

Life History and Reproductive Biology of the Short-Finned Pilot Whale, *Globicephala macrorhynchus*, off the Pacific Coast of Japan

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ABSTRACT

After a period of heavier exploitation in the 1940s, the short-finned pilot whale has been hunted at a lower rate of several hundreds per year by a small-type-whaling and drive fishery off the Pacific coast of Japan. Age data from 373 females and 170 males obtained from 27 schools which were stranded or driven during the 17-year period from 1965 cover all months except March, April, September and November. Breeding is diffusely seasonal, with a single parturition peak in July–August. A single calf is born at a mean body length of 140 cm after 14.9 months gestation and nursed for a minimum of about two years. Calves of older cows may be nursed for considerably longer than this. Females mature at 7–12 ($\bar{x} = 9.0$) years, produce an average of four to five calves, and have their last calf before age 40 years, even though they may live up to 63 years. In contrast, males have a maximum longevity of only 46 years and probably continue to be capable of reproduction until death. In males, puberty begins at 7 to 17 ($\bar{x} = 14.6$) years and social maturity at an average of 17 years.

The age composition suggests that the total mortality rate is lowest in the post-pubertal stage and that it increases after age 28 (male) or age 46 (female). Males have a higher total mortality rate than females at any given age. The juvenile total mortality rate is probably higher than that of post-pubertal animals. These differences in total mortality rates may reflect differences in natural mortality rates. Using an hypothetical stationary population model, we estimate that the total annual mortality rate over all age classes is 8.3% (male) and 4.5% (female). Thus there are more reproductive females than adult males. The mating system is polygynous. Males may migrate between schools after weaning. However, females probably stay in their mother's school for life, so that the breeding schools are essentially matrilineal kinship groups.

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1. INTRODUCTION

The genus *Globicephala* Lesson, 1828, includes two species (van Bree, 1971). The long-finned pilot whale, *G. melaena* (Traill, 1809), occurs in the higher latitudes of both hemispheres, while the short-finned pilot whale, *G. macrorhynchus* Gray, 1846, occurs in warm-temperate and tropical waters. *G. melaena edwardii* is considered to be a separate subspecies in the Southern Hemisphere (Davies, 1960). *G. macrorhynchus* also includes geographical forms (Anon. 1975; Polisini, 1980).

As *G. melaena* has not been confirmed from the North Pacific since the 12th century (Kasuya, 1975), *G. macrorhynchus* is the only extant member of the genus in this area. In the western North Pacific, *G. macrorhynchus* occurs in waters with surface temperatures above 15°–16 °C and under the influence of the Kuroshio Current and its tributaries. Thus distribution is seasonal along the Pacific coast of northern Japan and in the Sea of Japan (Kasuya, 1975). In this area, the short-finned pilot whale is thought to feed exclusively on squid, although there has not yet been a detailed study of its food habits.

Sergeant (1962a) published a study of the biology of *G. melaena* off the coast of Newfoundland. This was the first paper to detail the life history of a delphinid based on a reliable technique of age determination and was an important landmark in cetacean research. There have been several subsequent studies on the growth and reproduction of this species (e.g. Sergeant, 1962b; Cowan, 1966; Mercer, 1975).

A weakness of Sergeant's (1962a) study (which he recognized) was that because of a shortage of labour, he was forced to concentrate on collecting different data and samples at different times. This inevitably led to a lack of corroborative data from individual animals. In particular, detailed information about both age and reproductive status were generally not available. Another problem was Sergeant's inability to use cemental layer counts in the main part of his study.

Since then, there have been advances in the techniques of preparing teeth for age determination (see Perrin and

Myrick, 1980). However, up till now these techniques have not been applied to a significant sample of *Globicephala*. We report the results of a study on reproduction and life history of *G. macrorhynchus* parallel to that of Sergeant's (1962a) study of *G. melaena*. Our study is based on data of 565 females, 241 males and a few individuals of unknown sex in 27 schools caught or stranded off the Pacific coast of Japan in the 17 years since 1965. Two companion studies on *G. macrorhynchus*, one on the functional morphology of the ovaries (Marsh and Kasuya, 1984), the other on age determination and growth (Kasuya and Matsui, in press) have been reported separately.

2. MATERIALS AND METHODS

2.1. Data source

Most of the data and specimen materials were collected between 1965 and 1981 inclusive from 27 schools of *G. macrorhynchus* caught on the Pacific coast of Japan by the drive fishery at Taiji, Futo, or Arari, and from one school stranded at Choshi in the Chiba prefecture. The linear distance between the southernmost location, Taiji, and the northernmost, Choshi, is about 500 km (Fig. 1).

The quality and quantity of data and samples varied between the schools. In the early period of the study (Schools 1–6), effort was directed to the collection of materials for taxonomy, and the data obtained for the present analyses were limited and biased to adult individuals. These data have been used only for the analyses of postnatal and foetal growth. Information from four schools (Schools 8, 19, 20 and 21) examined by volunteers was usually limited to sex and body length, and thus the identification of reproductive condition was less precise. These data were also used in the analyses of foetal and neonatal growth and for some school-structure analyses. The 14 schools caught in the seven years from 1975 to 1980 and examined by Kasuya constituted the major source of data used for the study of reproduction and for the construction of the life table as well as for the analyses of growth and school structure. After most of the mathematical analyses of the present study were

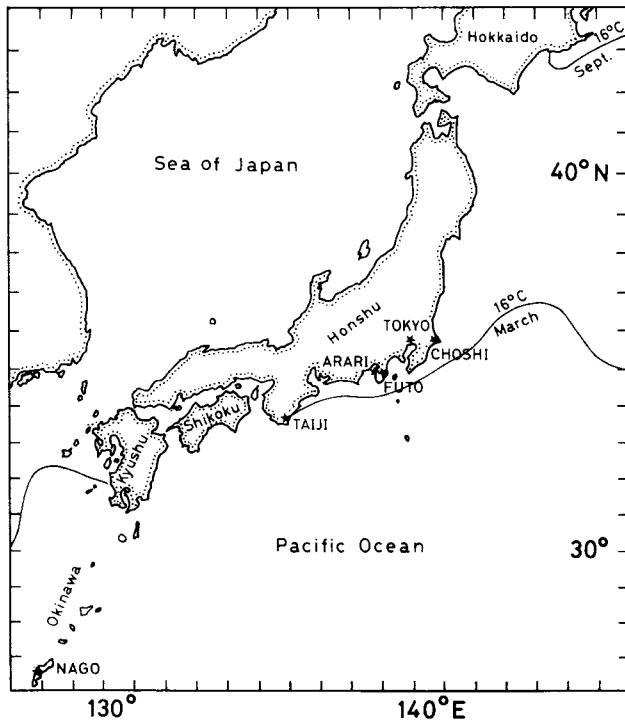


Fig. 1. Map of the waters adjacent to Japan showing the 16°C mean surface isothermal lines (Japan Oceanographic Data Center, 1978) in March and September.

completed using the data from the first 24 schools, Schools 25, 26 and 27 were examined; only adult females were aged. Data from the last three schools were not used in the main body of the study but have been included in the analysis of post-reproductive females, and where indicated in some text figures. The sex and body-length data of 19 fetuses examined between July 1976 and December 1980 and provided by Mr M. Yonekura or by Mr S. Matsui were also used.

Further details of the 27 schools are shown in Table 1. Additional information concerning the schools, which was usually collected by Kasuya from the chief of the driving team soon after the operation, is as follows:

School 1. Found 7 nautical miles NW of Arari. Six fetuses of unknown mothers were also examined. Record of female sexual condition was unsystematic.

School 2. Stranded. Large individuals were selected for skeleton and external measurements.

School 3. Large individuals were selected for skeleton and external measurements. Most of the catch was later freed.

School 4. Record of female sexual condition was unsystematic. One calf (142 cm, female) was born in captivity.

School 5. Record of female sexual condition was limited to few individuals. Two male calves (141 cm and 138 cm) were born in captivity.

School 6. No sample collected. Data for adult females probably not random.

Table 1
Materials used in this study

School no.	Locality	Date of		No. of individuals				Used for	Examined by
		Catch	Data collection	Driven	Examined	Aged	Lost		
1	Arari	20 Oct. '65	21 Oct. '65	33	18	8	15	A	KK, SO, TK
2	Choshi	13 Dec. '66	15 Dec. '66	ca. 90	9	3	80	A	KK, SO
3	Arari	— June '67	27, 28 June '67	> 30	14	4	16	A	RLB, TK
4	Taiji	22 July '69	July–Aug. '69	31	9	2	22	A	TK
5	Taiji	27 July '69	July–Aug. '69	46	23	10	23	A	KH, TK
6	Taiji	24 Feb. '71	24 Feb. '71	24	12	0	12	A	NM
7	Taiji	17 Jan. '75	18, 19 Jan. '75	28	28	26	0	A, B, C	RLB, TK
8	Taiji	21 Jan. '75	21, 22 Jan. '75	52	52	0	0	A, C	SM
9	Taiji	24 June '75	25 June–4 Jul. '75	ca. 230	173	125	57	A, B, C	CG, NM, TK
10	Taiji	22 July '75	22–24 July '75	33	32	18	1	A, B, C	SM, TK
11	Taiji	13 Jan. '76	13–17 Jan. '76	28	26	21	2	A, B, C	TK
12	Taiji	4 Feb. '76	5, 6 Feb. '76	20	20	18	0	A, B, C	TK
13	Taiji	7 Oct. '76	8, 9 Oct. '76	38	38	38	0	A, B, C	TK
14	Futo	20 Dec. '77	21 Dec. '77	25	25	22	0	A, B, C	NM, TK
15	Futo	24 Dec. '77	25 Dec. '77	48	48	45	0	A, B, C	ST, TK
16	Taiji	20 Feb. '78	20, 21 Feb. '78	27	27	27	0	A, B, C	TK
17	Futo	4 Dec. '78	5 Dec. '78	52	52	49	0	A, B, C	EM, TK, TO
18	Futo	13 Dec. '78	13, 14 Dec. '78	28	28	28	0	A, B, C	EM, TK, TO
19	Taiji	6 Jan. '80	6 Jan. '80	26	23	0	3	A, C	SS
20	Taiji	17 Jan. '80	17, 18 Jan. '80	14	14	7	0	A, C	SS
21	Taiji	2 Feb. '80	2 Feb. '80	19	17	0	2	A, C	SM
22	Taiji	20 Feb. '80	23 Feb. '80	15	15	15	0	A, B, C	TK
23	Taiji	21 Feb. '80	24 Feb. '80	23	23	23	0	A, B, C	TK
24	Taiji	30 May '80	31 May–3 June '80	38	38	38	0	A, B, C	TK
25	Taiji	3 Oct. '81	4–6 Oct. '81	ca. 35	16	9	19		TK
26	Taiji	3 Oct. '81	4–6 Oct. '81	ca. 35	29				TK
27	Taiji	5 Oct. '81	6 Oct. '81	—		14			TK

A: analyses of growth and seasonality of reproduction. B: analyses of mortality and pregnancy rate. C: analyses of school and population structure. CG: Miss Camille Goebel; EM: Miss Etsuko Miyahara; KH: Dr Keiji Hirose; KK: Mr Kazuo Kureha; NM: Dr Nobuyuki Miyazaki; RLB: Dr Robert L. Brownell Jr; SM: Mr Susumu Matsui; SO: Dr Seiji Ohsumi; SS: Mr Satoshi Shiraga; ST: Dr Sho Tanaka; TK: Dr Toshio Kasuya; TO: Mr Tsuguo Otake; Arari: 34° 49' N, 138° 46' E; Choshi: 35° 43' N, 140° 52' E; Futo: 34° 54' N, 139° 09' E; Taiji: 33° 34' N, 135° 54' E.

- School 7. All the members of the school were driven for four and a half hours after sighting. No other cetacean school was observed. Ages of two resting females (350 cm, 13 ovarian corpora; 352 cm, 10 corpora) were not estimated.
- School 8. All members were captured and examined for body length and sex. No samples collected.
- School 9. Several schools of *G. macrorhynchus* and a school of about 100 bottlenose dolphins, *Tursiops truncatus*, were found about 400 to 500 m from a school of killer whales, *Orcinus orca*. All members of the first two species are driven for 2.5 hours. Fishermen killed the larger pilot whales, and freed all the bottlenose dolphins and about 60 smaller pilot whales. The latter were probably adult females and immature individuals of both sexes. All the individuals processed (173 whales) were examined. The reproductive status of only 85 of the adult females were precisely recorded (Nos. 21–127).
- School 10. Three or four schools of *G. macrorhynchus* totalling about 200 individuals were found off Taiji. One school was driven and captured. No samples were collected from nine whales killed on 22 July and examined by S. Matsui.
- School 11. All members were driven into Taiji Port. After capture, one possible adult female was lost and two calves were released without examination. Several bottlenose dolphins found with the pilot whales were not captured.
- School 12. One of the five or six schools of *G. macrorhynchus* was driven to Taiji together with a school of bottlenose dolphins (about 20 individuals). No individuals were lost.
- School 13. Found alone, 10 to 20 nautical miles east of Taiji. All individuals were driven. Body-length measurements and collection of teeth from five individuals killed on 7 Oct. done by M. Yonekura.
- School 14. Found about 30 nautical miles off the Futo Port near schools of Pacific white-sided dolphins, *Lagenorhynchus obliquidens*, and *Tursiops truncatus* only. At the entrance of the port, one adult male was lost.
- School 15. Found about six nautical miles off Habu on the coast of the Ohshima Island, or about 25 nautical miles from Futo Port. One of several widely-scattered schools was driven. No whales were lost during the drive. Bottlenose dolphins were found with the whales but not driven.
- School 16. Several hundred pilot whales were found. One group closest to the port was driven without loss. Bottlenose dolphins were found with the pilot whales but not driven.
- School 17. Several *Globicephala* schools were found two to three nautical miles SE of Futo Port. The largest school was driven. *Tursiops* schools also present and one school driven with the pilot whales was released before arriving at the port. No whales were lost during the drive.
- School 18. Several pilot whale schools were found at about four to five nautical miles off Futo Port. None was lost during the drive.
- School 19. Found about five nautical miles south of Taiji (0805 hr); no other cetacean school present. Driven into Tsuga Port near Taiji (1430 hr). Twenty-two of the 26 whales caught were examined by S. Shiraga. One adult male, a juvenile, and two individuals of unknown sex were discarded by fishermen and not examined. Only body length and sex recorded. No samples collected.
- School 20. Found four to five nautical miles SE of Taiji (0800 hr), and driven into Taiji Port (0930 hr). No other cetacean school present. All individuals examined by S. Shiraga. Reproductive status not recorded for seven whales. Two live whales were sent to an aquarium.
- School 21. Seventeen of the catch of 19 whales were examined by S. Matsui for body length and sex. Reproductive status was not recorded systematically. No samples collected.
- School 22. Found in the morning five to six nautical miles off Taiji and driven into the nearby Tsuga Port that afternoon. All whales caught and examined. No other cetacean school found.
- School 23. Found in the morning four to five nautical miles off Taiji and driven into Taiji Port that morning. All individuals captured and examined. No other cetacean school found.
- School 24. Several *Globicephala* schools were found five to six nautical miles off Tawara with a school of bottlenose dolphins. One of the pilot whale schools was driven without loss to Taiji Port.
- School 25. Found about five nautical miles off Taiji and driven to Taiji Port. Only 16 of about 35 whales caught were examined.
- School 26. Found near school 25 and driven to Taiji Port by the other hunting team. Twenty-two of the catch of about 35 were examined.
- School 27. No information, mixed with the last two or three individuals of school 26.

2.2. Field procedures

Flensing was usually done within a few days of the drive, but occasionally whales were kept in a netted bay for up to 16 days. The information and samples listed below were collected by Kasuya, volunteers, or both, while the fishermen were flensing. At this stage, each pilot whale was assigned a sample number which is a hyphenated combination of the school number followed by the number of the animal within the school.

1. Sex.

2. *Body length*. Measured to the nearest 1 cm on a straight line parallel to the long axis of the body, from the anteriormost point to the bottom of the tail fluke notch. Although the tip of the upper jaw is the anteriormost point of the body of juveniles, it lies posterior to the front end of the melon after the whale is about 240 cm long and becomes difficult to distinguish (Yonekura, Matsui and Kasuya, 1980). Thus the measurement of body length is not exactly comparable for adults and calves less than one year old.

3. *Teeth*. One to three contiguous teeth were collected from the centre of the lower tooth row with a hammer and chisel and preserved in 10% buffered formalin. The largest available teeth were selected.

4. *Mammary glands*. The presence and colour of milk

was checked by pressing and then cutting the glands. If possible, the maximum thickness of one mammary gland was measured, and a histological sample was taken and fixed in 10% buffered formalin. The presence of colostrum or other fluid in the lumen was recorded.

5. *Testes*. Both testes were collected from 51 immature and adult individuals, cut transversely at mid-length and fixed in 10% buffered formalin. Only one testis from either side was collected from the remaining 112 whales. It was fixed as above if it weighed less than 500 g. Testes exceeding 500 g were weighed at flensing after removing the epididymis. A mid-length histological sample was then collected.

6. *Epididymides*. In the case of a small testis the entire epididymis was collected and fixed as well. In fully grown individuals, a histological sample was taken opposite the testis mid-length and fixed with the testis.

7. *Ovaries*. Both ovaries were collected from all females and fixed in buffered 10% formalin. The left ovary was marked with a nick. The presence of corpora lutea, corpora albicantia and large follicles was recorded.

8. *Uteri*. If time permitted, the maximum diameter of each uterine horn was measured, with the uterus on a flat floor. Histological samples were usually collected from the larger horn and fixed in 10% formalin.

9. *Foetuses*. Sex and body length were recorded. If a corpus luteum was found and there was no large foetus in the uterus, both uterine horns were saved and opened carefully to search for a small embryo, which could be detected more easily before fixation. A foetus was often not detected in spite of the presence of a corpus luteum. If the uterine cornua were fairly similar in size, the whale was classified as recently ovulated (not pregnant). On rare occasions non-lactating females were observed with one large asymmetric uterine horn with a congested endometrium suggesting a recent abortion.

10. *Stomach contents*. Stomach contents of the juveniles were, if time permitted, examined macroscopically for solid food or milk.

2.3. Laboratory procedures

1. *Age determination*. This was done by Kasuya, who counted the annual growth layers in dentine or cementum in haematoxylin-stained, decalcified sections 30–40 μm thick, as detailed in Kasuya and Matsui (in press).

The age of each individual was expressed as the number of growth layer cycles (equivalent to Growth Layer Groups – GLGs – of Perrin and Myrick (1980)). After studying the seasonal pattern of dentinal growth-layer deposition and seasonal changes in the thickness of the dentinal layer being laid down in the teeth of 270 females and 147 males which died in January, February, May, June, July, August, October and December, Kasuya and Matsui (in press) decided that dentinal growth-layer deposition was annual. For most whales in which dentine deposition was continuing (i.e. those with an open or closing pulp cavity), the counts of dentinal and cemental growth layers were very close. Kasuya and Matsui (in press) therefore concluded that cemental growth-layer deposition was also annual and used the cemental-layer count to estimate the age of individuals with teeth which had closed pulp cavities.

Kasuya and Matsui (in press) estimated the magnitude

of the errors likely to result from these methods of age determination and concluded that the 95% confidence range for the age estimates at ages 10, 20, 40 and 60 years are ± 0.9 , ± 1.8 , ± 2.6 and ± 3.4 years, respectively.

The ages of juveniles from which teeth for age determination were not available were estimated from their body lengths as outlined in Kasuya and Matsui (in press). Using this technique, it is possible to estimate age \pm two years for females below 280 cm (mean age about five years) or for males below 320 cm (mean age about eight years).

The age of individuals below 10 years was roughly estimated to the nearest $\frac{1}{4}$ year by considering the thickness and nature of the first and last postnatal dentinal layers of incomplete thickness. For whales over 10 years, the age was grouped into the nearest $n+0.5$ years ($n = \text{integer}$).

2. *Testes*. Each fixed testis was weighed to 0.1 g after removal of the epididymis. A testicular smear was taken from a transverse cross-section at the mid-length, dried, stained in 0.1% toluidine blue for a few minutes, rinsed in water, and air-dried. Samples for histology were taken from the centre (position 6 in Fig. 4) of one testis at mid-length for all individuals. In some whales, additional samples were taken from the periphery near the attachment of the cauda epididymis at the testis mid-length (position 7) and from the periphery opposite the cauda epididymis (position 5). In addition, histological samples were taken from 11 sites from one testis of two whales to see if different regions of the same testis were at different stages of maturity. Haematoxylin and eosin (H-E)-stained slides were prepared from paraffin sections of all histological samples, using standard techniques.

The stained and dried testicular smears were scanned with a microscope (10–20 \times) by Kasuya. The relative density of spermatozoa was classified as follows using a field diameter of 1.82 mm (see Fig. 10 for corresponding densities in epididymal smears).

- (a) Absent
- (b) Doubtfully present: one or two spermatozoa in several fields.
- (c) Scanty: less than 10 spermatozoa per field.
- (d) Intermediate: density between scanty and copious (maximum density observed for ordinary adult testes).
- (e) Copious: abundance similar to that usually found only on an epididymal smear.

The histological slides were examined by Kasuya at a magnification of 100–400 \times . By observing the entire section, which usually measured about 5 \times 7 mm, the ratio of the mature and immature tubules was calculated based on 70 to 150 tubules. Usually 20 diameters of the seminiferous tubules were measured for each sample on one or two enlarged black-and-white photoprints and the arithmetic mean diameter calculated.

3. *Epididymides*. An epididymal smear was taken from a position opposite the testis mid-length, and observed by Kasuya as described for the testicular smear. A sample for histology was taken from the same location, processed, H-E stained and mounted as above.

4. *Mammary glands and endometria*. Reference histology slides were prepared from paraffin sections using standard techniques. The mammary-gland sections were stained with H-E. The sections of endometrium were

Table 2
Catch of *G. macrorhynchus* off the Pacific coast of Japan

Year	Small-type whaling			Other fisheries, Pacific area					Total Pacific coast ^H
	A	B	Taiji ^C	Taiji ^D	Total Taiji ^E	Izu ^F	Okinawa ^G	Other areas ^D	
1948	725	426	38	—	—	—	—	—	—
1949	890	814	283	—	—	—	—	—	—
1950	715	668	233	—	—	224	—	—	—
1951	618	585	227	—	—	425	—	—	—
1952	335	322	131	—	—	650	—	—	—
1953	460	456	141	—	—	349	—	—	—
1954	75	80	20	—	—	31	—	—	—
1955	61	57	12	—	—	86	—	—	—
1956	297	275	141	—	—	126	—	—	—
1957	174	178	98	—	—	—	—	—	70
1958	197	—	—	—	—	—	—	—	266
1959	144	—	—	—	—	—	—	—	192
1960	168	—	—	—	—	—	243	—	560
1961	133	—	—	—	—	—	281	—	503
1962	80	—	—	—	—	—	0	—	73
1963	228	—	—	—	98	—	189	—	65
1964	217	—	—	—	146	—	318	—	145
1965	288	248	121	—	134	33*	0	—	57
1966	199	—	—	—	52	—	0	—	161
1967	237	—	—	—	68	30*	150	—	35
1968	166	121	97	—	96	—	150	—	10
1969	130	86	75	77*	77	—	500	—	10
1970	152	140	108	—	116	—	0	—	71
1971	181	140	111	24*	110	—	165	—	7
1972	91	66	60	30	91	0	170	0	6
1973	77	75	66	52	155	0	87	217	384
1974	62	76	65	94	193	0	53	23	54
1975	53	54	53	410	479	0	49	5	244
1976	11	14	14	371	369	0	36	19	830
1977	6	6	6	170	192	73*	301	0	215
1978	11	13	13	309	322	80*	0	70	129
1979	3	3	3	87	118	0	0	2	43
1980	—	1	0	605	—	0	80	0	—

A: Catch of all globicephalid species throughout Japan, from official whaling statistics. B: Catch of *G. macrorhynchus* off Pacific coast of Japan as in Table 3. C: From same source as Table 3. D: Data of Jap. Fish. Agency since 1972. E: Miyazaki, 1980b, includes both whaling and other fisheries. F: For Arari village (1950 to 1956, from Kasuya, 1976a) and for entire area (other seasons). G: Miyazaki, 1980a for 1960 to 1971 season, and J.F.A. data for 1972 to 1980. H: Statistics and Survey Div. Ministry of Agri. and Forestry, Pacific coast total, includes all kinds of 'whales'. Catch in Okinawa included since 1974.

* Catch examined by Kasuya but not listed in other records. Underlined: Statistics used in Fig. 2.

stained both with H-E and Aldehyde-fuchsin and Haematoxylin-light-green-chromotrope 2R.

5. *Ovaries*. Ovaries were weighed and checked in the laboratory by Kasuya to confirm the reproductive condition recorded at the flensing platform. Both authors examined the ovaries of Schools 7 and 17, while Marsh examined the ovaries of Schools 9 (No. 79 to 127)-18, 20 and 21-27 as outlined in Marsh and Kasuya (1984). Marsh classified corpora into four categories: 'corpus luteum (CL)', 'young corpus albicans (CA)', 'medium CA', and 'old CA' as outlined (loc. cit.).

3. HISTORY OF EXPLOITATION

3.1. Stock identity

The seasonal distribution of the short-finned pilot whale off the Pacific coast of Japan was analysed by Kasuya (1975) based on catch statistics (1949-52 inclusive) of the small-type whaling industry, which uses harpoon guns of 50 mm or smaller calibre and is licensed to hunt minke whales and all Odontoceti except sperm whales. He

showed that the whales migrate seasonally along the islands, expanding their range in summer up to eastern Hokkaido (ca 43° N) and retreating in winter to the south of the Kii Peninsula (ca 34° N).¹ Although some individuals are present throughout the year off the Kii coast, the bimodal distribution of the catch in this region suggests that the main wintering ground may be further south. Miyazaki (1980a) reported catch statistics for Nago (26° 34' N, 127° 59' E) on the west coast of Okinawa Island over the last 16 years. The catch had a

¹ Since completing this study, Miyazaki and Kasuya (unpublished) have observed two types of pilot whales off Ayukawa (38° 20' N) on the Pacific coast of Japan in November. This is near the northern boundary of the range of *G. macrorhynchus* at this time of year. Both types have skull features characteristic of *G. macrorhynchus* as described by van Bree (1971). The smaller type is identical to those taken off central Japan and studied in this paper. The other type is possibly a boreal form. It is from one to two metres larger, and has a more pronounced saddle mark. The forehead of the adult male is roundish rather than square as in the smaller type. The two forms may be geographical races corresponding to those reported by Polissini (1980) from the eastern North Pacific.

Table 3
Catch of *G. macrorhynchus* by small-type whaling¹

Year	Pacific Coast											
	Hokkaido ²			Sanriku ³			S/W Japan ⁴			Other areas ⁵		
	♂	♀	Total	♂	♀	Total	♂	♀	Total	♂	♀	Total
1948	0	0	0	200	121	321	69	35	104	0	0	0
1949	0	0	0	237	178	415	277	122	399	6	0	6
1950	0	0	0	126	163	289	231	130	361	3	1	4
1951	4	1	5	150	114	264	189	121	310	8	2	10
1952	3	4	7	64	56	120	118	76	194	6	3	9
1953	0	0	0	97	127	224	125	104	229	0	0	0
1954	1	0	1	25	18	43	24	12	36	0	0	0
1955	0	0	0	14	3	17	22	18	40	3	0	3
1956	53	29	82	11	8	19	99	70	169	2	1	3
1957	4	0	4	20	12	32	101	31	132	0	0	0
1965	7	7	14	76	37	113	101	10	121	0	0	0
1968	0	0	0	14	10	24	56	41	97	0	0	0
1969	0	0	0	7	4	11	53	22	75	0	0	0
1970	0	0	0	17	15	32	69	39	108	0	0	0
1971	0	0	0	15	14	29	51	60	101	5	5	10
1972	3	1	4	0	0	0	37	25	62	0	0	0
1973	5	4	9	0	0	0	37	29	66	0	0	0
1974	8	3	11	0	0	0	47	18	65	0	0	0
1975	0	0	0	1	0	1	25	28	53	0	0	0
1976	0	0	0	0	0	0	6	8	14	0	0	0
1977	0	0	0	0	0	0	3	3	6	0	0	0
1978	0	0	0	0	0	0	11	2	13	0	0	0
1979	0	0	0	0	0	0	1	2	3	0	0	0

¹ Compiled by Kasuya from the *Geiryō Geppo* (Monthly Report of Whaling Operation).

² 42° N–43° N.

⁴ 31° N–35° N.

³ 38° N–40° N.

⁵ Northern Kyushu and Sea of Japan.

single peak during March to May, before the spring peak off the Kii Peninsula in May and June. This suggests that the range of the population we have studied may extend to Okinawa.

The catch statistics for this species at Taiji (33° 34' N, 135° 54' E), the only pilot whaling locality on the Kii Peninsula, indicate that the fishing season has changed in recent years (Miyazaki, 1980b). There were two peaks in the catch before 1973, one in May through July, the other in November through January (Kasuya, 1975). However, only the latter peak persisted after 1973, probably the result of changes in fishing technique and interaction with other fisheries as outlined below.

From sometime before 1965 until 1973, the pilot whale fishery was conducted year-round with a small whaling boat (*Katsumaru*) equipped with a multi-barrelled harpoon gun. Regular drives started in 1971, and by 1974 the catch of pilot whales using this technique consistently exceeded that obtained by the whaling boat (Table 2 and Fig. 2). At Taiji, the drive fishery catches delphinids of several species during period when more lucrative alternatives are not available. The hunting team(s) usually break(s) up in May for trolling or some other small-scale net fishery.

3.2. Catch statistics

Significant catches of *G. macrorhynchus* have been limited to Taiji and Okinawa (Table 2). Although the drive fishery at Nago (Okinawa) seems to have a long history, the available statistics are limited to those of

Miyazaki (1980a) for 1960 to 1975 and those of the Japanese Fisheries Agency for 1972 to 1980. (When both sets of data are available for a given season they are identical). The catch was sporadic and ranged from 0 to 605 individuals per year (Table 2). The drive was carried out opportunistically by small fishing boats from other fisheries (Miyazaki, 1980a).

From the early 17th century, the pilot whale was hunted at Taiji by traditional whaling teams using hand harpoons (Hashiura, 1969). The first expansion of the fishery occurred in 1903 with the successful introduction of the multi-barrelled harpoon gun, and the second in 1921 with the first use of motor vessels. The usage of motor vessels rapidly increased (Hamanaka, 1979). Hamanaka reported catch statistics for the pilot whale at Taiji from 1920 to 1931. The catch of 120 whales by 11 traditional boats in 1920 increased to 381 in 1921 with the use of motor vessels. In the 11 years from 1921 to 1931, the annual catch ranged from 144 to 708 pilot whales ($\bar{x} = 483.6$). Although the fishery continued until recently, with a few years' interruption before and after 1945 (the last year of World War II), no catch statistics are available from before 1948. Table 2 summarizes the catch at Taiji since 1948. In addition to the catch statistics of the Japanese Government, Miyazaki (1980b) reported the catch of several delphinids at Taiji, including *G. macrorhynchus*, based on the records of number of viscera by species sold through the Taiji Fishery Co-operative Union from 1963 to 1979. The use of the visceral number covers carcasses which were occasionally sold through brokers and are missing from other records.

If all the statistics are correct, the sum of the columns C (whaling) and D (other fisheries) in Table 2 should be equal to the column E (Miyazaki, 1980b) of the same table. Error is inevitable in statistics, and the disagreement observed is not significant.

During the food crisis after the last war, the range of small-type whaling for pilot whales expanded from Taiji to waters off southern Kyushu (31° N) or to those off northeastern Hokkaido (43° N), as shown by Kasuya (1975). Table 3 lists the catch of the short-finned pilot whale (column B in Table 2) by small-type whaling compiled from the *Geiryō Geppo* (Monthly Reports of Whaling Operations) submitted by boat owners to the Fisheries Agency as well as the official statistics of 'globicephalid' whaling (column A in Table 2). In Table 2, Column A includes three globicephalid species, *Pseudorca crassidens*, *Grampus griseus*, and *Globicephala macrorhynchus*, but column B includes only pilot whales of known sex and excludes a small number (0 to 18 per year) of pilot whales of unknown sex. Although this is the main source of discrepancy between columns A and B of Table 2, there still remain some minor discrepancies which we cannot account for.

The catch of large numbers of pilot whales by this fishery lasted only from the late 1940s to the early 1950s, ceasing after the establishment of a whaling company for large cetaceans in 1951, when several small-type whaling boats were replaced with fewer larger boats licensed to catch large whales (Hamanaka, 1979). Another reason for the decline may be the intensified selection by small-type whaling boats of the more profitable minke whales, resulting from a decline in demand for dolphin meat (Kasuya, 1975). After the mid 1960s, significant catches of pilot whales by small-type whaling continued only at Taiji, because of the traditional food customs of the local people. Small-type whaling has now been almost totally displaced by the drive fishery, as discussed above.

Several Izu Peninsula villages are known to have operated a drive fishery for dolphins (Kasuya, 1976a). Arari Village caught pilot whales for an unknown part of the post-war period before 1960 (column F in Table 2). It is possible that the catch between 1948 and 1956 is under-estimated, because some other villages on the Izu coast may also have operated a drive fishery for pilot whales, but no data are available.

Fig. 2 shows the total annual catch of short-finned pilot whales off the Pacific coast of Japan, including recent records from Nago. The catch by fisheries other than whaling with harpoon guns is certainly under-estimated before 1957, because the catch of the Nago driving fishery is not included. The high catch in 1960 and 1961 resulted from the extraordinarily high catch in Shizuoka (501 individuals) and Miyagi (404 individuals) Prefectures. The former could have been caught by a drive fishery team on the Izu coast. The latter is difficult to explain, because there is no drive fishery in Miyagi Prefecture. A catch of 179 individuals is also recorded for this prefecture in 1958 (for details see Ohsumi, 1972). The high 1973 total catch is the result of the unusual catch of 217 pilot whales at Choshi in Chiba Prefecture (see column D (other area) in Table 2). These unusual catches could have been incidental or the result of a mass stranding.

We conclude that the total catch of the short-finned pilot whale off the Pacific coast of Japan may have been

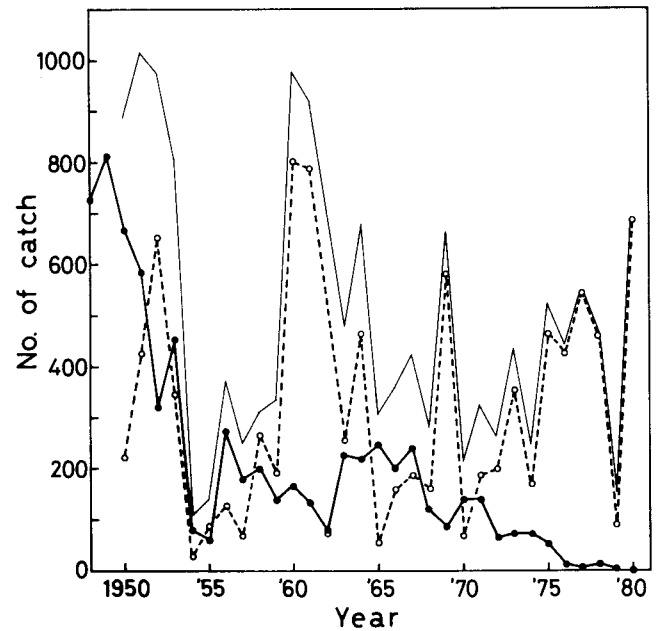


Fig. 2. Catch of *G. macrorhynchus* off the Pacific coast of Japan. The closed circles and thick solid line indicate the catch by small-type whaling (using 50-mm or smaller-caliber harpoon gun and licensed to take minke whale and toothed whales other than sperm whales). The open circles and dotted line indicate the catch by other fisheries, and the thin solid line the total. For data see Tables 2 and 3.

about one thousand individuals per year from the late 1940s to early 1950s and then declined, with a few exceptional years, to a level of 200–400 per year. The recent increase to 400–700 individuals per year results from the expansion of the drive fishery at Taiji.

4. MALE SEXUAL MATURITY AND BREEDING LONGEVITY

4.1. Maturity of testicular tissue

The maturity of testicular tissue was determined by examining all (70–150) seminiferous tubules in an H–E-stained histological section (approx. 5 mm × 7 mm or smaller). Tubules with spermatocytes, spermatids or spermatozoa were classified as mature. The tissue was then classified into one of the following categories (see Fig. 3):

- (1) immature: 100% immature tubules.
- (2) early-maturing: less than 50% of tubules examined mature.
- (3) late-maturing: between 50% (inclusive) and 100% of tubules examined mature.
- (4) mature: 100% mature tubules.

Although some of the tubules examined lacked one or two of the cell types of spermatocytes, spermatids and spermatozoa, there was no instance in which one or two of these three cell types were lacking in all tubules examined from a whale classified as early-maturing or later. For example, none of the testes classified as early-maturing had spermatocytes and/or spermatids only and no spermatozoa.

Different parts of the testis of the sperm whale, *Physeter macrocephalus*, (Best, 1969) and the sei whale, *Balaenoptera borealis*, (Masaki, 1976) have been shown to mature at different times. We sampled 11 sites on a

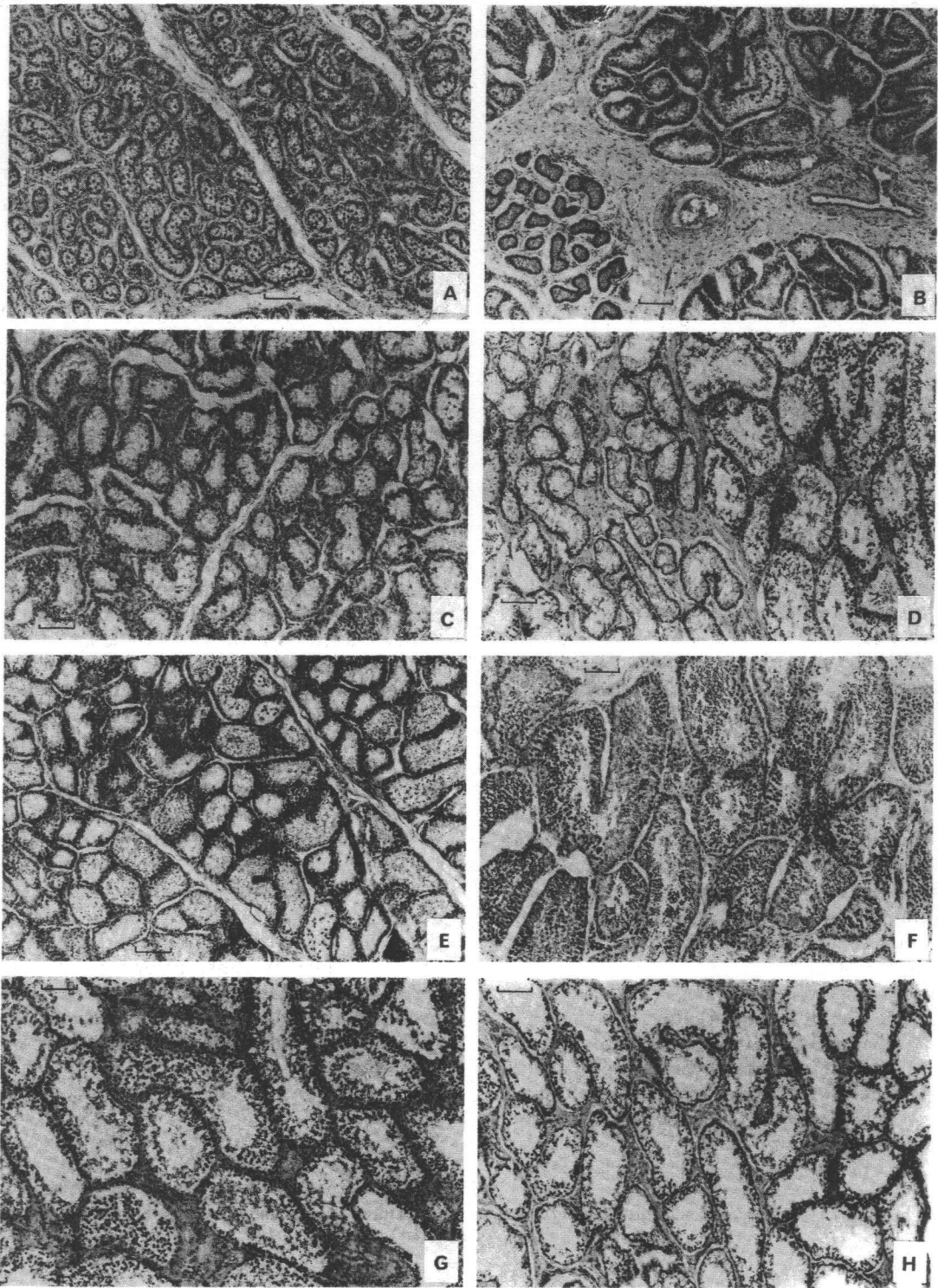


Fig. 3. Testis of *G. macrorhynchus*, haematoxylin and eosin-stained. In all photographs, the scale bar represents 0.1 mm.

- A. Immature (No. 18-34, 385 cm, 20.5 years old, weight of single testis 84.6 g). Spermatozoa were doubtfully present in testicular smear. None were seen in epididymal smear.
- B. Early-maturing (No. 15-34, 404 cm, age estimate not available, weight of single testis 122.3 g). Spermatozoa were absent from both smears.
- C. Early-maturing (No. 17-12, 390 cm, 16.5 years old, weight of single testis 154.0 g). Spermatozoa were absent from both smears (For epididymis, see Fig. 10B).
- D. Late-maturing (No. 18-42, 414 cm, 18.5 years old, weight of single testis 600 g). Spermatozoa were at 'intermediate' density in both smears.
- E. Late-maturing (No. 17-26, 420 cm, 18.5 years old, weight of single testis, 149.3 g). Spermatozoa were 'copious' in epididymis and at 'intermediate' density in testicular smear.
- F. Mature (No. 18-44, 465 cm, 20.5 years old, weight of single testis 1,000 g). Spermatozoa were 'copious' in epididymis and at 'intermediate' density in testicular smear.
- G. Mature (No. 18-36, 490 cm, 34.5 years old, weight of single testis 2,080 g). Spermatozoa were 'copious' in epididymis and at 'intermediate' density in testicular smear (For epididymis, see Fig. 10C).
- H. Mature (No. 18-39, 427 cm, 31.5 years old, weight of single testis 660 g). Spermatozoa were at 'intermediate' density in epididymis and 'scanty' in testicular smear.

Table 4

Maturity and diameter of seminiferous tubules at different positions in testis

Sample no. and position	Diameter (μm)		Mature tubules (%)	Maturity
	Mean	S.E.		
18-34				
1	67.4	1.30	0	immature
2	61.8	1.22	0	"
3	51.7	1.56	0	"
4	55.7	1.73	0	"
5	60.3	1.72	0	"
6	59.7	1.41	0	"
7	55.5	1.31	0	"
8	59.6	1.41	0	"
9	58.1	1.33	0	"
10	59.0	1.51	0	"
11	59.3	1.49	0	"
18-30				
1	95.7	3.01	60	late-maturing
2	96.0	2.90	59	"
3	89.0	3.28	54	"
4	95.3	2.64	66	"
5	90.2	3.23	63	"
6	81.1	3.05	65	"
7	88.4	2.44	59	"
8	84.3	3.93	55	"
9	89.8	2.06	63	"
10	93.1	3.54	46	early-maturing
11	88.2	2.46	58	late-maturing

No. 18-34: body length 385 cm, age 20.5 years, weight of a testis 94.6 g.
 No. 18-30: body length 420 cm, age 22.5 years, weight of a testis 171.8 g.

longitudinally-sliced testis (Fig. 4) of both a maturing male (No. 18-30) and a relatively old immature male (No. 18-34) to test whether *G. macrorhynchus* testes also mature differentially. In both animals, the mean diameter and status of the seminiferous tubules did not vary much between positions (Table 4).

Similar comparisons were made between tissues taken from positions 5, 6 and 7 (Fig. 4) for seven males of intermediate testis size (53.6-1,100 g). Again no differences were detected between different positions or between contralateral testes of the same whale. Therefore we considered that it was sufficient to base our assessment

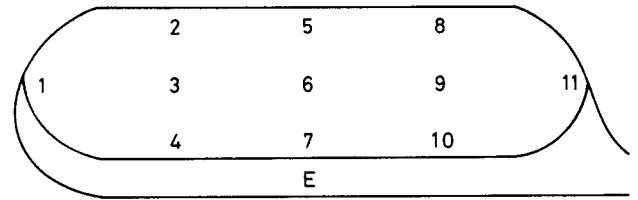


Fig. 4. Schematic diagram of a longitudinal section of a testis of *G. macrorhynchus* indicating the positions sampled. E indicates the position of the epididymal sample.

of testis maturity on one sample from position 6 (Fig. 4).

The results of these assessments of testis maturity were compared with the density of spermatozoa in the corresponding testicular and epididymal smears (Table 5). Whales with high densities of epididymal spermatozoa ('scanty' or greater (see Section 2)) exhibited similar densities on their testicular smears.

However, there are indications that there is an appreciable time lag between spermatogenesis and the appearance of sperm in the epididymis. Eleven individuals with large amounts of testicular spermatozoa had few or none in the epididymis (categories 'absent' or 'doubtfully-present', see Section 2). In contrast, only one of the 67 males studied (No. 18-41; body length 417 cm; age 21.5 years; histologically mature testis weighing 440 g) had a greater density of spermatozoa in its epididymis than in its testis. This male, which was sampled in December, may have only recently matured. Significant sperm production was often limited to the mating season (spring/summer) in such individuals (see Section 6.1).

Table 5 also shows that the testicular smears from 10 of the 50 whales with histologically-immature testes (20%) contained spermatozoa, but that only two of the 42 (4.8%) testes without spermatozoa in the smear were classified histologically as early-maturing. These contradictions indicate that about 20% of testes classified as immature may possibly belong to the early-maturing stage. The chance of misclassification should be much lower using the smear method because the smear was taken from a larger cross-section than was the histological block.

Table 5

Correspondence between three measures of male sexual maturity (histological maturity of testis and abundance of spermatozoa in testicular and epididymal smears)

Abundance of spermatozoa	Number of males in each category																		
	T/H	Im	EM	LM	M	Σ	E/H	Im	EM	LM	M	Σ	E/T	(a)	(b)	(c)	(d)	(e)	Σ
Absent	(a)	40	2	—	—	42	(a)	47	4	2	—	53	(a)	44	9	3	—	—	56
Doubtfully-present	(b)	8	3	—	1	12	(b)	3	5	2	1	11	(b)	1	2	8	—	—	11
Scanty	(c)	2	6	6	23	37	(c)	—	2	2	10	14	(c)	—	—	11	4	—	15
Intermediate	(d)	—	—	3	42	45	(d)	—	—	1	18	19	(d)	—	1	8	8	2	19
Copious	(e)	—	—	—	3	3	(e)	—	—	2	40	42	(e)	—	—	7	35	1	43
Σ		50	11	9	69	139	Σ	50	11	9	69	139	Σ	45	12	37	47	3	144

H: Histological maturity; Im: immature; EM: early-maturing; LM: late-maturing; M: mature.

T: Density of spermatozoa in testicular smear.

E: Density of spermatozoa in epididymal smear.

For details of the scale used in measuring the abundance of spermatozoa in smears see Section 2.

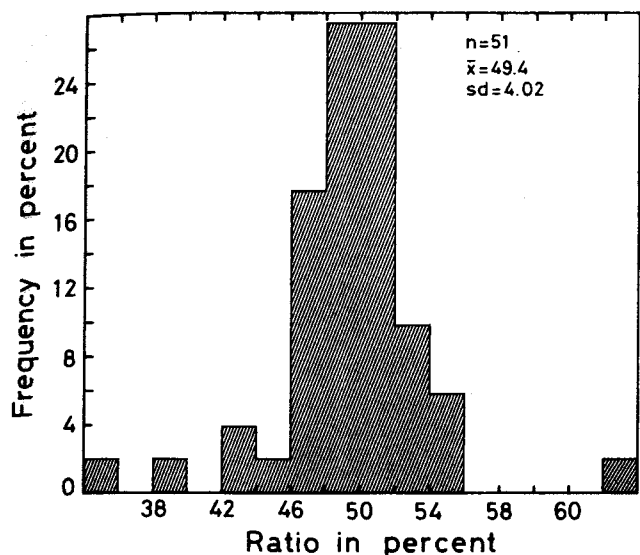


Fig. 5. Weight of the left testis expressed as the percentage of the combined weight of the testes in *G. macrorhynchus*.

4.2. Weight of testis

Contralateral comparison. The weights of the right and left testes were compared for 51 individuals ranging from immature to fully mature (Fig. 5). The weight of the left testis ranged between 34 and 66% of the combined testis weight ($\bar{x} = 49.4\%$; $SD = 4.02\%$). The testis of one side was not consistently heavier than that on the other. Thus the use of only one testis probably did not cause significant bias, although it may have caused apparently greater individual variation than would have the use of combined weights. Accordingly, we have usually used the arithmetic mean when the weights of both testes were

available; otherwise the weight of one testis from either side was used.

Increase in testis weight. Fig. 6 shows the relationships between single testis weight and body length and between testis weight and age. Testis weight (log scale) increased linearly from about 15 to 100 g (about sevenfold) as body length increased from 220 to 380 cm. After this, testis weight increased to about 700 g (also about sevenfold) while the body length increased only about 50 cm. Testis weight then increased at a rate intermediate between the above two rates (Fig. 6) until the whale reached a body length of about 500 cm (larger than the 95% confidence range for the asymptotic length ($473.5 \text{ cm} \pm 9.1 \text{ cm}$) (Kasuya and Matsui, in press)). This result suggests that for fully-grown males, those of large body size tend to have heavier testes than do smaller animals.

The relationship between testis weight and age shows a similar pattern (Fig. 6). Testis weight increased linearly from about 20 g at two years to about 100 g at 14 years of age, i.e. an annual increase of about 14%. Testis growth was most rapid between 14 and 17 years of age, with an increase from 100 g to about 700 g, an annual increase of about 90%. This was followed by a relatively slow increase until an age of about 25 years. After this age, testis weight varied from 700 to 3,000 g, a much wider range than the 1,700 to 3,000 g range in testis weight of males which have ceased growing.

As shown in Fig. 6, greatest growth occurred mostly in the early and late-maturing stages. This rapid weight increase may indicate puberty. Although our sample was small and seasonally limited and individual variations are expected, we estimate the weight of a testis at the four stages to be approximately as follows (also see Table 6):

Immature	≤ 100 g
Early-maturing	100 g–170 g
Late-maturing	170 g–400 g
Mature	≥ 400 g

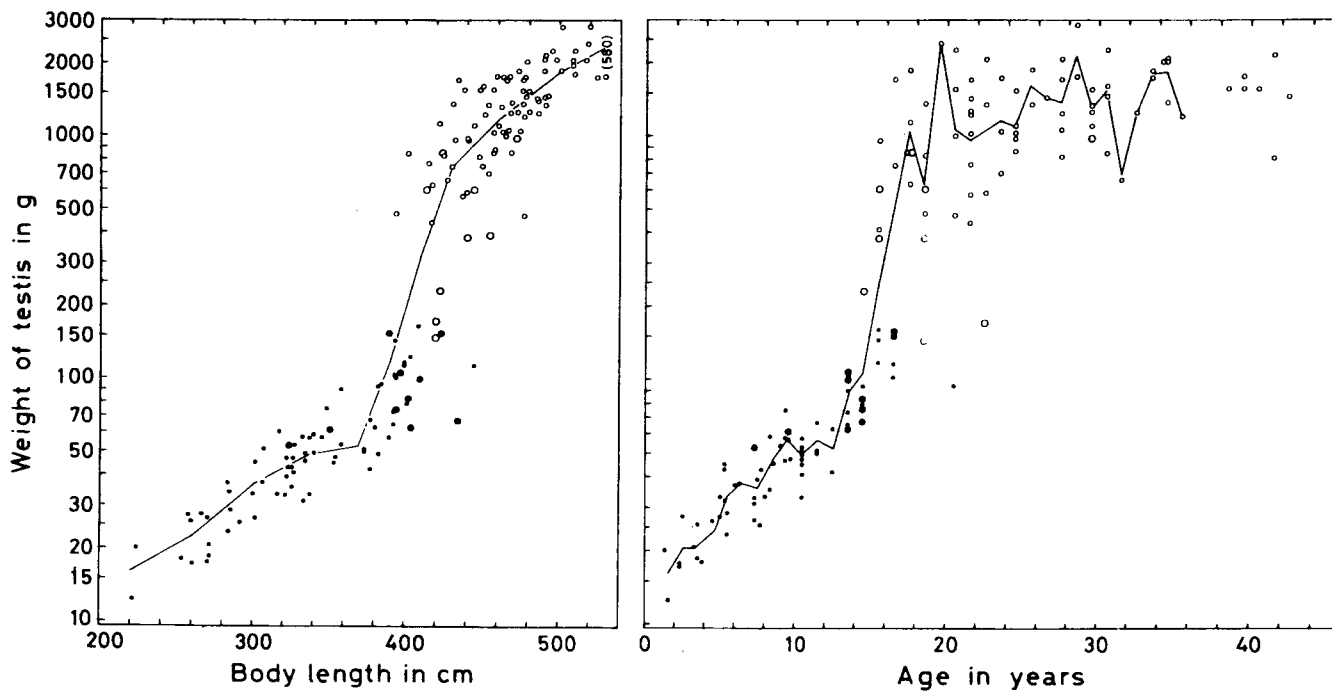


Fig. 6. Scatter-plot of weight of testis against body length (left) and age (right) in *G. macrorhynchus*. Small closed circle: 'immature' stage; large closed circle: 'early-maturing' stage; large open circle: 'late-maturing' stage; small open circle: 'mature' stage. The lines connect the arithmetic means of the testis weights for each body length (or age) class.

Table 6
Relationship between testis weight, histological maturity of testis, and spermatozoan density in epididymal smear¹

Range of testis weights (g)	Number of whales in each category				Σ
	Immature	Early-maturing	Late-maturing	Mature	
0-25	8a	—	—	—	8
25-50	26a	—	—	—	26
50-75	12a, 2b	1a, 3b	—	—	18
75-100	4a	1b, 1c	—	—	6
100-125	3a, 1b	2a, 1b	—	—	7
125-150	1a	—	1e	—	2
150-175	1a	1a, 1c	1a	—	4
175-200	—	—	—	—	0
200-225	—	—	—	—	0
225-250	—	—	1a	—	1
—	—	—	—	—	—
375-400	—	—	1b, 1c	—	2
400-425	—	—	—	1d	1
425-450	—	—	—	1d	1
450-475	—	—	—	1c	1
475-500	—	—	—	1d	1
—	—	—	—	—	—
550-575	—	—	—	1d	1
575-600	—	—	—	1e	1
600-625	—	—	1b, 1d	—	2
625-650	—	—	—	1e	1
650-675	—	—	—	1d	1
675-700	—	—	—	—	0
700-750	—	—	—	1c	1
750-800	—	—	—	1d, 1e	2
800-850	—	—	—	1d, 1e	2
850-900	—	—	1c	1c, 1d, 1e	4
900-950	—	—	—	—	0
950-1,000	—	—	1e	2e	3
≥ 1,000	—	—	—	50	50

¹ Spermatozoan density index in smear: a, absent; b, doubtfully present; c, scanty; d, intermediate; e, copious. For a description of each category see Section 2.

Diameter of seminiferous tubules. Seminiferous tubule diameter increased as the testis matured as shown in Table 7 and Fig. 7. In the immature and early-maturing stages, this increase was very slight compared to the corresponding changes in testis weight (Fig. 8). A rapid increase in tubule diameter was observed between the ages of 15 and 21 years (Fig. 7), when many testes were

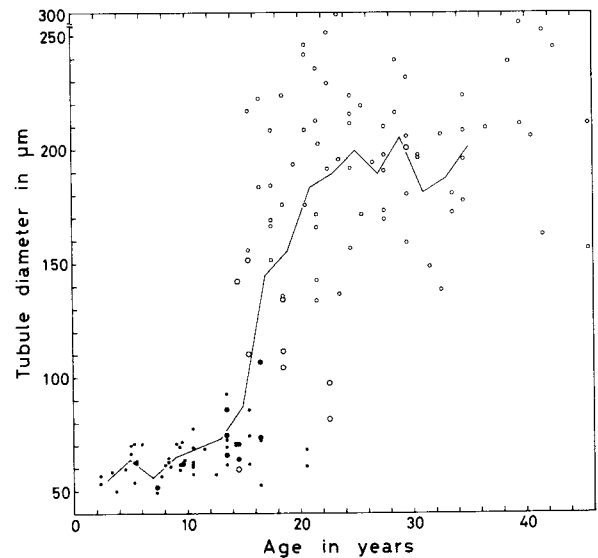


Fig. 7. Scatter-plot of diameter of seminiferous tubule against age in *G. macrorhynchus*. All of the dot symbols are as in Fig. 6. (Small closed circle: 'immature' stage; large closed circle: 'early-maturing' stage; large open circle: 'late-maturing' stage; small open circle: 'mature' stage.) Line connects mean diameters of each age class.

classified as late-maturing, suggesting that a rapid increase in tubule diameter is a feature of this stage. The wide individual variation in tubule diameter and testis histology (Fig. 3) observed in adult testes could reflect a seasonal or aseasonal reproductive cycle, but we had insufficient data to study this in detail.

Fig. 8 shows the relationship between tubule diameter and testis weight plotted on logarithmic scales. The immature and early-maturing testes formed one group; the late-maturing and mature testes another. The relationships (see Fig. 8) are described by the following least-squares equations:

$$\log Y = 0.1441 \cdot \log X + 36.5452 \quad (X < 80, r = 0.49) \quad (\text{Equation 4.1})$$

$$\log Y = 0.3828 \cdot \log X + 12.7160 \quad (X > 80, r = 0.93) \quad (\text{Equation 4.2})$$

where X indicates the single testis weight in g and Y the mean seminiferous tubule diameter in μm . Comparison

Table 7
Age (years) and diameter of seminiferous tubules (μm) of *G. macrorhynchus* at each stage of male sexual maturity

Age range	Diameter of seminiferous tubules at each stage							
	Immature		Early-maturing		Late-maturing		Mature	
	Range	Mean	Range	Mean	Range	Mean	Range	Mean
2-5	49.8-59.9	56.0	—	—	—	—	—	—
5-10	49.0-70.6	62.8	51.4-61.8	56.6	—	—	—	—
10-15	57.1-74.0	67.9	59.2-85.7	69.8	142.0	142.0	—	—
15-20	52.2-85.5	69.1	73.0-106.9	89.9	104.2-166.6	130.8	135.6-223.6	184.9
20-25	60.1	60.1	—	—	96.9	96.9	133.4-298.1	201.9
25-30	—	—	—	—	200.8	200.8	159.0-239.7	197.1
30-35	—	—	—	—	—	—	148.9-223.5	188.7
35-40	—	—	—	—	—	—	209.4-278.2	234.3
40-46	—	—	—	—	—	—	156.4-263.5	207.2
Overall figures	49.0-85.5	64.2	51.4-106.9	71.2	96.9-200.8	136.1	133.4-298.1	198.8

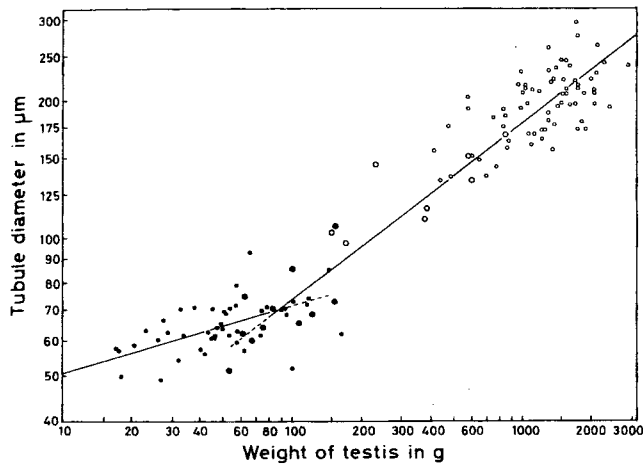


Fig. 8. Relationship between diameter (Y in μm) of seminiferous tubule and weight (X in g) of testis in *G. macrorhynchus* plotted on a double logarithmic scale. All of the dot symbols are as in Fig. 6. (Small closed circle: 'immature' stage; large closed circle: 'early-maturing' stage; large open circle: 'late-maturing' stage; small open circle: 'mature' stage.) Lines are least-square regressions of $\log Y$ and $\log X$ calculated separately for $X < 80$ (Equation 4.1) and $X > 80$ (Equation 4.2).

of the above correlation coefficients suggests that the increase in tubule diameter made a limited contribution to the testis weight increase in the immature and early-maturing stages, while in the late-maturing and mature stages most of the weight increase was accounted for by the expansion in tubule diameter. For a testis weighing more than about 1,500 g, tubule diameter and weight were no longer correlated (Fig. 8), supporting our earlier evidence that very high testis weight tends to correlate with large body size.

4.3. Growth and sperm-density changes in the epididymis

It is difficult to define when an individual male becomes sexually mature, i.e. physiologically capable of breeding, on the basis of the epididymal smear alone. Spermatozoa were absent from the epididymal smears of many males less than 17 years old (Fig. 9), and males whose smears were classified as 'sperm doubtfully present' (Fig. 10) were (with one exception) between 9 and 19 years old. Animals with 'scanty' epididymal sperm were all 14 years old or older, those with 'intermediate' amounts of epididymal sperm were all 15 years old or older, and those with copious amounts of epididymal sperm (see Fig. 10 for details) were all 15 years old or older (see Fig. 9). Although the first two stages were limited to the younger ages and seemed to be correlated with maturity as classified on the basis of testis histology, the latter three epididymal-smear stages correlate with neither age (≥ 15 years) nor the histological stages of 'late-maturing' and 'mature' (Table 5 and Fig. 9). Therefore, we consider that these last three stages of epididymal sperm density represent individual or seasonal variation within mature males rather than growth stages, i.e. many of the males with 'scanty' or more epididymal sperm were reproductively mature.

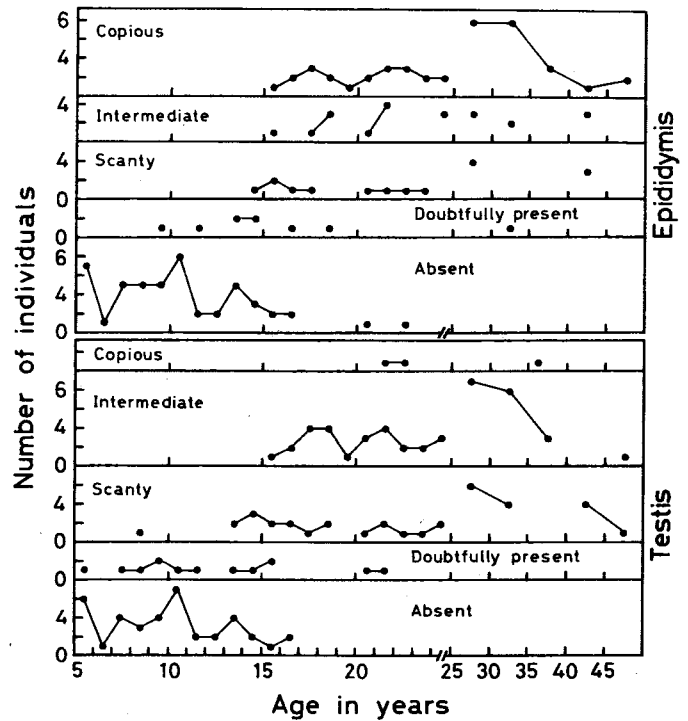


Fig. 9. Relationship between age and density of spermatozoa in epididymal (top set) and testicular smears (bottom set) in *G. macrorhynchus*.

4.4. Maturity, age and body length

Fig. 11 summarizes the relationship between testis maturity, age and body length. The immature and early-maturing stages were difficult to separate, as were the late-maturing and mature stages. However, immature and early-maturing individuals were distinct from late-maturing and mature whales. The boundary between these two major groupings was more closely related to body length than age, i.e., there was a tendency for males of large body size to mature younger.

For each stage of male sexual maturity (early-maturing, late-maturing, and mature), the percentage of individuals at or beyond this stage was plotted against both body length and age. The resultant linear regressions follow:

Maturity on body length (X , cm)

$$\text{Early-maturing and later} = 2.985X - 1,147.2 \quad (380 < X < 420, r = 0.94) \quad (\text{Equation 4.3})$$

$$\text{Late-maturing and mature} = 4.375X - 1,759.8 \quad (400 < X < 430, r = 0.90) \quad (\text{Equation 4.4})$$

$$\text{Mature} = 2.274X - 909.9 \quad (400 < X < 440, r = 0.83) \quad (\text{Equation 4.5})$$

Maturity on age (X , year)

$$\text{Early-maturing and later} = 16.206X - 186.6 \quad (13 < X < 18, r = 0.91) \quad (\text{Equation 4.6})$$

$$\text{Late-maturing and mature} = 21.660X - 293.2 \quad (14 < X < 18, r = 0.87) \quad (\text{Equation 4.7})$$

$$\text{Mature} = 16.691X - 233.6 \quad (14 < X < 20, r = 0.88) \quad (\text{Equation 4.8})$$

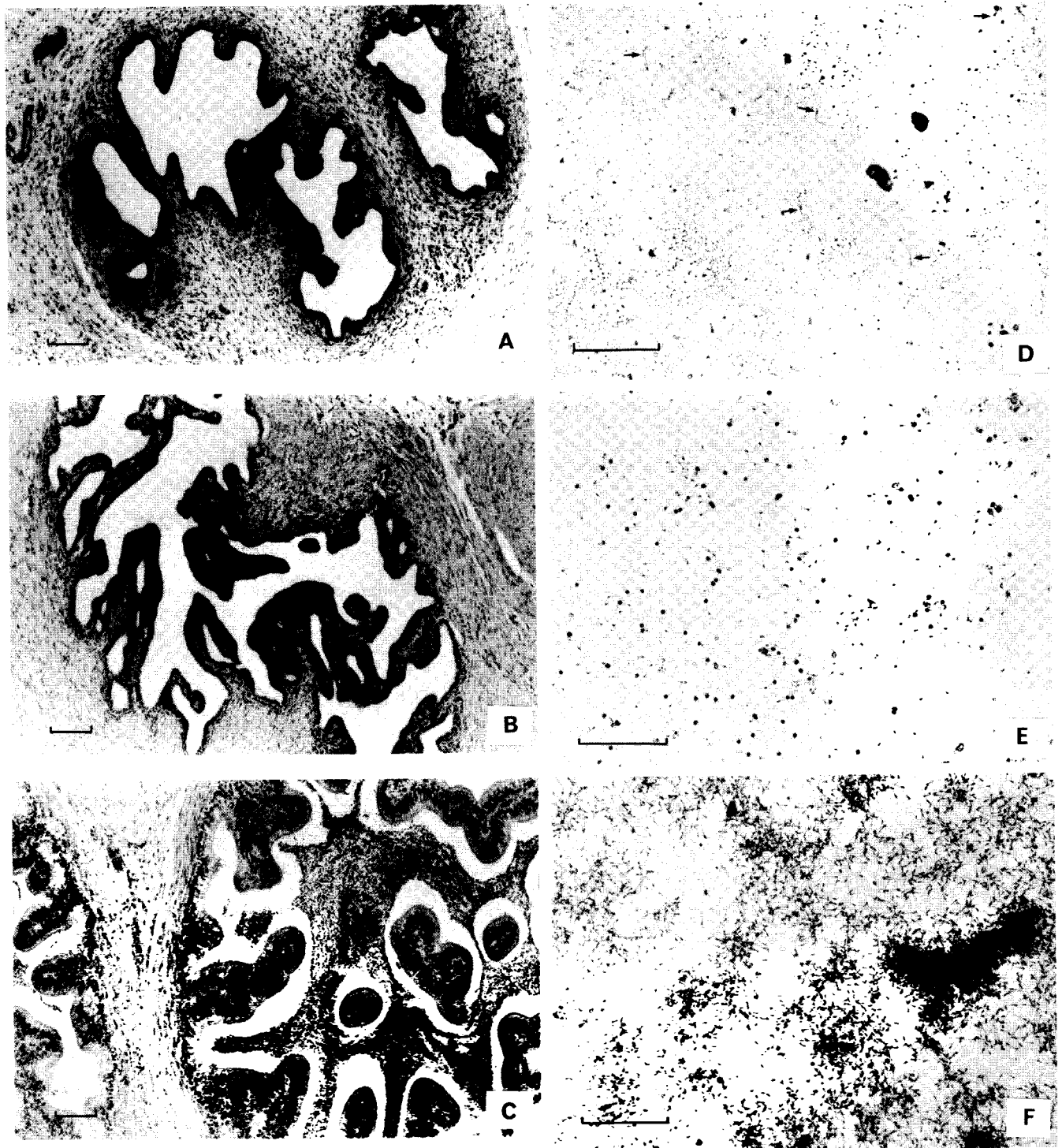


Fig. 10. Epididymis of *G. macrorhynchus*. In all photographs the scale bar represent 0.1 mm.

- A. Epididymis of an immature male (No. 15-9, 341 cm, 10.5 years old, weight of single testis 50.0 g). Spermatozoa were absent from both the epididymal and testicular smears. Haematoxylin and eosin-stained.
- B. Epididymis of a male at the early-maturing stage (No. 17-12, 390 cm, 16.5 years old, weight of single testis 154.0 g). Spermatozoa were absent from both the epididymal and testicular smears. Haematoxylin and eosin-stained. (For testis, see Fig. 3C).
- C. Epididymis of a mature male (No. 18-36, 490 cm, 34.5 years old, weight of single testis 2,080 g). Spermatozoa were 'copious' in the epididymal smear and at 'intermediate' density in the testicular smear. Haematoxylin and eosin-stained. (For testis, see Fig. 3G).
- D. Epididymal smear at the upper limit of the 'scanty' spermatozoan density stage. Each spermatozoon is indicated by an arrow.
- E. Epididymal smear at the 'intermediate' spermatozoan density stage.
- F. Epididymal smear at the 'copious' spermatozoan density stage.

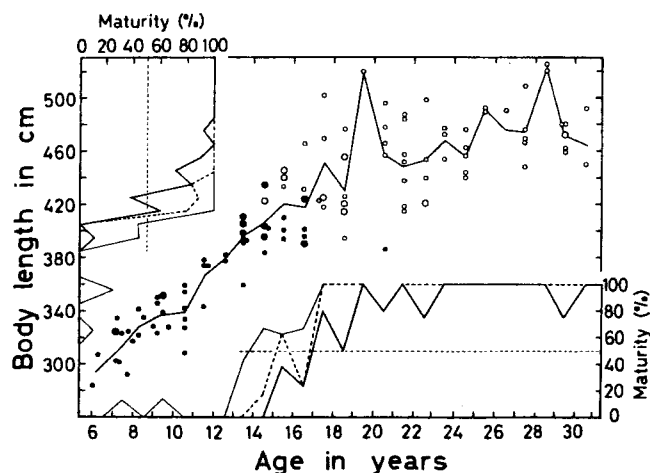


Fig. 11. Relationships between sexual maturity, body length and age in males of *G. macrorhynchus*. In the relationship between body length and age (centre), the dot symbols are as in Fig. 6. (Small closed circle: 'immature'; large closed circle: 'early-maturing'; large open circle: 'late-maturing'; and small open circle: 'mature'.) The line joins the mean body lengths in each age class. The symbols in the age-maturity (bottom) and body length-maturity (upper left) relationships are: thick solid line: 'mature'; dotted line: 'late-maturing' plus 'mature'; thin solid line: 'early-maturing' plus 'late-maturing' plus 'mature'. Individuals over 31 years are, as well as those below 31 years, included in the maturity-body length relationship.

Table 8

Range of data and mean (50% point on the linear regression*) at the attainment of each stage of sexual maturity in male of *G. macrorhynchus*

	Body length (cm)			Age (years)		
	Min.	Mean	Max.	Min.	Mean	Max.
Immature	—	—	409	—	—	20.5
Early-maturing	324	401.1	434	7.25	14.6	16.5
Late-maturing	414	413.7	455	14.5	15.8	29.5
Mature	394	422.1	525	15.5	17.0	45.5

* Equations 4.3 through 4.8 in text.

The body length and age at which 50% of individuals were at (or beyond) each stage, calculated from these regressions, are listed in Table 8. These values have been used in the latter sections of this study as the mean age (or body length) at the attainment of each stage.

4.5. Discussion

The epididymal smear is suitable for detecting the presence of spermatozoa (see Section 4.1). However, we consider that the density of sperm in an epididymal smear may not be a reliable index of the actual density of epididymal sperm. A further problem is that epididymal sperm density fluctuated seasonally in maturing individuals (see Section 6.1). Therefore we decided to use testis histology as the basis for recognizing male sexual maturity. We consider that males classified as 'late-maturing' or 'mature' were probably functionally mature. Thus functional maturity is attained at a mean age of 15.8 years, a mean body length of about 414 cm (Table 8) and a mean single-testis weight of 170 g (see Section 4.2).

As the body weight (Kasuya and Matsui, in press) and testis weight of males of *G. macrorhynchus* both continued to increase after the age of functional maturity until about age 25 years, we consider that it is likely that males do not mate successfully until several years after they are 'functionally mature'. Of course, this will be difficult to confirm even by behavioural observations (see Section 10).

Sergeant (1962a) used histology to study the maturity of the testis and epididymis of a limited number of samples of *G. melaena*. In both *G. melaena* and *G. macrorhynchus*, the tubule diameter was less than 80 μm in immature individuals and about 200 μm in fully-grown males. In *G. melaena*, dividing spermatocytes were first observed in a 75 g testis, and spermatids or spermatozoa were first observed in a testis weighing 573 g. However, in *G. macrorhynchus*, spermatocytes, spermatids and spermatozoa were all observed in every testis classified as early-maturing or later, and the smallest single testis in this category weighed about 50 g (Table 6). We suspect that these apparent 'species' differences may be due to the different techniques of preparation and examination.

Sergeant (1962a) considered that in *G. melaena*, sexual maturity occurred at a testis weight of 500–1,000 g and at ages between 11 and 16 years. According to his analysis, these corresponded to the stage of rapid testis-weight increase and to a seminiferous tubule diameter of 80–150 μm . Since both these phenomena occur in early-maturing and late-maturing individuals in *G. macrorhynchus*, we consider that Sergeant's criterion of sexual maturity in *G. melaena* corresponds to what we define as functional maturity in *G. macrorhynchus*. Thus according to Sergeant's criteria in the populations studied, males of *G. macrorhynchus* mature at 14–23 years, significantly later than in *G. melaena* (11–16 years).

5. FEMALE SEXUAL MATURITY AND BREEDING LONGEVITY

5.1. Puberty

Fig. 12 shows the diameters of the largest Graafian follicle in the ovaries of immature, pregnant, lactating and resting females (the last defined as sexually-mature females neither pregnant nor lactating).

The maximum follicle size in immature individuals was bimodally distributed. The larger mode (eight individuals) ranged from 4 to 8 mm, and the smaller mode (30 females) ranged below 4 mm, including follicles below measurable diameter (< 1.0 mm). Females younger than two years usually did not develop measurable follicles, an exception being a 0.25-year (190 cm in body length) female with one 1.0-mm follicle. Although some immature females had follicles more than 4 mm in diameter at ages over 2 years, individuals with no measurable follicles were still common up to the age of six years (about one year earlier than the age of the youngest mature females, estimated below).

The maximum follicle size in sexually-mature females varied with their reproductive status. In pregnant females, the follicles were least developed. The upper range was similar to that of immature individuals, but the boundary of the two modes lay between 1 and 2 mm. The size of follicles in lactating females showed a diffuse

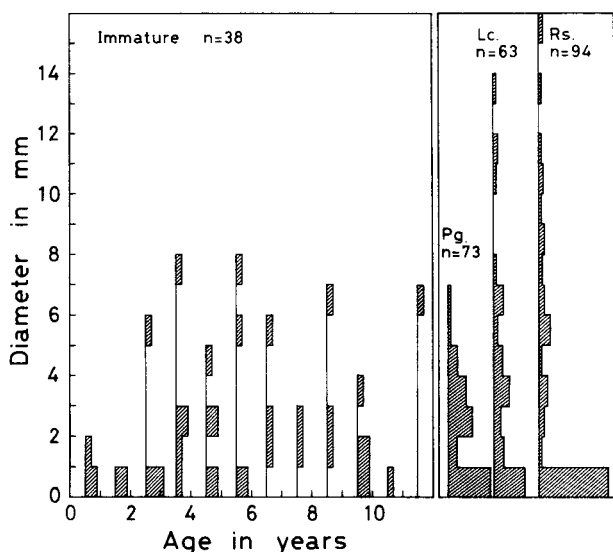


Fig. 12. Diameters of the largest Graafian follicles in the ovaries of immature, pregnant (Pg), lactating (Lc), and resting (Rs) females in *G. macrorhynchus*.

trimodal distribution. The smallest group included follicles below 3 mm (females without measurable follicles included), the intermediate mode range from 3 to 8 mm, and the largest group included a small number of follicles of 10 to 14 mm. The distribution of follicle diameters in resting females was similar to that of lactating females; however, the last two modes were continuous and the upper range of the largest group was slightly greater. Therefore we suspect that the diameter of follicles at rupture is close to the range of the largest-follicle group, i.e. 10–15 mm, and that the growth of follicles in mature ovaries is often suppressed at one of the first two stages, i.e. below 8 mm. The growth of follicles between the three stages, when it happens, is probably rapid.

The development of follicles to macroscopic size usually occurred in immature females at ages greater than two years, and further development appeared to follow the pattern of mature females. Although follicle size in some immature females varied seasonally from below 4 mm (outside the season) to 8 mm (during the mating season) (Marsh and Kasuya, 1984), further growth seemed to be suppressed for several years, probably until seven years or later, when the first ovulation occurred in some females. These data suggest that the length of time during which follicle growth is suppressed is flexible and that it may contribute to the change of age at attainment of sexual maturity of females of *G. macrorhynchus* brought on by a change in the environment or social structure.

5.2. Age at attainment of sexual maturity

We define sexually mature females as those which have ovulated at least once. As the corpus luteum formed after ovulation degenerates into a corpus albicans, which we believe persists for life in *G. macrorhynchus* (Marsh and Kasuya, 1984), the presence of one or more corpora was used as a direct indication of sexual maturity.

The relationship between age and sexual maturity is

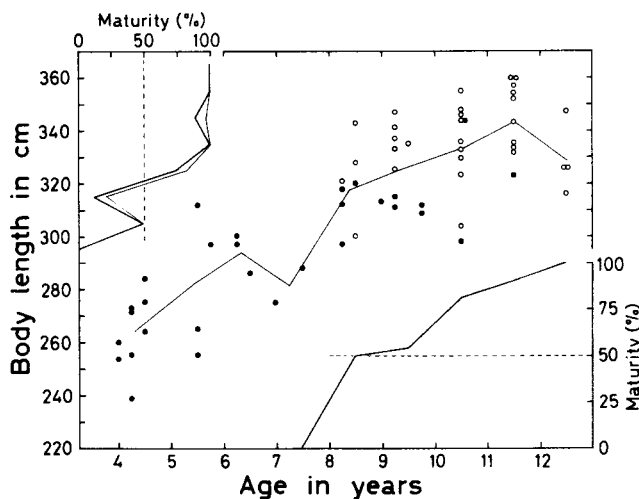


Fig. 13. Relationship between sexual maturity, body length and age in female *G. macrorhynchus*. In the body length – age relationship (centre), open circles indicate mature and closed circles immature animals, and the line connects the mean body length for each year class. In the maturity-body length relationship (upper left), the thick line includes only individuals less than 13 years old; thin line includes individuals over 13 years of age as well. The age-maturity relationship is shown at the lower left.

Table 9

Age at the most recent conception estimated for pregnant females less than 10 years old

Sample no.	Age at death (years)	No. of corpora	Foetal length (cm)	Pregnancy ¹		Age at conception (years)
				(days)	(years)	
7-17	8.25	1	90.0	306	0.84	7.4
26-9	8.25	1	40.5	160	0.44	7.8
17-2	8.5	1	66.5	237	0.65	7.9
9-122	8.5	4	3.0	50 ²	0.14	8.4
24-25	9.25	1	132.0	430	1.18	8.1
14-15	9.25	3	100.0	336	0.92	8.3

¹ Length of pregnancy (days) = $(452 \cdot 0.91 \cdot (\text{foetal length}) / 139.5) + (452 \cdot 0.09)$.

² Probable overestimate.

shown in Fig. 13. The youngest sexually mature female and the oldest immature female appeared at 8.25 and 11.5 years of age, respectively. A better estimate of the age at first ovulation was obtained from six pregnant females based on age at death, foetal body length and the mean foetal growth curve (Fig. 16, Table 9). Four of these females had only one corpus luteum, indicating that their first ovulation occurred between 7.4 and 8.1 years. Thus we conclude that the first ovulation occurs in *G. macrorhynchus* between the ages of 7.0 and 12.0 years.

Fig. 13 shows that 50% of females become sexually mature by 8.5 or 9.5 years. The least-squares regression between age (X , years) and proportion of mature females (Y , %) weighted by sample size, is as follows;

$$Y = 20.6111X - 135.81 \\ (7 < X < 11, r = 0.93). \quad (\text{Equation 5.1})$$

when $Y = 50$, $X = 9.0$. Accordingly, we have used 9.0 years as the mean age at the onset of female sexual maturity in *G. macrorhynchus*.

5.3. Body length at sexual maturity

The body lengths of the smallest sexually mature female and the largest immature female were 300 cm and 344 cm, respectively. The thin solid line in the upper left-hand corner of Fig. 13 shows the relationship between body length and the proportion of sexually mature females for 182 individuals ranging from 290 to 359 cm in body length. Our sample in the 290 to 310 cm range was very small. The least-squares regression between body length (X , cm) and the proportion of sexually mature females (Y , %) weighted by sample size is

$$Y = 2.5570X - 756.89 \\ (290 < X < 340, r = 0.93) \text{ (Equation 5.2)}$$

and when $Y = 50(\%)$, $X = 315.6$ (cm).

Thus we tentatively consider 316 cm as the mean body length at the onset of sexual maturity. An improved estimate will require more data. The body length on the mean growth curve (Kasuya and Matsui, in press) at 9.0 years of age (the mean age at the onset of sexual maturity) is about 320 cm, which is slightly larger than in the above estimation. This kind of discrepancy can occur when the growth rate declines soon after the attainment of sexual maturity, as observed in several small odontocetes (Kasuya, 1976a; Kasuya and Brownell, 1979).

5.4. Breeding longevity

The oldest pregnant female, which had a foetus 20 cm long, was aged at 34.5 years and was lactating. Assuming a normal termination of pregnancy, parturition would have been expected when the mother was about 35.5 years old (for method of estimation, see equation at the bottom of Table 9). Another indication of parturition at the same age came from a female (No. 9-116) that was observed to give birth in the harbour and was identified by a large nick on the dorsal fin. The next day this whale was killed, and very recent parturition was confirmed (lactating, uterine widths 16.0 cm (left) and 10.5 cm (right)). The next oldest pregnant females (four individuals) were 32.5 years old.

The oldest female with a corpus luteum of 'ovulation' was aged 39.5 years (No. 11-24, resting). The next oldest females with a corpus luteum of 'ovulation' were aged 38.5-years old (No. 9-3, resting) and 37.5-years old (Nos 7-26 and 24-9, resting; No. 10-15, lactating). Although the frequency of ovulations, the proportion of ovulations followed by conception, and possibly the proportion of conceptions ending at normal parturition rapidly decrease with increasing age of females (Marsh and Kasuya, 1984), there is still a possibility of parturition for whales in the 36.5- to 39.5-year classes.

Marsh and Kasuya (1984) tentatively identified post-reproductive females based on ovarian anatomy and age-related changes in fecundity (for further details, see Section 8). According to their criteria the youngest post-reproductive female appeared at age 29.5 years; the proportion increasing with increasing age, i.e. 8.5% at ages from 28 to 32 years, 19.6% at 32 to 36 years, 33.3% at 36 to 40 years, and 100% thereafter. We consider that these criteria probably underestimate the number of females less than 40 years old that have ceased to bear calves (see Section 8), and as such, are probably a more

reliable index of the minimum age of post-reproductive females (i.e. 29.5 years) than of the mean or maximum ages at which females become post-reproductive.

We conclude that females of *G. macrorhynchus* cease to bear calves when aged between 29.5 and 39.5 years inclusive. As sexual maturity occurs at 7.5 to 11.5 years, followed by first parturition between about 8.5 and 12.5 years inclusive, we estimate breeding longevity to be from about 17 to 31 years, with a probable mean of about 24 years.

5.5. Discussion

Sergeant (1962a) reported that the long-finned pilot whale in the western North Atlantic attained sexual maturity at 6-7 years (female) or at about 12 years (male). The corresponding figures for *G. macrorhynchus* are 9 and 16 years, respectively. Thus in both species the males mature about 6-7 years later than do the females. This delay is undoubtedly related to much larger male body size and possible polygynous breeding behaviour (see Section 10).

Even though *G. melaena* is larger than *G. macrorhynchus*, it attains sexual maturity several years earlier in both sexes. The cause of this difference is unknown. Our sample was taken from a stock subject to continuous fishing pressure at a relatively low level. In contrast, Sergeant's collection of samples from *G. melaena* was started in 1951 and continued during a period of heavy exploitation. However, the level of previous exploitation seems to have been low. In spite of these uncertainties, we consider that the earlier maturation and higher pregnancy rate in *G. melaena* (see Section 8) are parallel changes expected for a mammal population that lives in a better environment, and suggest that the observed difference in age at sexual maturity between the two *Globicephala* species may reflect differences in the history of exploitation or food availability.

For discussion of the incidence of post-reproductive females see Sections 8 and 10, and Marsh and Kasuya (1984 and in press).

6. SEASONALITY OF REPRODUCTION (INCLUDING FOETAL GROWTH AND NEONATAL LENGTH)

6.1. Male

Seasonal changes in male reproductive activity were investigated by studying testis weights, diameters of seminiferous tubules, and the density of spermatozoa in testicular and epididymal smears.

Weight of testis. Seasonal changes in single-testis weight are shown in Fig. 14. No significant seasonal fluctuation was detected in the mean weights of immature testes or maturing testes (early and late-maturing males combined). Because of the small sample sizes, the mean weight of histologically-mature testes was comparable only between February, May/June/July, and December. When the mean weights were compared between these three seasons, the value in May/June/July was slightly higher than that in December; the difference being just significant (T -test, $P = 0.05$). Although this apparent increase in testicular activity coincided with the breeding season estimated from the seasonality of the female

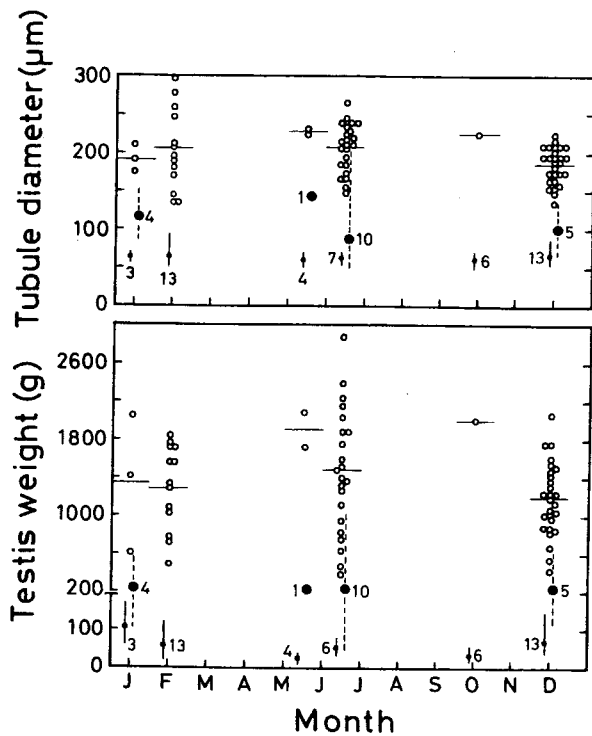


Fig. 14. Seasonal fluctuation of single-testis weight and diameter of seminiferous tubules. The open circles and bars indicate the individual and mean values for adult males respectively, the dotted lines and large closed circles the range and mean of the early and late-maturing males; and the solid lines and small closed circles the ranges and means of immature males in various seasons. The numerals indicate the sample size. Maturity was determined histologically. Data from 13 schools (nos 9 through 18, and 22 through 24).

reproductive organs, this may be a sampling artefact. The sample from May/June/July included 20 histologically-mature males from School 9, two from School 2 and two from School 24. School 9 contained adult males of large body size (Fig. 28). There was a positive correlation between body length and testis weight in mature males (Fig. 6). In order to examine the confounding effect of body size on the seasonal differences in mean testis weight, the testis weights in the months May to July were grouped by body length and compared with those in December (Table 10). The seasonal distribution of the heavier testis was variable between the body-length groups. The difference in mean testis weight was not significant for any of the body-length ranges (T -test, $P > 0.05$), and no seasonal fluctuation was detected. However, as the sample size is limited, we cannot conclude from this analysis that there is no seasonal change in the testis weight of adult pilot whales.

Seminiferous-tubule diameter. The mean seminiferous-tubule diameters of whales in various reproductive categories and body length classes are shown in Fig. 14 and Table 10, respectively. There was no significant seasonal difference in mean tubule diameter for either immature or maturing (early and late-maturing individuals combined) males (T -test, $P > 0.05$).

However, when the mean-tubule diameters of histologically-mature males in February, May/June/July and December were compared, a significant difference was found between May/June/July and December (T -test, $P < 0.01$), the mean tubule diameter being larger by about

Table 10

Comparison of single-testis weight and seminiferous-tubule diameter between whales examined in December and those examined in May–July

Range of body lengths (cm)	December			May–July		
	<i>N</i>	Mean	S.D.	<i>N</i>	Mean	S.D.
Testis weight (g)						
400–419	4	310.3	251.3	3	256.6	319.1
420–439	7	758.4	545.7	7	590.6	430.3
440–459	7	1,065.7	275.3	3	611.0	445.0
460–479	10	1,295.0	284.4	6	1,140.0	454.9
480–499	4	1,560.0	360.4	9	1,702.2	390.3
500–519				7	2,112.8	413.6
520–539				2	2,325.0	799.0
Tubule diameter (μ m)						
400–419	4	101.7	37.3	3	98.9	45.7
420–439	7	156.6	44.4	7	144.3	58.1
440–459	7	182.2	20.4			
460–479	10	194.9	22.0	6	208.4	26.2
480–499	4	189.7	12.1	8	224.7	27.1
500–519				5	211.5	16.3
520–539				2	227.9	16.6

22 μ m in May/June/July. When seasonal comparisons were made within body-length groups (Table 10) the tubule diameter of males more than 460 cm long in May/June/July also appeared to be consistently greater than in December, although the difference was statistically

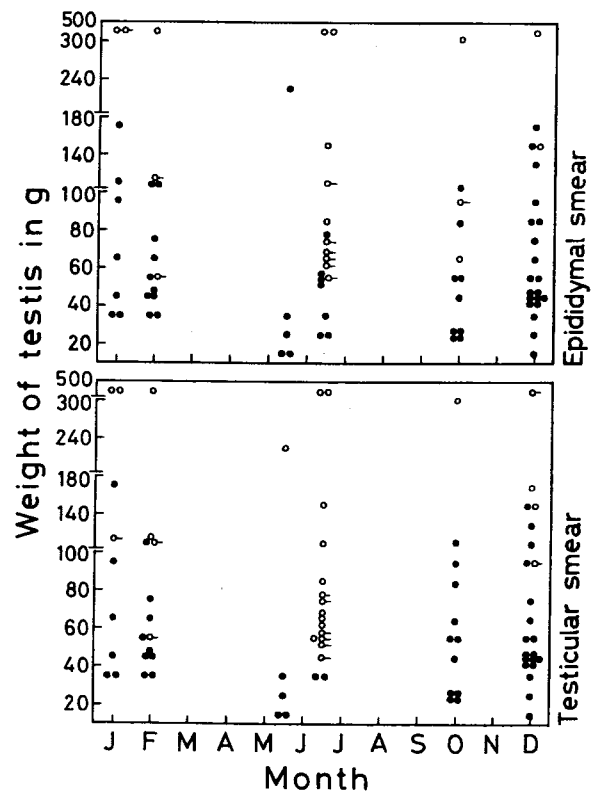


Fig. 15. Seasonal change in testes weight and density of spermatozoa in testicular (bottom) and epididymal (top) smears. Closed circles indicate individuals without spermatozoa, open circles with bars sperm 'doubtfully-present', and open circles without bars a higher sperm density. Only juvenile testes weighing less than 500 g (single testis) in 17 schools (nos 7, 9 through 18, and 22 through 27) are included.

Table 11

Seasonality of spermatozoan density in epididymal and testicular smears of males exceeding 600 g in single-testis weight

Month School no.	Number of whales						Σ
	Jan. 7, 11	Feb. 12, 16, 22, 23	May/June 24	June/July 9, 10	Oct. 13	Dec. 14, 15, 17, 18	
<i>Testicular smear</i>							
Absent	0	0	0	0	0	0	0
Doubtfully present	0	0	0	0	0	0	0
Scanty	1	5	0	5	0	10	21
Intermediate	4	6	2	17	1	15	45
Copious	0	1	0	0	0	1	2
<i>Epididymal smear</i>							
Absent	0	0	0	0	0	0	0
Doubtfully present	1	0	0	0	0	1	2
Scanty	1	4	0	4	0	2	11
Intermediate	0	4	0	2	0	9	15
Copious	3	4	2	16	1	14	40

significant only between length groups from 480 to 499 cm (*T*-test, $0.02 < P < 0.05$).

Density of spermatozoa in the smear. Fig. 15 shows the seasonal change in the relationship between the density of spermatozoa in epididymal (top) and testicular (bottom) smears for juveniles with a single-testis weight of less than 500 g. In May/June/July, spermatozoa were detected in the smears of all the testes exceeding 40 g. This threshold increased in December/January to between 90 and 160 g. The corresponding figures in October and in February were presumably intermediate between these two seasons. The epididymal smears showed the same seasonality, although the threshold level was slightly higher (testis weight 50 to 80 g in May/June/July and 140 to 180 g in December/January). This difference was expected, because further increase in testicular weight may take place from the stage of first spermiogenesis to the stage when the spermatozoa are transported to the epididymis. The density of spermatozoa found in the testis or epididymis of these juveniles was usually at the level of 'doubtfully present' and occasionally 'scanty' (Table 6), much lower than in adult males (below).

Table 11 shows the seasonal fluctuation in the density of spermatozoa of individuals with a single-testis weight of more than 600 g i.e. the approximate minimum testicular weight of fully-grown individuals (Fig. 6). There were 65 histologically-mature males and three late-maturing males with testicular weights in this category. With the exception of two epididymal smears, all samples had a sperm density of 'scanty' or greater. No seasonal difference was detected in these limited data.

Conclusion. The most definite indication of seasonal changes in the male reproductive tract is found in the threshold weights of testes producing spermatozoa. This threshold weight was low in summer and high in December/January. We consider that the reproductive activity indicated by this change probably starts in February, attains a peak in early summer, and gradually decreases towards October. This cycle is identical with the frequency of conceptions analysed below. The threshold testis weight at which sperm are produced increases from 40 to 100 g within about six months. However, it takes five years (from the ages of seven to 12 years) for the mean

testis weight to increase a corresponding amount (Fig. 6). This result and the absence of seasonal fluctuation in immature testis weights suggest that the seasonal change in threshold weight is not due to an increase in testis weight *per se* but reflects the seasonally-limited spermiogenesis of juveniles. The limited amounts of sperm thus produced suggest that these juveniles are probably not reproductively successful in the mating season.

We have no clear evidence for a seasonal cycle in the adult testis, although the wide variation in the testicular histology of mature males (Fig. 3) suggests that at least some individuals may exhibit fluctuations in reproductive activity. However, there is only a slight increase in seminiferous-tubule diameter in the mating season, and testis weights and testicular and epididymal sperm densities show no seasonality. We consider that a substantial proportion of the adult male population of *G. macrorhynchus* is probably capable of successful reproduction throughout the year.

6.2. Female

Neonatal body length. Table 12 shows the body-length frequency of 36 fetuses over 109 cm and 11 calves below 170 cm. The latter have been classified into neonates and older calves. The neonates included individuals with no neonatal line in their dentine and consequently no identifiable postnatal dentine. We do not consider these individuals to be stillbirths, because they had a healed or healing umbilicus and an erect dorsal fin. The largest foetus was 146 cm in males and 144 cm in females, and the smallest postnatal individual was 136 cm (males) and 142 cm (females). We have excluded one postnatal female of 117 cm from the following analyses, because it probably represented a premature birth. No difference between the sexes in neonatal length was detected in the somewhat scanty material presently available.

The body lengths of the five neonates were 136 cm (♂), 138 cm (♂), 141 cm (♂), 142 cm (♂) and 142 cm (♀). The mean (139.8 cm) is an estimate of the mean body length at birth. We consider that any growth between the birth and death of these neonates is probably insignificant.

Another estimate of the neonatal length was obtained from the proportion of postnatal individuals in each

Table 12
Estimation of neonatal body length

Range of body lengths (cm)	110	120	130	140	150	160	Σ
	to 119	to 129	to 139	to 149	to 159	to 169	
Number of whales in each category							
Males							
Prenatal	4	5	6	5	0	0	20
Postnatal, 0 years	0	0	2	2	0	0	4
Postnatal, older	0	0	0	0	1	0	1
Females							
Prenatal	3	4	8	1	0	0	16
Postnatal, 0 years	1	0	0	1	0	0	2
Postnatal, older	0	0	0	0	1	3	4
Males plus females							
Prenatal	7	9	14	6	0	0	36
Postnatal, 0 years	1	0	2	3	0	0	6
Postnatal, older	0	0	0	0	2	3	5
Corrected frequency*							
Postnatal	—	9	14	6	0	—	29
Postnatal, <i>n</i>	—	0	8.3	12.4	8.3	—	29
Postnatal, %	—	0	37.2	67.4	100.0	—	—

* Corrected for under-representation of young calves relative to pregnant females (see Section 8).

length group (Table 12). The method required a correction for the abundance of foetuses and postnatal calves in the sample. As shown in Table 12, 29 full-term foetuses but only seven calves between 120 and 159 cm long have been measured. Three reasons for this discrepancy are suggested: (1) not all small calves caught were measured, (2) many of the data were obtained in May to July, before the parturition peak in August, and (3) there was probably segregation of schools with lactating cows accompanied by small calves (see Section 8). Reasons (1) and (2) certainly apply to School 9, which was processed in June and July and had many full-term foetuses. A correction was made to equalize the number of foetuses and calves in the body-length range 120–159 cm (Table 12). The relationship between body length (X , cm) and the corrected proportion of postnatal calves (Y , %) is shown by the following least-squares regression.

$$Y = 3.302X - 409.479 \quad (r = 0.999)$$

(Equation 6.1)

The mean body length at birth 139.2 cm was calculated from the equation as the length corresponding to $Y = 50\%$. This value is close to the above estimate (139.8 cm). The mean of the two estimates, 139.5 cm, is used below as the mean body length at birth.

Foetal growth. Fig. 16 shows the seasonal change in body length frequency of 132 foetuses and 39 postnatal individuals below 210 cm. Although the distribution is diffuse, the data collected between May and August inclusive showed relatively high frequencies at body lengths from 120 to 150 cm (near-term foetuses and newborn calves) and below 20 cm (recently conceived smaller embryos). The frequency distribution of foetal lengths in the period October to February was also diffuse, but the values tended to be intermediate between the two size groups of foetuses in early summer. The foetal lengths also showed a gradual increase from October

Table 13
Monthly change in mean body length of hypothetical cohorts of foetuses and newborn calves of *G. macrorhynchus*

Month	Mean date ¹	Length range (cm)	N	Mean (cm)	S.D.
J./July	2 July	0–55	18	14.61 ²	18.83
August	15 Aug.	0–75	4	39.25 ²	36.55
October	13 Oct.	5–70	9	35.61	20.91
November	17 Nov.	5–85	4	48.62	31.20
December	16 Dec.	0–120	28	56.18	31.13
January	15 Jan.	15–115	17	70.97	29.38
February	14 Feb.	30–140	12	88.87	27.96
May/J.	1 June	70–145	7	120.28	27.01
J./July	2 July	65–170	32	123.79	22.61
August	15 Aug.	100–165	10	137.50	17.08
October	13 Oct.	140–195	3	171.33	25.71

¹ Mean date of data collection.

² Not used in Equation 6.2.

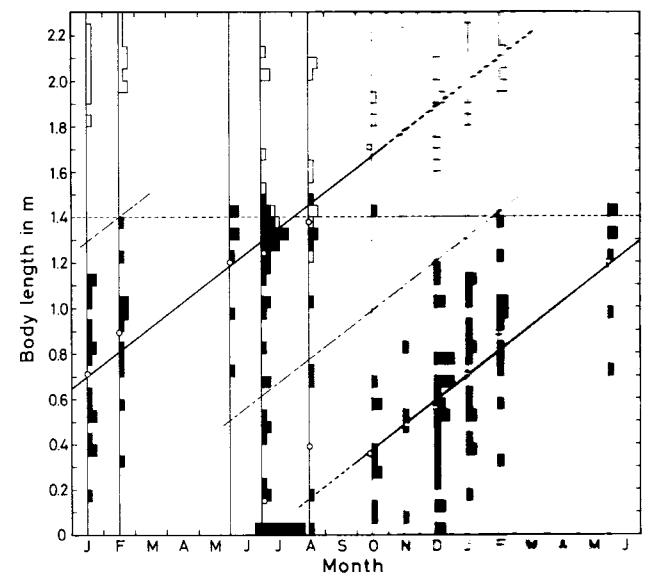


Fig. 16. Body length frequencies of foetuses (black) and neonates (white). Each open circle indicates a monthly mean of the hypothetical cohort and each thick solid line the least-squares equation fitted to the means weighted by sample size (Equation 6.2). The dotted lines are extrapolations beyond the range of the data. The dashed lines separate the two cohorts. The horizontal dotted line indicates the mean body length at birth. All data collected before July 1981 have been included.

to February. This suggests that gestation in *G. macrorhynchus* lasts more than one year, as indicated for the allied species *G. melaena* (Sergeant, 1962a), and that the seasonal changes in the foetal length-frequency distribution reflect foetal growth.

The monthly body lengths of foetuses and newborn calves were divided somewhat arbitrarily into two cohorts as shown by the dashed lines in Fig. 16, and their mean body lengths were calculated (Table 13). Of the 11 means listed in Table 13, nine (excluding the smallest two) increased linearly from one October to the next. However, the mean body lengths of the smaller foetuses for both June/July and August were situated slightly above the values expected from the trend in later months. We suggest two explanations for this result:

1. the samples were taken in the mating peak and were therefore biased by an over-representation of relatively larger foetuses conceived earlier in the season;

2. errors were caused by small sample size.

The first reason accounts for the large mean value of the June/July data. Both reasons probably contribute to the August value.

The least-squares regression equation fitted to the nine means weighted by sample size (the smallest two means are excluded) is

$$Y = 0.3398X - 60.1 \quad (r = 0.99)$$

(Equation 6.2)

where Y indicates body length in cm and X the number of days from the first of January. (Fitting individual data gives a similar equation, $Y = (0.3386 \pm 0.0425)X - 60.1$ $r = 0.82$, (95% confidence limits of the regression coefficient are also included)). Solving Equation 6.2 gives 11 August (day 588) as the date when $Y = 139.5$ cm (mean body length at birth) and 26 June (day 177) as the date when $Y = 0$. The time between the two dates is 411 days.

Hugget and Widdas (1951) suggested that foetal growth (expressed in terms of body weight) is curvilinear soon after conception and linear thereafter. They also suggested that the time from conception to the day when the extended linear-growth line cuts the axis of time (t_0) is a function of the total gestation time, being about 10% of gestation periods lasting more than 400 days. Laws (1959) established a similar pattern for the growth of cetaceans expressed in terms of body length. He indicated that t_0 of the body-length growth curve is about 90% of the corresponding value based on body weight. As we estimate the length of gestation in *G. macrorhynchus* to exceed 400 days, then t_0 of the body-length growth curve will be $0.1 \times 0.9 = 0.09$ of the total gestation time. The mean length of gestation of *G. macrorhynchus* is thus estimated as follows;

$$(588 - 177)/(1 - 0.1 \times 0.9) = 452 \text{ days or } 14.9 \text{ months}$$

(assuming 30.4 days per month)

(Equation 6.3)

The mean date of conception is thus 17 May. The 95% confidence interval for the gestation period is between 402 and 512 days.

Perrin, Holts and Miller (1977) obtained the following relationship for Delphinidae,

$$\log Y = 0.4586 \log X + 0.1659$$

(Equation 6.4)

where Y is the length of gestation in months, and X the length at birth in cm. Using this equation and 139.5 cm as the neonatal length of *G. macrorhynchus* (see above) gives a gestation length of 14.1 months, which is close to the 14.9 months estimated above.

Kasuya (1977) suggested the following relationship for delphinids;

$$Y = 0.001462X + 0.1622, \text{ (Equation 6.5)}$$

where Y indicates the daily foetal growth rate (cm) during the linear part of the growth, and X the neonatal length. The neonatal body length of *G. macrorhynchus* and the above equation suggest a foetal growth rate of 0.37 cm/day, which is similar to the growth rate of

Table 14

Mean date of parturition calculated from the body-length frequencies of foetuses and juveniles below one year of age

Length class	N	Mean date of parturition ¹	S.D.
Foetus < 10 cm	16	25th Aug.	70.5
Foetus 10-20 cm	7	9th Oct.	87.9
Foetus and calves, 21-155 cm	117	25th July	70.1
Total < 156 cm	140	2nd Aug.	73.3
Calves ≤ 213 cm (♀)	15	26th June	83.8
Calves ≤ 216 cm (♂)	13	5th July	83.5
Total calves	28	1st July	82.2

¹ Parturition season defined as 1 February to 31 January (see Section 6.2).

0.34 cm/day estimated above from the seasonal change in foetal body length.

Parturition season based on foetal lengths. The seasonal frequency of parturition was calculated from the mean foetal growth curve and the body-length frequencies of foetuses and newborn calves below 155 cm. The date of parturition was calculated for this purpose as the date when the foetus or calf is estimated to have passed the mean neonatal body length of 139.5 cm. The single linear growth curve obtained above (Equation 6.2) was fitted over the entire foetal size range, although it is probably strictly applicable only to foetuses more than 10 cm or 15 cm long. Because growth in the early embryonic stage is probably not linear and because our data were seasonally biased (we lack data for the months March, April and September), our estimated frequency distribution of parturition dates was subject to different biases for extrapolations based on different foetal lengths. We examined this problem by comparing the parturition seasons calculated separately for the three foetal-length groupings of under 10 cm, 10 to 20 cm and over 20 cm. The results are shown in Table 14 and Fig. 17. Although there were some differences in the mean parturition dates, all suggested that calving mainly occurs between May and November.

Ignoring these inaccuracies and combining the frequencies of the three foetal groups, we obtained the monthly distribution of births in Fig. 17. The distribution was unimodal, with a single peak in August, and reached a minimum in January. As breeding is annual, the estimated mean date of parturition will be affected by the arbitrarily chosen dates at which the annual breeding cycle is assumed to begin and end. We selected 1 February to 31 January, because this choice minimizes the variance of the dates of birth in comparison with the two other alternatives, i.e. from 1 January to 31 December or from 1 March to 28 February. The mean date of birth thus obtained was 2 August. This was not significantly different from our other estimates, e.g. 25 July estimated from the length frequency of the larger foetuses and newborn calves (Table 14) or 11 August estimated from the mean foetal growth curve and the mean neonatal length (see above). Although we have no special reason for concluding that 2 August is the best estimate, we have tentatively elected to use it below in our analysis of the seasonal change in apparent pregnancy rate.

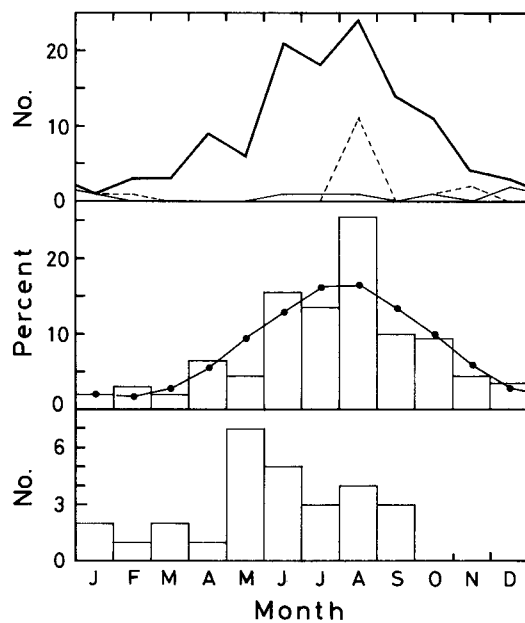


Fig. 17. Top: Estimated frequency of parturition calculated from the body lengths of foetuses and neonates between 20 and 155 cm long (thick solid line), those based on foetuses 10 to 20 cm inclusive (thin solid line), and those based on foetuses below 10 cm (dotted line). Middle: Sum of all the above parturition dates (histogram) and the normal distribution fitted to these data (closed circles and solid line). Bottom: Frequency histogram of the estimated dates of birth of neonates below one year of age calculated from the body length-age key.

Parturition season based on the lengths of calves. As discussed in Section 8, we consider that there is a significant segregation between pregnant females and lactating females accompanied by suckling calves. Consequently it is interesting to examine whether the parturition season estimated from calf lengths coincides with the above results based on foetal lengths. Fig. 17 shows the dates of birth of 28 calves below 214 cm (females) or below 217 cm (males) estimated using the body length - age key developed by Kasuya and Matsui (in press). The upper bounds of the lengths (213 and

216 cm respectively) corresponded to an age of about 1 year. The dates of birth were distributed from January to September, with relatively high frequency in the later part of this range. If the sample size and the over-simplifications inherent in our calculations are taken into consideration, the pattern of birth dates calculated by this method does not seem to be significantly different from that estimated from the foetal length data.

Seasonal change of apparent pregnancy rate. The above analyses indicate that gestation lasts more than one year and that breeding is seasonally unimodal, although some conceptions may occur in any month. This means that (1) the pregnant females in a sample may have resulted from more than one mating season (2) the proportion of pregnant females in the sample of adult females may be greater than the annual pregnancy rate (ratio of the number of females which conceive in a certain year to the total adult females in a population) and (3) the proportion of pregnant females may fluctuate seasonally as a function of the timing of parturition and conception. These problems are analysed below.

A normal distribution fitted to the predicted dates of parturition of 140 foetuses and newborn calves, assuming a mean of 2 August and a standard deviation of 73.3 days (Fig. 17), had a high chi-squared goodness-of-fit probability ($0.7 < P < 0.8$) and was therefore used to compute seasonal fluctuation in the apparent pregnancy rate. The monthly probability (relative frequency) of parturition was calculated from this distribution (Table 15). Then the normal distribution was moved forward 452 days to obtain the monthly relative frequency of conceptions (Table 15). The relative frequency of pregnancies for a cohort in a given month is the difference between the relative frequency of births and the cumulative relative frequency of conceptions for that cohort at that time. For example, let us trace the history of an imaginary cohort. The first conceptions occur in November. The relative frequency of pregnant females steadily increases until the mating season is completed in the following October. Parturition starts in the second February and the number of females in that cohort which are pregnant steadily falls until the next December. Thus

Table 15

Seasonal frequency of conceptions, births and pregnancies (see also Fig. 17)

Month	Conception frequency	Birth frequency	Frequency of pregnancies			Correction factor for pregnancy rate ²
			Cohort A	Cohort B	Cohort C	
November	0.017	0.059	0.017	1.000	0.050	1.067
December	0.026	0.031	0.043	1.000	0.019	1.062
January	0.054	0.019	0.097	1.000	—	1.097
February	0.081	0.017	0.178	0.983	—	1.161
March	0.131	0.028	0.309	0.955	—	1.264
April	0.155	0.055	0.464	0.900	—	1.364
May	0.166	0.096	0.630	0.804	—	1.434
June	0.141	0.132	0.771	0.672	—	1.443
July	0.107	0.162	0.878	0.510	—	1.388
August	0.066	0.165	0.944	0.345	—	1.289
September	0.033	0.136	0.977	0.209	—	1.186
October	0.023	0.100	1.000	0.109	—	1.109
Total	1.000	1.000	—	—	—	—

¹ All events are assumed to occur in the middle day of the month.

² Required to compensate for the seasonal change in the apparent pregnancy rate due to the 14.9-month gestation period and seasonality of breeding.

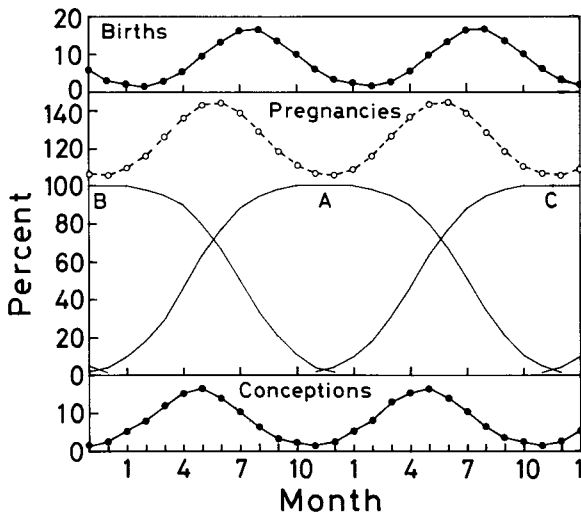


Fig. 18. Hypothetical seasonal frequencies of conception (bottom) and birth (top). Middle indicates frequencies of pregnancies for cohorts of three successive years (A, B and C), and the seasonal change of pregnant females (sum of the cohorts) expressed by open circles and dotted line.

it take two years and two months to complete this cycle. However, as the population is continually cycling, the pregnant females in the population in any one month represents two or three mating seasons (cohorts A, B and C in Table 15 and Fig. 18). Accordingly, the monthly abundance of pregnant females in a population (apparent pregnancy rate) is obtained by totalling the three cohorts for each month. The apparent pregnancy rate in June is thus 1.443 times higher than the annual pregnancy rate, whereas the corresponding figure for November is only 1.067 times the annual pregnancy rate. These figures can be used to estimate the annual pregnancy rate based on seasonally biased samples.

Table 16 compares the apparent pregnancy for each month estimated from samples and those estimated above. The two sets of figures show no correlation ($r = 0.35$), and the regression coefficient is not significantly different from zero (T -test, $0.5 < P < 0.7$). We consider that this is caused by the small sample size and the wide variation between schools in the proportion of pregnant females.

Conclusion. We conclude that breeding in this population is diffusely seasonal, with a single peak of

conception in April/May and of parturition in July/August. Gestation on the average lasts for 452 days. These figures suggest that the proportion of adult females which are pregnant fluctuates seasonally, ranging from about 107% (December) to about 144% (June) of the annual pregnancy rate, even though this pattern was not confirmed by the seasonal changes in pregnancy rate observed in our sample. However, the seasonal pattern of female reproduction reported here does coincide with the seasonal change in the abundance of nonpregnant females having a corpus luteum of 'ovulation' and with the seasonal change in the diameter of Graafian follicles in immature and lactating females as discussed by Marsh and Kasuya (1984).

7. LACTATION AND WEANING

7.1. Identification of lactation

The lactating female was identified visually by pressing the mammary gland externally and then cutting the gland with a knife. Colostrum was distinguished from ordinary milk. When a dense or thin brownish fluid was found in the lumen of the gland, it was recorded, but not as milk. The substance identified as milk in the present study had a texture like cow's milk and a colour varying from creamy white to a distinct green. The intensity of the green tinge is not dependent on the apparent quantity of milk present in the mammary gland or on the length of time between death and necropsy. Processing and subsequent biological examination of these whales were usually carried out within one hour of death, or rarely after 10-15 hours after death by drowning. The time between the drive and the slaughter does not seem to influence milk colour, because the proportion of lactating females secreting green milk in individuals processed the day after the drive did not differ from that for animals kept alive for more than one week (School 9). However, there is an indication that the occurrence of green milk is a seasonal phenomenon. The proportion of lactating whales secreting milk with some green tinge was high from February to October (Table 17). We suspect that the occurrence of green milk may depend on diet.

7.2. Analyses

We estimated the length of lactation by four different methods, (1) direct observation of stomach contents, (2)

Table 16
Seasonal variation in the reproductive status of all adult females sampled

Month	School no.	No. of adult females					Σ	CP ¹	APR ²
		Preg.	P. and L.	Lact.	Rest.				
January	7, 11	5	0	5	13	23	1.097	0.217	
February	12, 16, 22, 23	5	0	17	22	44	1.161	0.091	
May/June	24	7	0	8	8	23	1.439	0.304	
June/July	9, 10	40	1	19	39	99	1.416	0.414	
October	13	7	0	8	7	22	1.109	0.318	
December	14, 15, 17, 18	26	0	17	29	72	1.062	0.361	
Σ	14 schools	90	1	74	118	283	—	0.322	

¹ Correction factor for the overlap of pregnancies of animals from different cohorts (see Fig. 17 and Table 15).

² Apparent pregnancy rate, (P. + P. and L.)/Total adult females.

Abbreviations: preg.: pregnant; P. and L.: simultaneously pregnant and lactating; lact.: lactating; rest.: resting.

Table 17

Seasonality of females secreting green milk in *G. macrorhynchus*

Month	School no.	No. lact. females	Green milk (%)
January	7, 11	5	20.0
February	12, 16, 23	17	76.5
June/July	9, 10	17	82.5
October	13, 25, 26, 27	16	68.8
December	14, 15, 17, 18	17	0.0
Σ	—	72	54.2

Abbreviation: lact. = lactating.

comparison of the number of lactating females and the age of the corresponding number of juveniles caught at the same time, (3) computing the age difference between the greatest age at which a female was estimated to give birth and the age of all lactating females older than this, and (4) the ratio of the numbers of lactating females and pregnant females. As method (4) involves estimation of the number of pregnant females, we will consider it separately in Section 8. The results and deficiencies of the first three methods are discussed below.

Method 1. Age at which calf starts taking solid food

This is based on the direct evidence of the presence of solid food and/or milk in the stomach. Since the visual detection of a small amount of milk mixed with solid food is difficult, this method gives reliable information on the timing of the start of taking solid food rather than on the completion of weaning. All available data are shown in Table 18 together with corresponding observations on tooth eruption.

Eruption of the upper teeth started at between 0.25 and 0.75 year of age (body length of about 160 to 207 cm). Although eruption of the lower teeth tended to start after that of the upper teeth, the difference in timing was small. By the age of 0.75 years (body length of about 211 cm), all individuals had some erupted teeth in both jaws.

The stomach contents of eight small calves were examined. The smallest, 180 cm in body length and 0.5 year old, contained the remains of solid food, but no milk was detected. The oldest individual identified with milk in its stomach was 272 cm long and 2.75-years old. (Squid beaks were also present.) Records of two unidentified older suckling calves were obtained from School 14. We found two stomachs containing milk and squid remains in a pile of viscera from 23 individuals of this school processed on the same day. The other nine stomachs contained squid remains only. Although the suckling

Table 18

Information on tooth eruption and weaning in *G. macrorhynchus*

Sample no.	Body length (cm)	Sex	Age ¹ (years)	Tooth eruption status	Stomach contents ²
9-177	136	M	0 (0)	Not erupted	—
5-6B	138	M	0 (0)	Not erupted	—
5-4B	141	M	0 (0)	Not erupted	—
4-7A	142	F	— (0)	Not erupted	—
9-119	142	M	0 (0)	Not erupted	—
1-15	154	M	0.13 (0.11)	Not erupted	—
17-46	163	F	0.25 (0.18)	Several in up. and one in lower jaws	—
10-18	167	F	— (0.22)	Not erupted	—
15-1	170	F	0.50 (0.26)	One in each rami of upper jaw, none in lower jaw	—
7-20	180	F	0.50 (0.38)		Shrimps and squid beaks
13-19	182	M	0.25 (0.40)	Not erupted	—
13-20	190	F	0.25 (0.50)	Few in upper jaw, none in lower jaw	—
12-20	197	F	— (0.59)	Erupted in both jaws	Squid beaks (II)
12-19	207	M	0.75 (0.75)	Only upper teeth erupted	Squid beaks (II)
15-35	211	F	0.75 (0.91)	Erupted in both jaws	—
16-26	235	M	2.10 (1.70)	Erupted in both jaws	—
16-27	258	M	3.50 (2.75)	Erupted in both jaws	—
24-27	263	F	3.25 (3.9)	Erupted in both jaws	Squid beaks (I)
24-26	271	M	2.25 (4.0)	Erupted in both jaws	Squid beaks (I)
24-28	272	F	2.75 (4.5)	Erupted in both jaws	Milk (I) and squid beaks (II)
14-? ²	≥ 258	—	≥ 2.5	—	Milk and squid beaks (I)
14-? ²	≥ 258	—	≥ 3.0	—	Milk and squid beaks (I)

¹ Ages estimated from body length given in parentheses.² The stomachs from eleven whales over 258 cm and over 2.5 years were examined (see Section 7.2, Method 1). Individual whales not identified.³ Numeral indicates stomach compartment.

individuals were not identified, the youngest individual in the school was 2.5 years old and the second youngest 3.0 years. (Both had body lengths of 258 cm.) These data indicate that calves of *G. macrorhynchus* start taking solid food at between 0.5 and 1.0 year of age, the time when the teeth start to erupt, and that some calves continue to take both solid food and milk until the age of at least 3.0 years. Sergeant (1962a) estimated that *G. melaena* starts taking solid food at a similar age, 6–9 months.

Method 2. Age at which weaning is completed

This method is based on the comparison of the number of lactating females and the age composition of juveniles in a school, making the following assumptions: (1) *Each lactating female is nursing one calf at the time of her death.* If a female adopts a calf after the loss or weaning of her own, this will not cause error in estimating of the length of *suckling*. However, in this case, the calculated length of *lactation* will not be correct, the direction of bias depending on the age difference between the adopted and natural offspring. (The possibility of communal nursing will be discussed later.) (2) *There is no suckling calf older than any weaned calf in the same school.* This assumption may not be correct. The age of weaning is probably influenced by (a) individual variation in the behaviour of the cow or calf and by (b) the age of the cow. Although this assumption may underestimate individual variation in weaning age, it should not cause a large bias in the mean age. (3) *Both mother and calf are caught together without the loss of either during the drive.* A calf may not be able to swim as fast as its mother and may be lost if the driving is done too fast. This will cause an over-estimation in the age at weaning. However, a school of *G. macrorhynchus* which is being driven is usually small for the three to five driving boats involved, and the extent of the school can be seen from all boats, decreasing the chance of losing individuals. Although only schools which (in the fishermen's opinion) included the whole group were used in the following analysis, the possibility of loss has to be carefully examined when we compare these results with those obtained by other methods.

Results of the analysis using this method are shown in Fig. 19. The weaning status of two calves in school 10 could not be determined, because the sex and growth stage of one individual were unknown. Similarly, it is possible to say only that there were at least six suckling calves in school 12, because the reproductive status of three adult females was not known. These assumptions, applied to School 23, suggested that the oldest suckling individual was a 12.5-years old pregnant female. We find this conclusion difficult to accept without further evidence, even though lactating Steller's sea lions (*Eumetopias jubatus*) are known to suckle occasionally from another lactating female (Pitcher and Calkins, 1981). Accordingly, we have added a rider to our second assumption, i.e. that sexually-mature individuals shall be assumed to be completely weaned. If this rider is applied, a 15.5-year-old histologically-immature male in School 23 is classified as suckling instead of the 12.5-year-old pregnant female, and a 13.5-year-old immature male in School 12 is classified as suckling instead of a 11.5-year-old pregnant female. (However, the age of the oldest suckling calf in School 12 is not changed by this process). Our cumulative analysis of 12 schools is summarized at the

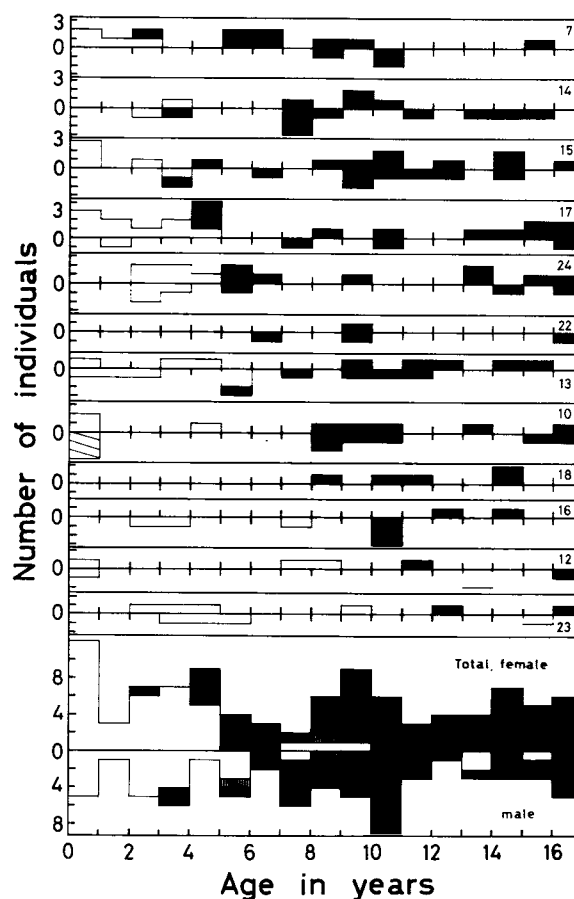


Fig. 19. Estimation of weaning age: the number of lactating females and the ages of juveniles in each school are compared. The number of the school is indicated on the right. The frequency histogram of the age distribution of females in each school is situated on top of the line; that for males is on the bottom. Code. White: presumed suckling calf; black: presumed weaned individual; vertical stripe: uncertain; diagonal stripe: sex unknown. For full data concerning these schools see Table 36 and Fig. 27.

bottom of Fig. 19. The youngest weaned calf appeared at 2.0 years, but suckling calves were abundant until the age of 6.0 years. The four calves apparently suckling when between seven and 10 years of age were from three different schools. Accordingly, we conclude (without any direct evidence) that some precocious calves complete weaning by the age of 2.0 years, but that a few calves continue to suckle until the age of 10 years.

The three immature males, from two schools, classified as suckling at the ages of 13.5 and 15.5 years were unexpected. The alternative explanation that smaller calves were lost during the drive necessitates assuming the loss of two suckling calves out of the six initially present in School 12 and one calf out of the eight in School 23. The sea state at the time of these captures did not differ from the usual calm conditions needed for driving. We consider that our conclusion that some calves suckle for up to 13 to 15 years is probably valid, especially as it is supported by the result of our third method of estimating the length of lactation (see below). Using the chemical identification of lactose in stomach contents, Best (1979) verified that some male sperm whale calves may suckle until they are 13 years old.

We examined the linear relationship between the mean

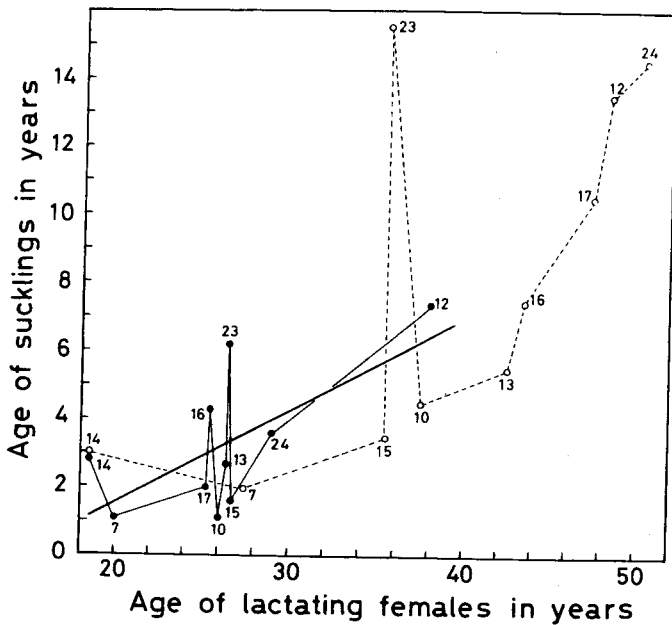


Fig. 20. Mean age of lactating females plotted against that of the probable suckling calves in the same school obtained by the second method (matching numbers of lactating cows and calves, Section 7.2) (closed circles and solid line). The age of the oldest suckling calves estimated either by the second method or third method (age of lactating cow older than oldest pregnant female, Section 7.2) has also been plotted against the age of oldest lactating cow in the school (open circles and dotted line). The thick solid line is the linear relationships between the mean age of the lactating females in a school and the mean age of the calves in the same school (Equation 7.1). Numerals indicate school number.

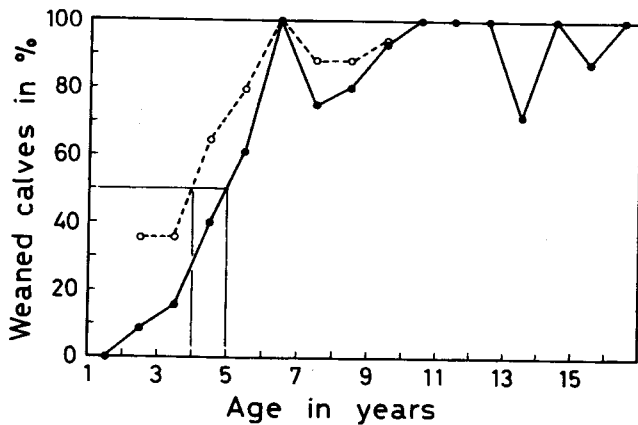


Fig. 21. Estimation of age at completion of weaning. The estimated proportion of weaned individuals in the total number of immature whales plotted against calf age. The closed circles and solid line indicate the figures calculated from Fig. 19, and the open circles and dotted line the corresponding figures assuming that weaned calves segregate.

age of the lactating females in each school (X , years) and the mean age of the calves in the same school (Y , years) which we classified as suckling using the assumptions outlined above. The relationship is expressed by the equation,

$$Y = 0.273X - 3.89, \\ r = 0.67 \text{ (Fig. 20)} \quad \text{(Equation 7.1)}$$

The regression coefficient is significantly different from 0 ($0.02 < P < 0.05$).

For each school, the age of the oldest suckling calf estimated by this method or by the third method (see below) was also plotted against the age of the oldest lactating female (Fig. 20). There are indications that older suckling calves were caught together with older lactating females, suggesting that older females may nurse their calves longer than do younger cows.

The analysis of calf age and the proportion of weaned calves in Fig. 21 is based on data in Fig. 19 and two alternative assumptions: (1) all the weaned calves remain in the mother's school, (2) there is no calf mortality below the age of 10 years, the differences between the observed frequencies of 0 to 1.0-year-old (17 individuals) and of other age groups over 2.0 years (see Fig. 19) being caused by segregation of the weaned calves. The former assumption gives 5.0 years as the age at which 50% of the calves have completed weaning and the latter an age of 4.0 years. The former assumption also suggests that weaning usually occurs between the ages of 3.5 and 5.5 years; and the second method at ages between 2.5 and 4.5 years.

We anticipate that there could be two kinds of segregation between weaned and suckling calves. (1) The segregation of *schools* which contain high numbers of either weaned or suckling calves. This case is not considered here, because we are analysing only mother-calf pairs in each school, but it is considered below (see Section 8). (2) In addition, it is possible that weaned calves segregate from their mother's school. Although such segregation is considered to occur in the western North Pacific populations of spotted (*Stenella attenuata*) and striped dolphins (*S. coeruleoalba*) (Kasuya, 1972; in press; Kasuya, Miyazaki and Dawbin, 1974; Miyazaki and Nishiwaki, 1978) and in the sperm whale (Best, 1979), there is no evidence for this behaviour in the long-finned pilot whale (Sergeant, 1962a) or in the killer whale pods which are under regular observation off Vancouver island (Bigg, 1982; Balcomb, Boran and Heimlich, 1982). The similarity between the breeding behaviour and school structure of short-finned pilot whales and killer whales suggests that weaned calves may not segregate in *G. macrorhynchus* to the same degree as in spotted and striped dolphins. We therefore suggest that weaning usually occurs between 3.5 and 5.5 years of age.

Method 3. Lactation in old females

This method is based on the age difference between the estimated age of last parturition and the ages of older lactating females. A defect of this method is the uncertainty that surrounds the ages of last parturition and the cessation of the subsequent lactation on a population basis. As outlined in Section 5, although the oldest age at parturition indicated by the pregnant females in our sample was 35.5 years, the age of the oldest females with a corpus luteum of 'ovulation' was 39.5 years. This suggests that conception followed by parturition and lactation may occasionally occur in animals up to 40 years old. On the other hand, many females probably cease to bear calves between the ages of 29.5 and 35.5 years (Marsh and Kasuya, 1984). However, we decided to use this method because: (1) a larger sample may find older pregnant females, but it may also find older lactating females, causing only a limited change in the result, and (2) the length of lactation

Table 19
Length of lactation after oldest estimated parturition

Sample no.	Age (years)	Female			Length of lactation after age 35.5 (years)	Maximum age and sex of sucklings in the school		Female Estimated age at last parturition ³
		Number of corpora				Calculated using		
		'CLO'	Medium CA	Old CA		Method 2 ¹	Revised Method 2 ²	
24-14	50.5	—	—	7	15	4.0 (♀)	14.5 (♂)	36
12-3	48.5	—	ovaries pathological		13	≥ 13.5 (♂)	—	35
17-41	47.5	—	—	7	12	4.25 (♀)	10.5 (♂)	37
9-47	45.5	—	—	—	10	—	—	—
12-11	43.5	—	—	10	8	≥ 13.5 (♂)	—	30
16-19	43.5	—	—	16	8	7.5 (♂)	—	36
12-12	42.5	—	1	10	7	8.25 (♀)	—	34
13-10	42.5	—	2	11	7	5.5 (♂)	—	37
9-25	41.5	—	—	—	6	—	—	—
13-31	40.5	—	—	13	5	5.5 (♂)	—	35
10-15	37.5	1	1	4	2	4.5-8.5	—	—
12-7	36.5	—	1	8	1	7.0 (♀)	—	29
Mean	43.4				7.83			34.3

¹ Based on the comparison of the number of lactating females and the age composition of juveniles in the school assuming that suckling calves are always younger than weaned calves.

² Based on revised assumption that suckling calves are not always younger than weaned calves (see Section 7.2, Method 2).

³ Female's age minus age of suggested suckling calf.

Abbreviations: 'CLO': corpus luteum of 'ovulation'; CA: corpus albicans. See Marsh and Kasuya (1984) for descriptions of medium and old CA. No young CAs were observed.

estimated by this method is not affected by the segregation of calves or by a sampling bias in estimating the pregnancy rate.

Assuming that each of the 12 'old' lactating females (Table 19) had its last calf at 35.5 years, we have estimated the length of the last lactation of each female as the difference between its age and 35.5 years. The 95% confidence interval of each of these estimates is between ± 2 and 2.5 years. (The coefficient of variation of each age reading is about 2%; see Kasuya and Matsui (in press).) Table 19 compares each of these 10 estimates of the length of the last lactation with the age of the oldest suckling calf in the same schools (estimated by Method 2 above). In six instances there was good agreement between the two methods. Two of the individuals for which there was a discrepancy were respectively 37.5 years old (No. 10-15) and 35.5 years old (No. 12-7). The discrepancy is eliminated if we assume that they had been nursing calves born when they were about 30 years old (Fig. 19).

Results for whale No. 24-14 (50.4 years old) were anomalous, as the oldest suckling calf estimated by Method 2 (above) was aged four years. This suggests that either (1) our identification of the 'oldest suckling calf' in this school was incorrect, i.e. the assumption that suckling calves are always younger than weaned calves in the same school is invalid, or (2) No. 24-14 was nursing a foster calf. We have no evidence pertinent to the second hypothesis. If we accept the first alternative, Fig. 19 suggests that a 14.5 year old male might have been suckling instead of one of the eight calves less than five years old. (The three females in the school between nine and 14 years old were pregnant.) The testis of this male was at the late-maturing stage (weight of testis was 230 g and 60% of the tubules were mature), and no

spermatozoa were detected in its epididymis. Thus this male had not yet matured. If this male was indeed the calf of No. 24-14, this female would have last given birth at 36 years of age.

Results for whale No. 17-41 (47.5 years) were similarly anomalous (Fig. 19). In School 17 the oldest suckling calf identified by Method 2 (above) was only 4.25 years old, while two females between the ages of 8 and 11 years were pregnant. However, if the 10.5 year old immature male was the calf of No. 17-41, this whale would have last given birth when 37 years old.

7.3. Discussion

Milk as a major source of nutrition may be essential for odontocetes for only the first few months of life. In aquaria, bottlenose dolphins have been variously observed to start taking solid food at 3.5 months (Tavolga, 1966), 205 days (6.7 months) and 195 days (6.4 months) (Nakajima, Takahashi, Ogura and Sawaura, 1963) or 9 months (Tavolga and Essapian, 1957), and *Neophocaena phocaenoides* at eight months (T. Kataoka, pers. com. 1982). Although suckling was considered to be infrequent by the time a *T. truncatus* calf was between 12 and 16 months old, the mother's mammary gland was still active at the time of her death when the calf was 2.5 years old (Nakajima, 1963). We suggest that the minimum requirement for suckling as a *nutritional* source may be about a year, by which time a calf may have also gained the minimum skills required for independence, e.g. *T. truncatus* calves do not establish the frequency modulation and stereotypy of their whistles (characteristics common to all adult bottlenose dolphins) until they are about a year old (Caldwell and Caldwell, 1979). Weaning

is usually completed by eighteen months, but the mother-calf bond is retained for more than two years if the mother is not pregnant (Tavolga, 1966).

Brodie (1969) observed that four species of odontocetes, i.e. sperm whale, white whale (*Delphinapterus leucas*), long-finned pilot whale and bottlenose dolphin, had prolonged nursing periods (of about two years) compared to those of mysticetes. He postulated that lengthy lactations were related to training period required by these animals with their complex social structure. The nursing period of the common porpoise (*Phocoena phocoena*) has been estimated at eight months (Mohl-Hansen, 1954) and that of *Pontoporia blainvillei* at less than nine months (Kasuya and Brownell, 1979). A nursing period of about one year was estimated for eastern tropical Pacific *Stenella attenuata* (Perrin, Coe and Zweifel, 1976) and *S. longirostris* (Perrin *et al.*, 1977). In the western North Pacific, a lactation period of about two years was estimated for *S. attenuata*. For the more heavily exploited *S. coeruleoalba*, Kasuya (in press) has demonstrated a decrease in the lactation period from 2.64 years in 1955 to 1.59 years in 1977. Both the lactating and resting periods are considered to increase with age in these populations of *Stenella* species. A wide individual variation of up to five years in the length of the nursing period was suggested for *S. attenuata* by Kasuya, Miyazaki and Dawbin (1974). These results suggest the potential both for a relatively extended lactation period and for considerable flexibility in lactation length in accordance with the physiological or social requirements of the population. Although the mean lactation length for the sperm whale is believed to be about two years (Ohsumi, 1965; Best, 1968), there are indications of large individual variation extending up to 7.5 years for female calves and up to 13 years for male calves (Best, Canham and MacLeod, 1984). Longer suckling may serve to maintain the cow-calf bond while the calf improves its communicational ability under the protective and perhaps educational care of its mother (Brodie, 1969).

Of the three methods used in this study to estimate length of lactation or weaning age, the analysis of stomach contents (Method 1) provides firm data on the start of taking of solid food (0.5 year) and verification of suckling up to 3.0 years.

School analysis (Method 2) is based on an unconfirmed assumption that each calf suckles from its own mother. Although this is generally accepted for most mammals, a captive *Neophocaena phocaenoides* calf has been observed to occasionally suckle from a non-lactating adult female while it was suckling from its own mother. Also in captivity, another orphan calf of the same species was adopted by a lactating female soon after the abortion of her own near-term foetus (T. Kataoka, pers. comm. 1982). This behaviour was not observed on all possible occasions in the aquarium and might be due to crowded conditions. However, communal nursing has been reported in several species of wild land mammals (see Gubernick, 1981 for details). The third method of analysis (lactation length in old females) is not affected by communal nursing.

Our results using these three methods were in good agreement. The result of the fourth method (mean lactation length and its increase with age of cow, see Section 8) were similar to those produced by the second

method. We consider this indicates that communal nursing is uncommon in *G. macrorhynchus* and that the extended lactation period of the older females will be attributable, in most cases, to the suckling of their own calves. The last calf of a female seems to be sometimes nursed for a very long time, possibly up to 13 or 15 years.

The rapid increase in mean lactation length after 24 years of age is partially related to the lengthy lactation by some post-reproductive females, as discussed in Section 8. An increase in mean nursing period with increasing maternal age has been observed in four stocks of *Stenella* (see above) as well as *G. macrorhynchus*. The occasional long nursing periods suggested for *G. macrorhynchus* are similar to those reported for the sperm whale (Best *et al.*, 1984). Although we are not certain whether the maximum duration of suckling in *G. macrorhynchus* is longer for male than female calves (as in the sperm whale), we suggest that this result is highly probable, because both species exhibit a parallel marked difference in the age of sexual maturation of males and females (Best, 1970).

Once lactation is established, it will be maintained by the stimulus of regular suckling. However, there are at least two requirements for this. (1) The calf has to maintain a close relationship with its mother, and (2) the mother has to continue to allow the calf to suckle. Although suckling may inhibit the onset of estrus it clearly does not always prevent estrus or subsequent conception in *G. macrorhynchus*, since three simultaneously pregnant and lactating females were observed in our sample. As we have no information on the effect of the behaviour of the mother at estrus on her interaction with her calf, we do not know whether this tends to terminate suckling behaviour. However, by analogy with other mammals, lactation will almost certainly be terminated towards the end of pregnancy at the latest. In domestic cows, *Bos taurus*, for example, pregnancy has no measurable effect on milk production before the fifth or sixth month, but by eight months, production usually falls rapidly. It is, however, well known that barren cows can lactate for extended period (Lascalles and Lee, 1978). Similarly, in the case of post-reproductive females of *G. macrorhynchus*, lactation will not be interrupted by estrus or pregnancy and can continue as long as the suckling stimulus is maintained. A similar situation can occur in human societies. Lee (1980) reported that it is not uncommon for women in the !Kung tribe (an African hunter-gatherer community) to undergo menopause while still nursing.

We thus consider that the extended suckling of the last calf of post-reproductive females is the result of the long mother-calf bond and stable school structure, not the cause of that bond. A large proportion of calves are certainly weaned at a younger age, and most post-reproductive females are not lactating. The reasons for stable long-lasting school structure in *G. macrorhynchus* are considered separately below (see Section 10).

We further suggest that this extended period of maternal care is likely to be much more common in some species of odontocetes than others. We do not expect spotted and striped dolphins to have such an extended suckling period as *G. macrorhynchus*. Not only does sexual maturity occur earlier in both sexes (7-10 years) of these species, but most of the weaned juveniles

segregate from the breeding schools until puberty (Kasuya, 1972; Miyazaki, 1977; Miyazaki and Nishiwaki, 1978; Kasuya, in press). In contrast, sperm whales do not segregate into bachelor schools until after puberty at 10–13 years (Best, 1970; 1979). Thus even male sperm whales have the opportunity to suckle for many years, as observed by Best (1979).

8. REPRODUCTIVE CYCLE

8.1. Outline of reproductive cycle

We have classified adult female of *G. macrochynchus* as pregnant, lactating (defined above), pregnant and simultaneously lactating, or resting. The resting category comprises all adult females which were neither pregnant nor lactating, including the post-reproductive 'resting' females identified by Marsh and Kasuya (1984). Lactation and pregnancy usually do not overlap. Only three females (Nos. 26–8 (12.5 years), 25–38 (13.5 years) and 10–12 (34.5 years)) were simultaneously pregnant and lactating, compared with 94 pregnant, 81 lactating and 129 resting females (Schools 25, 26 and 27 included). As shown in Table 20, some of the lactating and resting females had an ovarian corpus luteum even though their uteri showed no indication of recent parturition or abortion. These females are considered to have ovulated shortly before death.

Fig. 22 compares the width of the uterine horn between females of different reproductive status. The horn width was below 3 cm in immature females. In most lactating females, the uterine width ranged from 2 to 4 cm (with no obvious contralateral size differences). However, some exceptionally large uteri of lactating females (who presumably had recently given birth) measured over 20 cm. The uteri of resting (but not recently ovulated) females exhibited slight contralateral size differences, and the upper range of widths was about 7 cm above that of most of the lactating females. This suggests that some of the resting females were killed at about the time of estrus and had slightly distended uteri as a result. The two uterine horns of one whale (No. 25–1, 28.5 years old), one of the two pregnant females in Fig. 22, measured 4.5 and 6.0 cm. Although the larger horn contained an embryonic membrane about 10 cm long, it was pathological and presumably represented a degenerating pre-implantation stage of pregnancy (see Benirschke and Marsh, 1984).

The uteri of recently ovulated, non-pregnant females were intermediate in width between those of resting females and females in early pregnancy. This suggests that the ova shed by these females were either (1) not fertilized, (2) aborted before implantation, or (3) at the pre-implantation stage. In view of the high number of ovulations per reproductive cycle (see Table 23) and the significant increase in the proportion of females having a corpus luteum of 'ovulation' at ages between 20 and 40 years (when the pregnancy rate was declining (Marsh and Kasuya, 1984)), we expect that many of these corpora had resulted from infertile ovulations. As pointed out by Benirschke, Johnson and Benirschke (1980) and confirmed by the large size of the membranes found in whale (No. 25–1) above, a small embryo in a relatively large embryonic membrane is unlikely to be missed.

Although our estimates of the length of the lactating

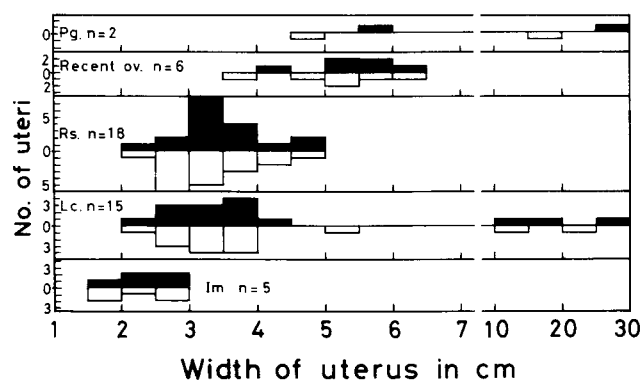


Fig. 22. The width of the uterus of pregnant (top), recently-ovulated/non-pregnant (2nd), resting (3rd), lactating (fourth), and immature females (bottom). Black squares indicate the larger horns, and white squares the smaller.

and resting periods based on a gestation period of 452 days are likely to be over-estimates, we used these values in this section because we do not know when pregnancy first becomes macroscopically visible. We presume that the length of invisible pregnancy will be less than 45 days ($= t_0$, estimated in Section 6). Thus the error produced by using 452 days as the length of visible pregnancy should be less than 10%.

Another error in the calving cycle estimation in Sections 8.2 and 8.3 comes from ignoring pre- and post-natal mortality and undetectable early pregnancies in the correction for overrepresented pregnant females. We do not know the resultant effect of these factors, although it is expected that they will act in opposite ways, i.e. the first will cause overestimation and the second, underestimation of pregnant females.

All the estimates below are correct to only one or at most two decimal places. However, the subsequent calculations were made on the unrounded estimates to avoid rounding-off errors. Unrounded figures have been given to aid the reader who wishes to check the calculations.

8.2. Mean reproductive cycle

The annual pregnancy rate and mean length of the reproductive cycle are estimated from the proportion of mature females that are pregnant, by assuming (1) that the length of each reproductive stage is proportional to the relative frequency of adult females at that stage in the sample, and (2) that the gestation period is 452 days. This method is affected by two types of biases: (1) seasonal biases in both sample collection and reproductive status, (2) the school-specific bias, i.e. the fact that the proportion of females at each reproductive stage in a school may not be representative of the proportions in the population.

If both biases are neglected, the annual pregnancy rate (APR) can be calculated from the following equation:

$$APR = \frac{P_m + PL_m}{S_m} \frac{365}{452} \quad (\text{Equation 8.1})$$

where P_m indicates the number of pregnant (but not lactating) females, PL_m the number of females pregnant and simultaneously lactating, and S_m the total number of

Table 20

Reproductive status and apparent pregnancy rate of adult females in various age classes: Schools 7, 9 through 18, 22, 23 and 24

Age class (years)	Number of whales at each reproductive stage			A.P.R. (%)
	Preg.	Lact.	Rest.	
6-9	3	0	1	75.0
9-12	12	3	5 (2)	60.0
12-15	13	3 (1)	3	68.4
15-18	9	9	3	38.1
18-21	14	6	6 (4)	53.8
21-24	14	9 (2)	5 (3)	50.0
24-27	6	9	7	27.3
27-30	7	4 (1)	8 (3)	36.8
30-33	7	4	5 (2)	43.8
33-36	1*	10 (1)	6 (1)	5.9
36-39	0	2 (1)	17 (5)	0
39-42	0	2	8	0
42-45	0	4	14	0
45-48	0	2	13	0
48-51	0	2	2	0
51-54	0	0	3	0
54-57	0	0	4	0
57-60	0	0	1	0
60-63	0	0	2	0
< 36	86	57 (5)	49 (15)	44.8
N/A	5	5	5	33.3
Total	91	74 (6)	118 (20)	32.2

* Pregnant and simultaneously lactating.

Non-pregnant females with a corpus luteum of 'recent ovulation' are given in brackets.

Abbreviations: Preg.: pregnant; Lact.: lactating; Rest.: resting; A.P.R.: apparent pregnancy rate; N/A: age estimate not available.

adult females whose reproductive status was determined. Using this Equation 8.1 and the data for 283 adult females in 14 schools (Table 20), the annual pregnancy rate not corrected for other biases is given as

$$\frac{90+1}{283} \cdot \frac{365}{452} = 0.2597$$

However, if the sample is seasonally biased, it is better to estimate the annual pregnancy rate as follows;

$$APR = \frac{\Sigma((P_m + PL_m)/C_m)}{\Sigma S_m} \quad (\text{Equation 8.2})$$

where m indicates month and C_m the proportion of mature females that are pregnant in each month (last column of Table 15). The other abbreviations are as in the first equation. The same data and this equation give the corresponding value as

$$\frac{72.77}{283} = 0.2571$$

The figures obtained by the two methods are similar. This may be partially because (1) the present sample covered nearly all seasons of the year and (2) the between-school variation in the apparent pregnancy rate was almost large enough to mask the seasonal change. We used the first method to calculate the annual pregnancy rate below, solely because of the simplicity of calculation. In view of the apparent unimportance of the correction for seasonality, we have ignored the seasonal bias in the number of lactating females, because we expect the

seasonality of weaning to be more diffuse than that of mating or parturition.

A school-specific bias is indicated by Table 21, which shows that the number of calves below the age of 452 days (equivalent to the length of gestation) was only 20 individuals, in contrast to the estimate of 60.7 pregnant (plus pregnant and simultaneously lactating) females in the sample (adjusted to include females of unknown status, see Table 21). This difference seems unreasonable even assuming a high neonatal mortality rate and the inaccuracies discussed in Section 6.2. The number of calves of suckling size (not necessarily below the age 452 days) missing in this comparison is only two, in School 11 (see Fig. 28). Among several hypotheses tested, the assumption that pregnant females were over-represented relative to the other two reproductive stages of adult females was the only hypothesis that did not contradict the other biological results obtained in this study.*

For this reason, our analysis of the reproductive cycle is based on this assumption. The other hypotheses tested and rejected are detailed below (Section 8.4).

The data from School 9 are initially excluded from the following analyses because females below 15 years of age are under-represented in our sample from this school (see Section 9.4). However, they are included in the final calculation with appropriate corrections (see Section 8.3).

If pre- and post-natal mortality is ignored, $P+PL$ should equal the number of calves below the age of 452 days, which is 20.

$$PL = 1 \therefore P = 19.0$$

$$PL + L = 1 + 63.5$$

$$R = 84.8$$

where P = No. pregnant, PL = No. pregnant and simultaneously lactating, L = No. lactating, R = No. resting (All figures have been adjusted to include adults of unknown reproductive status in Table 21). The mean length of each reproductive stage in years is calculated from

$$\frac{X}{P+PL} \cdot \frac{452}{365} \quad (\text{Equation 8.3})$$

where X indicates the number of females at the reproductive stage being considered (see Table 21).

The mean calving interval for all adult females (10.42 years (excluding School 9) or 10.13 years (with School 9)) is the sum of the length of each stage. Inclusion of School 9 does not affect the length of the resting period but shortens the mean lactation length (sum of periods of

* Footnote: After completing the present analysis, Kasuya examined 178 short-finned pilot whales caught in six drives at Taiji. The reproductive status of the adult females was as follows:

School	Date	Preg.	PL	Lact.	Rest.	Total	Missing
25	Oct. '81	2	1	0	6	9	1 or 2
26+27	Oct. '81	1	1	7	4	13	10% (26)
27	Oct. '81	—	—	—	—	—	80% (27)
28	Jan. '82	2	0	6	4	12	0
29	Oct. '82	4	1	10	7	22	3
30	Oct. '82	9	0	13	6	28	0
Total		18	3	36	27	84	—

The number of lactating females in these schools was about twice that of pregnant females, close to the value estimated in this study and suggesting that segregation of schools based on female reproductive status may be more apparent in the summer, e.g. School 9, than in the fall/winter.

Table 21
Estimates of mean reproductive cycle with and without corrections for sample bias and including and excluding School 9

	No. of adult females of all ages						No. of calves ²
	Preg.	P. and L.	Lact.	Rest.	Unknown	Total	
<i>13 schools¹ (excluding School 9)</i>							
No. of whales at each stage	59	1	61	81	7	209	20
No. extrapolated to include whales of unknown reproductive status	59.7	1.0	63.5	84.8	0	209	20
% at each stage	28.5	0.5	30.4	40.6	0	100	—
With correction for sample bias							
No. of whales	19.0	1.0	63.5	84.8	0	168.3	—
%	11.3	0.6	37.7	50.4	0	100	—
Estimated length of stage (years)	1.18	0.06	3.93	5.25	0	10.42	—
<i>14 schools (including School 9)</i>							
With correction for sample bias (all adult females)							
Estimated length of stage (years)	1.19	0.05	3.43	5.46	—	10.13	—
With correction for sample bias (excluding post-reproductive females)							
Estimated length of stage (years)	1.20	0.04	2.86	2.78	—	6.88	—

¹ Schools 7, 10, 11 through 18, and 22 through 24.

² Calves below the age corresponding to length of gestation (female < 219 cm, male < 223 cm).

Abbreviations: Preg.: pregnant; P. and L.: simultaneously pregnant and lactating; Lact.: lactating; Rest.: resting.

lactation and lactation and simultaneous pregnancy) from 3.99 to 3.48 years.

The difference is probably caused by the low number of lactating females in School 9, i.e. 35.1% of the resting females (P, 31; R, 37; L, 13 individuals) compared with 76.5% (P, 59; PL, 1; L, 61; R, 81 individuals) for the other 13 schools. At this stage, we have to conclude that the estimates produced by including School 9 are better, because they are based on a larger number of samples (Table 21).

The resultant estimate of the mean *length of lactation* (3.48 years) is about one year shorter than the mean *weaning age* (i.e. the age at which the number of suckling and weaned calves were equal (Section 7.2)). Half of this discrepancy (3.99 - 3.48 = 0.51 year) can be attributed to the low number of lactating females in School 9. We attribute the remaining 0.5 year to the fact that these analyses are dealing with two different biological phenomena. The mean *length of lactation* does not distinguish lactations terminated by weaning from those terminated prematurely by death, whereas the estimation of mean *weaning age* excludes those cases and thus should be longer. The mean *length of lactation* is more relevant to our analysis of the reproductive parameters of the population; the mean *weaning age* is a better indication of juvenile growth.

Correction for post-reproductive females: According to the criteria of Marsh and Kasuya (their Fig. 8, 1984), 15.5% of 71 lactating females and 49.0% of 100 resting females were post-reproductive. The sample on which Marsh and Kasuya's (loc. cit.) analysis was based was almost identical with that in Table 20. Therefore Marsh and Kasuya's estimates of the proportions of post-reproductive females are used to compute the mean lactating and resting periods for reproductive females only, as follows:

$$\begin{aligned} \text{lactation} &= 3.43 \times (1 - 0.155) \\ &= 2.90 \text{ years} \quad (\text{Equation 8.4}) \end{aligned}$$

$$\begin{aligned} \text{resting period} &= 5.46 \times (1 - 0.490) \\ &= 2.78 \text{ years} \quad (\text{Equation 8.5}) \end{aligned}$$

This reduces the mean calving interval to 6.92 years.

8.3. Age-specific reproductive cycle

As the pregnancy rate is strongly affected by maternal age, we have also computed the reproductive cycle on an age-specific basis. The analysis requires a large sample size, and so we have included School 9 data (appropriately corrected for the under-representation of young adult females). As the inclusion of School 9 changes the ratio of the number of pregnant (plus pregnant and simultaneously lactating) females to the total number of adult females from 60.7/209 (Table 21), to 91/283 (Table 20) the correction factor F_1 required if School 9 is included is

$$F_1 = (60.7/209)/(91/283) = 0.903$$

(This correction factor is needed because the correction for the seasonality of pregnancy (see Table 15) was computed excluding School 9).

Corrections are also necessary because of the sample bias resulting from the segregation of pregnant and lactating females (Section 8.2) i.e. the frequency of the pregnant females has to be decreased by

$$F_2 = 19.0/59.7 = 0.318$$

Using these correction, Y_t (the mean length of one of the reproductive stages) and C_t (the mean calving interval), both at age t years, can be calculated as follows:

$$Y_t = \frac{X_t}{(PL_t + P_t \cdot F_2) F_1} \cdot \frac{452}{365} \text{ years} \quad (\text{Equation 8.6})$$

Table 22

Linear-regression equations ($Y = aX + b$) describing the relationships between the length of the various reproductive stages (Y , years) or the annual pregnancy rate (Y , %), and age (X , years)

Y variable	Age range (years)	Constants		Correlation coefficient r
		a	b	
Lactation period (years)	< 24	0.186	-0.95	0.68
	> 21	0.597	-11.42	0.58
Resting period (years)	< 24	0.011	1.35	0.19
	> 21	0.381	-6.30	0.72
Calving interval (years)	< 24	0.196	1.64	0.70
	> 21	0.978	-16.48	0.65
Annual pregnancy rate %	< 18	-2.077	51.65	0.82
	> 15	-0.737	31.26	0.78

$$C_t = \frac{R_t + L_t + (PL_t + P_t \cdot F_2) F_1}{(PL_t + P_t \cdot F_2) F_1} \cdot \frac{452}{365} \text{ years} \quad (\text{Equation 8.7})$$

where X_t indicates the number of whales in age group t in one of the four reproductive stages. Other notations are as above. The annual pregnancy rate for the age group of t years is calculated as $1/C$. The calculations are based on data from 268 adult females grouped in three-year age classes as shown in Table 20.

Table 22 details the constants of the least-squares regression equations describing the relationships between age and each of the following parameters; annual pregnancy rate, lactation period, resting period, and calving interval.

Two regressions (one for age classes < 18 years, the other for classes > 15 years) are necessary to describe satisfactorily the relationship between annual pregnancy rate and age (Fig. 23 and Table 22). According to these equations, the annual pregnancy rate falls from 30.9% at 10 years to 4.7% at 36 years. The equations over-estimate the annual pregnancy rate for whales older than 36 years, which is zero.

Females attain sexual maturity between 7 and 12 years, and few give birth before 9 years of age. After the age of 9 years, lactating females start to appear, and the proportion gradually increases with increasing age. The mean length of lactation increases from 1.8 years at age 15 years to 3.2 years at age 24 years. After this, the rate of increase of the mean length of lactation increases, so that by the time a whale is 36 years old, the mean lactation period has increased to 9.4 years.

The mean resting period is almost constant at 1.5 years in the age range below 24 years. However, as in the case of the length of lactation, the resting period increases at a faster rate after age 24 years. The mean resting period at 36 years of age is estimated to be 7.4 years.

This method is not applicable to age classes over 36 years because of the absence of pregnant females as the standard for time calibration. However, comparison of the age composition of lactating females with that of pregnant females (Method 3 in Section 7.2) shows that females which are lactating at age 35.5 years will continue lactation for an average of 7.83 years. The mean length of lactation after 36 years is, therefore, estimated as

$$7.83 - (36 - 35.5) = 7.33 \text{ years} \quad (\text{Equation 8.8})$$

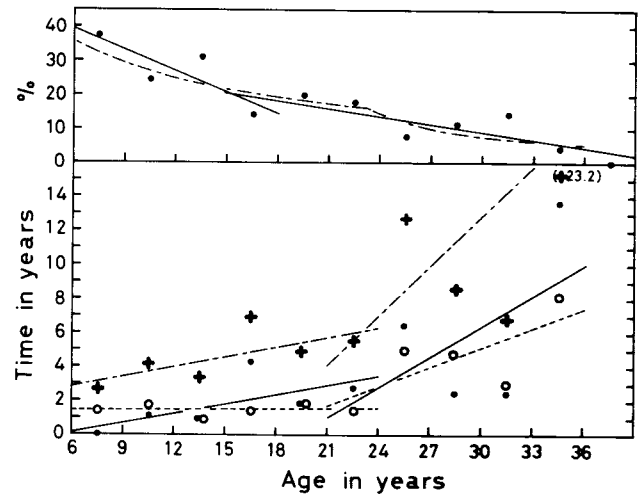


Fig. 23. Corrected age-specific reproductive parameters: annual pregnancy rate (top), mean calving interval (bottom, crosses and chain), mean length of lactation (bottom, closed circles and solid line), and mean length of resting period (bottom, open circles and dotted line). The dashed line at the top of the diagram indicates the annual pregnancy rate calculated as the reciprocal of the linear regression of mean calving interval.

An independent estimate of the mean length of lactation of females more than 36 years old is obtained from the relative proportion of lactating females younger and older than this age (Table 20). The lactation period for 58 females less than 36-years old is

$$\frac{57 + 1}{(1 + 85 \cdot 0.318) \cdot 0.903} \cdot \frac{452}{365} = 2.84 \text{ years} \quad (\text{using Equation 8.6})$$

The overall mean of the lactation period calculated for 70 individuals is 3.48 years (3.43 years (lactation period) + 0.05 years (lactation and simultaneous pregnancy)) (see Table 21). Thus we can estimate the mean lactation period (X) after 36 years of age from the following equation:

$$2.84(57 + 1) + X \cdot 12 = 3.48 \cdot 70 \quad (X = 6.57 \text{ years}) \quad (\text{Equation 8.9})$$

This figure is close to 7.33 years, the estimate obtained independently above.

The mean resting period after the age of 36 years can also be calculated in this way. Using the data in Table 20, we can obtain the following estimate of the mean resting period for all animals less than 36 years old:

$$\frac{49}{(1 + 86 \cdot 0.318) \cdot 0.903} \cdot \frac{452}{365} = 2.37 \text{ years} \quad (\text{Equation 8.10})$$

Comparing this with the overall mean of the resting period (5.46 years), obtained from 14 schools (including School 9), we can obtain an estimate (X) of the mean length of the resting period for the 64 females over 36 years of age using the following equation:

$$(2.37 \cdot 49) + (X \cdot 64) = 5.46(49 + 64) \quad (X = 7.83 \text{ years}) \quad (\text{Equation 8.11})$$

The mean life expectancy of a female at age n years is calculated using the following equation based on the

Table 23

Outline of the age-specific reproductive cycle of *G. macrorhynchus* (based on data from Table 24, including School 9)

Age range (years)	6-12	12-18	18-24	24-30	30-36	≥ 36	Total
Corrected for sample bias (all adult females)							
Lactating period (years)	0.86	2.35	2.31	4.31	6.38	6.57	3.48
Resting period (years)	1.73	1.18	1.69	4.98	4.68	7.83	5.46
Calving cycle (years)	3.83	4.77	5.24	10.53	11.87	—	10.13
No. of ovulations/cycle ²	2.43	2.23	1.80	2.66	2.20	—	—
Corrected for sample bias (post-reproductive females excluded)							
Lactation period (years)	0.86	2.35	2.31	4.31	4.91	0.66	2.86
Resting period (years)	1.73	1.18	1.69	4.60	3.83	1.51	2.78
Calving cycle (years)	3.83	4.77	5.24	10.15	9.51	—	6.88
No. of ovulations/cycle	2.43	2.23	1.80	—	—	—	—
Not corrected for sample bias (all adult females)							
Lactation period (years)	0.25	0.68	0.66	1.24	2.32	2.22	1.02
Resting period (years)	0.50	0.34	0.49	1.43	1.70	2.25	1.61
Calving cycle (years)	1.98	2.25	2.39	3.91	5.11	—	3.85
No. of ovulations/cycle	1.26	1.05	0.82	0.99	0.95	—	—

¹ For details of corrections for sample bias and School 9 see Section 8.

² Calculated as the product of the age-specific ovulation rate at the mid-point of the age range and the length of the calving cycle. The number of ovulations per year (*y*) at age *x* years was calculated from the formula $y = 1.008 (0.95)^x$ (Marsh and Kasuya, 1984).

Table 24

Frequency of post-reproductive females in *G. macrorhynchus* constructed from Fig. 8 in Marsh and Kasuya (1984)

Age range (years)	Pregnant <i>N</i>	Lactating		Resting		Total	
		<i>N</i>	PRP (%)	<i>N</i>	PRP (%)	<i>N</i>	PRP (%)
With correction for sample bias ¹							
28-32	1.72	3	0.0	7	14.3	11.72	8.5
32-36	1.44	11	18.2	8	25.0	20.44	19.6
36-40	0	1	0.0	17	35.3	18.00	33.3
≥ 40	0	9	100.0	40	100.0	49.00	100.0
Without correction for sample bias							
28-32	6	3	0.0	7	14.3	16	6.3
32-36	5	11	18.2	8	25.0	24	16.7
36-40	0	1	0.0	17	54.5	18	33.3
≥ 40	0	9	100.0	40	100.0	49	100.0

¹ No. pregnant (corrected) = No. pregnant · 0.318 · 0.903.

Note: 0.318 (correction for sample bias); 0.903 (correction for School 9) see Section 8.

Abbreviations: PRP: post-reproductive.

annual survival rate in the life table constructed below (Section 9):

$$\left(\sum_{t=n}^m t(L_{t-0.5} - L_{t+0.5}) \right) / (L_{n-0.5} - n) \quad \text{(Equation 8.12)}$$

where L_t indicates number of females at age t years, and m the maximum longevity (errors in the value of m cause no significant change in the result). If $m = 63$, the mean life expectancy of a 36-year old female is 14.1 years. Since we assume a stationary population, this figure should be close to the mean longevity of females that live to the age of 36 years, i.e. to the sum of the lactation and resting periods after this age, and is calculated from the above results as $6.57 + 7.83 = 14.40$ years. The two figures are close.

Table 23 shows the results of the above analyses for

six-year age classes. The period of lactation and simultaneous pregnancy is included in lactation for the age group from 30 to 36 years. We calculated the mean number of ovulations per calving cycle by multiplying the length of the mean calving cycle by the mean ovulation rate at the mid-point of each age group, using the equation for ovulation rate developed by Marsh and Kasuya (1984).

Correction for post-reproductive females. Marsh and Kasuya (1984) identified post-reproductive females as (1) females below 40 years of age having old corpora albicantia only and no macroscopic follicles that were not atretic in their ovaries, or (2) any females older than 40 years. This standard is likely to underestimate the young post-reproductive females compared with those above 40 years of age. The proportions of post-reproductive females in various age groups (Table 24) were computed from Fig. 8 in Marsh and Kasuya using the corrections developed earlier. The youngest post-reproductive female appeared at the age of 29.5 years, and the proportion increased rapidly with age.

By correcting for the proportion of post-reproductive females in an age group, the length of the lactation or resting periods of the reproductive females in that age group are calculated (Table 23) using the following equation:

$$X_t = Y_t \cdot \frac{R_t}{(R_t + S_t)} \quad \text{(Equation 8.13)}$$

where X_t indicates mean length of the resting period for reproductive females in each age group of t years, Y_t is mean length of the resting period for all adult females in the same age group, R_t the number of reproductive resting females in the age group, and S_t the number of post-reproductive resting females in the age group. Y_t was estimated from Equation 8.6 above, and R_t and S_t were calculated from data in Marsh and Kasuya (1984). The corresponding figures for the lactation period were also estimated using this method.

Since our criteria for classifying a female as post-reproductive are somewhat arbitrary and we do not know

exactly when each female became post-reproductive, these figures may not be very accurate. However, we can safely conclude that both the lactating and resting periods of reproductive females increase after the age of 24 years. We cannot estimate the mean number of ovulations per calving cycle for the reproductive females alone, because the annual ovulation rate calculated by Marsh and Kasuya is based on data for both reproductive and post-reproductive females.

8.4. Other hypothesis tested and rejected

In our attempt to explain our apparently anomalous observation that the number of pregnant females in our sample was about three times the number of calves less than 452 days old, we tested several hypotheses. The only one that withstood this scrutiny was that pregnant females were over-represented in our sample. The other hypotheses and our reasons for rejecting them are discussed below.

Alternative hypothesis 1: sample is not biased. This hypothesis assumes that the difference between the numbers of foetuses (corrected estimate = 60.7 individuals) and of calves younger than the age of 452 days (20 individuals) was caused by mortality between birth and age 452 days, i.e. a mortality rate of 59.2% per year. If we accept this mortality rate, then we have to accept an extremely low or negative mortality rate between the second and the tenth year (assuming a stationary population) (see Section 9). Although such a high first-year mortality seems unrealistic, we do not consider this a valid reason to reject this hypothesis in the absence of data on mortality or population status.

Under this hypothesis, the mean reproductive cycle is estimated from the proportion of females at each reproductive stage using only the corrections for gestation length (452/365) and for School 9 ($F_1 = 0.903$). The results are shown in Table 23. The mean length of lactation is estimated at about 0.6 to 0.7 year for females below 24 years of age and 1.02 years for all females. These figures contradict the results of (1) stomach-contents analysis (Section 7.2, Method 1) (which indicate that calves start to take solid food at about 0.5 year but may not be weaned until between 2 and 3 years of age), (2) school analysis (Section 7.2, Method 2) (which suggest that weaning will be completed at a variable age of between 2 and 15 years with a mean estimate of 4 or 5 years), and (3) the mean lactation length (7.33 years) for the 12 females that were still lactating after age 36 years (Equation 8.8). Assuming the mean lactation period in the population to be 1.02 years, the mean length of lactation for the 58 lactating females below 36 years (X) is calculated as;

$$1.02 \cdot 70 = (58 \cdot X) + (7.33 \cdot 12) \quad (\text{Equation 8.14})$$

i.e. $X = -0.29$ year, which is clearly impossible.

We also examined the possible effect of using cemental-layer counts to estimate the ages of these old lactating females (even though Kasuya and Matsui (in press) considered that the reading of cemental layers is not difficult in *G. macrorhynchus* and that the error is similar to that for dentine reading). Replacing the cemental ages by the corresponding dentinal-layer

counts reduced the ages of five lactating individuals in Table 20 the ages of three animals to less than 36 years. The resultant mean lactation period for the nine remaining females over 36 years old is 4.72 years. Assuming an overall mean lactation length of 1.02 years, the estimate of the mean lactation time for 61 females less than 36 years old is 0.47 years, which still contradicts the age at which the stomach-contents analyses indicate that solid food is first taken. Therefore we conclude that, even if the reading of cemental layers was inaccurate, the above discussion is not affected.

The mean number of ovulations per reproductive cycle (Table 23) is also inconsistent with this hypothesis. Correcting for the over-representation of pregnant females, the number of ovulations per cycle is greater than two for most age groups (Table 23). However, assuming that the sample is not biased, the numbers of ovulations per cycle is reduced to about one or less. This is unrealistic in view of the presence of a significant proportion of females with a corpus luteum of 'ovulation', and the other evidence of sterile cycles presented in Marsh and Kasuya (1984) (see also below).

The sum of the lactating and resting period for animals older than 36 years of age based on this hypothesis (4.47 years, Table 23) is also markedly different from the mean life expectancy of females at 36 years of age (14.1 years) (The mean lengths of the lactation and resting periods for animals older than 36 years of age have been calculated by the method outlined by Equations 8.9 to 8.11 using only $F_1 = 0.903$ for inclusion of School 9). Replacing cemental ages by dentinal ages changes the age composition. The life expectancy of 36-years old females then becomes 10.9 years instead of 14 years as calculated above.

Alternative hypothesis 2: Lactating females are under-represented. In this case, the sample bias is corrected by increasing the number of females lactating, or pregnant and simultaneously lactating, by

$$F_3 = (59.7 + 1)/20 = 3.035$$

where 59.7 = No. of pregnant females

1 = No. of pregnant/lactating females,

20 = No. of calves less than 452 days old.

Then Y_t , the mean length of a reproductive stage, and C_t , the mean calving interval at the age of t years, are estimated as follows:

$$Y_t = \frac{X_t}{(P_t + PL_t \cdot F_3) F_1} \cdot \frac{452}{365} \text{ year} \quad (\text{Equation 8.15})$$

$$C_t = \frac{R_t + L_t \cdot F_3 + (PL_t \cdot F_3 + P_t) F_1}{(PL_t \cdot F_3 + P_t) F_1} \cdot \frac{452}{365} \text{ year} \quad (\text{Equation 8.16})$$

where X_t indicates the number of whales in age group t in one of the four reproductive stages, P_t the number of pregnant whales, PL_t the number of pregnant and simultaneously lactating, F_1 the correction factor for inclusion of School 9 (0.903), and $X_t = PL_t \cdot F_3$ or $L_t \cdot F_3$ instead of $X_t = PL_t$ or L_t .

The following estimates of the lactating and resting periods were then calculated as in Sections 8.2 and 8.3 based on the proportion of females at each reproductive stage:

- Resting period, overall = 1.76 years
- Resting period, < 36 years = 0.76 years
- Resting period, > 36 years = 2.53 years
- Lactation, overall = 3.31 years
- Lactation, < 36 years = 2.74 years
- Lactation, > 36 years = 6.07 years

This estimate of the mean resting period for females over 36 years (2.5 years) is obviously unrealistic for the 64 resting females, which include a significant proportion of individuals older than the oldest lactating female. The sum of the lactating and resting periods for females over 36 years is $2.53 + 6.07 = 8.6$ years, much shorter than the mean life expectancy (14.1 years) of a 36-year-old female. We therefore consider that this hypothesis is inferior to the alternative assumption used in Sections 8.2 and 8.3, i.e. that pregnant females are over-represented.

Alternative hypothesis 3: incorrect juvenile age estimates. Another possible explanation of the disparity between the numbers of pregnant females and calves less than 452 days old is that the ages of young calves have been over-estimated. In order to investigate the implications of this explanation, we estimated the growth rate of neonates that would be necessary if (1) the sample was not biased and (2) the postnatal mortality during the period in which calves grew to lengths of 219 cm (female) or 223 cm (male) (the lengths corresponding to an age of 452 days, see Kasuya and Matsui, in press) were (a) zero or (b) $\frac{1}{3}$ (i.e., annual mortality of 48%). The results are as follows:

Postnatal mortality	Estimated age at 219 cm (female), 223 cm (male)	Estimated daily growth rate cm/day
0	$452 \cdot \frac{20}{60} = 151$ days	0.52 (females) 0.55 (males)
48%	$452 \cdot \frac{20/2}{60/3} = 226$ days	0.35 (females) 0.37 (males)

As these values are larger than 0.34 cm/day (the estimated rate during the linear stage of fetal growth), they are obviously unreasonable.

As discussed in Kasuya and Matsui (in press), the body length of *G. macrorhynchus* at 452 days estimated using the equation of Perrin *et al.* (1976) (assuming a gestation period of 452 days and a neonatal length of 139.5 cm) is 197.4 cm. The corresponding length on the mean growth curve for *G. macrorhynchus* developed by Kasuya and Matsui (in press) is approximately 228 cm. If the age estimates, and hence the growth curve, are modified in accordance with Hypothesis 3 above, the estimated body length at 452 days is 243 cm (0 mortality) and 265 cm (0.48 mortality per year) respectively. Thus the estimate based on the original growth curve is in closer agreement with the Perrin *et al.* (1976) prediction than either of the modifications.

Hypothesis 3 also assumes that the proportions of adult females at various reproductive stages in the sample are representative of those in the population. Thus all the problems discussed above for Hypothesis 1 also apply.

Alternative Hypothesis 4: suckling calves were lost during the drive. From the fishermen's accounts, it seems

improbable that both mothers and calves were lost during the drive. However, if this were the case, this situation becomes effectively identical to that discussed under Hypothesis 2 above.

If only the calves were lost, the proportions of adult females at the various stages in the reproductive cycle would be unaffected and the problems inherent in Hypothesis 1 remain. In addition, although the nursing-period analysis (Section 7.2, Method 2) becomes invalid, Hypothesis 4 does not affect the conclusions derived from the stomach-contents analysis (Section 7.2, Method 1) and the extended lactation of females older than 36 years (Section 7.2, Method 3).

Thus even if some suckling calves were lost during the drive, the relatively small number of lactating females in the sample is still inconsistent with the independent evidence of extended lactation.

Alternative Hypothesis 5: rapid increase in pregnancy rate during sampling period. If this happens, the proportion of pregnant females in the sample will be disproportionately higher than that of mature females at other reproductive stages. As indicated in Table 1 and the footnote to page 288, our sample was obtained over a seven-year period (longer than one reproductive cycle for most reproductive females), during which there was no significant change in the apparent pregnancy rate (0.37 in 1975, 0.26 in 1976, 0.32 in 1977, 0.33 in 1978, 0.18 in 1980, 0.23 in 1981, 0.25 in 1982). We therefore reject this hypothesis.

8.5. Discussion

The reproductive life of the short-finned pilot whale can be divided into three phases. Whales less than about 24 years old have a relatively high reproductive potential and a reproductive cycle which is fairly similar to that of most other odontocetes, except that the resting period tends to be about one year longer. We have called the period between 24 and 40 years the transitional period, because it is during this time that the proportion of post-reproductive females increases from about 9% (ages 28 to 32 years), to 20% (ages 32 to 36 years), to 33% (ages 36-40 years) and then to 100% (> 40 years). We have no direct evidence of conception in females over 35 years, even though some animals may ovulate up till the age of about 40 years (Marsh and Kasuya, 1984). Thus the post-reproductive stage starts when a female is between 29 and 40 years of age. Some females may have a post-reproductive life span of 20 to 30 years, and the mean post-reproductive life span is about 14 years.

As discussed in Marsh and Kasuya (1984 and in press) such a significant post-reproductive stage is very unusual in wild mammals. We have confirmed that about one sixth of the post-reproductive females appear to lactate for extended periods. (The oldest lactating female was 50.5 years). However, we have no knowledge of whether these old females participate in the other reproductive activities of their school.

Comparison with G. melaena. Sergeant (1962a) detailed the reproductive status of 500 adult females from a population of the closely related long-finned pilot whale, *G. melaena*. His data have been rearranged in Table 25 so that they can be compared with our data for *G. macrorhynchus*. (We have assumed a 16-month gestation

Table 25

Comparison of reproductive status of 500 specimens of *G. melaena* (rearranged from Sergeant (1962a) assuming a gestation period of 16 months) and 297 specimens of *G. macrorhynchus* (numbers in parentheses)

	Pregnant	Pregnant/ lactating	Lactating	Resting	Total
No. individuals	159 (86)	10 (1)	280 (69)	51 (113)	500 (269)
Proportion (%)	31.8 (32.0)	2.0 (0.4)	56.0 (25.7)	10.2 (42.0)	100.0 (100.0)
Length of phase (years)	1.25 (1.19)	0.08 (0.05)	2.21 (3.43)	0.40 (5.46)	3.94 (10.13)

period for *G. melaena*). A major difference between the reproductive cycles of the two pilot whale species lies in the abundance of resting females. Both the numbers of reproductive resting females and of post-reproductive resting females seem to be much lower in the long-finned pilot whale (but see also Marsh and Kasuya, 1984). Conversely, the pregnancy rate in *G. melaena* seems to remain high until the age of 50 years, the estimated age of the oldest female (Sergeant, 1962a).

Evidence that the reproductive potential of G. macrorhynchus is suppressed. Using the equation developed by Marsh and Kasuya (1984), we estimate that the ovulation rate of *G. macrorhynchus* is about 0.6 ovulations per year at 10 years, 0.36 at age 20 years and 0.21 at age 30 years. Females cease to ovulate by age 40 years, as discussed above. In comparison, the mean annual ovulation rate for striped and spotted dolphins is 0.41 ovulations per year (Kasuya, 1976b) while the mean annual ovulation rate for sperm whales less than 20 years old is 0.31 (Ohsumi, 1965). Thus the ovulation rate for specimens of *G. macrorhynchus* younger than 20 years is not less than that of the other odontocetes for which comparable figures are available.

However, an important between-species difference exists in the observed frequency of corpora lutea of 'ovulation'. The proportion of the total number of corpora lutea which were accompanied by a recognizable pregnancy (excluding those of recognized abortion) was 0.78 (91/(91 + 26)) in the short-finned pilot whale (Table 20), 0.75 (384/509) in the sperm whale (Best, 1967), 0.94 in the striped dolphin and 0.97 in the spotted dolphin (Kasuya, in press). The difference between the pilot and sperm whales and the dolphins is more pronounced if the difference in the gestation periods (14–16 months against 11–12 months) is taken into account. The relative frequencies of ovulation apparently not followed by pregnancy is approximately $(1 - 0.778)/14.9 = 0.015$ in the short-finned pilot whale, 0.016 in the sperm whale off South Africa, 0.005 in the striped dolphin and 0.003 in the spotted dolphin. These figures suggest that the proportions of unsuccessful ovulations in short-finned pilot whales and sperm whales are similar and three to five times higher than those in the striped and spotted dolphins. These calculations are independent of calving-interval estimates. We conclude that the apparently high proportion of 'wasted' ova in *G. macrorhynchus* in comparison with the dolphins is a cause of the long calving interval and suggests that the reproductive potential may be suppressed in this population.

Further evidence of possible suppression is given by comparison of the estimated mean lengths of the resting period in several odontocetes. All estimates have been derived using similar methodology and are as follows: *G. melaena*: 0.4 year (Sergeant, 1962a); sperm whale: 0.67 year (Ohsumi, 1965) or 0.75 year (Best, 1968); spotted and striped dolphins: 0.2–0.6 year (Perrin *et al.*, 1976; Kasuya, in press). These estimates are all much less than 1.2–1.7 years, the mean resting period of *G. macrorhynchus*, even in its most fecund phase below 24 years of age.

These results suggest that the reproductive potential of this population of *G. macrorhynchus* may be suppressed by population density, food shortage, or other unknown environmental factors. It is also possible that the high proportion of adult females which are post-reproductive (about 25% of adult females) is suppressing breeding in the younger females.

Comparison with the killer whale. Bigg (1982) analysed the reproductive biology of a killer-whale population off Vancouver Island, based on eight years of observation of about 260 whales in 30 schools, some of which had a short history of selective cropping. Although the birth-rate of the cropped killer whale pods exceeded that of the unexploited pods by about 2–3%, the combined birth-rate was 9.17 or 11.43% per cow per year, depending on the method of calculation. The resultant estimates of mean calving interval are 10.9 years or 8.7 years, respectively. These values are very similar to the mean calving interval of the short-finned pilot whale calculated above (10.13 years). Bigg's observations on 26 individually-identified cows provide data on individual variation in the calving interval. The confirmed intervals were relatively short cycles and occurred only in the cropped pods. There were five intervals of three years and one interval of four years. These intervals are only slightly shorter than the mean interval of four to five years estimated for female pilot whales below 24 years. The density changes produced in the killer whale schools by cropping may have stimulated the possibly suppressed (Bigg, 1982) reproductive potential of young females in the school. However, Bigg recorded for both cropped and uncropped pods a total of 17 occasions where the minimum calving interval was six or seven years. Our data suggest that such a long lactation and/or resting period is very common in short-finned pilot whales older than 24 years. Although Bigg (1982) doubted that such a large component of the killer whale population was barren, we suggest that a significant proportion of females that

did not breed for long periods were probably post-reproductive.

In contrast to the population studied by Bigg (1982), the pregnancy rate of a killer whale population in Norwegian waters (Christensen, 1984) is considerably higher. This difference may reflect differences in food availability and/or social structure which may have resulted from the apparently larger-scale selective cropping by small-type whaling in Norwegian waters.

Implications for management. Bigg (1982) indicated that the effect of exploitation on the reproductive rate of killer whales might have appeared only in the schools where the cropping had occurred. Because of the cohesiveness of the school, the effect of the density change may not have been directly transmitted to other schools. This may be also true in the short-finned pilot whale schools, where the movement of members between schools is apparently less common than in striped dolphins (Kasuya, 1972; and Miyazaki and Nishiwaki, 1978). Thus the effect of the removal of an entire school, which is common in a driving fishery, may not produce a density-dependent change in the reproductive rate of the remaining schools. Although either selective cropping or whole-school cropping may increase the available food supply, the population reproductive rate may respond more rapidly to cropping individuals from many schools rather than the removal of a small number of entire schools. However, the social consequences of selective cropping are likely to vary with the age and sex of the cropped individuals, as discussed in the Workshop Report for the Conference on the Behaviour of Whales (IWC, in press).

9. LIFE TABLE

9.1. Litter size

A single foetus was present in all 141 pregnancies examined, indicating that multiples are uncommon in this species and that the mean litter size is close to one.

9.2. Neonatal sex ratio

Table 26 shows the sex of all available foetuses (excluding those below 5 cm in body length, which cannot be sexed reliably) and of juveniles below 220 cm in body length. The 95% confidence interval for the age of calves of this length is about 0.5 to 1.5 years (\bar{X} = 1.1 years (males); 1.2 years (females), (Kasuya and Matsui, in press). The difference between the sex ratios of foetuses and juveniles is not significant. If both stages are combined, 48.4% of neonates examined were female. This discrepancy from a 1:1 sex ratio is not statistically significant (chi-square test, $P > 0.8$).

There are two reasons for using both foetal and juvenile sex ratios in order to estimate the neonatal sex ratio: (1) to increase the sample size and to improve the precision of the estimate, (2) to correct for any difference between foetal and neonatal sex ratios. If intrauterine mortality is different between sexes, the sex ratio may change with increasing foetal age and the foetal sex ratio may not necessarily represent the neonatal sex ratio. A similar phenomenon is expected for postnatal mortality. Even though nothing is known of any sexual difference in survival rates in the foetal and early postnatal periods,

Table 26
Neonatal sex ratio

	Foetus > 5 cm		Postnatal < 220 cm		Total	
	Female	Male	Female	Male	Female	Male
N	58	61	17	19	75	80
% Female	48.7	—	47.2	—	48.4	—

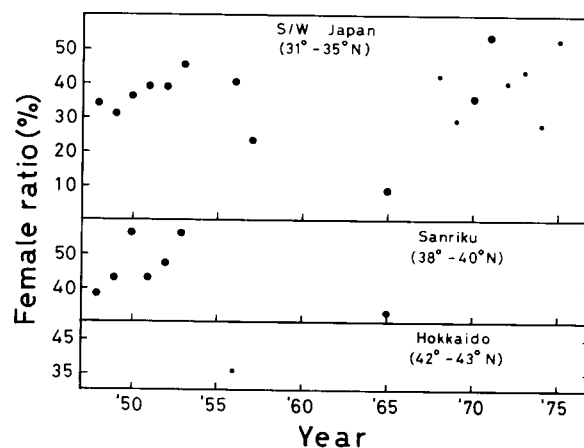


Fig. 24. Annual change of sex ratio of *G. macrorhynchus* in the catch of small-type whaling in Japan. Larger circles represent the total catches of over 100 whales and smaller circles the catches of between 50 and 100 whales inclusive. Catches of less than 50 whales are not listed. Data in Table 3.

both sets of data were tentatively combined in the present study.

9.3. Postnatal sex ratio

The postnatal sex ratio has been analysed separately for two sets of data: (1) the catch records of the small-type whaling and (2) the drive-fishery catch. The first data set is biased by the size of the animals caught (see below) but provides information from outside the geographical range of the drive fishery.

Catch by harpoon gun ('small-type whaling'). The sex ratios for various years in Fig. 24 have been calculated from the data in Table 3. The proportion of females in the catch in southwestern Japan was about 30% in 1948 and gradually increased to about 45% in 1953. A similar pattern was observed in the catch off the Sanriku region on the Pacific coast of northern Honshu. The proportion of females gradually increased from about 40% in 1948 to about 55% in 1953. After 1953, the catch was small, and no trend was detected in either area (Table 27).

As shown by Kasuya and Matsui (in press), the body weight of a male at the mean asymptotic length (473.5 cm) is estimated to be 1,210 kg, approximately twice the weight of an adult female (569 kg) at the mean asymptotic length (364.0 cm). The difference in body size between sexes probably caused males to be fished selectively by the harpoon-gun fishery. However, this selectivity can also be affected by other factors, such as the capability of the gunner, the density of whales, the availability of other profitable species such as the minke whale, and consumer

Table 27

Sex ratio of *G. macrorhynchus* in the catch of small-type whaling off the Pacific coast of Japan

Year	South western Japan		Sanriku ¹		Total Pacific	
	Both sexes	Female	Both sexes	Female	Both sexes	Female
	<i>N</i>	(%)	<i>N</i>	(%)	<i>N</i>	(%)
1948	104	33.7	321	37.7	425	36.7
1949	399	30.6	415	42.9	814	36.9
1950	361	36.0	289	56.4	650	45.1
1951	310	39.0	264	43.2	574	40.9
1952	194	39.2	120	46.7	314	42.0
1953	229	45.4	224	56.7	453	51.0
1954-57	377	34.7	111	36.9	575	35.0
1965-69	293	24.9	148	34.5	455	28.8
1970-75	455	43.7	62	46.8	541	43.6
1976-79	36	41.7	0	—	36	41.7

¹ Pacific coast of north-eastern Honshu, approximately between 38° N and 40° N.

preference. At Taiji, the people prefer to eat the meat of adult males, which is fattier than the meat from adult females. This may not be true, however, in other regions.

Thus the only definite conclusion we can make is that the true sex ratio of *G. macrorhynchus* must have been similar between southwest Japan and the Sanriku coast. In both regions, there was a steady increase in the female ratio from 1948 to 1953 followed by a reversion to initial levels after the 1954 season. There was little change in the number of pilot whales caught in the first six years. The number of fishing vessels was nearly constant, fluctuating slightly between 66 and 74 from 1949 to 1952 (Kasuya, 1975) and does not seem to have affected the sex ratio of the catch.

To examine the possibility that the increase over years in the proportion of females was due to the selective catch of males by small-type whaling, we shall assume (without proof) that the internal structure of the population in 1948 was similar to that being exploited by the present drive fishery. (The whales wintering at or south of southwestern Japan are considered to migrate in summer to the waters off northern Japan (Kasuya, 1975)). We shall also assume that the small-type-whaling operation hunted only sexually mature females and males. This assumption is probably not unreasonable, because few immature and early-maturing males exceed the mean asymptotic length for the female (see Kasuya and Matsui, in press). Recruitment is ignored. Then the intensity of the selection for males over females, (*b*), is calculated by

$$b = \frac{1}{c} \cdot \frac{\text{Male whaling catch 1948}}{\text{Female whaling catch 1948}} \quad (\text{Equation 9.1})$$

where *c* indicates the ratio of adult males to adult females in the population. Using data from the life table (Table 33) gives

$$c = (1 - 0.7742)/0.7742 = 0.292$$

therefore

$$b = \frac{1}{0.292} \cdot \frac{269}{156} = 5.91$$

If the selectivity remained the same until 1953, we get the following equation:

$$\frac{c \cdot P - M}{P - F} \cdot b = \frac{\text{Male whaling catch 1953}}{\text{Female whaling catch 1953}} \quad (\text{Equation 9.2})$$

where *P* equals the number of adult females in the population in 1948, *M* the total adult males caught from 1948 to 1953, and *F* the catch of adult females in the corresponding period.

The catch by harpoon gun in 1953 was 222 males and 231 females (Table 3). *M* is the sum of the adult-male catch by the small-type-whaling fishery (1890 whales, Table 3) and the drive fishery, for which total catch is uncertain. The annual catch off the Izu coast in 1948 and 1949 (statistics are not available) is assumed to be 412 (the mean annual catch in the area from 1950 to 1953). The catch of *G. macrorhynchus* at Nago (Okinawa) is assumed to be 183 per year (the mean of the catch of the 10 years from 1960 to 1969). Then the total catch by the two drive fisheries in the six years is estimated to have been $(412 + 183) \times 6 = 3,750$ individuals. The proportion of adult females in the catch of the drive fishery was 0.5253, and that in the adults of both sexes was 0.7742 (Table 33). Therefore the catch of adult males is calculated as $3,750 \cdot 0.5253 \cdot (1 - 0.7742)/0.7742 = 575$, and the total catch of males by both fisheries as $1,890 + 575 = 2,465$. In the same way the catch of adult females is calculated as $1,352 + (3,750 \cdot 0.5253) = 3,322$. This calculation is based on the unrealistic simplification that the male proportion in the drive fishery catch was constant, thus over-estimating the male catch and consequently under-estimating the population.

Using the above figures to solve Equation 9.2 gives $P = 15,200$, the population of adult females in the 1948 season. Since the proportion of adult females is about 52% of the population, the size of the total exploited population is estimated as $15,200/0.52 = 28,600$ individuals, which can be rounded to 30,000.*

The above calculation suggests that the change of sex ratio in the catch of small-type whaling can be explained by the selective exploitation of adult males, if the above assumptions are correct and if the total population of the species was over 30 thousand in the 1948 season. This is of the same order as the population of the long-finned pilot whale in the Newfoundland area (less than 60,000, Mercer, 1975). Ignoring annual recruitment, the adult-male population, $15,000 \cdot (1 - 0.7742) = 3,400$ in 1948, is estimated to have decreased during the exploitation to $3,400 - 2,400 = 1,000$ by the 1953 season, while the population of adult females decreased from 15,200 to $(15,200 - 3,300) = 12,000$. If it is assumed (without a definite basis) that the fishery has exploited a coastal population, the above catch figures may be large enough for the selective hunting to cause an obvious change in the sex ratio of the catch (but also see 'Fishing selection' below).

Catch of the drive fishery: Fig. 25 and Table 28 show the sex ratio of the short-finned pilot whales caught by the drive fishery from 1975 to 1981. Females comprised

* Footnote: In view of information obtained after this study, this figure must include a population off the Pacific coast of northern Japan, from which no samples have been obtained in the present study (see footnote page 264).

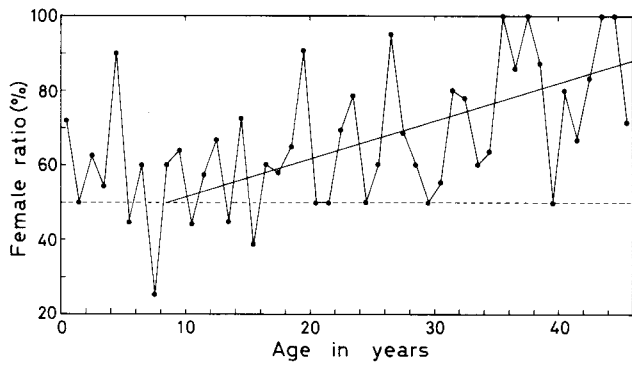


Fig. 25. Age-specific sex ratios of *G. macrorhynchus* in the catch of the driving fishery. The straight line indicates the least-squares regression between age and sex ratio (Equation 9.3).

Table 28
Postnatal sex ratio in *G. macrorhynchus*¹

Age range (years)	Male N	Female		χ^2 probability ²
		N	%	
0-10	46	69	60.0	0.2-0.3
10-20	49	71	59.2	0.2-0.3
20-30	40	74	64.9	0.01-0.02
30-40	17	54	76.1	0.02-0.05
40-46	6	31	83.8	< 0.001
46-63	0	26	100.0	< 0.001
Total	158	325	67.3	< 0.001

¹ Schools 7, 8, 9 (> 15 years), 10 through 18, 22 and 23.

² Chi-square test to see whether the sex-ratio is significantly different from 1:1.

67.3% of all postnatal individuals. This proportion is about 7% lower than the corresponding figure for the long-finned pilot whale, *G. melaena*, in the western-North-Atlantic drive fishery reported by Sergeant (1962a). The difference in male to female ratios between 158:325 (*G. macrorhynchus*) and 1,825:2,778 (*G. melaena*) is statistically significant (chi-square test, $P < 0.01$).

Since the sample size is small, an irregular short-term fluctuation of the age-specific sex ratio (Fig. 25) is not significant, but the longer general trend may be important. The apparent decrease in the proportion of females between zero and eight years of age may not be significant, because both the neonatal sex ratio and the overall sex ratio between zero and 10 years are close to parity. However, it is possible that females comprise more than 50% of the age classes below 10 years (Table 28). The continual increase in the proportion of females starts somewhere between the ages of eight and fifteen years (Fig. 25). After age 16 years, females definitely exceed males, and they continue to increase in proportion until they attain 100% at 46 years and thereafter. The least-squares regression of the age-specific sex ratio (Fig. 25) is shown by

$$Y = 0.991X + 41.74 \quad 10 < X < 47 \quad (r = 0.59)$$

(Equation 9.3)

where Y indicates the proportion of females in %, and X the age in years. If this line is extrapolated towards the left it crosses the parity level at age 8.3 years (Fig. 25), the age which coincides with the start of the early-maturing

stage in some males. By the age of 16 years (when females definitely exceed males), most males have reached at least the early-maturing stage of their reproductive development. We therefore conclude that the disparate sex ratio is associated with the later arrival of puberty in the male.

The previous analysis showed that the small-type whaling selectively exploited the adult males until 1953 and could have changed the population sex ratio. At about age 13 years, the mean male growth curve exceeds 390 cm, which is the upper limit of female length (see Kasuya and Matsui, in press). Therefore the sex-ratio bias caused by small-type whaling is expected to occur in age classes above 13 years in 1953, i.e. this bias would have applied to whales born in 1940 or before. However, this bias would have been greater in older cohorts, because these males would have attained larger body sizes (growth lasts 25 years) and would therefore be more heavily selected. Also, animals in older cohorts would have been exposed to the selective fishery for longer than animals in the younger cohorts. However, the animals from cohorts before 1940 would have been 35 years or older in 1975 at the start of the collection of materials for this study, and 41 years in 1981 when it ended. Since the maximum age of males in our sample is 46 years, the male population which would have been hunted most severely by the small-type whaling would have almost died off when our data collection started. Accordingly, we conclude that the age-specific sex ratio indicated by our sample is not an artefact caused by selective whaling.

Although the drive fishery probably provides less biased information on school and population structure, it still leaves some possibility of sex-ratio bias (see Section 10). We offer the following explanations for the decreasing proportion of males with increasing age after puberty: (1) Adult males may segregate outside the driving fishery area (perhaps in the northern part of the range or in offshore waters), or leave the breeding school to assume a solitary life. (2) Males have a higher natural mortality rate. The analysis of the catch by small-type whaling revealed that the sex ratio is almost the same in the Sanriku region as in southwest Japan. This result is easily explained by the fact that, as indicated by Kasuya (1975), the individuals migrating between eastern Hokkaido and southwest Japan are following the seasonal movement of the northern boundary of the Kuroshio current and staying in the same oceanographic environment throughout the year.

Segregation of adult males out of the fishing ground, or into a solitary existence either inside or outside the fishing ground, cannot be confirmed. A drive fishery does not kill single individuals, and even small-type-whaling vessels would have had a smaller chance of finding solitary adult males. However, we consider that the disparate sex ratio is more likely to be due to higher natural mortality rate. The age of the oldest male in the present study is 17 years younger than that of the oldest female, and there are 26 females older than the oldest male. The continual and steady decrease of the male sex ratio with age also supports the above assumption. The slight excess of females in the age classes below 10 years (Table 28) also suggests that male mortality is slightly higher in the immature stage.

A similar between-sex difference in mortality was also

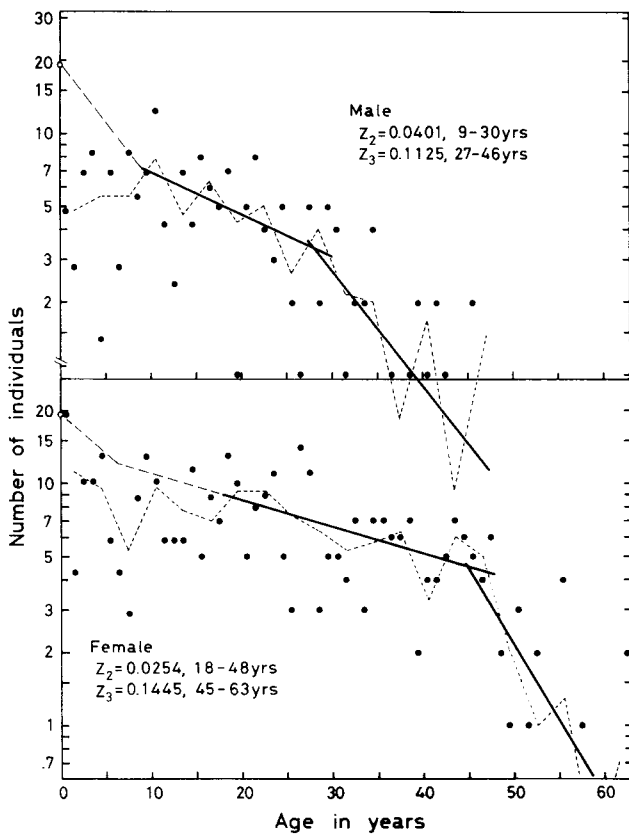


Fig. 26. Age frequency and total mortality coefficient (Z) of *G. macrorhynchus* in the catch of the driving fishery. The closed circles and fine dotted lines indicate the frequency of each age and the means of each three-year age group respectively; the thick straight lines the least-squares regressions fitted to the means for the three-year age groups, the open circles the estimated annual production, and the straight dotted lines the hypothetical age frequencies of juveniles.

found in *G. melaena* in the western North Atlantic (Sergeant, 1962a). In this population, the age of the oldest male was 40 years, 10 years younger than the oldest female, and the male sex ratio was shown to decrease throughout the age series.

In another polygynous cetacean species, the sperm whale, there is no obvious difference in mortality between sexes. However, the sex ratio in the breeding schools is strongly skewed by the geographical segregation of adult males (Ohsumi, 1966; Best, 1979). A similar segregation would explain the skewed sex ratio of the short-finned pilot whale. However, the maximum age of the male sperm whale in the breeding area is not different from that of the females in the same area (Ohsumi, 1966). This is a distinctly different situation from that for the pilot whale, where the female lives much longer than the male. We therefore conclude that the skewed sex ratio in *G. macrorhynchus* is due to sex differences in mortality rather than to segregation.

9.4. Age composition and mortality rate

The age-frequency diagram (Fig. 26) has been constructed from 150 males and 318 females in 14 schools (nos 7, 9 (> 15 years) through 18, and 22 through 24). In addition, the three juveniles of unknown sex less than one year of age have been arbitrarily divided equally between the

sexes. Among this total of 471 individuals, the ages of two males (5.5 and 8.5 years), three females (< 1 year), and three individuals of unknown sex (< 1 year) have been estimated from their body lengths. There are 21 females (18 adult and three of unknown growth stage), four males (immature, early-maturing, late-maturing, and mature), and three individuals of unknown sex (two suckling) missing from the 13 schools other than School 9. (For details see Fig. 27).

The School-9 data are biased more heavily. The school was composed of about 230 individuals. Each day the fishermen selectively killed the larger individuals. After 10 days, about 60 smaller whales were released. During this operation, the male ratio in the kill decreased gradually while the ratio of immature males increased. However, the number of immature females killed was negligible throughout. As shown in Figs 28 and 27 respectively, the lower range of body lengths of the whales slaughtered from this school is about 320 cm, while the youngest whales killed were aged eight years (female) and five years (male). Females measuring 320 cm in body length were below 15 years of age; males of the same body length were less than 11 years of age (see Kasuya and Matsui, in press). In the present analysis, it is assumed that the age frequency of the sample represents that of the school for age classes over 15 years for both sexes.

The age frequency of whales more than 15 years old (Fig. 26) has been constructed by combining all data from the 14 schools, while that below 15 years (Fig. 26) has been calculated as follows:

$$L_t = K \cdot B_t \quad (t < 15) \quad (\text{Equation 9.4})$$

$$K = \frac{\sum_{t=15}^{\infty} A_t}{\sum_{t=15}^{\infty} B_t} \quad (\text{Equation 9.5})$$

where L_t indicates the frequency at age t years corrected for the exclusion of School 9, A_t the number of individuals at age t including School 9, and B_t that without School 9. The value of K has been estimated empirically as 1.45 for females and 1.38 for males.

Because of the small sample size, there are large fluctuations in the age-frequency distribution. These fluctuations have been smoothed by using the means of three-year age classes (indicated by the dotted line on Fig. 26). For simplification, the age-frequency distribution for each sex has been divided into three portions (age groups) and the mortality coefficient (Z) calculated separately for each. The least-squares regressions fitted to the age-frequency distribution based on the means of the three year age classes for the intermediate and oldest age groups are given here; those for the youngest age group will be considered below (Section 9.5).

Females:

$$\ln Y = -0.0254X + \log 14.23 \quad (18 < X < 48, r = 0.76) \quad (\text{Equation 9.6})$$

$$\ln Y = -0.1445X + \log 2,926.01 \quad (45 < X < 63, r = 0.87) \quad (\text{Equation 9.7})$$

Males:

$$\ln Y = -0.0401X + \log 10.34 \quad (9 < X < 30, r = 0.75) \quad (\text{Equation 9.8})$$

Table 29

Comparison of survival rate estimated from age composition by two different methods

Method		A	B
Female	18-47 years	0.9749	0.9751 ± 0.0164
	45-63 years	0.8655	0.8544 ± 0.0668
Male	9-30 years	0.9607	0.9567 ± 0.0315
	27-46 years	0.8936	0.9030 ± 0.0609

A: From Z_2 or Z_3 calculated by linear regression (Equations 9.6 through 9.9).

B: By segment analysis (Robson and Chapman, 1961), best point estimate with 95% confidence interval.

$$\ln Y = -0.1125X + \log 84.52$$

$$(27 < X < 46, r = 0.83)$$

(Equation 9.9)

where Y indicates the frequency, and X the age in years. The slope of each of these lines is an estimate of the total mortality coefficient Z for the respective sex/age class. The corresponding annual survival rates are listed in Table 29.

The merit of using the means of the three-year age classes is obvious for older ages. If the actual frequencies had been used in the calculations, the data for the age classes with a zero frequency would have to be excluded, with a resultant over-estimation of the survival rates.

Robson and Chapman (1961) detailed mathematical methods to estimate the survival rate and its confidence interval from the age-frequency distribution. The results of their segment-analysis method applied to each age frequency in our sample are listed in Table 29. Each of these figures is in good agreement with the survival rates calculated from the gradient, Z , of the corresponding least-squares regression (above).

The slopes of the linear regressions (Fig. 26) are the sum of the annual natural mortality coefficient at the time of recruitment to the fishery, the annual fishing mortality coefficient at the same time, and the annual change in the amount of recruitment. The last factor can probably be ignored, because, except for the post-war period, the present population seems to have sustained an annual catch of 200 to 500 individuals since the early 1920s (if this last assumption is untrue, the following analyses of mortality are invalid). It is obviously not possible to separate the natural mortality rate and the fishing mortality rate. Accordingly we referred only to the total mortality rate in this study.

In *G. macrorhynchus*, the mortality rate is higher in older animals than in young adults. In our sample, the difference is significant only in the female (Table 29), but the pattern is similar in both sexes. In males, the mortality rate starts to increase at about age 27 years, 15 years earlier than in females. This is consistent with the shorter maximum longevity of males. Each point estimate of male mortality is higher than the corresponding value for females of the same age. Although sexual differences in mortality are not always significant, we consider that this is probably an artefact of the small sample size.

There is little change in the age frequency of juvenile females during the first few years of life, but the frequency of males less than 10 years old is lower than that at 10

Table 30

Actual frequencies of juvenile males and females compared with expected frequencies calculated from life table

Age (years)	Actual frequency			Expected frequency
	Female	Male	Σ	
0.5	19.6	4.8	24.4	37.1
1.5	4.3	2.8	7.1	33.9
2.5	10.1	6.9	17.0	31.0
3.5	10.1	8.3	18.4	28.2
4.5	13.0	1.4	14.4	25.8
5.5	5.8	6.9	12.7	23.6
6.5	4.3	2.8	7.1	21.6
7.5	2.9	8.3	11.2	20.3
8.5	8.7	5.5	14.2	19.1
9.5	13.0	6.9	19.9	18.3
10.5	10.1	12.5	22.6	17.7
$\Sigma < 5$	57.1	24.2	81.3	156.0
$\Sigma 5-10$	34.7	30.4	65.1	102.9

years. The difference between sexes may not be significant. If the age frequencies of both sexes are combined (Table 30) and an exponential survival curve is fitted to the resulting points, using the least-squares method, the following equation is obtained:

$$\log Y = 0.0136X + \log 13.24 \quad (0 < X < 11)$$

(Equation 9.10)

where Y indicates the frequency and X age in years. The slope obtained here is greatly affected by minor changes in the age range included in the calculation (presumably due to the small sample size). However, this equation clearly suggests that the apparent mortality rate is negative or very close to zero in the immature stage. If juveniles are not under-represented in the present material, either juvenile mortality must be extremely low or the annual recruitment must have been decreasing in recent years. The first alternative is improbable, because the mortality between birth and weaning would be higher than that of the mother (2.5% per year, 18 to 46 years of age). We also reject the second explanation for the following reasons. Firstly, the recent catch increase started in 1975 coincident with the start of the collection of the present materials and is therefore too recent to be the cause of the recent reduction of recruits (see Sections 3.2 and 8.4 for the possible response of the population to the drive fishery). Secondly, although some years of high catch were recorded between 1954 and 1975, they were sporadic and could hardly have caused destruction of the population and thereby decreased recruitment in recent years. Accordingly, the only plausible explanation is a sampling bias against juveniles. Estimates of the true juvenile mortality rate and of the magnitude of the sample bias are made in the next section.

9.5. Life table

Assumptions and equations used. The mortality rate can only be legitimately estimated from an age-frequency distribution (as we have done) if the population is stable or has a known rate of increase (Caughley, 1977). We have assumed without supporting evidence that this population is stationary. Therefore, we regard our

estimates of the mortality rate for whales of various ages as tentative.

Caughley (1966, 1977) suggested that the typical mammalian mortality pattern is 'U-shaped', consisting of a juvenile phase in which the rate of mortality is initially high but rapidly decreases, followed by an initially low but steadily increasing rate of mortality. For simplification, we have divided the life of a female pilot whale into three stages; $0 < t \leq 6.5$ years, $6.5 < t \leq 46.5$ years, and $46.5 < t < 70$ years; and have assumed that the mortality rates Z_1, Z_2, Z_3 respectively are constant at each stage.

The female life table (Table 31) is constructed assuming a stationary population and is based on the following equations:

$$L_0 = \sum L_t \cdot A_t \cdot P_t \cdot F \cdot R \quad (\text{Equation 9.11})$$

$$L_t = L_0 \cdot e^{-Z_1 \cdot t} \quad (0 < t \leq 6.5) \quad (\text{Equation 9.12})$$

$$L_t = L_{6.5} \cdot e^{-Z_2(t-6.5)} \quad (6.5 < t \leq 46.5) \quad (\text{Equation 9.13})$$

$$L_t = L_{46.5} \cdot e^{-Z_3(t-46.5)} \quad (46.5 < t \leq 70) \quad (\text{Equation 9.14})$$

where

- F : mean litter size
- R : neonatal female sex ratio
- Z_1 : total mortality coefficient below 6.5 years of age
- Z_2 : total mortality coefficient between 6.5 and 46.5 years of age
- Z_3 : total mortality coefficient above 46.5 years of age
- L_t : number of individuals at age t years
- A_t : proportion of sexually-mature individuals at age t years

P_t : annual pregnancy rate at age t years

With the exception of the mortality rate of whales less than 18 years of age, all parameters have been calculated above as follows:

$$F = 1.0 \quad (\text{see Section 9.1})$$

$$R = 0.5 \quad (\text{see Section 9.2})$$

$$Z_2 = 0.0254 \quad (6.5 < t \leq 46.5) \quad (\text{see Equation 9.6})$$

$$Z_3 = 0.1445 \quad (46.5 < t < 70) \quad (\text{see Equation 9.7})$$

$$A_t = 0.2061t - 1.358 \quad (6 < t < 12) \quad (\text{from Equation 5.1})$$

$$P_t = -0.02077t + 0.5165 \quad (6 < t \leq 15) \quad (\text{from equation in Table 22})$$

$$P_t = -0.00737t + 0.3126 \quad (15 < t < 42) \quad (\text{from equation in Table 22})$$

All values for A_t, P_t and L_t were calculated at the mid-point of each year class except for A_t at the extremes of its range (i.e. between six and seven years, and 11 and 12 years), when the function is integrated over the one-year range in each case.

As a simplification, the upper or lower boundaries of the equations for A_t and P_t were extended outside the actual ranges of the data in our model. For example, our sample suggests that the age of the youngest sexually mature female is between seven and eight years old, while the above equation is based on an estimate of between six and seven years. This bias is minimal. Similarly, all pregnant females in our sample were less than 35 years old, while the model assumes that females bear their last calf at age 42 years. The resultant overestimation of

Table 31

Simplified life table for females of *G. macrorhynchus* based on an imaginary cohort of 1,000 females. Only selected ages are listed here, but the total is based on all age classes

Age (years) (t)	Maturity rate	Annual pregnancy rate	Number of females			
			Immature	Adult	Giving birth	Dying in year between t and $t+1$
0			(1,000)			
0.5	0	—	964	0	0	68
5.5	0	—	668	0	0	47
6.5	0.042	0.381	595	26	10	16
7.5	0.188	0.361	491	114	41	15
8.5	0.394	0.340	359	231	79	15
9.5	0.600	0.319	230	345	110	14
10.5	0.806	0.298	105	456	135	15
11.5	0.955	0.278	25	521	145	13
12.5	1	0.257	0	533	137	14
15.5	1	0.198	0	494	98	13
20.5	1	0.162	0	435	70	11
25.5	1	0.125	0	383	48	10
30.5	1	0.088	0	337	30	8
35.5	1	0.051	0	297	15	7
40.5	1	0.014	0	262	4	7
45.5	1	0	0	230	0	5
50.5	1	0	0	126	0	17
55.5	1	0	0	61	0	8
60.5	1	0	0	30	0	4
65.5	1	0	0	14	0	2
69.5	1	0	0	8	0	8
Total	—	—	6,660	15,591	2,003	1,000

Table 32

Simplified life table for males of *G. macrorhynchus* based on an imaginary cohort of 1,000 males. Only selected ages are listed here, but the total is based on all age classes

Age (years) (t)	Maturity rate	Number of males		
		Immature	Adult	Dying in year between t and t+1
0		(1,000)		
0.5	0	946	0	98
5.5	0	545	0	56
10.5	0	349	0	13
12.5	0	322	0	12
13.5	0.023	303	7	13
14.5	0.208	235	62	11
15.5	0.425	164	122	11
16.5	0.642	98	177	11
17.5	0.858	37	227	11
18.5	0.997	1	252	10
19.5	1	0	243	9
20.5	1	0	234	9
25.5	1	0	191	7
30.5	1	0	136	15
35.5	1	0	77	8
40.5	1	0	49	5
45.5	1	0	25	3
49.5	1		16	16
Total	—	7,915	4,183	1,000

the number of births is only 58 out of 2,003 whales, an error which can be ignored.

Although the use of age at first ovulation instead of the age at first conception or at first parturition probably overestimates the true number of reproductive females, this does not bias our estimate of the reproductive rate, because the annual pregnancy rate has been calculated including those adult females. We also assumed that the mortality rate of females between the age of 6.5 years, the age when sexually-mature females are assumed by the model to first start to appear (see below), and 18 years is the same as that derived from the age-frequency distribution of females between 18 and 48 years of age (Z_2).

The mortality rate of females less than 6.5 years of age ($Z_1 = 0.0734$) was calculated assuming a uniform rate of decrease from L_0 (calculated from Equation 9.11) to 12.06 (the actual frequency at 6.5 years of age extrapolated from Equation 9.6).

The life table for males (Table 32) has been constructed on the same principle as that for females. The total mortality rate between 0 and 9 years of age ($Z_1 = 0.1102$, $0 < t \leq 9$) was calculated assuming a constant rate of decrease from L_0 (calculated from Equation 9.11 above) to 7.207 (the estimated frequency at nine years using Equation 9.8).

In the model, sexually mature males have been defined as those at the late-maturing stage or mature stages, because of the evidence that attainment of the histological 'late-maturing stage' coincides with functional maturity (see Section 4.5). The proportion of adult males at age t years was calculated from

$$A_t = 0.2166t - 2.932 \quad (13 < t < 19)$$

(from Equation 4.7)

Comparison of the model with the original data. The juvenile age frequencies observed in our sample are compared with those predicted by the model in Table 30. The total number of individuals between zero and five years of age in the sample (81.3 animals) is only 52% of the frequency estimated from the model. Similarly, the observed frequency for the 5- to 10-year age classes is only 63% of that predicted by the model. These discrepancies can be explained by the sample bias against females with young calves discussed in Section 8.

The mean ages calculated from the model using the equation

$$\frac{\sum ((n+0.5) \cdot (L_{n+0.5}))}{\sum L_{n+0.5}}$$

($n = \text{integer in this section}$)

(Equation 9.15)

are about 20 years (female) and 13 years (male). The difference between these values and those calculated from our raw data is small in females but larger in males (Table 33). This may be because of a relatively greater fishing selection for adult males in the drive fishery (see 'Fishing selection' below).

The mean life expectancy of newborn calves, or the mean age at death,

$$\frac{(\sum n \cdot (L_{n-0.5} - L_{n+0.5}))}{L_0}$$

(Equation 9.16)

calculated from the model is 22 years in females and 12 years in males (Table 33). This value will be strongly affected by the errors in our estimate of juvenile mortality.

In the model, the ratio of adult females to functionally mature (late-maturing) males is 3.7:1 (Table 33). This value is not significantly different from the ratio in the original data (3.4:1), calculated assuming that males older than 16.0 years and females older than 9.0 years were at those stages. These values have been compared with Sergeant's (1962a) figures for *G. melaena* as detailed in his Table XXVII. In *G. melaena*, if (1) all females six years or older, (2) all males 11 years or older, and (3) all whales of both sexes with a closed pulp-cavity are considered to be sexually mature, the female to male ratio is 227:61 or 3.7:1, which is identical with the value in the present model.

In *G. macrorhynchus*, the ratio of adult females to total females is lower in the model than that in the sample (Table 33). This difference can be explained by the sample bias in favour of pregnant females (see Section 8).

The overall annual pregnancy rate of the sample (corrected only for the inclusion of School 9 (see Section 8)), is

$$(365 \cdot (P + PL)) / (452 \cdot (P + PL + L + R)) = 0.2345$$

This estimate (Table 33) decreases to the more reasonable value of 0.0961 when corrected for the sample bias in the pregnancy rate (see Section 8.3). The corresponding value estimated from the model (0.1285) is intermediate between these two figures. It is probably too high, because our extrapolation of the mortality rate for ages between 18 and 48 years back to the age of 6.5 years has increased the relative abundance of young adult females and thus the population pregnancy rate. If the mortality rate between 6.5 and 18 years of age is lower, the overall annual pregnancy rate will be close to 0.096, the observed

Table 33
Summary of reproductive parameters of *G. macrorhynchus*

Parameter			Original data	Life-table data
1. Onset of sexual maturity,	female	year	9.02	—
	male	year	15.85	—
2. Mortality rate, annual,	female, 0.0–6.5 years	%	—	7.08
	6.5–18.0 year	%	—	2.51
	18.0–46.5 year	%	2.51	—
	46.5–70.0 year	%	13.45	—
	all ages	%	—	4.49
	male 0.0–9.0 year	%	—	10.43
	9.0–28.5 year	%	3.93	—
	28.5–50.0 year	%	10.64	—
	all ages	%	—	8.27
	in the population	%	—	5.82
3. Mean age,	female	year	21.98	19.98
	male	year	16.72	13.05
4. Mean longevity	female	year	—	22.26
	male	year	—	12.11
5. Sex ratio (female ratio),	neonatal	%	48.98	50.00
	all ages	%	67.26	64.78
	adult	%	77.42	78.85
6. Adult females	in the female population	%	78.11	70.07
	in the total population	%	52.53	45.39
7. Annual pregnancy rate		%	23.45	12.85
8. Gross annual reproductive rate,	female calves/female population	%	9.16	4.50
	all calves/total population	%	12.32	5.83
9. Average calf production per female living to post-reproductive age		no.	—	4.39
10. Reproductive females in the female population		%	58.31	52.36
11. Post-reproductive females in the adult female population		%	25.34	24.51

value (corrected for sample bias). We suggest that the overall annual pregnancy rate of this population is probably between about 9.6 and 13%.

The population pregnancy rate may be significantly altered by a minor change in age structure, even when the age-specific pregnancy rate is kept unchanged. This will be particularly important in the short-finned pilot whale, where the pregnancy rate is strongly dependent on age, especially in this population which contains a large proportion of old post-reproductive females.

The gross annual reproductive rates (the annual production of female calves by the female population), are calculated as above, based on previously derived parameters (Table 33). The value without correction for the sample bias in pregnancy rate (Section 8) is $0.2345 \times 0.5 \times 0.7811 = 0.0916$. This figure will be lowered to $0.0916 \times 0.5 \times 0.7811 = 0.036$, with correction for this bias. As the model assumes that the population is stationary, the corresponding figure estimated by the model ($0.1285 \times 0.5 \times 0.7007 = 0.0450$) has to equal the overall annual mortality rate calculated for females from the equation

$$\frac{\Sigma (L_{n-0.5} - L_{n+0.5})}{\Sigma L_{n+0.5}} = L_0 / \Sigma L_{n+0.5} \quad (\text{Equation 9.17})$$

which is 0.045. The annual rate of female calf production by the female population is probably about 4–5%.

The sample suggests that the number of calves of both sexes produced annually by the entire population, the gross annual reproductive rate in the ordinary sense, is

$0.2345 \times 0.5 \times 0.7811 = 0.0916$. This figure will be lowered to $0.0916 \times 0.5 \times 0.7811 = 0.036$, with correction for this bias. As the model assumes that the population is stationary, the corresponding figure estimated by the an estimate of 0.058 (Table 33). The gross annual reproductive rate of the population is probably about 5–6%.

The mean number of calves produced by an adult female living to the post-reproductive stage is estimated as the sum of age-specific pregnancy rates, $\Sigma P_{n+0.5}$. Assuming sexual maturity at 9.0 years (the mean for the population) and the age of the last parturition at 42 years (possible maximum from the age/pregnancy rate-regression equation), the number of calves is estimated as 4.39. If breeding longevity is assumed to be 35 years, then the calf production is estimated at 4.19. The difference is negligible.

The age-specific abundance of post-reproductive females given in Section 8 can be used to calculate the number of post-reproductive females as $\Sigma (A_t \cdot S_t)$, where S_t indicates the proportion of post-reproductive females at age t years. The approximate number of post-reproductive females, 25% of the adult females (Table 33), is calculated using the corrected abundance of these females, i.e. 8.5% (28–32 years), 19.6% (32–36 years), 33.3% (36–40 years) and 100% (over 40 years) in Table 24. The values observed from the data and predicted by the model are very similar.

Table 34

Criteria used to allocate individual specimens of *G. macrorhynchus* to the appropriate growth stage when gonad data incomplete

Order of preference	1	2	3
Male	Single-testis weight (g)	Age (years)	Body length (cm)
Immature	< 100	≤ 14.5	≤ 401
Early-maturing	100 to 170	15.5	402 to 413
Late-maturing	170 to 400	16.5	414 to 422
Mature	≥ 400	≥ 17.5	≥ 423
Female	Age (years)	Body length (cm)	
Immature	< 9	≤ 320	
Mature	≥ 9	≥ 321	

10. SCHOOL STRUCTURE, SOCIAL MATURITY AND FISHING SELECTION

10.1. Materials and methods

The analysis is based on data from 18 schools (Nos. 7 through 24, see Table 1). The 13 schools shown in Table 36 are the most important with respect to the quality of the information obtained from them. Since these data were collected during six years, from 1975 to 1980, we

firstly examined whether the school structure had changed during this period by plotting various school parameters against the year of catch and calculating the resultant least-squares regression equations. In no instance was the regression coefficient significantly different from zero (*T*-test, $P > 0.05$). The parameters tested were (1) school size, $n = 18$, $a = -2.73$, $r = -0.4$, $0.05 < P < 0.1$, (2) proportion of adult males, $n = 13$, $a = 1.98$, $r = 0.2$, $0.3 < P < 0.5$, (3) proportion of immature individuals of both sexes, $n = 13$, $a = -1.69$, $r = -0.2$, $0.3 < P < 0.5$, (4) proportion of females, $n = 17$, $a = -0.01$, $r = -0.001$, $P > 0.9$, (5) proportion of pregnant females, $n = 14$, $a = -3.64$, $r = -0.3$, $P > 0.9$, (6) proportion of lactating females, $n = 14$, $a = -0.77$, $r = -0.77$, $r = -0.07$, $P > 0.9$, (7) proportion of resting females, $n = 14$, $a = 4.11$, $r = 0.3$, $0.3 < P < 0.5$, (8) proportion of post-reproductive females, $n = 12$, $a = 6.16$, $r = 0.4$, $0.1 < P < 0.2$ (all proportions are in %, and those in (5)–(8) relative to number of total adult females). We therefore discounted any change in school structure during the sampling period.

The composition of the 18 schools of *G. macrorhynchus* classified on the basis of age, body length and reproductive status is illustrated in Figs. 27 and 28. Ages were estimated using annual growth layers in dentine or cementum, except for eight whales for which the

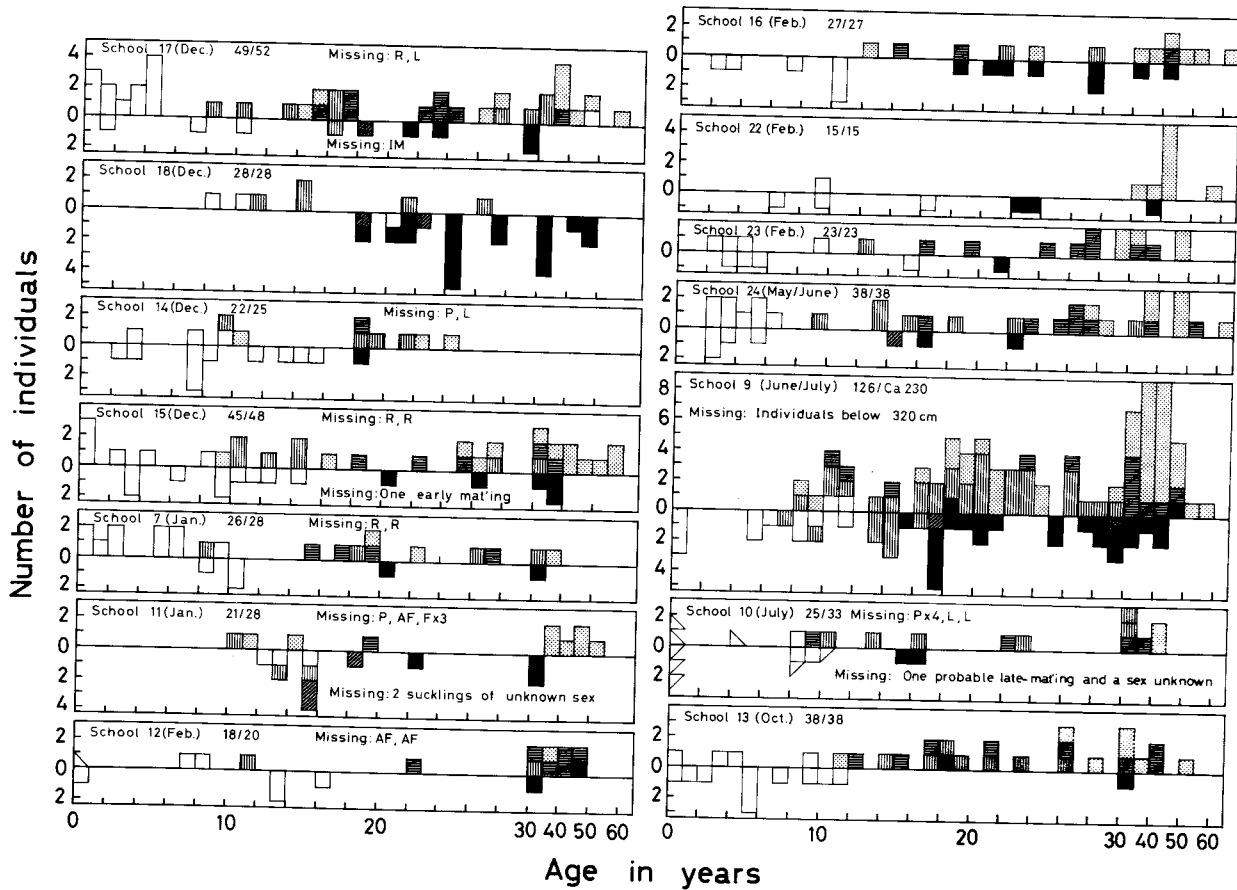


Fig. 27. School structure of *G. macrorhynchus* plotted against age. The school number, month of catch, number listed/number caught, and number and reproductive status of missing individuals are indicated at the top (IM-immature, AF-adult female, AM-adult male, F-female, M-male, L-lactating, P-pregnant, R-resting). Triangles indicate whales the ages of which have been estimated from body length. The frequency histograms for the females are on the top of the lines, those for males below the lines. Code for females. White: immature; vertical lines: pregnant; horizontal lines: lactating; dots: resting; black: known only as mature. Code for males. White: immature; vertical line: early-maturing; oblique line: late-maturing; black: mature.

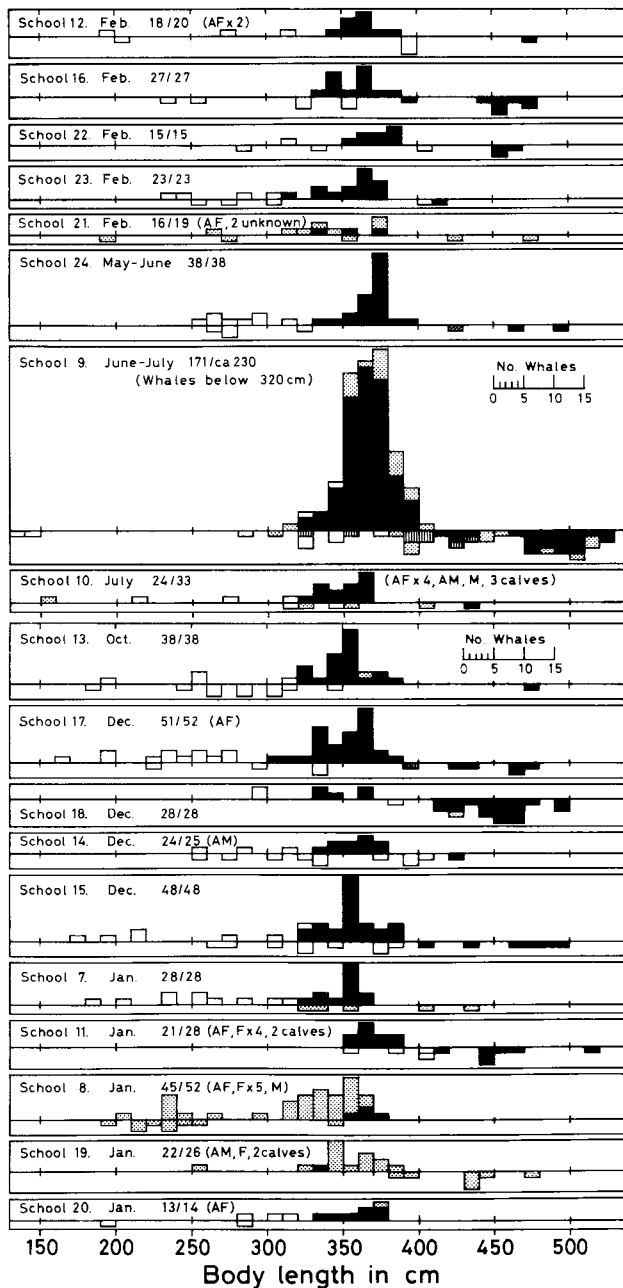


Fig. 28. School structure of *G. macrorhynchus* plotted against body length. Code for females (on the top of lines): white: immature; black: mature; dots: unknown. Code for male (below the lines): white: immature; vertical lines: early-maturing; oblique lines: late-maturing; black: mature; dots: unknown. Other marks (as in Fig. 27) are school number, month of catch, number listed/number caught, and number and reproductive status of missing individuals indicated at the top (IM-immature, AF-adult female, AM-adult male, F-female, M-male, L-lactating, P-pregnant, R-resting).

length-age relationship was used (see Kasuya and Matsui, in press). This method was applied to females under 290 cm or males under 385 cm, which correspond to ages of 6.0 and 14.0 years, respectively. The ages of 21 individuals (excluding those in School 9) were not estimated, either because their body lengths were not known (two calves in school 11) or because they were greater than the range for which the age-length relationship can usefully be applied. The sexual maturity of 11 males and three females was estimated using the

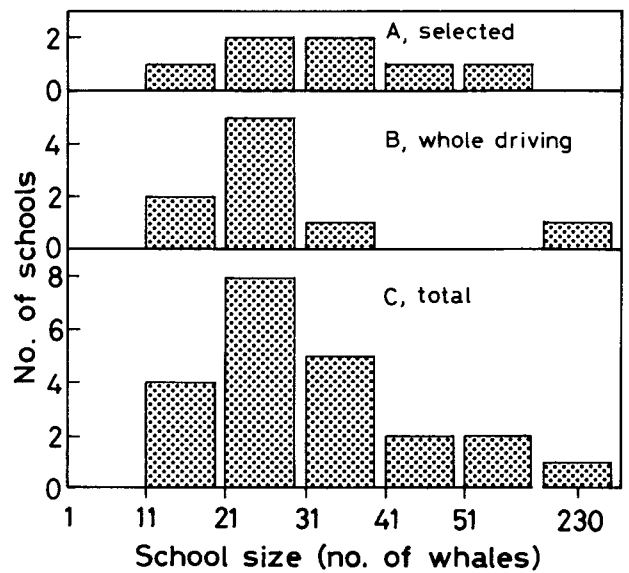


Fig. 29. School-size frequencies of *G. macrorhynchus* caught by the driving fishery. A: eight schools selected from aggregations, B; seven schools found alone, C: total of 21 schools including six schools of unknown status.

criteria in Table 34, while the reproductive status of most whales was determined by examining reproductive organs (Sections 4 and 5).

10.2. School size

As indicated in Section 2, eight schools were found alone and driven to shore (nos. 7, 11, 13, 14, 19, 20, 22 and 23), while seven schools were each driven from aggregations of several schools (nos. 10, 12, 15, 16, 17, 18 and 24). The fishermen reported that these aggregations were scattered over an area of several square nautical miles but that the smaller groups ('school', ordinary unit of driving) were more tightly grouped and distinct. The aggregations also often contained school(s) of another delphinid species, as analysed below.

School 9 was actually an aggregation containing, at first sighting, eight schools of *G. macrorhynchus* and one or more schools of *Tursiops truncatus* scattered over a wide area. Later the aggregation became tighter (presumably because of a nearby killer whale school) and was driven to port. The total number of pilot whales caught was about 230 ($\bar{x} = 29$ whales per school, close to the mean school size calculated below).

Fig. 29 shows the school-size frequency for 22 drives, for 16 of which information was available about the school before driving commenced. The sizes of these 21 schools (excluding School 9) ranged from 14 to 52 whales ($\bar{x} = 30.9$). The eight schools found alone consisted of 14 to 38 whales ($\bar{x} = 24.6$) and were often smaller than seven schools taken from aggregations, which contained 20 to 52 whales ($\bar{x} = 35.1$). Although the difference between the two means is not significant, we believe that the selected schools tend to be larger than the schools found alone, because the fishermen tend to select one of the larger schools in an aggregation if they can.

Kasuya (unpublished) has 21 shipboard observations of schools of *G. macrorhynchus* in the western North

Pacific with reliable estimates of school size. On two occasions, two schools were found 100 to 200 m apart. These groupings may correspond to the aggregations mentioned above. The school sizes ranged from five to 50 whales ($\bar{x} = 20.6$; $SD = 12.8$). Admitting inaccuracy in the shipboard estimation of school size, we conclude that this figure is close both to the sizes discussed above, and to the mean school size (25) reported for *G. macrorhynchus* off the coast of southern California (Brown and Norris, 1956).

Sergeant (1962a) reported that the 'herd' size of *G. melaena* averaged about 20 whales in pelagic waters and rarely exceeded 100, but that the size of schools stranded or driven ashore averaged about 85 whales and frequently exceeded 200. Sergeant also observed that many small 'groups' of about 15 to 25 whales scattered in Trinity Bay, Newfoundland, tended to come together when alarmed by aircraft.

We conclude that the groupings of short-finned pilot whales vary from solitary schools to loose aggregations of several schools and may comprise tight aggregations in certain (alarm) situations, e.g. when disturbed by aircraft (Sergeant, 1962a) or killer whales (School 9). The 'school' discussed below is probably the only long-lasting identifiable social unit of this species. Aggregations may provide member schools with occasional opportunities to mate or exchange individuals.

10.3. Effect of fishing bias on school composition

Tables 35 and 36 detail the differences in the composition of six schools found alone and seven schools taken from aggregations. (The incomplete data available from School 9 have been excluded).

The reproductive status of the males in aggregations and solitary schools is significantly different (chi-square test, $0.02 < P < 0.05$) because of the higher number of adult males in the schools selected from aggregations (range 1 to 18; $\bar{x} = 5.7$) compared with that in solitary schools (range 1 to 3; $\bar{x} = 2.0$) (Table 36). This fishing bias is due to the fishermen's preference for adult males because of their large body size and preferred meat. The proportion of immature and maturing males is not different between the two catch types.

The proportion of the total females that are pregnant is higher in the schools taken from aggregations, while the proportion of resting females is lower, but the differences are not statistically significant (chi-square test on actual number of whales, $0.3 < P < 0.5$). We know of no reasons why pregnant females would be caught in preference to resting females and consider that there is probably no conscious fishing bias in their favour.

Thus we conclude that the drive fishery may select (1) larger schools and (2) schools containing a higher number of adult males. This will cause the number of adult males in the population in Section 9 to be over-estimated. The ratio of mature males to mature females in the schools taken from aggregations is $40/128 = 0.31$, in contrast to $12/80 = 0.15$ in the solitary schools (Table 35).

10.4. Inter-relationship of school members

The composition of the schools of *G. macrorhynchus* in our sample was highly variable with respect to the sex,

Table 35
Comparison of schools taken from aggregations and solitary schools

Sex and reproductive status	Aggregations		Solitary schools	
	No. of whales	%	No. of whales	%
Male				
Immature	33.5 ¹	41.6	34 ²	66.7
Early-maturing	2	2.5	2	3.9
Late-maturing	5	6.2	3	5.9
Mature	40	49.7	12	23.5
Total	80.5	100	51	100
Female				
Immature	36.5 ¹	22.2	23 ²	22.3
Resting	45	27.4	36	35.0
Lactating	38	23.1	23	22.3
Pregnant	42	25.5	19	18.4
Mature unclassified	3	1.8	2	1.9
Total mature	128	77.8	80	77.7
Total	164.5	100	103	100
Missing (♀ and ♂)	1		0	

¹ Half of three calves of unknown sex included.

² Half of two calves of unknown sex included.

age and reproductive status of school members (Table 36, Figs 27 and 28).

Mature males. With the exception of School 20, each of the 27 schools examined contained at least one mature male. The number of mature males in solitary schools ranged from one to three. In contrast, four of seven schools taken from aggregation contained four to 18 mature males. We consider that these schools were selected and that they may be over-represented in our sample. Thus in the thirteen schools for which detailed figures are available (Table 36) the ratio of mature females to mature males varies from 1.6 to 23.0 (excluding 0.3 in School 18, which contained 18 adult males). When the apparently post-reproductive resting females are excluded, the mature male: mature female ratios of 11 schools in Table 36 are between 1.1 and 21.0 (excluding 0.3 values for unusual Schools 18 and 22). Since all these 11 schools contained both pregnant and lactating females, they are certainly breeding schools. Thus we conclude that there is usually an excess of reproductive females over mature males in breeding schools of *G. macrorhynchus*, and that the species is polygynous like *G. melaena* (Sergeant, 1962a).

School 18 was exceptional, with 18 mature and two 'late-maturing' males. Only one of the five pregnant females in School 18 was classified as being in 'recent oestrus', the remaining four females being in various stages of pregnancy (Fig. 30 and Table 36). In contrast, Schools 13, 10 and 24 had more oestrous females than school 18 but fewer mature males. Thus it seems unlikely that males congregate around oestrous females. We also tested the correlation between the number of adult males and that of other members in the school. None of the correlations was statistically significant. These results suggest that either mature males stay in the same breeding school for a period exceeding one female breeding cycle, or that their movement between breeding schools is controlled by (unknown) factors other than the female reproductive cycle.

Table 36
School composition in *G. macrorhynchus*

School no.	School taken from aggregation								Solitary school				
	10 ²	12	15	16	17	18	24	7	11	13	14	22	23
Male maturity													
1. Immature	5.5 ³	4	9	6	4	1	4	3	4 ⁵	10	10	3	4
2. Early-maturing	0	0	1	0	1	0	0	0	2	0	0	0	0
3. Late-maturing	1	0	0	0	1	2	1	0	3	0	0	0	0
4. Mature	2	1	5	8	4	18	2	2	3	1	2	3	1
5. Unclassified	0	0	0	0	0	0	0	0	0	0	0	0	0
6. Total	8.5	5	15	14	10	21	7	5	12	11	12	6	5
Female maturity													
7. Immature	5.5 ³	3	6	0	12	2	8	10	1 ⁵	4	3	1	4
8. Mature	18	12	27	13	30	5	23	13	12	23	10	8	14
9. Unclassified	0	0	0	0	0	0	0	0	3	0	0	0	0
10. Total	23.5	15	33	13	42	7	31	23	16	27	13	9	18
Reproductive status of adult female													
11. Oestrous ¹	3	0	1	0	0	1	5	2	0-4	5-6	0	0	0
12. Pregnant	10 ⁴	2	7	2	9	5	7	4	2-6	7-8	5	0	1
13. Lactating, all	7 ⁴	6-9	5	3	10	0	8	4	1-5	8-9	2	0	8
14. Lactating, post-reproductive	0-2	3-4	0	1	1	0	1	0	0-4	2	0-1	0	2
15. Resting, reproductive	0	0-2	9	4	8	0	3	5	4-8	6-7	3	1	3
16. Resting, post-reproductive	2	1-2	6	4	3	0	5	0	4-8	1	0	7	2
17. Unclassified	0	3	0	0	0	0	0	0	4	1	0	0	0
18. Total	18	12	27	13	30	5	23	13	12-15	23	10	8	14
Age composition, male													
19. < 9 years	3.5 ³	1	3	3	3	0	4	1	1 ⁵	7	6	1	3
20. 9 to 23 years	4-5	3	8	6	4	7	3	3	9	3	5-6	3	2
21. > 23 years	0-1	1	4	5	3	14	0	1	2	1	0-1	2	0
22. Unclassified	1	0	0	0	0	0	0	0	0	0	1	0	0
23. Total	8.5	5	15	14	10	21	7	5	12	11	12	6	5
Age composition, female													
24. < 9 years	5.5 ³	3	6	0	13	1	8	10	1 ⁵ -4	3	2-4	0	3
25. 9 to 35 years	9-15	4-6	17-19	7	19-21	6	15	10-12	4-8	20	9-11	2	12
26. > 35 years	3-9	6-8	8-10	6	8-10	0	8	1-3	6-10	4	0-2	7	3
27. Unclassified	6	2	2	0	2	0	0	2	4	0	2	0	0
28. Total	23.5	15	33	13	42	7	31	23	16	27	13	9	18

¹ Females with corpus luteum of 'ovulation' or with foetus smaller than 10 cm in body length.

² One individual of unknown sex excluded.

³ Half of three suckling calves of unknown sex included.

⁴ One pregnant and simultaneously lactating female included.

⁵ Half of two suckling calves of unknown sex included.

The wide variation in the proportion of mature males in breeding schools (Table 36) and the polymodal mature-male age frequency in some schools (Schools 9 and 24) (Fig. 27) suggest that males do not necessarily stay in one breeding school for their entire lifetime but may aggregate (School 18) or move away from a school (as in Schools 13 and 20) to another breeding school. However, as mentioned below, there is no indication that any particular component of the adult male population is geographically segregated from the sampling area (also see Section 9.3).

Maturing male. The maturing stage (early and late-maturing stages combined) includes whales ranging from the immature to the fully sexually-mature stages. We expect the social behaviour of these individuals to vary widely. The 13 schools contained a total of only 12 maturing males.

As shown in Table 36, the maturing males were not evenly distributed among schools. Only six schools contained males at this stage; five maturing males were

present in School 11. This school contained an additional three immature males of similar age (Fig. 27). These findings suggest that males may tend to aggregate at the arrival of puberty (usually between 10 and 20 years of age) and may occasionally leave their mothers' school to join with other pubertal males. This is also supported indirectly by the occasional lack of males in these age ranges (Schools 13, 16 and 18).

Adult females and immature individuals. As expected, the number of lactating females in a school shows significant positive correlation with the number of immature individuals (Spearman rank correlation coefficient, $P < 0.025$). The number of pregnant females is also positively correlated with the number of immature individuals ($P < 0.025$), presumably because a calf remains in the breeding school for some time after weaning. The significant positive correlation between the number of immature individuals and the number of reproductive resting females in a school also supports this conclusion ($P < 0.025$).

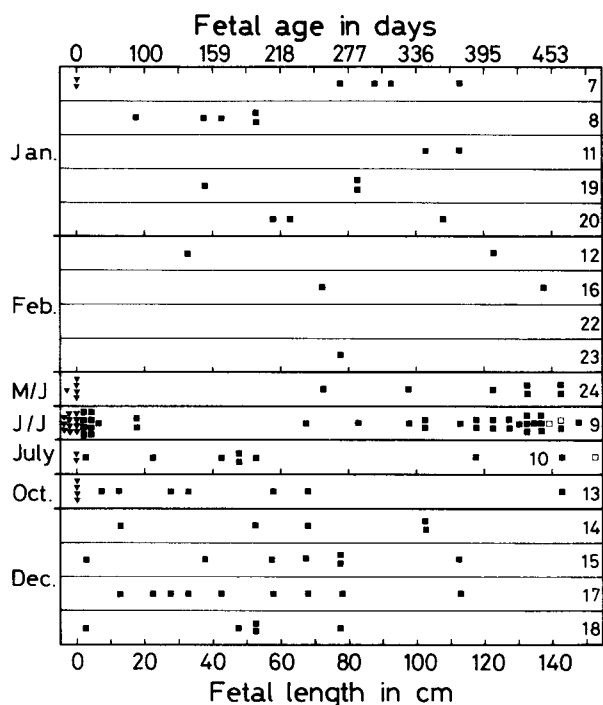


Fig. 30. Body-length frequencies of foetuses (black squares) and newborn calves (white squares) below 155 cm in body length. The school number is indicated at the right. Nonpregnant females with corpus luteum of 'ovulation' (triangles) are plotted on 0 cm length. The foetal age indicated at the top has been calculated from foetal length using the equation at the base of Table 9.

The age composition of the females within schools of *G. macrorhynchus* (Fig. 27) suggests that pubertal females, unlike males, do not aggregate or move between schools. Thus a female probably remains in its mother's school for life.

Fig. 30 shows the body-length frequency of foetuses and calves under 155 cm. The corpus luteum of 'ovulation' of non-pregnant females is plotted on zero body length. This is an obvious over-simplification, because a corpus luteum of 'ovulation' persists for an unknown (but probably short) time (Marsh and Kasuya, 1984). In contrast to the pattern in *Stenella attenuata* (Kasuya *et al.*, 1974) and *S. coeruleoalba* (Kasuya, 1972), the calculated dates of conceptions are not synchronized in most schools of *G. macrorhynchus* but dispersed over several months. This lack of synchrony could occur either when a school is a cohesive long-term unit in which oestrus is not synchronized, or when school members are recombined randomly at frequent intervals. In view of the results discussed above, we reject the second explanation.

The number of post-reproductive resting females in a school is not correlated with the number of immature whales ($P > 0.05$). We suggest that this is because the last lactation (> 6 years) and the post-reproductive life time (about 14 years on average) of females is long enough for most of their calves to attain puberty or sexual maturity.

The number of resting females classified as post-reproductive per school ranged from zero to seven individuals, with modes at zero and four. However, the number of such females is almost certainly higher than

this because (1) our classification of a female as post-reproductive is conservative (Section 8), and (2) information is incomplete for some whales (Table 36 and Figs 27 and 28). Our results certainly do not suggest that the presence of post-reproductive resting females and/or old (> 40 years) lactating females is essential for a school (Table 36).

Post-reproductive females usually seemed to be associated with adult females of other reproductive stages. School 22 is an exception to this pattern, with eight resting females, one immature female (9.5 years), three immature males (ages six to 17 years) and three mature males. Seven of the eight resting females were classified as post-reproductive, using the criteria of Marsh and Kasuya (1984). The ovaries of the remaining adult female, aged 35.5 years, contained one large follicle (15.1 mm) and a young corpus albicans, indicating that it had ovulated recently. School 22 might be the result of a recent school split. Alternatively, the immature whales might have been the offspring of the youngest two or three adult females (aged 33.5, 38.5 and 40.5 years at capture), none of which had managed to bear and rear a calf for the previous six years. Thus even this unusual school is not inconsistent with our thesis that each school is a stable matrilineal kinship group.

10.5. Social maturity

We estimated in Section 4.5 that males attain 'functional maturity' when their testes reach the 'late-maturing' stage. We will now attempt to identify when males reach 'social maturity', the stage when they can successfully impregnate females, as defined by Best (1969) and Ohsumi (1971) for another polygynous species, the sperm whale.

The data available are limited to 14 breeding schools (13 schools in Table 36 and School 20 in Fig. 28). One school (no. 20) contained neither mature nor maturing males (by histological criteria), but all of the remainder contained at least one mature male, while only four had both mature and maturing males. No school was found with maturing but no mature males. This suggests that maturing males cannot substitute for mature males.

We examined the age of the youngest histologically-mature male in relation to the number of males at this stage in the same school. Their ages ranged from 18.5 to 34.5 years ($\bar{x} = 26.8$) for the four schools containing one mature male; 15.5 to 20.5 years ($\bar{x} = 17.5$) for three schools having two mature males; 22.5 years for both schools having three mature males; and from 18.5 to 21.5 years ($\bar{x} = 19.8$) for four schools with more than three mature males. If the lower range of the first group was higher than those of the latter groups, it could be suggested that some of the histologically mature males may not be socially mature. However the similarity of the lower ranges suggests that 'social maturity' is not different from 'histological maturity'. The sperm whale is similar (Best, 1969). In *G. macrorhynchus*, therefore, 'social maturity' (= histological 'mature stage') is attained at about 17 years, or two years after the start of puberty (= histological 'early-maturing stage') and 10 years before the cessation of growth in mean body length.

10.6. Interspecific aggregations

Five of the 12 drives of pilot whales for which this information was available were not accompanied by other cetaceans. (Four of these drives were of solitary schools.)

Bottlenose dolphins were found near the pilot whales in six drives, five of which were of aggregations of pilot whale schools. One solitary school (no. 14) was found near schools of both bottlenose dolphins and Pacific white-sided dolphins, *Lagenorhynchus obliquidens*.

Twenty-three schools (21 encounters) of *G. macrorhynchus* in the western North Pacific were observed from ships (Kasuya, unpublished). Bottlenose dolphins were observed near the pilot whales on seven occasions, including one aggregation of two schools. Pacific white-sided dolphins were also seen near one pilot whale school. Thirteen encounters (14 schools) were with pilot whales only. Interspecific aggregations were limited to coastal waters, perhaps because of their higher productivity and the relatively coastal habitat of *Tursiops* and *Lagenorhynchus*.

We conclude that short-finned pilot whale schools are often associated with bottlenose dolphins or Pacific white-sided dolphins, particularly when in a large aggregation, and suggest that such an aggregation is a temporary concentration of schools, probably in a feeding area.

10.7. Discussion

School structure. We conclude from the above analyses that the *G. macrorhynchus* school is usually a breeding unit composed of adult males, adult females of various reproductive stages (including post-reproductive individuals), and immature and pubertal individuals of both sexes. At puberty, some males may leave the school where they were nursed to join with other males of the same stage, presumably when schools aggregate in a feeding area. Adult males, usually one to three per school, may also move between schools occasionally and form schools dominated by adult males. We have no evidence of social or geographical segregation of pubertal or mature males. Females probably attain sexual maturity in their mother's school. The association of females persists for a long time, at least for more than one calving cycle, and presumably usually for life. Females and juvenile males in one school are probably consanguineous.

We tentatively suggest that the school structure of *G. macrorhynchus* differs from that of the sperm whale (Ohsumi, 1971; Best, 1979) as follows: (1) some immature male and female sperm whales apparently segregate from their breeding schools; (2) some adult male sperm whales segregate from the breeding schools socially and geographically. Although the sperm whale is polygynous, there appears to be little difference between the natural mortality rates in the two sexes (Ohsumi, 1966) and there are large numbers of 'surplus' males which segregate geographically from the breeding area (Ohsumi, 1971; Best, 1979). This segregation perhaps allows the surplus adult males to avoid competition for resources with the breeding population. In contrast, our results for *G. macrorhynchus* suggest that the male mortality rate is

much higher than that of the female, so that there does not appear to be many 'surplus' males in the population. Therefore, assuming that intrasexual competition among adult males is not a major source of mortality, we suggest that such competition is not great in *G. macrorhynchus*, as already indicated for *G. melaena* (Sergeant, 1962a). It is of course possible that our results are an artefact of a sampling bias caused by geographical segregation. However, the sex differences we have observed in maximum longevity (46 years for males, 63 years for females) suggest that this is not the case and contrast with Ohsumi's (1966) results for sperm whales in the breeding areas off Japan. As both pilot whales and sperm whales have been subjected to fishing pressures which have selected for adult males, it does not seem likely that these results are historical consequences of the respective fisheries.

Fishing selection. Adult males are probably over-represented in our sample because of the selection of schools with a large number of adult males from aggregations. The adult male/female ratio in the 'solitary' schools is 0.15, in contrast to 0.29 for the whole sample (Tables 35 and 36). Assuming that the ratio in the 'unselected' catch is close to the true population parameter we suspect that the ratio obtained in Section 9 (Table 33) is nearly twice the true figure. Although this bias may actually cause an under-estimation of the male mortality rate and of the population size in the 1940's (Section 9), we consider that we do not have enough data to make meaningful corrections.

Over-representation of pregnant females. Our analyses of school structure indicate that the percentage of adult females that were lactating varied from 0 to 50% ($\bar{x} = 26.5\%$; $SD = 17.3\%$) but do not suggest fishery selection for pregnant females or against lactating females. Thus we conclude that the sample bias discussed in Section 8 may have been caused by the geographical concentration of schools that contain a high proportion of pregnant females in our sampling area, which was limited to coastal waters near the northern limit of the range.

The drive fishery for striped dolphins also shows a similar but less intense bias towards pregnant females. However, the fishery for the spotted dolphin shows the opposite bias (Kasuya, in press). In Dall's porpoise (*Phocoenoides dalli*) in the western North Pacific, mother and calf pairs are known to segregate from the other animals in August in the northern part of the range of this species (Kasuya and Jones, in press). There is also some evidence of segregation in the white whale (Brodie, 1971). In Mysticeti, reproductive status affects the timing of the migrations of humpback and gray whales (Lockyer and Brown, 1981; Lockyer, 1984).

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