependent changes of the life history parameters suggested in the present study. Therefore, I consider that the stock of the striped dolphin exploited off the Pacific coast of Japan could not sustain the annual catch of 3,600 to 16,000 individuals ($\bar{x}=7{,}915$), off Izu and Taiji in 1961 to 1981 (Miyazaki, 1983; Anon., 1984; 1985). This figure does not include the individuals shot and lost by the past harpoon fishery off Taiji, which used hand-held harpoon and shot gun and seemed to have landed only about half of the total kill).

Kasuya and Marsh (1984) suggested for *G. macrorhynchus* that, even when the total catch was the same, the population might respond more effectively to cropping from many schools rather than to the capture of whole schools.

However, because the schools of the striped dolphin seem to be more fluid than those of the pilot whale (Miyazaki and Nishiwaki, 1978) it is questionable if this is strictly applicable to the striped dolphin.

The magnitude of the contribution of the changes in life history parameters to the improvement of population productivity can be roughly estimated as follows.

The average age of female striped dolphins at the attainment of sexual maturity declined from 9.7 years at around 1966 (for the 1957 cohort, using Equation 1) to 7.4 years in 1976 (for the 1969 cohort), i.e. a decline of about 2.3 years during about 10 years. In the 1636 striped dolphins for which ages were estimated (both sexes combined to smooth age frequency), there were 787 individuals over 10 years old and 949 over 8 years old. Thus the observed decline in the age at maturation could have increased population productivity by about 20.6% in this period. However, this figure has to be considered as tentative, because it is affected by the biased juvenile age composition and assumes that the age composition was unchanged for 10 years.

On the other hand, if the calving interval of the striped dolphin really declined in the same period (10 years) to 83.6% of the initial level (Equation 8), it could have contributed to the 19.6% increase in the annual pregnancy rate. If this change was accompanied by the decline in age at maturation mentioned above, the gross reproductive rate could have increased by about 44% ($1.206 \times 1.196 = 1.44$) of the initial level. However, this figure is less certain than that above (20.6% increase), because the change in the pregnancy rate is more uncertain.

The only detectable change in the life history parameters of female spotted dolphins off the Pacific coast of Japan was the possible decline of the minimum age at the attainment of sexual maturity. Ohsumi (in press) analyzed the age of female fin whales at maturation for the exploited population in the North Pacific, using individuals with only one corpus in the ovaries. He found that the density dependent change appeared first as an increase of early-maturing individuals, which had little effect on the age where 50% of the females were sexually mature. This change was followed by a decline in the age of 50% maturation, but some females still attained maturity at a higher age as before. The last phase of the change was the disappearance of these relatively old immature females. Thus females that matured at between 8 and 17 years of age ($\bar{x} = 12.4$) in the 1957–'58 seasons matured in 1974–'75 seasons at about 4 to 11 ($\bar{x} = 7.0$) years of age (Fig. 3 in Ohsumi, in press).

Laws *et al.* (1975) also showed for populations of the African elephant, *Loxodonta africana*, in different habitats, that sexual maturation occurred among females at ages of 10 to 34 years in unfavorable habitat (50% maturation at about 22 years), but at ages of 10 to 22 years in more favorable habitat (50% maturation at about 17 years). Both studies suggest that a change in the age at sexual maturation may not occur equally in all age classes.

I believe that this kind of change could have started recently in the population of spotted dolphins. The drive fishery for the spotted dolphin may have started in 1959 (Table 3), but annual catches were small (less than 1,000) in most of the seasons before 1973 (Miyazaki *et al.*, 1974), and increased only after 1976 to an average of 1,251 (0 to 4,184) concurrent with the decline of the striped dolphin catch (Kasuya and Miyazaki, 1982; Miyazaki, 1983). However, the catch was still low, even in recent seasons (1,441 in 1982 and 629 in 1,983, Anon., 1984; 1985) compared with that of the striped dolphins in the area (Miyazaki, 1983). This suggests that if a change of the minimum age at sexual maturity has really occurred in the spotted dolphin population, it could be the result of not only the decline of the population of spotted dolphins but also that of the striped dolphin population in the same geographical area, due to reduced competition for food.

The limited catches and almost indetectable changes in life history parameters suggest that the apparent mortality rate of the spotted dolphins calculated in this study might be close to the natural mortality rate of the species, even though it may be an overestimate due to the calculation technique (de la Mare, 1984).

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