GROWTH OF DALL'S PORPOISE IN THE WESTERN NORTH PACIFIC AND SUGGESTED GEOGRAPHICAL GROWTH DIFFERENTIATION

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ABSTRACT

Some growth parameters of the western North Pacific *dalli*-type Dall's porpoise were estimated from 167 specimens taken with hand-held harpoons on two cruises and compared with data obtained previously from porpoises killed incidentally in the salmon gill net fishery. These parameters were compared with previously published figures for the Japanese coastal population. Individuals from the Pacific coast of Japan (96% were *truei*-type) attained sexual maturity at body lengths 12 to 17cm larger than *dalli*-type individuals in the offshore waters. This is an indication of genetic differentiation between the two populations in addition to the previously reported external pigmentation. The possible usefulness of the growth parameters for the detection of genetic isolation between two major color types off the Pacific coast of Japan is indicated.

INTRODUCTION

Using specimens obtained from a harpoon fishery, Kasuya (1978) analyzed the life history of the Dall's porpoise, *Phocoenoides dalli* (True, 1885), off the Pacific coast of Japan, and suggested that the *dalli*-type individuals which comprised about 4% of the total catch might be migrants from the offshore Pacific or Sea of Japan populations which were mainly composed of *dalli*-type individuals. His conclusion was based on seasonal changes in the frequency of the color types and analysis of mixed schools with both two color types. Miyazaki, Jones and Beach (1984) supported this conclusion by reanalyzing the school structure using additional records of mixed schools. However, there was still uncertainty concerning the genetic isolation of the two color types as suggested by Wilke, Taniwaki and Kuroda (1953) and Houck (1976).

Based on limited number of samples taken in the offshore western North Pacific, Kasuya and Jones (1984) suggested, that both the incidental take by

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the salmon gill net fishery and the intended catch with hand-held harpoons are biased (1) by the tendency of different growth stages to be geographically segregated and (2) bow riding behaviour to be predominant among individuals between weaning and sexual maturity. They also suggested that *dalli*-type individuals in the offshore waters mature at smaller body size than the Japanese coastal population (mostly *truei*-type) studied by Kasuya (1978).

Using additional materials caught by hand-held harpoon, the present study analyzes the effect of different sampling methods on life history parameter analysis, and the growth difference between the Dall's porpoises from the two areas.

MATERIALS AND METHODS

This study is based on *dalli*-type Dall's porpoises taken with hand-held harpoon in the western North Pacific in 1982 (80 individuals) and 1983 (87) during the two cruises of the *Hoyomaru No. 12* chartered by the Fisheries Agency of Japan (Kasuya and Jones, 1984; Ogi and Fujise, 1984). Few *truei*-type individuals taken during the cruises (8 in 1982, and 2 in 1983) were excluded from the analyses, but one black-type taken at 43°27′N, 163°00′E in 1983 cruise was included. Since the black-type, which lacks white area on the flank and is entirely dark, is known in the entire range of the species (Kasuya, 1978; Morejohn, 1979), it is reasonable to assume that it belongs to the same population as that of the major color type of the area.

The periods of sampling were from 21 August to 17 September in 1982 and 16 August to 7 September in 1983. This corresponds to early mating season after the parturition peak in mid June to early August (Newby, 1982). The samples were collected in the area surrounded by the USSR Fishery Control Zone (FCZ), US FCZ, 180° longitude, and 42°N latitude. The majority of animals (82% in 1982 and 92% in 1983) were taken in the Subarctic Convergence Zone and within a radius of 180 nautical miles centered at 45°N and 160°E (Fig. 1). Over 94% of individuals were caught in a region where the surface water temperature was between 11° and 19°C, and where weaned juveniles segregated (Kasuya and Jones, 1984).

In contrast to the present sample, that used by Newby (1982) were collected in early June to late July (during the parturition season), in a northern region (majority of them in an area surrounded by 49°N, 56°N, 170°E, and 175°E), from the incidental take by the salmon gill net fishery, and in the three seasons from 1978 to 1980. Materials used by Kasuya (1978) were taken in winter (January to April), off the Pacific coast of Japan (39° to 40°N), from the harpoon fishery, between 1972 and 1976.

The age determination and classification of female reproductive status were done after Kasuya and Jones (1984). In the case of the 1982 sample male sexual maturity was assessed histologically (Kasuya and Jones, 1984)

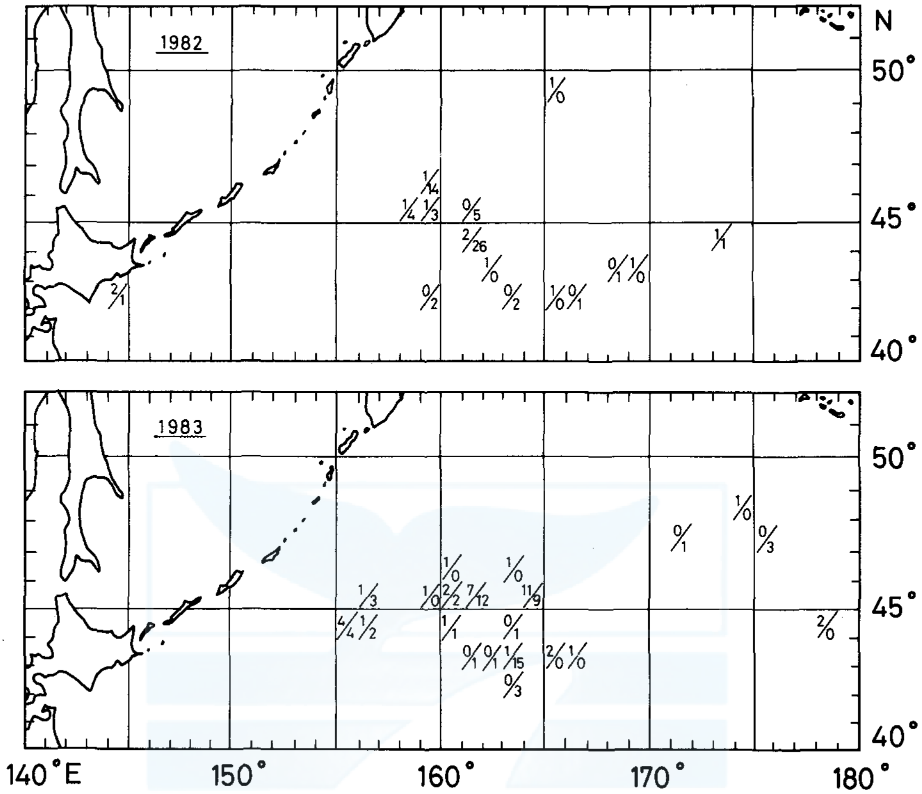

Fig. 1. Position of catch of the present sample. Numbers of females/males are indicated in one degree of longitude and latitude.

However, early (more than 0% and less than 50% of the seminiferous tubules had spermatocyte, spermatid or spermatozoon) and late maturing (50% or more but less than 100% of the tubules had at least one of the cell stages) individuals were included with immature and mature individuals respectively. For the 1983 sample, male maturity was determined using the testis weight criteria of Kasuya and Jones (1984); individuals whose left testis weighed 40g or more in August-September were considered mature and others immature, the inclusion of the late maturing males into mature stage does not cause significant bias in the following analysis, and meets the weight criteria.

RESULTS

Sex ratio, an additional indication of segregation

The number of males in the sample exceeded females for all cruises and maturity groups (Table 1), but the imbalance was statistically significant only for the 1982 sample (Chi-square test, $p < 0.02$). As suggested by Kasuya and

TABLE 1. BODY LENGTH FRENQUENCY OF *DALLI*-TYPES TAKEN BY THE *HOYOMARU NO.12* CRUISES IN 1982 AND 1983

Body length (cm)	Male					Female				
	immature		mature		total	immature		mature		total
	'82	'83	'82	'83		'82	'83	'82	'83	
148-					0		1			1
152-					0					0
156-					0		1			1
160-		4			4		3			3
164-	3	3			6	1	5		5	11
168-	4	6		1	11		2	1	1	4
172-	7	4	2		13	1	2	1	4	8
176-	3	5	3	3	14		1		2	3
180-	10	6	1	4	21		2	2	4	8
184-			8	3*	11*		1	2	3	6
188-	1	5	5	8	19					0
192-		1	4	2	7			1		1
196-	1		4	3	8					0
200-			1		1			1		1
204-			1		1			1		1
208-			1		1					0
212-					0			1		1
216-			1		1					0
Total	29	34	31	24*	118*	2	18	10	19	49

*: Includes one black type.

Jones (1984), there could be more males than females in the Subarctic Convergence. This is supported by the predominance of males in the present sample aged at 2 or 3 years (57:32, see Table 2) and the reverse sex ratio in the gill net sample in the northern area (54:96, see Newby 1982). The sex ratio of immature individuals was significantly different between the 1982 and 1983 samples (Chi-square test, $p < 0.02$). This suggests that there may exist some kind of sexual segregation of immature individuals in the Subarctic Convergence Zone.

Body length frequency

Body length ranged from 148 to 220 cm. However, there were few individuals with body length less than 160 cm or above 188 cm (females) or 196 cm (males) (Table 1), despite the abundance of individuals in these size ranges in the catch of the salmon gill net fishery to the north of our sampling area (Fig. 2).

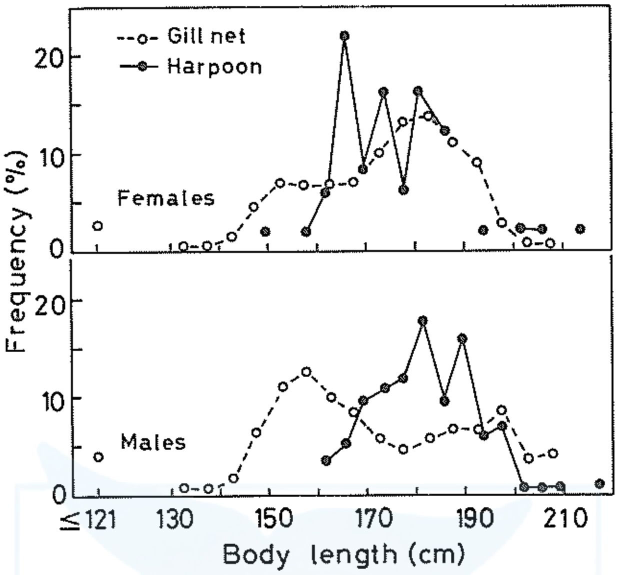

Fig. 2. Body length frequency of *dalli*-type Dall's porpoise taken using hand-held harpoon (present material) or by salmon gill net fishery (Newby, 1982). Sample sizes are 49 females and 118 males (harpoon catch), and 1,140 females and 708 males (gill net catch).

TABLE 2. AGE FREQUENCY OF *DALLI*-TYPES TAKEN BY THE *HOYOMARU NO.12* CRUISES IN 1982 AND 1983

Age (years)	Male					Female				
	immature		mature		total	immature		mature		total
	'82	'83	'82	'83		'82	'83	'82	'83	
0					0					0
1					0		2			2
2	9	11	2	2	24	1	11		4	16
3	6	13	5	9	33		4	2	10	16
4	6	6	6	3	21	1	1	3	1	6
5	4	2	7	5*	18*			1	2	3
6	2	1	3		6				1	1
7	1		1	1	3				1	1
8			1		1					0
9				1	1			1		1
10			1		1			1		1
17			1		1					0
no age	1	1	4	3	9			2		2
Total	29	34	31	24*	118*	2	18	10	19	49

*: Includes one black-type.

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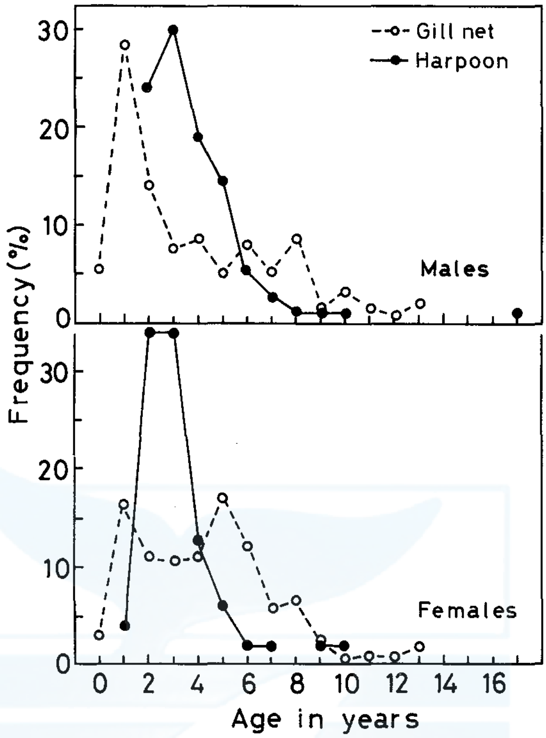

Fig. 3. Age frequency of *dalli*-type Dall's porpoise taken using hand-held harpoon (present material) or by salmon gill net fishery (Newby, 1982). Sample sizes are 47 females and 109 males (harpoon catch), and 427 females and 234 males (gill net catch).

Age frequency

There are some indications that the readability of tooth layers decreases with increasing age (Newby, 1982), but the proportion of individuals which were not aged due to shedding of whole teeth from the jaw or extreme ware of teeth did not differ significantly between mature and immature individuals of the present sample (Chi-square test, $p > 0.2$).

Ages of the present sample ranged from 1 to 17 years, but there were few individuals less than 2 years or older than 6 years (females) or 8 years (males) (Table 2). These results are consistent with the body length frequency data, and quite different from composition of the gill net catch (Newby, 1982; Kasuya, 1978) (Fig. 3). We conclude that the harpoon and gill net samples represent different components of the population because of segregational and behavioral differences related to age and reproductive status (Kasuya and Jones, 1984). Kasuya and Jones (1984) suggested that the waters north of the Subarctic Convergence Zone were inhabited by adult *P. dalli*, weaned calves, and mother-calf pairs all of which were rare in the southern area.

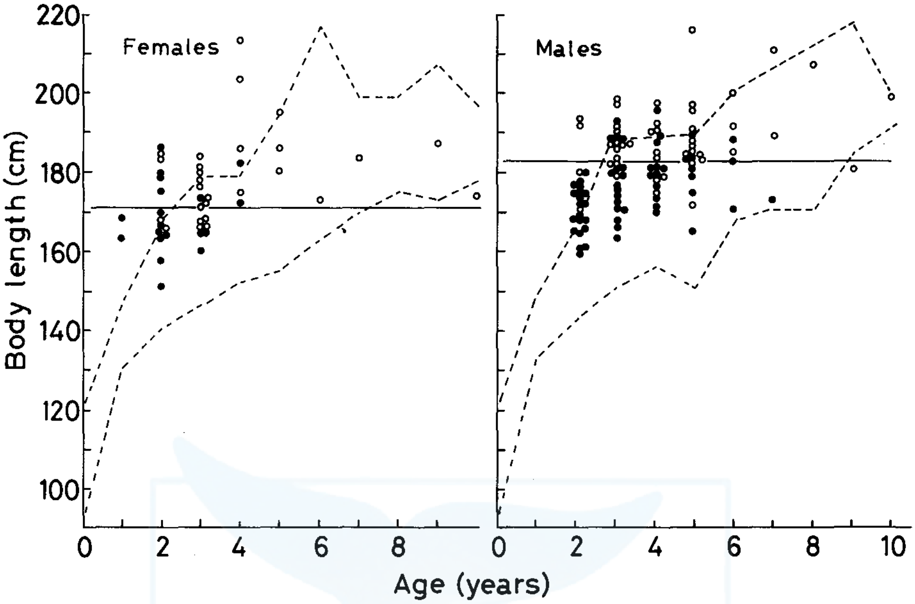

Fig. 4. Age-body length relationship in *dalli*-type Dall's porpoise taken by hand-held harpoon (present material) or salmon gill net fishery (Newby, 1982). Dotted lines indicate range of the gill net sample and circles individuals taken with harpoons (closed circle: immature, open circle: mature). Horizontal line indicates mean body length at the attainment of sexual maturity of the offshore *dalli*-type population.

Growth curve

Newby (1982) estimated the average body length at birth for the offshore population as 94.83 cm. This could be an underestimation because he used all the available fetuses and neonates (363 fetuses and 62 newborns, 61 to 123cm in body length) to correct the unbalanced frequencies of the two categories. It would have been more appropriate to include only length range where both fetuses and calves were present, i.e. 90 to 111 cm. If this procedure is used the average birth length is estimated at about 99 cm. Kasuya (1978) obtained a similar figure (99.7 cm) using a limited number of samples.

Fig. 4 compares the growth curves of the *dalli*-type porpoises suggested by the harpoon and gill net samples. The growth curves generated from the samples from the two harpooning cruises are similar, but different from that suggested by the gill net sample; harpoon samples below 4 (females) or 5 years (males) generally giving larger body size.

A plausible explanation for this is that faster growing individuals migrate to south and start to be attracted to a ship's bow wave at an earlier age than slower growing individuals, and that these individuals mature at younger age and segregate to the mothership gill net fishing ground and become less attracted to vessels at younger age than the slow growing smaller individuals. Thus, neither of the harpoon catch nor the gill net catch alone will correctly indicate the mean growth curve of the population.

Male sexual maturity

Body lengths of the smallest sexually mature male and of the largest immature one were in the body length groups of 168-171 cm and 196-199 cm, respectively (Table 1). The correlation between sexual maturity and body length was high compared with that between age and maturity. The materials from the two different sampling methods indicated an identical pattern (Fig. 5).

The attainment of sexual maturity and accompanying behavioral change in this species apparently depend on body size rather than age. Therefore we consider that the mean body length at the attainment of sexual maturity is correctly estimated by either sampling methods. Newby (1982) gave 182.5 cm, using larger sample, as the body length where 50% of the males were sexually mature. This will be the best available figure for the population.

In the harpoon sample, ages of the youngest mature male and of the oldest immature one were 2 years and 7 years, respectively, and there was observed almost no correlation between the proportion of mature individuals and the age (for ages 3 to 6 years) (Fig. 5). This is different from the result obtained from the gill net sample (Newby, 1982). We interpret this as indicating a balance between males which reach maturity and become takable by harpooning and those which become unavailable for capture by harpooning after a certain stage because of a geographical segregation of reproductive males and/or a change in their response to vessels (Kasuya and Jones, 1984).

Therefore, it is difficult to estimate from the harpoon samples the age where 50% of individuals are sexually mature. A similar phenomenon was reported by Kasuya (1978) for the harpoon sample of the Japanese coastal population of the Dall's porpoise. We do not know how the gill net sample cause bias in estimating the mean age at the attainment of sexual maturity. However, in view of the better correlation between age and maturity and the fact that the mean age estimated from the gill net sample (5.67 years, see Newby, 1982) is within the above range (3 to 7 years), we consider that males of this population will on average be reproductive at about 5 to 6 years of age.

Female sexual maturity

Using the presence of a corpus luteum or albicans as the indicator, the sexual maturity of females was identified more accurately than that of males. The smallest mature female and the largest immature one appeared between body lengths of 164-167 and 184-187 cm, respectively (Table 1). The relationship between the percentage of sexually mature females and body length in the harpooned sample is almost identical with that in the gill net sample (Fig. 5). Newby (1982) estimated the body length at which 50% of individuals were

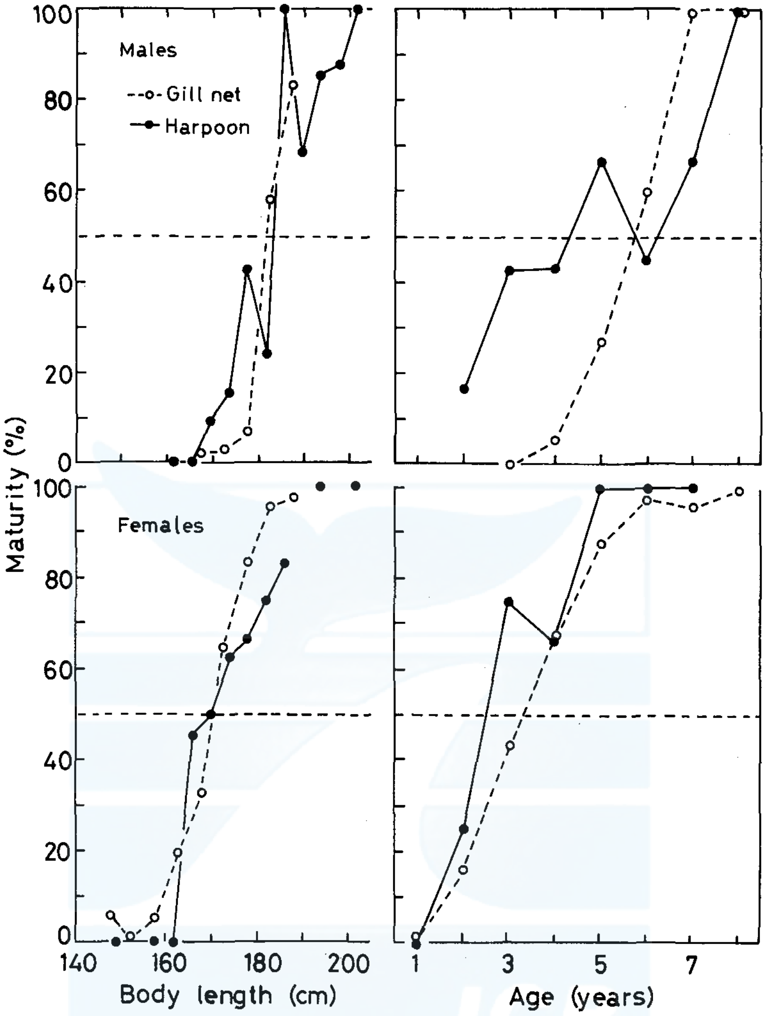

Fig. 5. Body length or age related change of the proportion of sexually mature individuals in *dalli*-type Dall's porpoise taken by harpooning (present material) and gill net fishery (Newby, 1982).

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sexually mature as 170.5 cm. This is considered as the present best available figure, because it is based on a large sample.

The mean body length of 21 females in the present material having only one corpus luteum and no corpus albicans ranged from 164 to 186 cm. The mean was 175.0 cm (sd=7.14). The fact that these two figures differ is not necessarily important, because the maturity-body length relationship is not necessarily symmetrical.

The ages of the youngest sexually mature female and the oldest immature one were 2 and 4 years, respectively (Table 2). The disagreement between the maturity-age relationships of the harpooned material and that of the gill net sample is smaller in females than in the males (Fig. 5). The segregation by growth stage may be less intense in females (Kasuya and Jones, 1984). We consider that the age when 50% of the females are sexually mature will be close to 3.3 years as estimated by Newby (1982) using a large number of samples taken in gill nets.

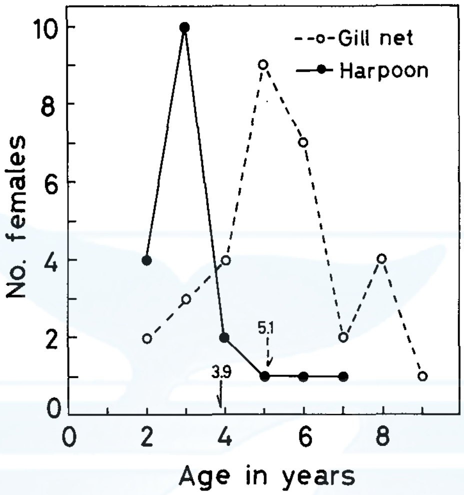

Fig. 6. Age composition of female *dalli*-type Dall's porpoise having corpus luteum of the first ovulation. Arrow indicates mean age.

Another estimate of the age at the attainment of sexual maturity is indicated by the ages of females with only one corpus luteum and no corpus albicans in the ovaries (Newby, 1982). Newby estimated the mean age as 5.1 years (range: 2 to 9 layers (years)). The corresponding figure for the present harpoon sample (19 aged individuals) was 3.9 years (range: 2 to 7 years). There is about one year difference between the two mean values, and two years difference in the peak ages of the two separate samples (Fig. 6). The one year difference of the mean is reasonable because the gill net sample of Newby (1982) was obtained in June and July and was represented by pregnant females with near term fetuses, whereas the present material was taken in August and September, or about 10 months earlier, and was represented by females at the early stage of pregnancy or shortly after ovulation (Table 3).

Even after taking account of the one year difference mentioned above, there still remains another one year discrepancy between the peak ages of the two data sets. The age frequency of females having only one ovarian corpus in the gill net sample was symmetrical (Fig. 6) as expected from the sigmoidal age-maturity relationship (Fig. 5). However that of the harpoon sample is skewed to the left. This suggests that the harpoon sample represents relatively precocious individuals, and will underestimate the age of first ovulation. This also implies that the gill net sample may overestimate the age of first ovulation to some degree. Therefore the mean age of the first ovulation in this population would be between 3 (peak age represented by harpoon sample, Fig. 6) and 4 years (peak represented by gill net sample, with correction for the length of the gestation period). This coincides well with the age of females at which 50% of the individuals are sexually mature estimated above (3.3 years, from Newby, 1982).

TABLE 3. REPRODUCTIVE STATUS OF ADULT *DALLI*-TYPES TAKEN BY THE *HOYOMARU NO.12* CRUISES IN 1982 AND 1983

No. of corpora	Pregnant		Preg. & lact.*		Ovulated**		Total
	'82	'83	'82	'83	'82	'83	
1	1	7			3	11	22
2	1						1
3		1			1		2
4	1						1
5			1				1
6					1		1
12	1						1
Total	4	8	1	0	5	11	29

*: Pregnant and simultaneously lactating.

**: Females having corpus luteum and neither pregnant nor pregnant and lactating. Pregnancy was identified by the presence of embryo recognizable under dissecting microscope or of embryonic membrane (7 embryonic membranes). Among the latter, recognizable embryos (over 4 mm) were found only in those over 10 cm in length (2 individuals), but none in those from 5 to 6 cm (5).

DISCUSSION

The validity of our conclusions relating to segregation and sample bias depend on the correspondence between our age determination technique and those of Newby (1982). We believe that our methods are in good agreement because (1) Kasuya and Newby cross checked each others readings (Newby, 1982), and (2) the age composition of 107 *dalli*-type porpoises that were taken in the gill net fishery and aged by Kasuya (1978) showed features similar to these obtained by Newby (1982), i.e. the highest peak at age one year and subsequent trough (Fig. 3). Similar age related selectivity of hand-held harpoons was reported by Kasuya (1978) on the Dall's porpoise off the Pacific coast of Japan and the striped dolphin, *Stenella coeruleoalba* (Meyen, 1833). Thus, we consider that the conclusions of the present study are not artifacts of age determination error.

Using harpoon sample (96% were *truei*-types), Kasuya (1978) analyzed the life history of Dall's porpoise off the Pacific coast of Japan and concluded that the individuals of the population attained sexual maturity at a mean body length of about 195 cm (male) or 187 cm (female). These figures are larger than the corresponding figures of the offshore western North Pacific population (*dalli*-types) by about 12 cm for males and 17 cm for females.

Age at the attainment of sexual maturity also seems to differ between the two populations. In the harpoon sample from the Japanese coastal population the proportion of the sexually mature individuals in the sample first attains 50% at the age of about 6.5 (male) or between 5.5 and 6.5 years (female). Taking account of the bias of harpoon sample, Kasuya (1978) estimated the mean ages at the attainment of sexual maturity as about 8 years (male) and 6.8 years (female). These are later than the corresponding figures of the offshore population by about 2 or 3 years (0.5 year difference of sampling season adjusted).

Therefore we conclude, as suggested by Kasuya and Jones (1984) based on smaller samples, that individuals in the population off the Pacific coast of Japan mature at a larger body length and possibly later. We believe that the size difference is the more direct information and reliable.

Since maturation is dependent on body size rather than age (see above), if the growth difference between the two populations resulted from a density dependent change in growth rate, we should expect a shortening of the prereproductive period, which may not be accompanied by a change in body length at the attainment of sexual maturity. However, the present study showed the different feature; maturation occurring at a lower age in the population of smaller body size. This suggests that the growth difference between the two populations is not a result of the density dependent change in the growth rate but the result of genetic differentiation.

The differentiation in age and body length at the attainment of sexual maturity indicated above for the two populations of the Dall's porpoise suggests the presence of a parallel difference in the body length at physical maturity. However, the analysis is not possible in the present study because of the sample bias in the catch of the harpoon fishery off the Japanese coast.

Kasuya (1978) suggested that the *dalli*-type individuals off the Pacific coast of Japan might not be inherent to the population but could be migrants from the offshore western North Pacific population or Sea of Japan population. He based his conclusion on the facts that the proportion of *dalli*-type in the catch by the fishery increased during the fishing season, and that the frequency of mixed schools of the two color types was lower than that expected from the assumption of random combination. After this study more data were accumulated to indicate that the geographical segregation of the two color types was rather distinct, and that in the area where both color types were present the occurrence of mixed schools of the two color types was much less than random combination and it was close to frequency of the hetero-specific mixed schools of other dolphin species (Kasuya and Jones, 1984; Miyazaki *et al.*, 1984).

Kasuya and Jones (1984) also showed that the *dalli*-type population in the western North Pacific segregated by growth and reproductive status and that the majority of breeding population was segregated (at least in the mating season) in the northern waters, where the *truei*-type was not recorded. Although it is not known at present how the members of the Japanese coastal population are segregated within its range, this is an additional information suggesting that the interbreeding between the two color types will be less frequent than it might be expected from their geographical coexistence or presence of the mixed schools.

We admit that the results of the present study alone do not provide a firm conclusion on the question of interbreeding between the two color types off the Pacific coast of Japan. However they suggest that the analyses of the growth of the *dalli*-type individuals found among *truei*-types in the Japanese coastal waters will be benefitial. If the growth difference is indicated, it is a strong indication of the genetic isolation between the color types. Then, in view of geographical segregation and minor genetic differenciation other than pigmentation, it will be reasonable to deal them as separate subspecies as proposed by Morejohn (1979). However, if they interbreed, we are unable to individually identify the two populations in the western North Pacific and the idea to deal the two color types as color morphs of one species (Houck, 1976) will be justified.

In view of the recent information on the segregation between the color types, the conclusion of Kuroda (1954; also see Wilke, Taniwaki and Kuroda, 1953) on *truei*-type fetuses found in the *dalli*-type cows should be reexamined based on the knowledge of the ontogenetic development of fetal pigmentation.

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