RE-EXAMINATION OF LIFE HISTORY PARAMETERS OF LONG-FINNED PILOT WHALES IN THE NEWFOUNDLAND WATERS*

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ABSTRACT

Age dependent life history parameters of the long-finned pilot whale were analyzed using recent technique of aging which allowed accurate age estimate for old individuals and materials taken in 1954 from the drive fishery off Newfoundland and once used by Sergeant (1962). In both sexes mean growth ceases at ages between 21 and 25 years, when natural mortality increases. Males live to age 36 years or about 10 years shorter than females. Natural mortality is dependent on age in both sexes, and male mortality exceeds that of females of the same age, thus causing age related decline of male proportion in the population. Pregnancy rate is not apparently dependent on age of females and the possibility of a large proportion of postreproductive females is rejected, which is different from feature known on the short-finned pilot whale. Additionally, long-finned pilot whales differ from short-finned pilot whales in the younger age at maturation, shorter longevity and higher proportion of adult males, suggesting less specialized reproductive strategy and difference in the social structure.

INTRODUCTION

A study on life history and reproductive biology of the long-finned pilot whale, *Globicephala melaena* (Traill, 1809), was published by Sergeant (1962) using materials obtained from the drive fishery off Newfoundland. This was the first delphinid biology based on reliable age determination. However, as recognized by himself, the age of older individuals tended to be under estimated due to the decrease of readability of dentine layers or cessation of the deposition at an age between 8 and 16 years, and reliable life history parameters were not available for older individuals. Recent study of Martin (1987) on long-finned pilot whales mass stranded on the British coast probably retained similar problem (IWC, 1987).

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After Sergeant (1962), there was a progress in age determination technique of toothed whales (Perrin and Myrick, 1981), and Kasuya and Matsui (1984) established age determination method for the short-finned pilot whale, *G. macrorhynchus* Gray, 1846, using annual growth layers in dentine and cementum apparent in decalcified and haematoxylin stained longitudinal section of the tooth. Based on this aging technique, Kasuya and Marsh (1984), Marsh and Kasuya (1984) and Kasuya (1986) analyzed the life history and reproductive biology of short-finned pilot whales taken by the drive fishery or small-type whaling with harpoon gun off the Pacific coast of Japan. These studies showed that the short-finned pilot whale exhibits a large longevity difference between males (46 years) and females (63 years), age dependent change in the pregnancy rate, and post-reproductive life time of females extending over 20 years. Marsh and Kasuya (1986) indicated further need to examine the presence of postreproductive females in *g. melaena*.

We reanalyzed in the present study some of the life history parameters of the long-finned pilot whale using materials of Sergeant (1962) and age determination method of Kasuya and Matsui (1984), and compared them with the results of short-finned pilot whales off Japan to find difference of the reproductive strategy between the two pilot whale species.

MATERIALS AND METHODS

This study is based on teeth of 437 long-finned pilot whales obtained from the drive fishery off Newfoundland and some accompanying biological data (Table 1). They were collected in June to October 1954 and were the major portion of the materials used by Sergeant (1962) for the study of age and growth. The teeth had been preserved in glycerin with a tag having specimen number, body length (measured to a nearest inch), sex and date on it.

Information was not available for male maturity. The reproductive status data of females (usually pregnancy and lactation only) were available for some limitted number of individuals. Although these data did not seem to be biased to certain body length classes (Fig. 2), our data contained high proportion of females of unknown reproductive status and very low number of resting females (adult females neither pregnant nor lactating), the former being close to the sum of the females in pregnancy or in lactation, and the latter amounts only 16% of the pregnant females (Table 2). This was because only females which were obviously pregnant or lactating were fully recorded and mature females of another reproductive status (resting) were underrecorded in the sample (Sergeant, 1962: p.56). Therefore mature females of unknown reproductive status were more likely to be in the resting status rather than pregnant or lactating.

The teeth had been cut transversely near the cingulum for the previous age determination. For the present age determination, we usually used only the root portion of the tooth. The crown side of old individuals did not usually

TABLE 1. MATERIALS USED IN THE PRESENT STUDY

Sex	Month*	With age and body length	With age but without body length**	Total
Male	July	43	0	43
	August	101	1	102
	Sept.	8	0	8
	Oct.	0	0	0
	Total	152	1	153
Female	July	67	1	68
	August	200	6	206
	Sept.	8	2	10
	Total	275	9	284

* All the materials were collected in 1954.

** Used for only age composition and age dependent sex ratio analysis.

have the most recent layers due to sawing off. The few exceptions were for 0 to 2 years old young tooth where the crown side of the tooth was used because the root was too short and thin. Either root or crown portion of the tooth was firstly rinsed in running water for one to two nights to remove the glycerin, longitudinally half sectioned, glued on a plastic plate, polished to a thickness of about 30 to 40 μm, decalcified in 5% formic acid for several hours, stained with Mayer's haematoxylin and mounted with Canadian balsam (Kasuya and Matsui, 1984).

Kasuya aged all the individuals without referring to any data of the specimen (including the date of sampling) and using method of Kasuya and Matsui (1984) outlined below:

(1) To have three independent counts for both cementum and dentine.
(2) To choose the middle figure as the best for each tissue.
(3) To use the best dentinal count if the pulp cavity is wide and the deposition of dentine was considered to be continuing on the entire pulp wall (open pulp cavity) or on part of the wall (closing one), or to use the best cemental count if the pulp cavity was narrow and lined by thin uniformly stainable dentine suggesting cease of the deposition (closed pulp cavity).
(4) A pair of stainable and unstainable layer was assumed to represent one year as deduced by Sergeant (1962), and any age between n and n+1 year was expressed by n+0.5 (n being an integer).

After aging all the individuals, the body length was plotted on age, and five individuals (two females and three males, see Figs 3 and 4) were found in the body length/age relationship to be apart from rest of the individuals. These individuals were excluded from the subsequent analyses, but ages of rest of the individuals were accepted as they stand (including 10 individuals having no body length data).

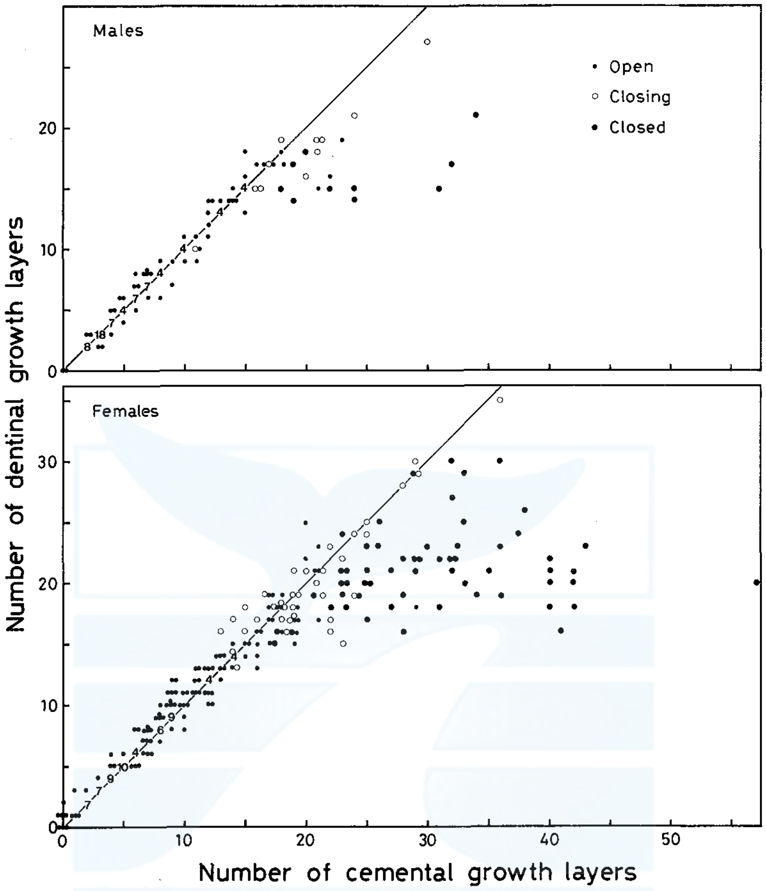

Fig. 1. Scatter plot of number of dentinal growth layers on that of cemental layers in the same tooth slide. Symbols distinguish the condition of pulp cavity. Numerals represent the number of individuals having open pulp cavity, and each of other mark represents one individual. The solid line represent equal deposition of layers in both issues.

RESULTS

Comparison between dentinal and cemental layer counts

Fig. 1 compares the number of growth layers in cementum and that in dentine of the same teeth. Since these tooth had been cut transversely to remove a piece of thin section for the previous age determination (Sergeant, 1962), we could not confirm on most of the present preparations if all the cemental or postnatal dentine layers were present (neonatal line in dentine could be identified only on the slide of juveniles prepared from the crown portion of the tooth). Although this did not necessarily imply loss of the first postnatal growth layer in either of the tissues, we were uncertain on tooth showing disagreement of counts in the two tissues if it came from the error of reading or from the deficit of the preparation. The readability of cemental and dentinal layers was slightly inferior to that of the short-finned pilot whales studied by Kasuya (1986) and Kasuya and Matsui (1984).

Admitting possible minor disagreement expected from the above deficit, we considered that growth layer counts in the two different tissues in a tooth slide were similar on most of the teeth having open or closing pulp cavity, but the correlation was lost on teeth with closed pulp cavity. The number of cemental layers exceeded that of the dentinal layers after ages between 15 to 20 years, and the magnitude of the disagreement increased with increasing age (Fig. 1).

We conclude therefore that growth layers in the two dental tissues are deposited at a same rate on young individuals, but on older individuals only the cemental layers continue deposition. And we assumed without direct evidence that the rate of cemental layer deposition stays same (annual) for the entire lifetime after the start of its deposition in early postnatal time (Kasuya and Matsui, 1984).

Body length composition and neonatal length

Body lengths of the 152 males ranged between the half-foot length groups of 5.5–6.0 feet (1.68–1.83m) and 19.5–20.0 feet (5.94–6.10m) (Fig. 2). A peak of large individuals was present between 17.5 and 19.0 feet (5.33 to 5.79m)

Body lengths of the 275 females were found between length groups of 6.0–6.5 feet (1.83–1.98m) and 16.0–16.5 feet (4.88–5.03m). A peak of larger individuals was present at lengths between 14.0 and 15.0 feet (4.27 to 4.57m), which was about 1 m smaller than that of the male. These features are similar to the body length frequencies presented by Sergeant (1962).

We had five (three female and two male) postnatal individuals having no neonatal layer in dentine, an indication of newborn calves (Kasuya and Marsh, 1984). Their body lengths were 175 and 198cm in males, and 173, 183, and 183cm in females (Figs 3 and 4). Mean of the five body lengths was 182.4cm. The range was nearly within the range of neonatal lengths of both sexes (165 to 191 cm) reported by Sergeant (1962), and the mean was close to the mean neonatal lengths (174 cm in females and 178 cm in males) estimated by him. We found no reason to change the neonatal length estimate of Sergeant (1962).

Male growth

The correlation between body length and age was very good before age 20 years, with most of the plots within the range of 70 cm, but it was apparently lost after an age between 21 and 25 years (Fig. 3). The male growth is rapid till the age of 2.5 years, or the body length of 2.7 to 3.3 m. After this

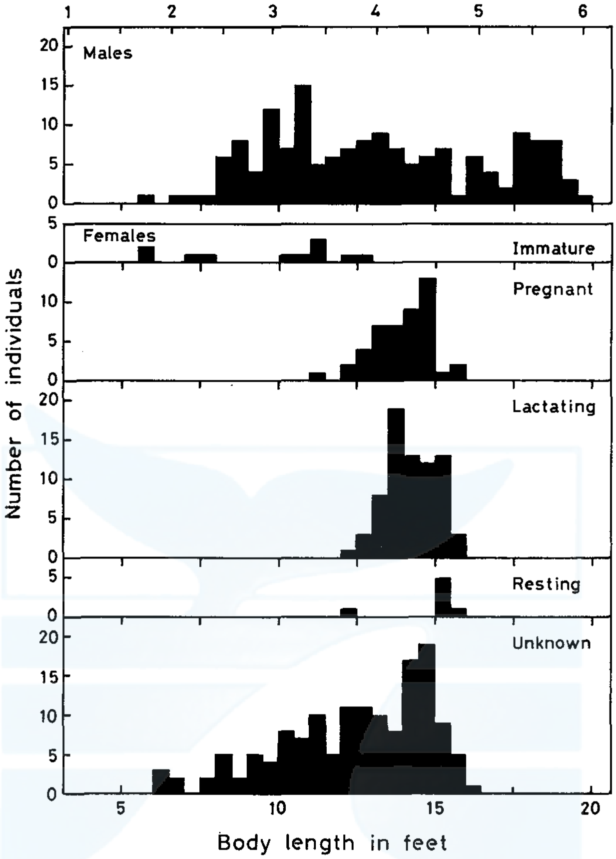

Fig. 2 Body length frequency of materials used in the present study. Scale at the top indicates body length in meter.

age, males grew at a slower but almost constant rate till the age of about 20 years. The inconspicuous secondary growth spurt probably started at about 12-13 years.

Although the mean body length seemed to stop increasing at an age between 21 and 25 years, and the mean body length of males over 25 years was 557 cm (n=5), we were unable to consider this figure as a reliable estimate of the mean asymptotic length of males due to the small sample size (Appendix Table 1).

The age at the start of secondary growth spurt (12-13 years) probably corresponds to the mean age at the attainment of breeding maturity 12 years estimated by Sergeant (1962). Due to the lack of adequate number of samples on age and maturity, Sergeant (1962) firstly estimated the mean age of breeding maturity (12 years) from a limited number of samples with good age estimate, then he read the mean body length of 4.88 m at breeding maturity on his mean growth curve corresponding to the age at the attainment of

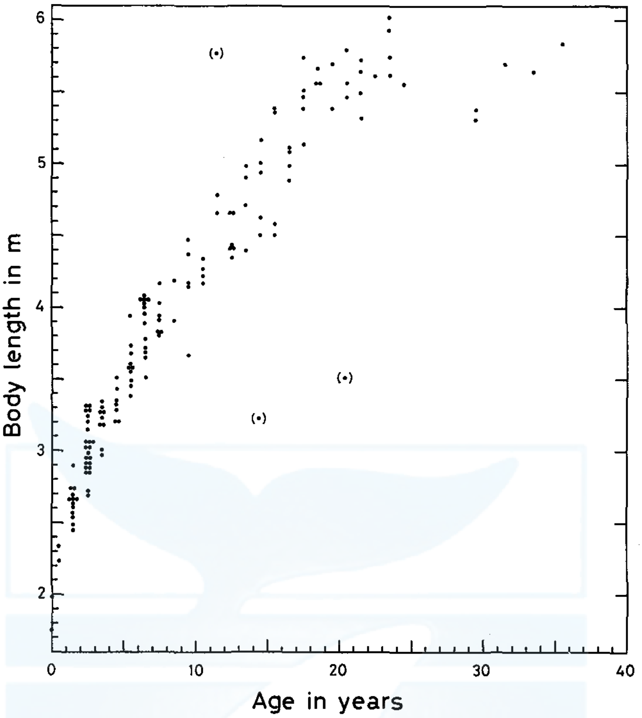

Fig. 3. Scatter plot of body length on age, males. Each mark represents one individual. Marks in parentheses indicate ages that were not used in the present alalyses.

breeding maturity. If the same method was adopted to the growth curve constructed in the present study, males were estimated to attain the length of 4.3 to 4.9 m at the mean age of breeding maturity (12 years). The middle value of this range, 4.6 m, was about 30 cm smaller than the estimate of Sergeant (1962). We consider that the difference is significant in view of the narrow individual variation of body length (see above).

This disagreement probably came from the overestimation of male growth by Sergeant (1962) due to the underestimation of age of many individuals over 8 to 16 years. Therefore, the present estimate of 4.6 m can be a better estimate of the mean male length at age 12 years (age at breeding maturity estimated by Sergeant (1962)). However, in view of slow and complicated procedure of maturation of males of the short-finned pilot whale (Kasuya and Marsh, 1984) and rather limited number of samples available for the long-finned pilot whale study (Sergeant, 1962), we feel that parameters relating to male maturity of the latter species require further investigation.

Female growth curve

Female body length increased almost at the same rate as that of the

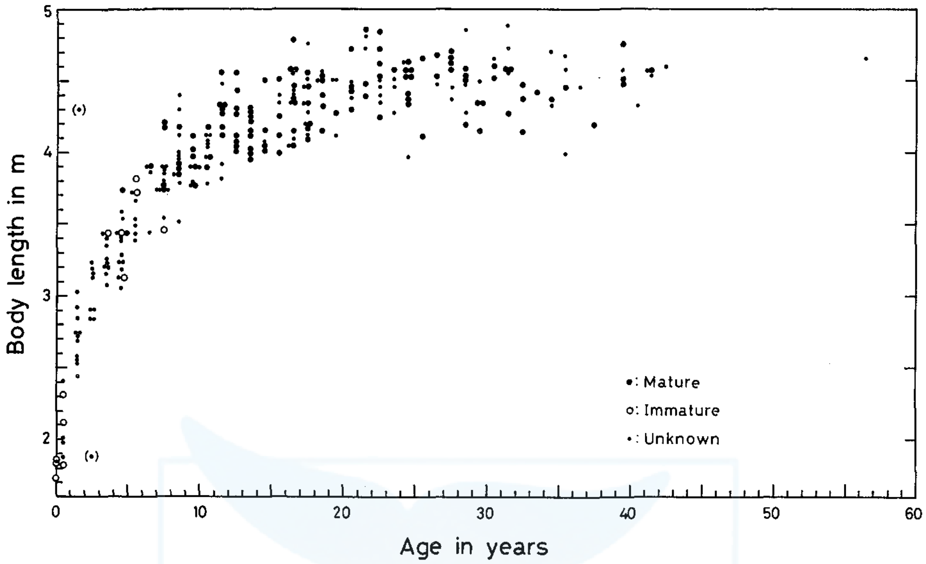

Fig. 4 Scatter plot of body length on age, females. Each mark represents one individual. Marks in parentheses indicate ages that were not used in the present analyses.

males till the age of 6 years (mean age of females at sexual maturity, see below) as indicated by Sergeant (1962) (Fig. 4), then the growth rate declined rapidly with increasing age, and the mean body length apparently ceased to increase at an age between 21 and 25 years. The mean body length of females over 25 years was 488.8cm (n=53, sd=18.6). This is the mean asymptotic length of females of this population.

Both mature and immature females were present at the body lengths between 11.0 and 13.0 feet (3.35 and 3.96m), and at the ages between 4 and 8 years (Figs 4 and 5). These ranges did not differ from corresponding figures estimated by Sergeant (1962). His estimation of the mean age and body length of females at the attainment of sexual maturity were 6 years and 12 feet (3.66m), respectively.

Age related change in female reproductive activity

Three resting females identified as senile by Sergeant (1962) were aged by us at 22.5, 30.5, and 41.5 years, and they were not always old. Marsh and Kasuya (1984) indicated the difficulty of identifying postreproductive females by macroscopic observation of ovaries. The oldest females of the present study at the pregnant, lactating, or resting status were aged at 39.5, 39.5 and 41.5 years, respectively (Fig. 5), which were close each other. Ages of three resting femals having corpus luteum of ovulation were 4.5, 24.5, and 25.5 years, and the age of a lactating female having corpus luteum of ovulation

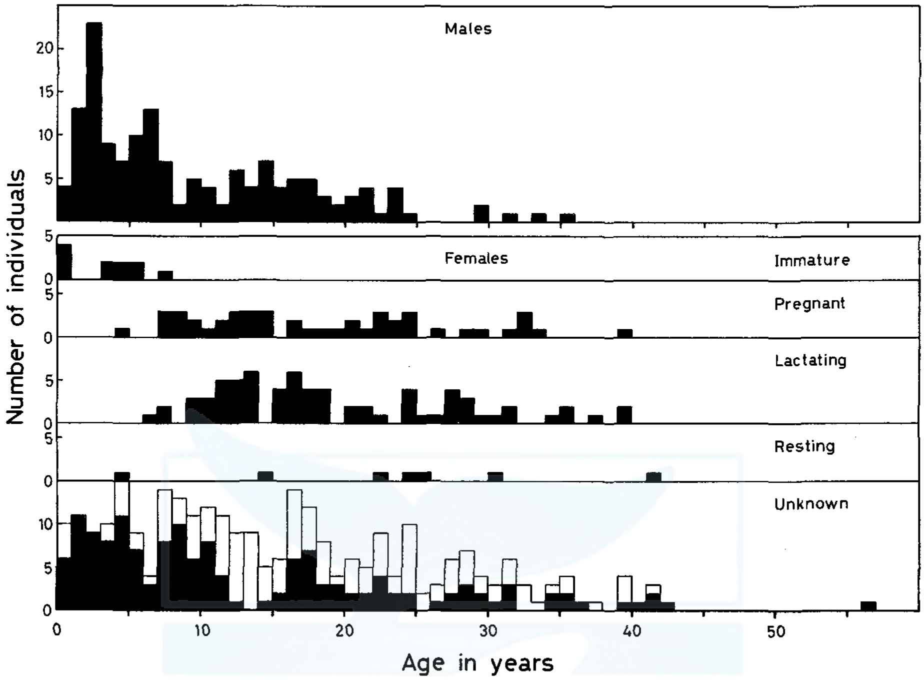

Fig. 5. Age composition and reproductive status of the long-finned pilot whale sample. White square at the bottom indicates sum of the females of known reproductive status.

was 31.5 years. These ages are younger than that of the oldest confirmed pregnancy.

Table 2 lists two kinds of pregnancy rates; (1) proportion of pregnant females in sexually mature females of known reproductive status, and (2) proportion of pregnant females in all the females including both immature and unknown reproductive status. Since females of unknown reproductive status in our sample probably tended to include more resting females than the pregnant or lactating ones (see above), the former figure will overestimate level of the apparent pregnancy rate of the sample, and this underrepresent, if it exists, the age dependent decline in the pregnancy rate. To the contrary, the latter will underestimate the apparent pregnancy rate (the degree of which will depend on the number of pregnant females classified to the unknown category), but will better reflect the age dependent change in the pregnancy rate if it exists.

None of the two pregnancy rate series in Table 2 showed significant age dependent change (Chi-square tests for ages over 10 years, $p > 0.5$). Thus, we were unable to conclude that the females of long-finned pilot whales off Newfoundland exhibit age dependent decline of reproductive activity, which was very distinct in the short-finned pilot whale populations off Japan and

TABLE 2. AGE DEPENDENT CHANGE IN APPARENT PREGNANCY RATE IN *GLOBICEPHALA MELAENA*.

Age (years)	Immature	Mature*				No. data	Pregnancy rate (%) **	
		P	L	R	T		(1)	(2)
0–10	11	8	6	1	15	75	53.3	8.8
10–20	0	17	37	1	55	28	30.9	20.5
20–30	0	14	19	3	36	20	38.9	25.0
30–40	0	6	9	1	16	10	37.5	23.1
40–50	0	0	0	1	1	4	0	0
50–60	0	0	0	0	0	1	–	0
Total	11	45	71	7	123	138	36.6	16.5

* P=pregnant, L=lactating, R=resting, T=total.

** (1) indicates proportion of pregnant females in mature females of known reproductive status, and (2) that in total females including females of immature and unknown maturity.

was an indication of the presence of postreproductive females (Kasuya and Marsh, 1984; Marsh and Kasuya, 1984; Kasuya, 1986).

The uncertainty that surrounds above analysis comes from the adult females of unknown reproductive status. If a 39.5 years old pregnant female is excluded, then all the 18 females over 33.5 years are non-pregnant or of unknown reproductive status (Appendix Table 2). Females of the latter category has high probability of not being pregnant, and might leave a possibility for postreproductive females. However, even under extreme assumption that they were all in the resting status, the number of pregnant females in the total females over 35 years (1/15) was not significantly different from that at 10-35 years (36/119) (Chi-square test, $0.2 > p > 0.1$), making it impossible to conclude the presence of significant number of postreproductive females in the population.

From the above analyses we conclude that the population of long-finned pilot whales has high reproductive capacity till the observed oldest age, although a larger sample may perhaps prove the presence of some postreproductive females among old females.

Sex ratio, age composition and mortality rate

The proportion of females in the sample increased from parity at ages below 10 years to 100% at age over 36 years (Table 3 and Appendix Table 2), or about 5 years earlier than the corresponding age for the short-finned pilot whale populations off Japan (Kasuya and Marsh, 1984; Kasuya, 1986). The decline of male proportion with increasing age will reflect the sexual difference of mortality rates and longevity (see below).

Sergeant (1962), using cementum age of limited number of selected individuals, showed that males lived to age of only 36 to 40 years while females did to age of 46 to 50 years. Ages of the oldest individuals of the present

TABLE 3. AGE RELATED CHANGE OF THE SEX RATIO IN *GLOBICEPHALA MELAENA.*

Age (years)	No. females	No. males	Total	Females (%)
0– 5	55	56	111	49.5
5–10	51	37	88	58.0
10–15	46	23	69	66.7
15–20	44	19	63	69.8
20–25	34	13	47	72.3
25–30	22	2	24	91.7
30–35	16	2	18	88.9
35–40	10	1	11	90.9
40–45	5	0	5	100.0
45–50	0	0	0	–
50–55	0	0	0	–
55–60	1	0	1	100.0
Total	284	153	437	65.0

material were 35.5 years in males and 56.5 years in females. However, the age of the oldest female seemed to be an outlier, and the ages of the next oldest male and female were 33.5 and 42.5 years, respectively (Appendix Table 2). Thus reasonable longevity difference between sexes of the long-finned pilot whale will be about 10 years as suggested by Sergeant (1962).

Age frequencies plotted on a logarithmic scale (Fig. 6) showed an apparent gradient change in both sexes at an age between 21 and 25 years. Additionally, there was observed in the male age composition a slight depression at ages between 8 and 17 years or at the age of puberty, suggesting a possible segregation of some pubertal males from the breeding schools. The similar feature was indicated for short-finned pilot whales off Japan (Kasuya and Marsh, 1984).

Ignoring the slight underrepresentation of pubertal males indicated above, we estimated the apparent annual mortality rate of males as about 0.07 at ages below 25 years (Table 4). The corresponding figure for ages between 21 and 36 years (the oldest male age) was calculated to be about 0.15 using very limited number of samples. For females, we estimated the corresponding figure of the mortality rates to be slightly over 0.02 (< 25 years) and about 0.1 (from 21 to the oldest individual). The male apparent mortalities are always higher than that of the females of the same age, as observed on the short-finned pilot whale off Japan (Kasuya and Marsh, 1984; Kasuya, 1986).

DISCUSSION

We re-examined several biological parameters of long-finned pilot whales off the Newfoundland waters using materials once used by Sergeant (1962) and

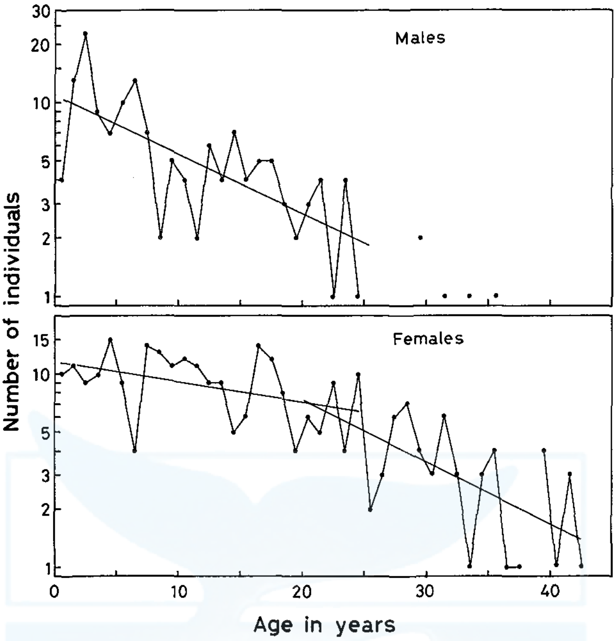

Fig. 6. Age frequency of long-finned pilot whale samples plotted on logarithmic scale. Straight line indicate linear regression of the frequency on age (see Table 4).

recently improved age determination method, which could give higher ages for many of individuals aged over 10 years by the previous method of aging using only dentinal layers. Among biological parameters examined, we found no reason to alter the previous estimate of Sergeant (1962) on neonatal body length, longevity, female age at the attainment of sexual maturity, and juvenile sex ratio. The growth curves of both sexes were altered slightly, and the mean asymptotic length of females and the age at the length were newly estimated in the present study.

In particular, we obtained new estimate of age composition of the catch and biological parameters derived from it. These allowed us to compare some life history parameters of long-finned pilot whales in the Newfoundland waters and those of short-finned pilot whales off Japan studied by Kasuya and Marsh (1984), Marsh and Kasuya (1984) and Kasuya (1986).

Apparent mortality rates calculated above are sums of natural mortality rate, fishing mortality rate and annual change in recruitment. Effect of the fishery on the latter two components is probably significant in the population of long-finned pilot whales, which had long history of hunting of relatively small scale (probably less than 500 individuals per year) by highly selective harpoon fishery and 3 years large scale harvest just prior to the commencement of present sampling (about 3,000 individuals per year) by less selective

TABLE 4. APPARENT ANNUAL MORTALITY RATES OF *GLOBICEPHALA MELAENA* ESTIMATED FROM AGE COMPOSITION.

Method		A	B
Female	0 – 25 years	0.0231	0.0201 ±0.0090
	21 – 43 years	0.0696	0.0682 ±0.0160
	21 – 57 years	–	0.0985 ±0.0122
Male	0 – 25 years	0.0683	0.0716 ±0.0115
	21 – 36 years	–	0.1497 ±0.0507

A: From the gradient of the linear regression in Fig. 6.
B: By segment analysis (Robson and Champman, 1961), best point estimate and standard error.

(Kasuya and Marsh, 1984) drive fishery (Sergeant, 1953; 1962; Mercer, 1975).

We consider that the drive fishery could have decreased absolute number of recruitment in the last 2 years preceding the sampling, but did not cause severe change in the age composition of older individuals. Thus we feel that the present age composition data are not suitable for the analysis of age dependent change in juvenile mortality rate.

To the contrary, the history of harpoon fishery over 7 years could have selectively killed larger individuals and changed the age composition and sex ratio of older individuals as observed on the short-finned pilot whales off Japan (Kasuya and Marsh, 1984). This causes difficulty to make meaningful comparison of apparent age dependent mortality rates between sexes. However, we consider that the present sample size is probably large enough to give a rough estimate of the maximum age which is allowed physiologically for the species, and that our finding of the shorter longevity of males allows our deduction of above result that males will have natural mortality rate exceeding that of the females of same age.

Ages of the oldest individuals in the sample of long-finned pilot whales were younger than those of short-finned pilot whale populations off Japan by 6 (including an outlier) or 20 years (excluding an outlier) in females or by 10 years in males, and were close to those of less specialized delphinid species such as striped dolphin, *Stenella coeruleoalba*, and spotted dolphin, *S. attenuata*, studied by Kasuya (1985). The difference of longevity between the two pilot whale species was in parallel with that of the age at sexual maturity (*G. melaena* of shorter life matures younger). Although reliable estimates of natural mortality rate are not available for either of the two pilot whale species, above longevity difference suggests a higher natural mortality of the long-finned pilot whale.

Although there remains a possibility that a larger sample may find some postreproductive females in old age classes, we have been unable to confirm age dependent decline of pregnancy rate in the long-finned pilot whale. This is in clear contrast with the life history observed on the short-finned pilot whale populations off Japan, where the confirmed pregnancy occurred below age of 36 years and lactation below 51 years while females lived for 63 years, and additionally their pregnancy rate declined with increasing age for all the age range over 8 years (Kasuya and Marsh, 1984; Marsh and Kasuya, 1984; Kasuya, 1986). We conclude therefore that female long-finned pilot whales have a shorter lifespan and breed till older age at a more constant rate than the short-finned pilot whale. We do not have data to compare the absolute annual pregnancy rates of the two species. Not denying the possibility that the above features of reproduction of long-finned pilot whale could have been enhanced in some degree by the continued expolitation, we suggest that the differences indicated between the two pilot whale species are principally species specific.

In a short-finned pilot whale population off Japan, individuals become reproductive at the mean ages of 9 years (female) and 17 years (male), and the sex ratio of adult individuals is 0.27 (adult males/adult females) (Kasuya and Marsh, 1984). In the population of long-finned pilot whales, males mature at a lower age (probably at 12 years) relative to the age of female maturity (6 years), and the natural mortality rate of both sexes appear to increase at a similar age (21-25 years) while there is large difference in the short-finned pilot whale off Japan (28 years in males and 46 years in females). These resulted in the higher adult male ratio of 153/220=0.70 (estimated from the age composition), which is closer to those of more generalized delphinids, e.g. 0.77 of *Stenella attenuata* (Perrin, Coe and Zweifel, 1976), 0.91 of *S. longirostris* (Perrin, Holts and Miller, 1977) and 1.1 (=1278/1191) of *S. coeruleoalba* (Miyazaki and Nishiwaki, 1978)

Above analyses indicate that the long-finned pilot whale has life history parameters which are apparently less specialized than those of the short-finned pilot whale, and that its reproductive strategy and social structure will not be the same with those of the short-finned pilot whale. The cohesive matrilineal school structure and long maternal care of the latter species (Kasuya and Marsh, 1984) may not be so pronounced in the long-finned pilot whale population off Newfoundland.

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APPENDIX TABLE 1. AGE–LENGTH KEY OF *GLOBICEPHALA MELAENA* (CM).

Age (years)	Males			Females		
	no. samples	mean	sd	no. samples	mean	sd
0.5	4	207.8	23.0	10	199.3	21.4
1.5	13	264.3	11.4	11	270.6	16.7
2.5	23	303.0	17.9	8	302.0	15.4
3.5	9	319.7	12.3	10	327.1	11.9
4.5	7	332.9	10.6	15	333.5	17.9
5.5	10	360.1	15.0	8	358.9	14.5
6.5	13	387.7	17.9	4	376.5	19.4
7.5	7	393.1	11.7	14	379.5	19.4
8.5	2	405.0	14.0	13	398.4	22.2
9.5	5	416.8	26.9	9	389.4	11.2
10.5	4	425.0	6.3	10	401.1	11.0
11.5	2	471.5	6.5	10	422.2	21.9
12.5	6	448.3	12.1	8	421.9	18.4
13.5	4	474.3	22.8	9	413.4	12.3
14.5	6	481.8	23.0	5	415.0	18.0
15.5	4	495.3	41.8	6	426.2	17.2
16.5	5	508.2	16.1	14	436.4	21.4
17.5	5	544.4	19.7	12	435.9	18.0
18.5	3	559.3	4.7	7	441.7	13.6
19.5	2	553.5	15.5	4	434.5	16.5
20.5	3	560.3	13.8	6	445.3	13.3
21.5	4	554.0	15.6	5	464.6	18.3
22.5	1	561.0	–	9	451.2	18.0
23.5	4	582.3	15.8	4	444.0	12.3
24.5	1	556.0	–	10	444.8	18.9
≥25.5	5	557.2	19.8	53	448.8	18.6

APPENDIX TABLE 2. AGE AND REPRODUCTIVE STATUS OF *GLOBICEPHALA MELAENA*.

Age	Females						Males
(year)	immat.	mature			unknown	total	
		preg.	lact.	rest.			
0.5	4				6	10	4
1.5					11	11	13
2.5					9	9	23
3.5	2				8	10	9
4.5	2	1		1*	11	15	7
5.5	2				7	9	10
6.5			1		3	4	13
7.5	1	3	2		8	14	7
8.5		3			10	13	2
9.5		2	3		6	11	5
10.5		1	3		8	12	4
11.5		2	5		4	11	2
12.5		3	5		1	9	6
13.5		3	6			9	4
14.5		3		1	1	5	7
15.5			4		2	6	4
16.5		2	6		6	14	5
17.5		1	4		7	12	5
18.5		1	4		3	8	3
19.5		1			3	4	2
20.5		2	2		2	6	3
21.5		1	2		2	5	4
22.5		3	1	1**	4	9	1
23.5		2			2	4	4
24.5		3	4	1*	2	10	1
25.5			1	1*		2	
26.5		1	1		1	3	
27.5			4		2	6	
28.5		1	3		3	7	
29.5		1	1		2	4	2
30.5			1	1**	1	3	
31.5		1	2*		3	6	1
32.5		3				3	
33.5		1				1	1
34.5			1		2	3	
35.5			2		2	4	1
36.5					1	1	
37.5			1			1	
38.5							
39.5		1	2		1	4	
40.5					1	1	
41.5				1**	2	3	
42.5					1	1	
56.5					1	1	
Total	11	46	71	7	149	284	153

* Includes one female having corpus luteum of ovulation.

** Classified as "senile" by Sergeant (1962).