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Biological Analysis of a Mass Stranding of Melon-headed Whales (*Peponocephala electra*) at Aoshima, Japan

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Abstract We examined 119 melon-headed whales, *Peponocephala electra*, which stranded on a stretch of about 1.6 km of coast at Aoshima (31°47′N, 131°29′E), Miyazaki Prefecture, Japan, in the early morning of 6 January 1982. We confirmed the presence of 84 live animals (70.6% of the total animals examined) during our 4-hour examination (10:00 a.m.–14:00 p.m.) on 7 January. Body length of 109 animals (68 males and 41 females) examined ranged from 211 to 264 cm for males and from 209 to 256.5 cm for females. The relationship between body weight (Y in kg) and body length (X in cm) is shown by the following equation: $Y=0.0000192X^{2.91}$. The sex ratio (female % of the total) of 119 animals was 39.5%. Of 39 females examined on reproductive condition, 34 (87.2% of the total number of females) were sexually mature, comprising 10 pregnant (29.4% of the sexual mature females), 13 lactating (38.2%) and 11 resting animals (32.4%). Sexually mature females ranged from 11.5 to 44.5 years of age and from 231 to 256.5 cm in body length. The annual ovulation rate was estimated at 0.28. Possible sexually mature males having a testis weight of 200 g or more ranged from 16.5 to 38.5 years of age and from 244 to 264 cm in body length. The rate of sexual maturity of 36 males examined was estimated at 72.2%. Maximum testis weight was 1040 g. Physically mature animals were found to be 13.5 years or older, and all 14 animals of over 17 years were physically mature. The vertebral formula was C7+T(13–16)+L(15–18)+Ca(39–45)=78–83. *Nasitrema gondo* was found in the tympanic cavity of all 20 animals dissected in the laboratory.
Keywords: Biological analysis, mass stranding, melon-headed whale, *Peponocephala electra*, Aoshima, Japan.

The melon-headed whale, *Peponocephala electra*, is distributed in tropical and subtropical waters (Nishiwaki, 1972; Perrin,1976; Jefferson *et al.*, 1993; Perryman *et al.*, 1994). The species has an oceanic distribution and occurs in groups of up to 500 individuals (Nishiwaki & Norris, 1966; Lodi *et al.*, 1990; Mullin *et al.*, 1994). Little is known about the life history of the species, although some biological studies were made using samples collected sporadically on the east coast of Australia by Bryden *et al.* (1977), in South Africa by Best & Shallowness (1981), in the eastern Pacific by

Perrin (1976), and on the Pacific coast of Japan by Nakajima & Nishiwaki (1965) and Miyazaki (1983 a).

Japan is the northernmost locality from which the species has been recorded in the Pacific Ocean (Perryman *et al.*, 1994). Since 1963 eight records (six catches and two strandings) have been reported from the Pacific coast of Japan, between 26°32′N and 35°20′N (Nakajima & Nishiwaki, 1965; Nishiwaki & Norris 1966; Miyazaki, 1980, 1983 a, 1983 b; Anonymous, 1981, 1992, 1993; Uchida, 1982; Amano & Miyazaki, 1996). The present mass stranding constituted the sixth record of the species at the Pacific coast of Japan. The first record was of one melon-headed whale stranded on Hiratsuka Beach (35°20′N, 139°21′E), Kanagawa Prefecture, on 12 August 1963 (Nakajima & Nishiwaki, 1965). The second was of a school of about 500 animals which came into Suruga Bay, about half of which were caught at Tabi (35°03′N, 138°54′E), Shizuoka Prefecture, on 23 March 1965 (Nishiwaki & Norris, 1966). The third comprised 140 melon-headed whales captured at Nago (26°32′N, 128°00′E), Okinawa Prefecture, on 9 July 1979 (Uchida, 1982). The fourth and fifth records were of about 200 and 10 animals, respectively, driven into the harbor of Taiji (33°36′N, 135°56′E), Wakayama Prefecture, in the early morning on 20 February 1980 (Miyazaki, 1980). After the sixth record, being of the mass stranding (Miyazaki, 1983 a), two catches have also been recorded from Taiji: 80 animals captured in the dolphin drive-fishery in 1990 (Anonymous, 1992), and a mixed school of about 500 individuals composed of Fraser's dolphins (*Lagenodelphis hosei*) and melon-headed whales driven into a cove on 29 January 1991 (Amano & Miyazaki, 1996). Despite this, the biological characteristics of the melon-headed whale have not been studied in detail.

In the present study we describe the background information on the 1982 stranding of melon-headed whales in Japan and analyze the biological samples, in order to increase our general knowledge of mass strandings and to improve knowledge of the morphological characters and life history parameters of the species. With this knowledge, the probable cause of the event is discussed.

Materials and Methods

Background information

The 119 melon-headed whales were found widely scattered over a stretch of about 1.6 km of coast at Aoshima (31°47′N, 131°29′E), Miyazaki Prefecture, Japan, in the early morning of 6 January 1982 (Figs. 1–2). The surface water temperature here was about 20°C. At 07:00 a.m. the manager of "Children's Park" had discovered the animals and informed the Fisheries Research Institute of Miyazaki Prefecture. The news was then broadcasted by local radio and TV, after which the local people gathered on the beach to see the stranded whales. Although the staff of the Fisheries Research Institute of Miyazaki Prefecture tried to return the animals to the sea, the

Fig. 1. The 119 melon-headed whales, *Peponocephala electra* stranded on the coast of Aoshima (31°47′N, 131°29′E) in the early morning on 6 January 1982.

attempt was not successful. Then, four live animals were transported by truck to the Fisheries Research Institute, where they were put into the pool. However, all died before the evening on 7 January, without having taken food. Prof. T. Morimitu of the Miyazaki Medical University collected parasite samples from the inner ear of one dead specimen on 7 January 1982 and examined damage to the octavus nerve caused by the parasite *Nasitrema gondo* (Morimitu *et al.*, 1986).

Field investigation

From 10:00 a.m. till 14:00 p.m. on 7 January we examined the 115 melon-headed whales on the beach, as well as the 4 animals in the laboratory of the Fisheries Reserch Institute. Although some people told us that the total number of the stranded animals was 135, in this report we maintain the total of 119, because we were unable to confirm the presence of the remaining 16 animals. On 6 January the tide level in this area was 145 cm in the highest at 03:16 a.m. and was 82 cm in the lowest at 08:47 a.m., based on data from the Maritime Safety Agency. All stranded whales were lying around the flood tidal line. As we were assured that nobody had observed the stranded animals on the coast between midnight and 07:00 a.m. when the manager of "Children's Park" first found them, we assume that the whales have stranded on the coast during higher tide.

Body length was measured to the nearest 0.5 centimeter in a straight line from

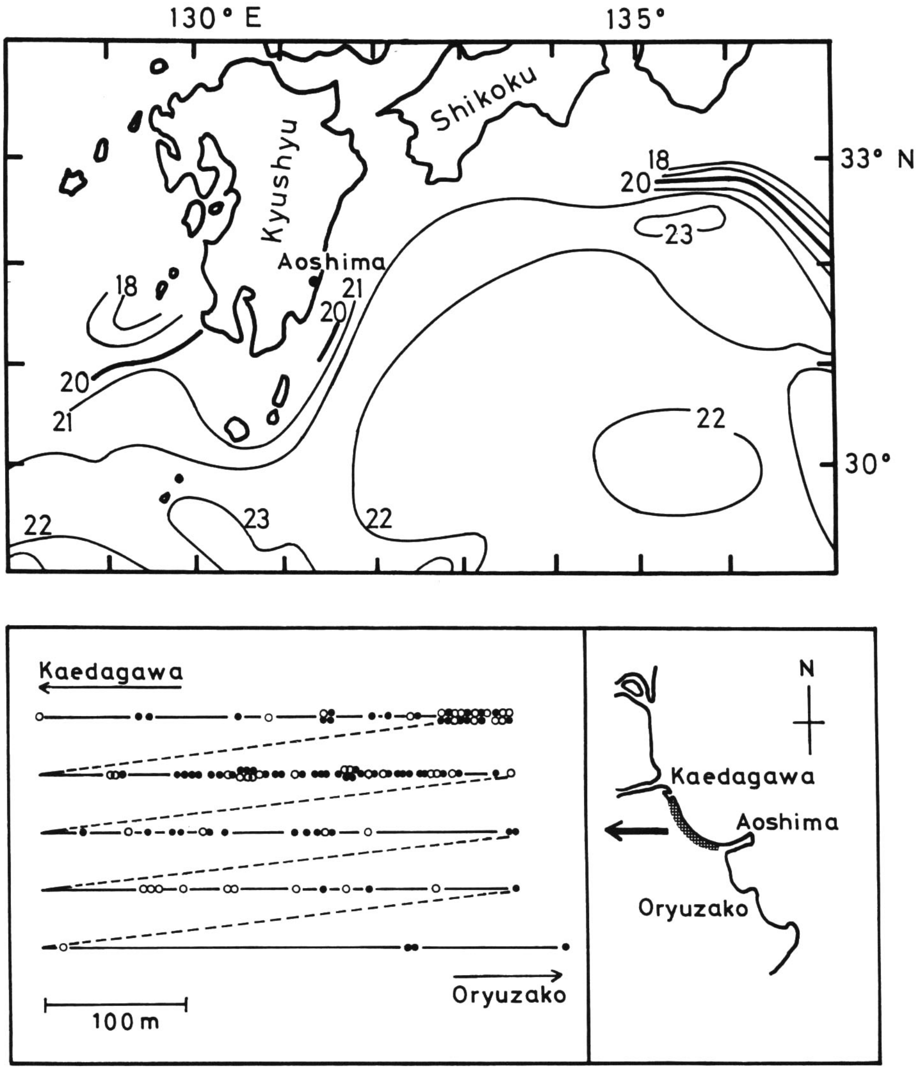

Fig. 2. Surface isotherms (°C) off Aoshima during 23 December 1981 and 13 January 1982 (Japanese Maritime Safety Agency, 1982) and relative position of the stranded whales on the coast (about 1.6 km). Males indicate closed circles and females open ones. Relative position was estimated by taking footsteps of about 1 m.

the tip of the upper jaw to the notch of the tail flukes. The distance between the stranded animals was estimated by taking footsteps of about 1 m. The stranded animals were widely scattered over a distance of 1640 m but were concentrated in two areas, 280–320 m (relative density: 0.5 animal/m) and 400–600 m (0.2) south of Kaetagawa (Fig. 2). No sexual segregation was observed. Of the 119 animals examined, including the 4 kept in the pool of the Fisheries Research Institute, 84 (70.6% of the total animals examined) were observed to breath faintly during our investigation. The other ones were already dead.

As the Aoshima region is within the Nichinan Coastal Seminational Park, we were unable to examine anatomically the animals on the beach. Thus, for scientific study we selected 20 animals comprising various stages of both sexes and transported them by truck to Ehime University, where they were kept in the freezer at −20°C pending a detailed examination. Since the coast had to be cleaned as soon as possible, the other 99 animals were brought to the oil company at Nagasaki Prefecture for incineration, following the advise of the administrator of Miyazaki Prefecture. During several hours before incineration, the second author examined the body length and sex of 50, and collected the teeth and the reproductive organs of 42 animals there.

Laboratory study

At Ehime University we photographed the selected 20 animals, took the external measurements, and weighed the internal organs and tissues after dissection on 21 and 27 April 1982 (Table 1). Samples were collected from blubber, muscle, liver, kidney and other internal organs, to be used for biometry and a chemical analysis for organochlorine compounds and heavy metals. One skeletal sample was also used for chemical analysis. Complete skeletal samples of the other 19 animals have been deposited in the National Science Museum, Tokyo (Museum nos. M23727–M23745) (Miyazaki, 1986).

The senior author took skull measurements of these 19 specimens, and examined the numbers of vertebrae and the state of ossification of the vertebral epiphyses. The skulls were measured with an anthropometer to the nearest millimeter.

Age was estimated from the higher number of either dentinal or cemental growth layers in the teeth, which were prepared by staining thin ground sections (10 to 20 μm) with haematoxylin after decalcification in a 5% water solution of formic acid following Kasuya (1976).

The ovaries from 35 females were collected and fixed in 10% formalin. The numbers of corpora albicantia and/or corpora lutea on ovaries were counted. Mature females were defined as those with at least one corpus luteum or corpus albicans. Resting females were defined as mature females being neither pregnant nor lactating. Testis weight of males was recorded to the nearest gram.

Results

Size frequency and sex ratio

Among the 119 stranded melon-headed whales, 10 animals (4 males and 6 females) lacked their tail flukes. Thus, size frequency was calculated from 109 animals

Table 1. Biological data of 20 samples of *Peponocephala electra* collected

Specimen no.*	Age (yr)	Sex	Sexual** condition	Body length (cm)	Body weight (kg)	Sexual organ weight (g) left	Sexual organ weight (g) right
M23727	2.5	M	Immature	214.0	105.4	8.2	8.2
M23728	11.5	F	Immature	231.5	131.5	2.0	2.6
M23729	21.5	F	Pregnant	240.0	173.2	11.6	2.1
M23730	20.5	F	Lactating	239.0	141.2	3.1	1.5
M23731	26.5	F	Lactating	235.0	145.0	2.7	2.5
M23732	5.5	M	Immature	223.0	114.4	15.7	19.8
M23733	17.5	F	Lactating	231.0	134.4	2.3	1.0
M23734	23.5	F	Lactating	251.5	184.0	6.5	5.9
M23735	22.5	F	Lactating	235.5	156.4	4.6	2.7
M23736	20.5	F	Lactating	242.0	159.6	6.5	3.2
M23737	31.5	M	Mature	264.0	228.6	930.4	917.0
M23738	13.5	F	Lactating	246.0	166.0	3.5	2.3
M23739	13.5	M	Immature	236.0	144.2	43.9	48.6
M23740	9.5	F	Immature	215.0	110.6	1.5	1.5
M23741	27.5	F	Pregnant	234.5	182.1	2.8	15.2
M23742	27.5	M	Mature	251.0	198.4	927.0	912.4
M23743	21.5	M	Mature	247.5	175.6	593.0	444.8
M23744	26.5	F	Resting	252.0	181.1	4.7	4.7
M23745	37.5	M	Mature	247.0	196.5	820.0	761.7
82106-15	—	M	Mature	258.0	211.7	864.5	782.3

* Skeletons of the samples (Museum no.: M23727–M23745) are deposited in the National Science
** Males having testis of 200 g or more are definited as mature.
*** The species was identified as *Nasitrema gondo* (Morimitsu *et al.*, 1986; *J. Parasit.*, **72** (3): 469–472).

(68 males and 41 females) examined in the field and at the Fisheries Research Institute (Fig. 3). The body length ranged from 211 to 262 cm for males and from 209 to 252 cm for females. The peak at 250–255 cm for males is obviously on higher figures than that (235–240 cm) for females. In the laboratory, the collected animals were measured again. Then the largest body length was recorded as 256.5 cm for females and 264 cm for males. Comparison of 24 adult males and 29 adult females of over 15 years old indicated males were significantly larger than females (t-test, $p<0.05$). In the present stranding, no newborn calf or animal less than 209 cm was found, in spite of the recognition of 13 lactating females. Body length of 10 fetuses ranged from 29.3 to 101.0 cm with a slight peak at 80–85 cm.

The sex ratio (female % of the total) of 119 animals was 39.5%, which did not differ greatly from that of 10 fetuses (30%). Among 74 animals whose age was determined, the sex ratio of 57 animals of over 15 years old was 56.1%, which was larger at Aoshima (31°47′N, 131°29′E), Japan on 6 January 1982.

No. of corpora				No. of vertebrae	Physical maturity	No. of parasites in the tympanic cavity***
left		right		C+T+L+Ca=Tol.		
c.l.	c.a.	c.l.	c.a.			
				7+14+16+43=80	No	+
0	0	0	0	7+14+18+42=81	No	+
1	3	0	1	7+14+18+41=80	Yes	132
0	6	0	0	7+14+17+41=79	Yes	185
0	6	0	0	7+13+18+42=80	Yes	125
				7+14+17+40=78	No	20
0	1	0	0	7+14+18+40=79	Yes	47
0	0	0	11	7+16+16+40=79	Yes	98
0	2	0	0	7+14+16+43=80	Yes	161
0	5	0	0	7+14+17+42=80	Yes	25
				7+14+16+42=79	Yes	230
0	5	0	0	7+15+15+42=79	Yes	98
				7+14+16+43=80	No	50
0	0	0	0	7+15+18+39=79	No	6
1	1	0	1	7+14+16+42=79	Yes	135
				7+13+17+44=81	Yes	54
				7+14+15+45=81	Yes	15
0	4	0	2	7+15+15+43=80	Yes	352
				7+15+16+45=83	Yes	324
—	—			—	—	197

Museum, Tokyo.

than that of the 17 younger animals (41.2%).

Age composition

Figure 4 shows a comparison of the number of dentinal and cemental growth layers of decalcified and stained sections of the teeth. The number of dentinal and cemental growth layers was almost the same in the animals of 20 dentinal growth layers or less. In the animals of over 20 dentinal growth layers, the number of cemental growth layers exceeds that of the dentinal growth layers in nearly all specimens. In the present study, the age was estimated from the higher number of either dentinal or cemental growth layers of the same animal. The age ranged from 5.5 to 45.5 years for females and from 2.5 to 38.5 years for males. Age frequency showed a peak at 3.5, 12.5, 19.5 and 35–37 years for males, and at 11.5 and 22–25 years for females (Fig. 5).

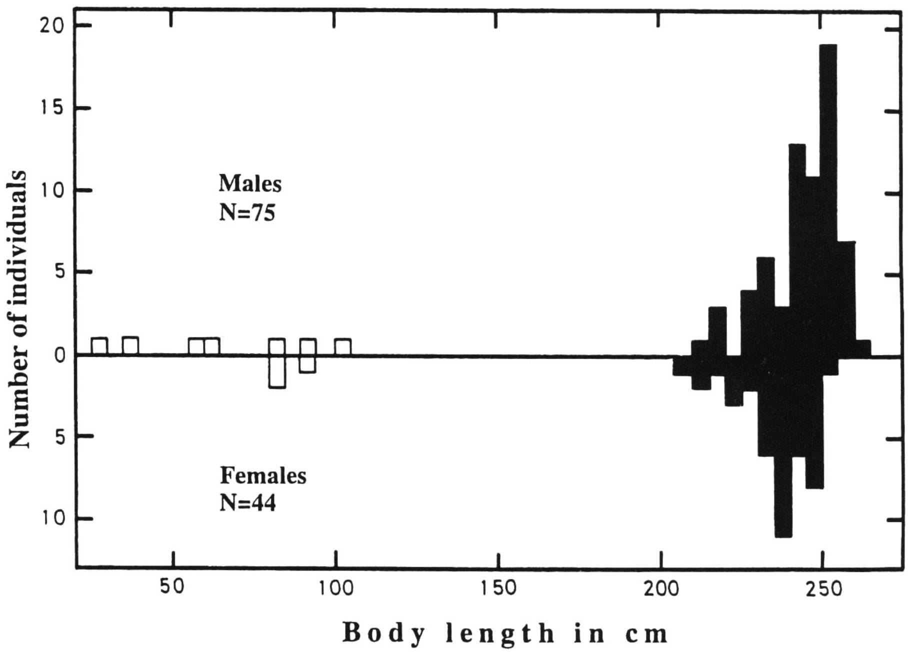

Fig. 3. Body length frequency of 109 postnatal animals (68 males and 41 females) and 10 fetuses (7 males and 3 females) in *Peponocephala electra*. Black boxes indicate postnatal animals and white ones fetuses.

External appearance and morphology

Coloration

The melon-headed whales have a black or dark grey overall body coloration, with white lips and a light throat chevron, midventral streak and genital patch (terminology of Mitchell, 1970) (Fig. 6). This specific ventral color pattern is white in most animals whereas pink in some. This coloration shows some individual variation in position, size and shape. There is no sexual difference in color pattern except for the genital patch, which extends from around the anterior part of umbilicus to the end of the anus in males, whereas to the end of the mammary slits in females.

In order to investigate the development of this color pattern in the fetal stage, the patterns of the fetuses are compared at various stages (Figs. 7–8). In a female fetus of 39 cm in body length, the black color was observed in both sides of dorsal fin, flippers and flukes as well as around the eye, and a grey color was observed in the tip of upper and lower jaw, and overall head, while in the other areas of the ventral and dorsal side this coloration was not present (Fig. 7). In a male fetus of 63.5 cm, all of the dorsal area was black, whereas on the ventral side the black color had not been formed. In a female fetus of 81.5 cm, the ventral area between both flippers, the area below both eyes, and some area around chin became black as well as all of the area

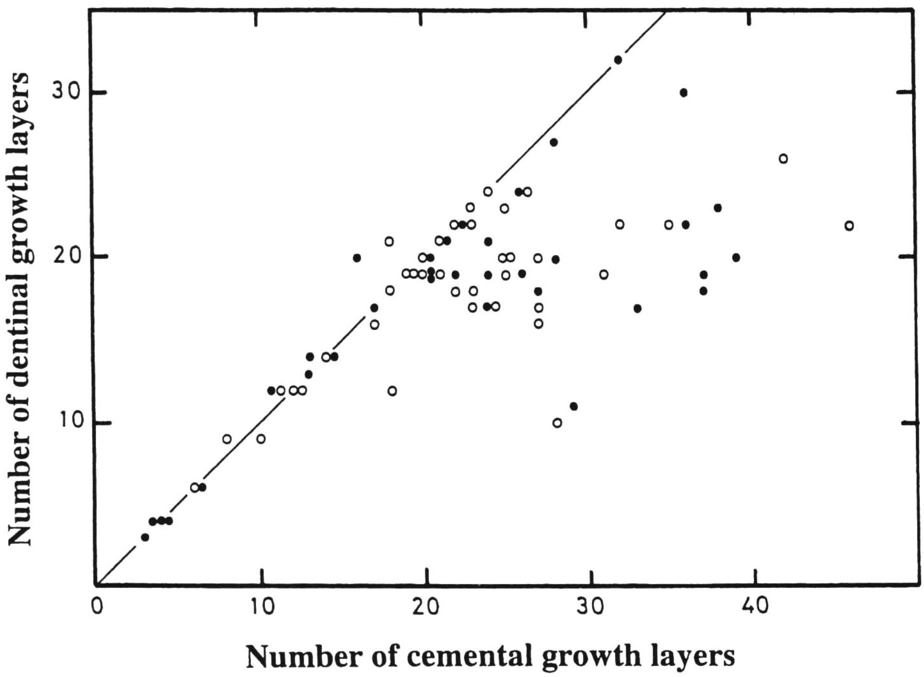

Fig. 4. Relationship between number of dentinal and cemental growth layers of 74 *Peponocephala electra*. Closed circles indicate males and open ones females. Solid line was drawn by the same number between them.

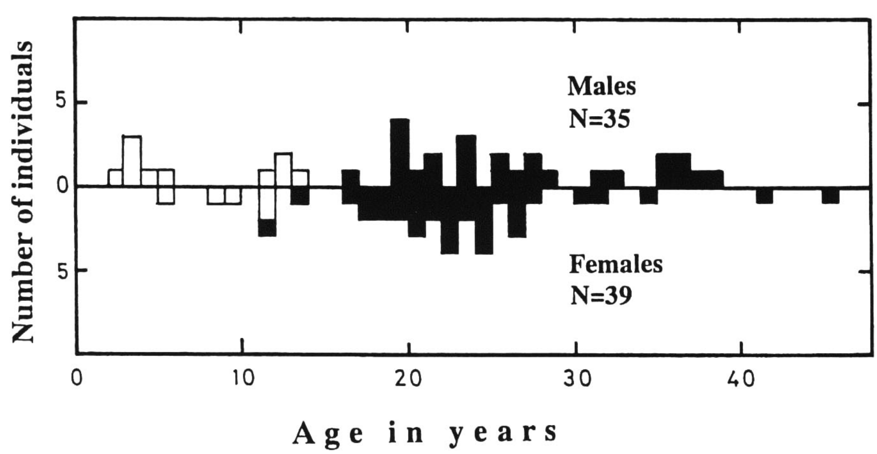

Fig. 5. Age composition of 74 *Peponocephala electra* (35 males and 39 females). Black boxes indicate mature animals and white ones immature. Mature males were defined as animal having a testis weight of 200 g or more (see Fig. 14), and mature females as those with at least one corpus luteum or corpus albicans on ovaries.

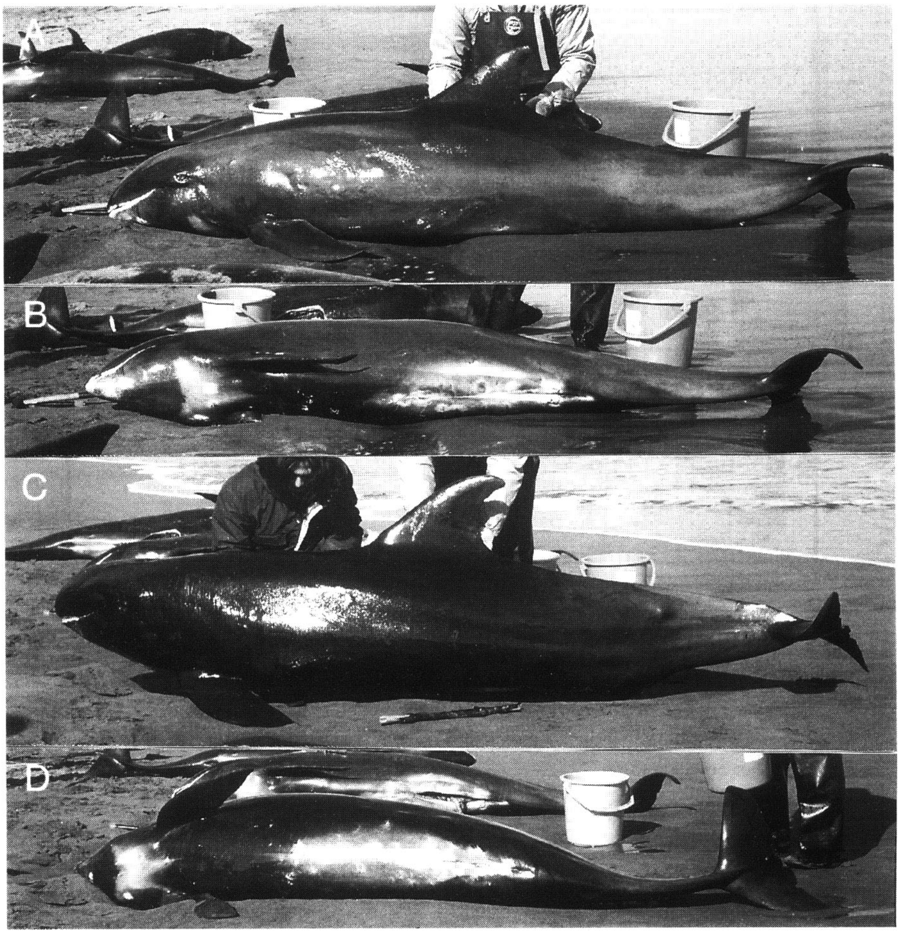

Fig. 6. Coloration and external morphology of the adult *Peponocephala electra*. —— A, An adult female (Field no.: 82107-19, BL: 246.5 cm, Age: 45.5 years); B, ventral side of the same animal of A; C, an adult male (Field no.: 82107-20, BL: 259 cm, Age: 36.5 years); D, ventral side of the same animal of C.

on the dorsal surface, whereas in both lips and the other ventral areas black color was not formed. The same color pattern of the postnatal individuals was also found in male fetuses of 92 and 101 cm, indicating the characteristic color pattern of the species is formed till the fetal stage of about 80 cm or more. Thus, it is concluded that lips, throat chevron, midventral streak and genital patch are white for the life. No sexual difference in coloration is not observed.

External morphology

Development of some external characters is shown using data for the fetuses of

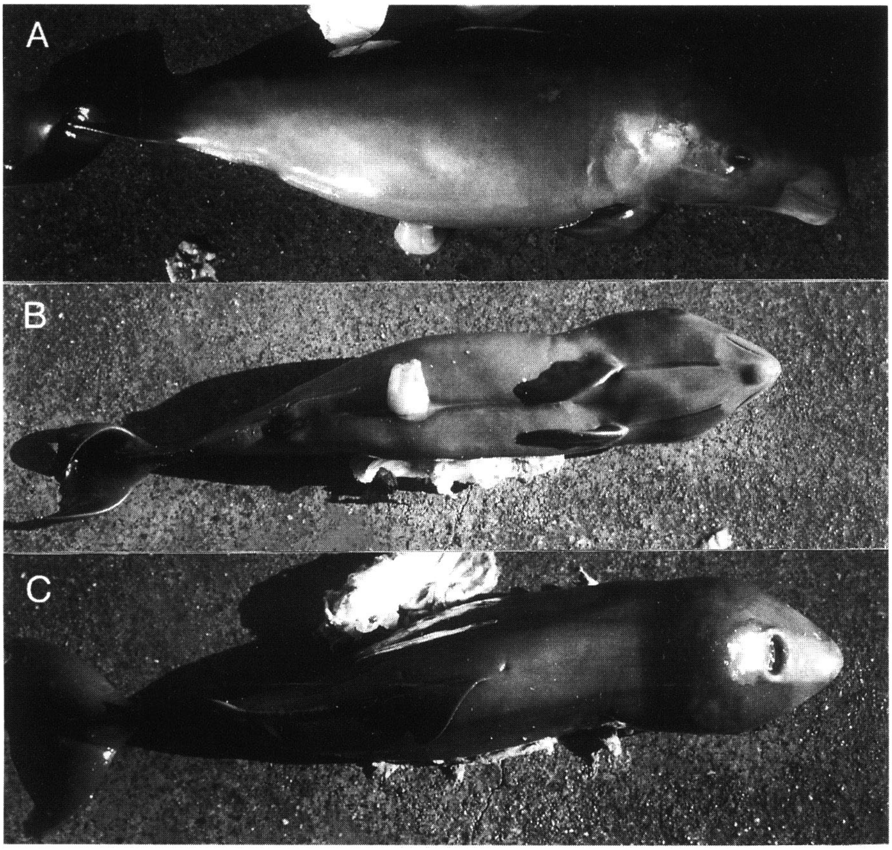

Fig. 7. Color pattern on a fetus *Peponocephala electra* of 39 cm in body length. —— A, Lateral side of the fetus; B, ventral side of the fetus; C, dorsal side of the fetus.

39 to 101 cm and for the 14 postnatal animals of 214 to 259 cm in body length (Fig. 9). The relative position of gape, eye and blowhole to the body length (Measurement nos. 2, 3 and 6 in Table 2) decreased after birth, as well as that of the flipper, dorsal fin and umbilicus (7, 8 and 9). The relative position of the anus and genitals slightly decreased with growth. The relative position of the genital aperture in males was about 7% further forward than it was in females, and this difference seemed to be almost constant in the prenatal and postnatal stages. Thus, the thoracic and caudal parts of melon-headed whales becomes relatively larger with growth, whereas the head becomes smaller.

Among 31 characters of 14 adult animals of over 15 years old, a significant sexual difference was observed in flipper (Measurement nos. 12, 15, 16 of Table 2), dorsal fin (17, 19, 20), flukes (21, 22, 23, 24, 25, 26, 27, 28) and girth at anus (31) (t-test, $p<0.05$), indicating that males were larger than females in these 15 characters,

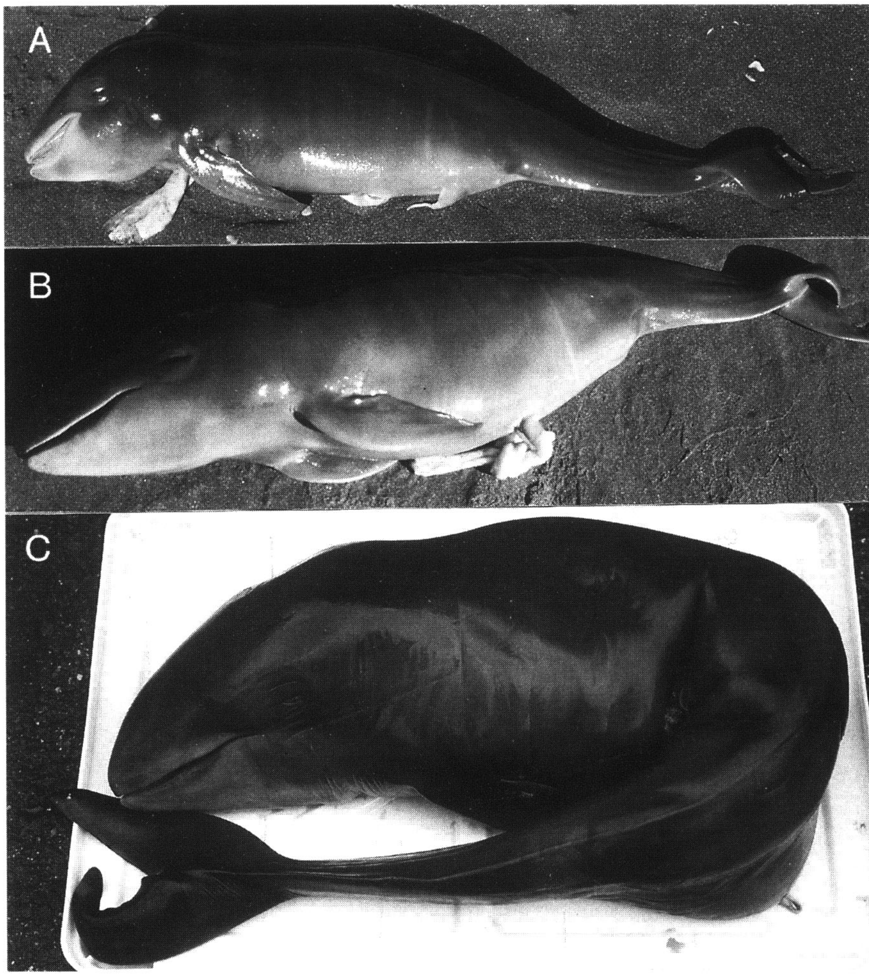

Fig. 8. Comparison of color pattern of fetuses in *Peponocephala electra*. —— A, A male fetus of 63.5 cm; B, a female fetus of 81.5 cm; C, a male fetus of 101.0 cm.

whereas in the length from the tip of upper jaw to genital aperture (10) this was the reverse (Table 2).

We also found sexual dimorphism in the development of a ventral keel and in the shape of the anterior part of the head. In adult males a pronounced keel posterior to the anus (Fig. 10) was present, and the head was more rounded in shape as compared with adult females (Fig. 6). Development of the keel with growth is shown in Table 3. The keel was recognized in males of 231 cm or more and of 21.5 years or more. Its maximum height was 2.8 cm in the middle class and 4.3–5.5 cm in the well developed class.

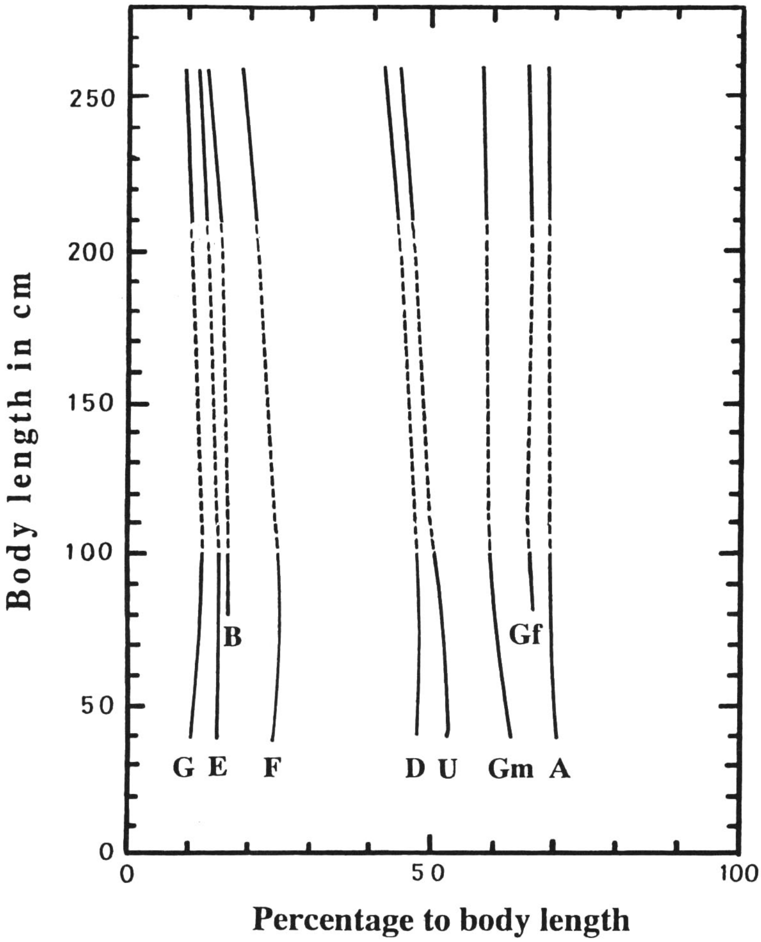

Fig. 9. Development of external characters of *Peponocephala electra* with growth. Solid line is drawn with data of 24 postnatal animals ranged from 211 cm to 259 cm and 6 fetuses ranged from 39 cm to 101 cm, and broken line without data between the smallest postnatal animals of 211 cm and the largest fetus of 101 cm.

Healed scars which probably are to be attributed to the small shark *Isistius* (Jones, 1971) were found on the ventral and lateral sides of several animals (Fig. 11). They were more often found in the ventral than in the lateral or dorsal areas, indicating that the shark attaches itself more easily to the ventral side. These scars were already present in a young animal of 214 cm in body length. There was no significant difference in the position of the healed scars between sexes and between growth stages.

Table 2. External measurements (cm) of adult males and females of *Peponocephala electra*.

Measurements	Males			Females		
	No.	range	mean	No.	range	mean
1. Body length	24*	244.0~264.0	253.1±5.5**	29*	231.0~256.5	242.6±7.6**
2. Length of gape	4	21.5–23.1	22.3	10	20.1–24.2	22.0
3. Tip of upper jaw to center of eye	4	28.4–30.8	25.6	10	27.9–31.0	25.5
4. Tip of upper jaw to center of ear	4	35.4–40.4	37.4	10	33.6–39.0	36.6
5. Eye to ear	4	7.9–8.5	8.3	10	7.9–9.4	8.6
6. Tip of upper jaw to center of blowhole	4	29.5–34.5	32.1	10	27.5–35.3	31.5
7. Tip of upper jaw to anterior insertion of flipper	4	43.6–48.0	45.4	10	44.2–51.0	47.5
8. Tip of upper jaw to anterior insertion of dorsal fin	4	100.8–109.0	103.1	10	100.5–110.0	104.6
9. Tip of upper jaw to center of umbilicus	4	105.3–115.2	109.2	10	100.5–111.5	108.3
10. Tip of upper jaw to genital aperture	4	139.0–147.0	141.6**	10	147.2–168.0	158.1**
11. Tip of upper jaw to anus	4	162.2–177.0	168.8	10	154.1–175.0	165.3
12. Flipper length, anterior insertion to tip	4	47.6–51.7	49.4**	10	40.5–50.4	45.2**
13. Flipper length, posterior insertion to tip	4	31.4–37.8	34.3	10	29.1–33.7	32.1
14. Flipper width at base	4	15.2–17.0	15.9	10	14.0–16.0	15.1
15. Flipper width at maximum	4	12.8–15.0	14.1**	10	11.6–13.7	12.5**
16. Length of dorsal fin at base	4	40.0–48.7	45.2**	10	32.5–43.4	38.7**
17. Anterior insertion of dorsal fin to tip	4	42.8–49.5	46.2**	10	36.5–43.0	39.7**
18. Posterior insertion of dorsal fin to tip	4	20.0–26.5	22.9	10	16.7–22.2	20.5
19. Height of dorsal fin	4	20.0–26.0	21.9**	10	16.7–21.5	19.2**
20. Height of dorsal fin at maximum	4	21.4–26.9	23.2**	10	18.6–23.1	20.5**
21. Width of flukes	4	61.0–66.0	62.5**	10	43.8–60.0	50.4**
22. Anterior insertion of left fluke to tip	4	39.4–43.3	41.4**	10	34.0–43.0	36.9**
23. Anterior insertion of right fluke to tip	4	39.5–43.6	41.8**	10	32.6–43.5	37.0**
24. Tip of left fluke to center of notch	4	32.1–35.0	33.6**	10	25.5–34.5	28.3**
25. Tip of right fluke to center of notch	4	31.8–35.1	33.4**	10	25.3–34.5	28.3**
26. Anterior insertion of left fluke to notch	4	18.2–19.0	18.6**	10	14.3–18.2	16.6**
27. Anterior insertion of right fluke to notch	4	18.0–19.8	18.8**	10	15.0–17.6	16.5**
28. Depth of notch at maximum	4	3.2–4.5	3.9**	10	2.2–3.8	2.9**
29. Girth at axilla	4	114–124	118.9	10	103–121	113.0
30. Girth at anterior insertion of dorsal fin	3	132–154	142.7	10	123–146	134.1
31. Girth at anus	4	86.5–108	99.6**	10	70.2–83.0	76.5**

* Samples of 15.5 years or more were used for comparison.
** Statistically significant difference at the level of $P<0.05$.

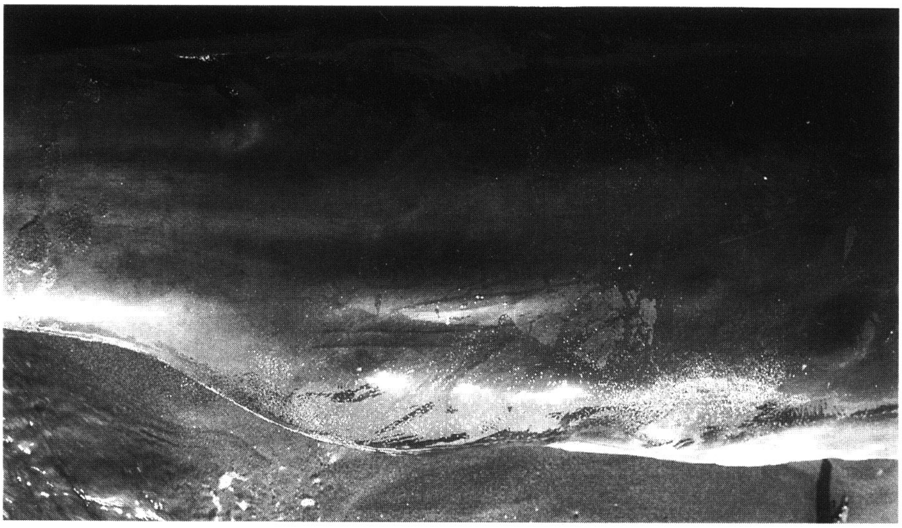

Fig. 10. A developed keel posterior to anus in an adult males of 259 cm (Field no. 82107-20).

Table 3. Development of the ventral keel in males of *Peponocephala electra*.

Body length (cm)	Grade of development*			Age (yr)	Grade of development**		
	well	middle	no		well	middle	no
220–	0	0	0	2.5[A]			1
225–	0	0	2	5.5[B]			1
230–	1	1	1	13.5[C]			1
235–	0	1	0	21.5[D]		1	
240–	4	0	0	27.5[E]	1		
245–	2	0	0	31.5[F]	1		
250–	8	0	0	37.5[G]	1		
255–	2	0	0				
260–	1	0	0				
265–	0	0	0				
Total	18	2	3		3	1	3

* Data were obtained from observation in the field.

** Data were corresponding to the specimens in Table 1. A: M23727 (Height of hump: 0 mm), B: M23732 (0 mm), C: M23739 (0 mm), D: M23743 (28 mm), E: M23742 (55 mm), F: M23737 (not measured) and G: M23745 (44 mm).

Skull morphology and vertebral formula

A comparison of 51 skull measurements of 14 adult animals of over 15 years old is given in Table 4. The dental formula was 17–25/18–25 left and 14–23/19–23 right.

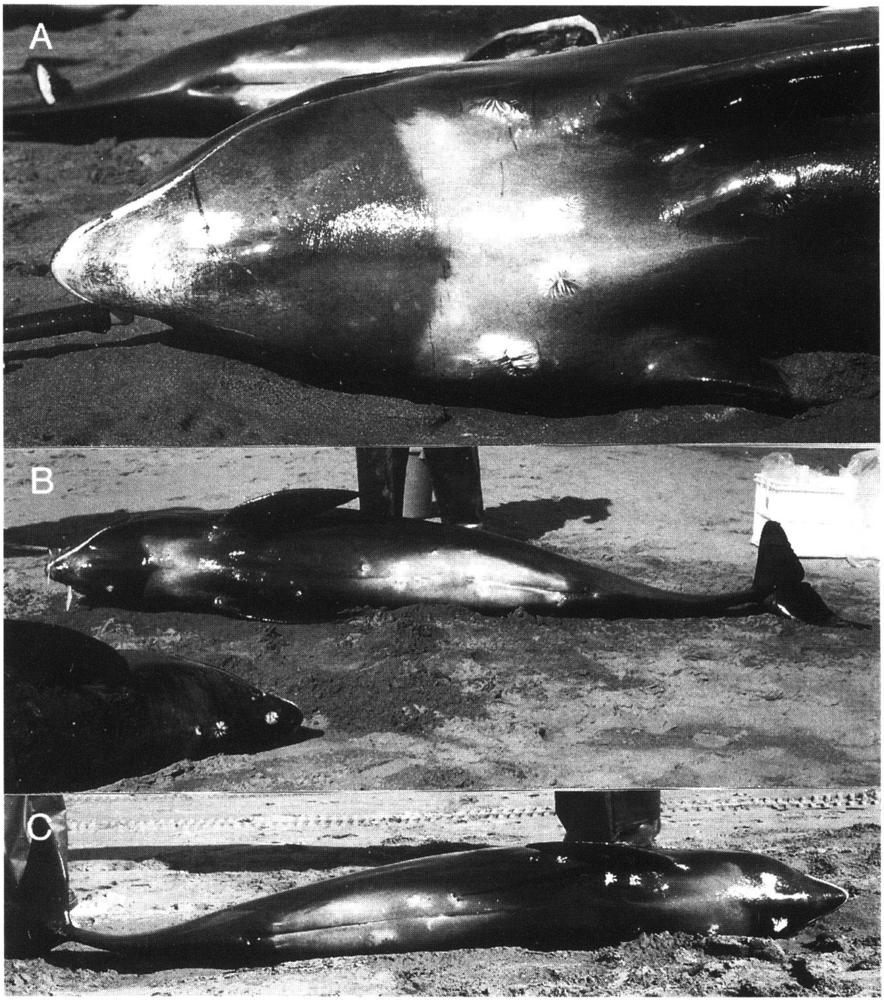

Fig. 11. Several healed scars probably attributed to the small shark *Isistius* on the ventral side of *Peponocephala electra.* —— A, An adult female (Field no.: 82107-19, BL: 246.5 cm, Age: 45.5 years); B, an adult female (82107-12, 235 cm); C, a subadult female (82107-5, 214 cm).

Most skull measurements (94%) showed no sexual difference except for the following three characters: width of premaxillaries at 3/4 length from the base (Measurement no. 10), parietal width (19) and lacrimal length (29), indicating males were significantly larger than females in the first character whereas in the other two it was the reverse.

In all 19 specimens coalescence of the first three cervical vertebrae was observed. In addition, coalescence of the fifth and sixth, and of the sixth and seventh

Table 4. Skull measurements (mm) of adult males and females of *Peponocephala electra*.

Measurements	Males			Females		
	No.	range	mean	No.	range	mean
1. Condylobasal length	4	452–478	461.8	10	442–477	459.6
2. Length of rostrum	4	248–262	253.0	10	244–266	252.1
3. Width of rostrum at base	4	133–138	136.0	10	132–142	137.2
4. Width of premaxillaries at base	4	79–83	81.5	10	75–87	81.0
5. Width of rostrum at 60 mm from base	4	109–119	114.3	10	106–120	110.9
6. Width of premaxillaries at 60 mm from base	4	48–70	63.5	10	57–85	67.0
7. Width of rostrum at midlength	4	90–98	94.0	10	85–98	91.1
8. Width of premaxillaries at midlength of rostrum	4	58–62	60.5	10	52–66	58.8
9. Width of rostrum at 3/4 length from base	4	67–78	73.0	10	61–75	69.4
10. Width of premaxillaries at 3/4 length from base	4	41–45	43.5*	10	38–45	40.4*
11. Distance from tip of rostrum to external nares	4	308–322	312.8	10	298–329	312.9
12. Distance from tip of rostrum to internal nares	4	291–307	299.3	10	239–311	289.5
13. Greatest preorbital width	4	239–273	253.3	10	237–259	250.6
14. Greatest postorbital width	4	260–275	265.5	10	256–284	267.5
15. Least supraorbital width	4	243–260	249.3	10	235–259	249.7
16. Greatest width of external nares	4	61–63	62.3	10	58–68	61.8
17. Greatest width across zygomatic processes	4	253–270	261.5	10	253–274	261.9
18. Greatest width of premaxillaries	4	93–98	96.3	10	90–103	96.9
19. Greatest parietal width	4	194–207	199.3*	10	199–216	206.8*
20. Vertical external height of braincase	4	133–149	142.8	10	136–152	143.9
21. Internal length of braincase	4	117–127	122.0	10	121–130	125.0
22. Greatest length of left posttemporal fossa	4	87–92	89.0	10	79–95	86.7
23. Greatest width of left posttemporal fossa	4	58–69	62.3	10	46–65	58.5
24. Major diameter of left temporal fossa proper	4	40–49	45.0	10	38–52	44.7
25. Minor diameter of left temporal fossa proper	4	49–52	50.5	10	45–58	52.0
26. Projection of premaxillaries beyond maxillaries	4	10–18	14.8	10	8–18	13.4

Table 4. Continued.

Measurements	Males			Females		
	No.	range	mean	No.	range	mean
27. Distance from foremost end of junction between nasals to hindmost point of margin of supraoccipital crest	4	28–39	34.3	10	20–35	28.6
28. Length of left orbit	4	67–72	69.3	10	69–76	71.5
29. Length of antorbital process of left lacrimal	4	40–47	44.5*	10	45–55	49.9*
30. Greatest width of internal nares	4	72–81	75.3	10	71–81	74.1
31. Greatest length of left pterygoid	4	74–97	84.0	10	80–91	84.7
32. Greatest width of anterior overhang of supraoccipital crest	4	58–138	109.3	10	72–184	126.1
33. Greatest length of bulla of left tympanoperiotic	4	34–36	35.3	10	35–37	35.9
34. Greatest width of bulla of left tympanoperiotic	4	21–22	21.3	10	20–22	20.9
35. Greatest length of periotic of left tympanoperiotic	4	31–33	31.5	10	30–34	32.0
36. Greatest width of periotic of left tympanoperiotic	4	21–24	22.5	10	22–24	23.0
37. Length of upper left tooth row	4	171–186	177.0	10	162–190	175.2
38. Number of teeth (upper left)	4	17–22	20.5	10	19–25	21.2
39. Number of teeth (upper right)	4	14–22	19.3	10	18–23	20.9
40. Number of teeth (lower left)	4	20–24	21.8	10	18–25	21.4
41. Number of teeth (lower right)	4	19–22	21.0	10	19–23	21.4
42. Length of lower left tooth row	4	154–178	166.5	10	149–176	161.4
43. Greatest length of left ramus	4	359–377	367.0	10	350–389	368.9
44. Greatest height of left ramus	4	89–93	90.8	10	87–93	89.3
45. Length of left mandibular fossa	4	137–147	142.5	10	136–154	145.4
46. Length of basihyal along midline	4	46–56	52.8	10	41–62	50.1
47. Greatest width of basihyal	4	50–61	55.5	10	55–66	60.2
48. Greatest width of left thyrohyal proximally	4	27–35	30.0	10	26–31	28.2
49. Greatest length of left thylohyal	4	76–87	79.8	10	77–88	82.4
50. Greatest width of left stylohyal	4	22–26	23.0	10	19–26	23.1
51. Greatest length of left stylohyal	4	101–109	105.3	10	98–114	105.5

* Statistically significant difference at the level of $P<0.05$.

cervical vertebrae was found in four specimens (M23729, M23731, M23735, M23736) and in one (M23728), respectively. The number of ribs including floating ribs (0 to 2) ranged from 13 to 16. This number was the same on both sides in 18 specimens, whereas one male (M23743) had 14 left and 13 right. In most (78.9%) of the specimens one floating rib was found on both sides. However, there were individual variations, such as: (1) two floating ribs left and one right (M23743), (2) two floating ribs on both sides (M23745), and (3) no floating rib (M23731). The first caudal vertebra is defined as the vertebra in which the first chevron is attached to its posterior edge. The vertebral formula of 19 melon-headed whales varied as follows: C7+T(13–16)+L(15–18)+Ca(39–45)=78–83 (Table 1).

Internal organs

Table 5 gives the organ and tissue weights of 14 adult animals of over 15 years old. Intestine length is also given in this Table. The body weight of adult males was significantly greater than that of adult females, as well as the weight of muscle, blubber and bones (t-test, $p<0.05$), whereas the weight of the viscera showed no sexual

Table 5. Organ and tissue weights of adult males and females of *Peponocephala electra*.

Measurements	Males			Females		
	No.	range	mean	No.	range	mean
1. Body weight (kg)	4	175.6–228.6	199.8*	10	134.4–184.0	160.6*
2. Muscle weight (kg)	4	89.1–117.6	101.9*	10	63.3–96.2	79.0*
3. Blubber weight (kg)	4	43.1–55.8	49.0*	10	34.3–43.4	38.4*
4. Bone weight (kg)	4	16.4–19.7	17.6*	10	12.7–16.4	14.8*
5. Viscera weight (kg)	4	20.6–26.8	23.0	10	18.2–25.5	21.6
6. Brain weight (g)	4	1200–1520	1370	10	1060–1481	1255
7. Other tissues (g)	4	1680–4520	2853	10	1070–2710	2044
8. Heart weight (g)	4	778.2–1300	1004	10	746.6–1400	956.5
9. Lungs weight (g)	4	4040–6530	5021.8	10	4110–6100	5238
10. Liver weight (g)	4	2932–4260	3523	10	3130–4896	3807.6
11. Left kidney weight (g)	4	404.8–561.3	465.9	10	373.7–499.6	437.5
12. Right kidney weight (g)	4	453.1–527.9	482.8	10	337.4–505	430.6
13. Spleen weight (g)	4	52.7–69.1	60.3	10	32.0–67.9	49.7
14. Pancreas weight (g)	4	95.2–172.9	135.0	10	90.1–167.9	131.8
15. First stomach weight (g)	2	842.7–956.7	899.7	10	656–1210	865.6
16. Second stomach weight (g)	2	367–403.5	385.3	10	361–484.2	429
17. Third stomach weight (g)	2	175.1–218.1	196.6	10	125.9–208.3	157.4
18. Fourth stomach weight (g)	2	61.7–64.5	63.1	10	74.0–151.5	92.5
19. Intestine weight (g)	4	3440–4225	3778.8	10	2910–4050	3580
20. Intestine length (cm)	4	1630–1950	1788.8	10	1520–1830	1650.6

* Statistically significant difference at the level of $P<0.05$.

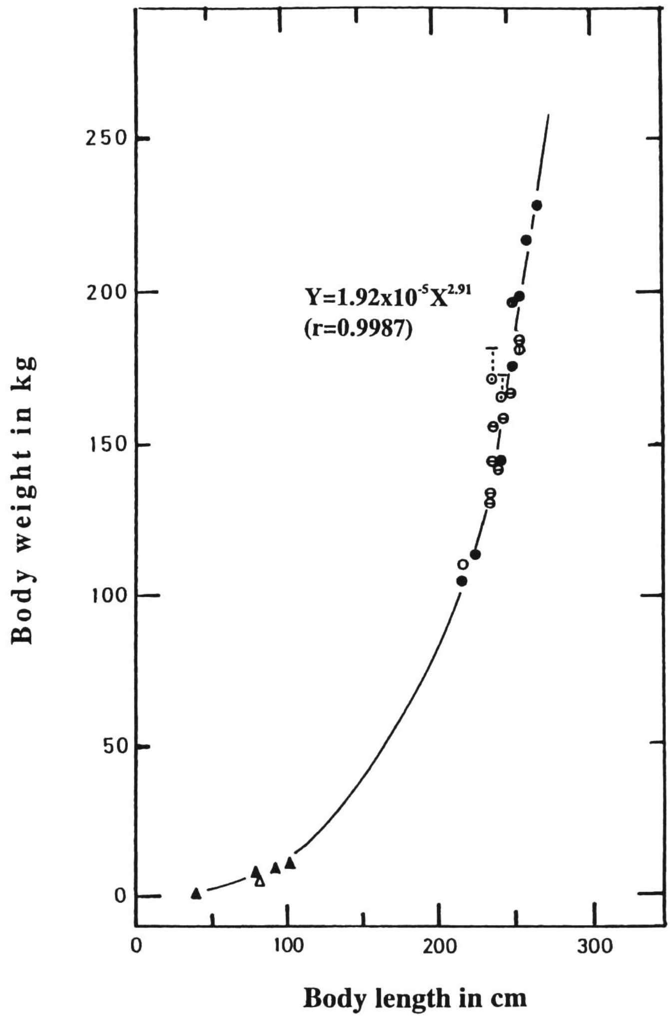

Fig. 12. Relationship between body weight and body length in *Peponocephala electra*. Closed circles indicate males, open circle immature female, open circle with vertical line resting female, open circles with horizontal line lactating females, open circles with dot pregnant females, open triangle female fetus and closed triangles male fetuses. The body weight of a pregnant female was calculated as body weight minus fetus weight.

difference. Muscle, blubber, viscera and bone weights were about half (males: 51.9%, females: 49.2%), a quarter (24.5%, 23.9%), slightly more than one tenth (11.5%, 13.4%) and slightly less than one tenth (8.8%, 9.2%), respectively, of the body weight. No significant sexual difference was observed in the weight of heart, lungs, liver, kidney, spleen, pancreas, four stomachs and intestine as well as in the length of the intestine. Comparison of mean left and right kidney weight showed no significant difference at the level of $p=0.05$.

Life history

Growth

Figure 12 shows the relationship between body weight and body length in a sample of 25 animals ranging from a fetus of 38.5 cm to the largest specimen of 264 cm in length. The maximum body weight was 228.6 kg for males and 184 kg for females (Table 1). The body weight of pregnant female was calculated as body weight minus fetus weight. The relationship is expressed by the following equation: $Y=0.0000192X^{2.91}$ $(r=0.999)$, where Y indicates body weight in kg, X body length in cm, and r the correlation coefficient.

The relationship between body length and age is shown in Fig. 13. The growth curve was drawn by eye, using the length at birth of 112 cm given by Perrin (1976). Body length increased rapidly during the first years after birth, and then increased at a constant rate. Growth of both females and males ceased at 13 and 15 years old, respectively. The body length of the animals of over 15 years old showed a sexual dif-

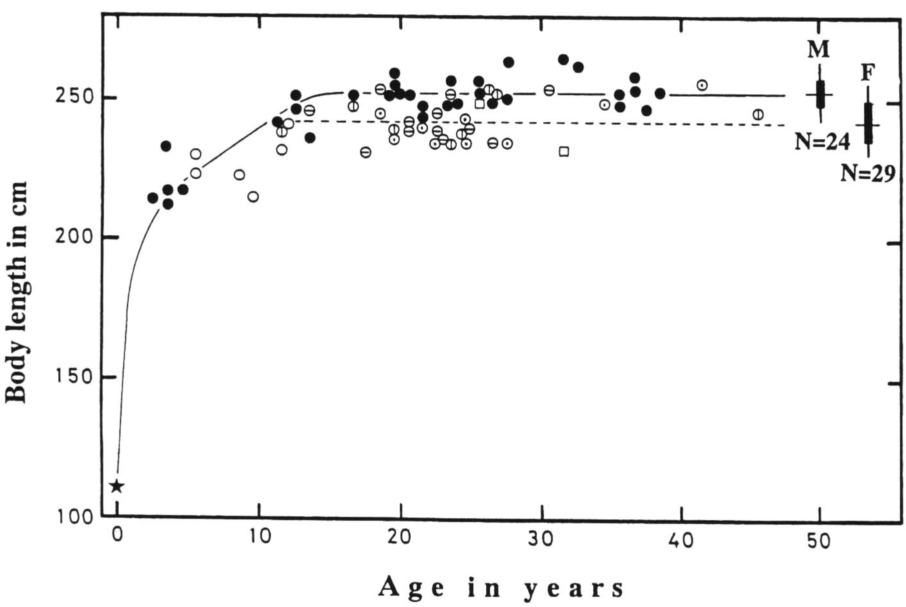

Fig. 13. Relationship of body length and age of 70 *Peponocephala electra*. Open squares adult females of reproductive condition unknown. Star indicates the smallest newborn of 112 cm cited from Perrin (1976). See Fig. 12 for the other marks. Solid line is the mean growth curve for immature animals in both sexes and for mature males, and dotted line is the mean for mature females. Vertical lines indicate ranges, horizontal midlines means and black boxes standard deviations.

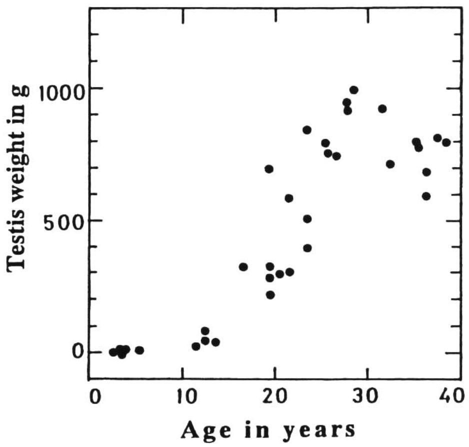

Fig. 14. Relationship between a testis weight and age of 34 males in *Peponocephala electra*.

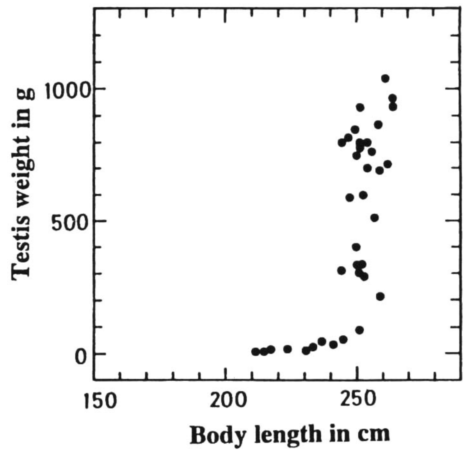

Fig. 15. Relationship between a testis weight and body length of 36 males in *Peponocephala electra*.

ference, in that the average body length (252.4 cm) of the males was significantly greater than that (242.7 cm) of the females (t-test, $P<0.05$). Thus, the asymptotic length of the species was considered as 242.7 cm for females and 252.4 cm for males, respectively.

Reproduction of males

To determine the sexual condition of the males, the testis obtained from either the left or right side was measured for 36 animals. Testis weight of males increased gradually from 2.5 to 13.5 years old and rapidly after 15 years of age. Thus, males seem to attain sexual maturity at the age of around 15 years (Fig. 14). However, we can not determined precisely the age when 50% of the males attain sexual maturity, because of the small sample size and the lack of histological examination. Maximum testis weight was 1040 g. Testis weight increased rapidly around a length of 245–250 cm (Fig. 15). The possibly mature males having a testis of 200 g or more ranged from 16.5 to 38.5 years old and from 244 to 264 cm in body length. Using this criterion, the rate of sexual maturity among the 36 stranded males examined was estimated at 72.2%.

Reproduction of females

Among 44 females examined, 5 were determined as immature, and 34 as sexually mature, whereas the other 5 were in unknown reproductive condition. Thus, 87.2% of the stranded females excluding the unknown individuals was sexually mature. Of the 34 sexual mature females, 10 were pregnant (29.4% of the total sexual mature females), 13 lactating (38.2%) and 11 resting animals (32.4%). The sexually mature fe-

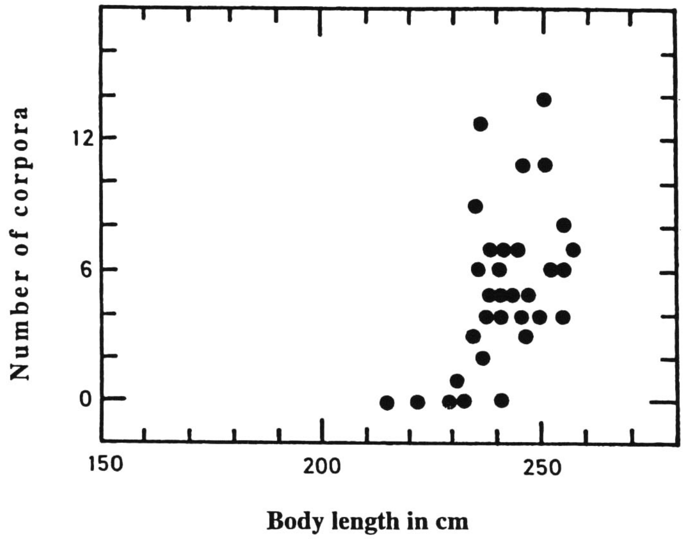

Fig. 16. Relationship between number of corpora and body length of 32 females in *Peponocephala electra*.

males ranged from 11.5 to 44.5 years old and from 231 to 256.5 cm in body length. The oldest and largest sexually immature female was 11.5 years old and 241 cm in body length, respectively, and the youngest and smallest sexual mature female was 11.5 years old and 231 cm, respectively. Thus, females appear to attain sexual maturity at around 11.5 years old and a body length of around 235 cm (Figs. 16–17). The youngest animal in either lactating or pregnant female was 13.5 years old. As the female of 41.5 years old was pregnant, females seem to breed till at least this age, but no post-reproductive female was found.

Comparison of the number of corpora between the left and right ovary in 20 mature females shows that all corpora were in the left ovary in 14 animals (70%), whereas in one animal they were in the right. In the other 5 animals corpora were found in both ovaries. This suggests that in most mature females the left ovary is more functional than the right. The largest number of corpora was 14 for the animal of 34.5 years old. The relationship between the number of corpora and age is shown in a sample of 32 sexually mature females and 2 immature females of 11.5 years, and is expressed by the following least-squares equation: $Y=0.28X-0.83$ ($r=0.62$), where X indicates age in years and Y the number of corpora, and r the correlation coefficient (Fig. 17). Thus, the annual ovulation rate was estimated at 0.28.

Physical maturity

We examined the number of vertebrae and the condition of ossification in the

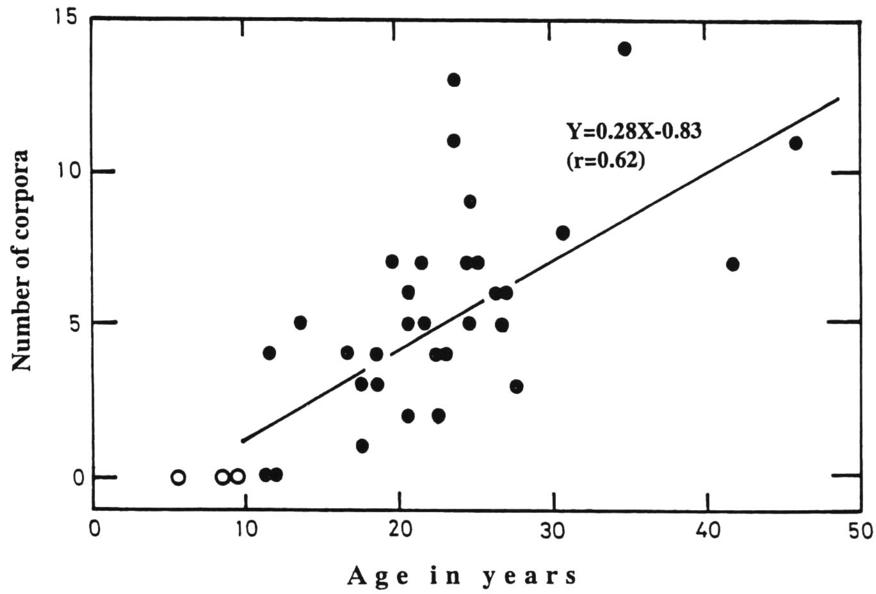

Fig. 17. Relationship between number of corpora and age of 32 mature females (closed circles) and 3 immature ones (open circles) in *Peponocephala electra*. The linear regression line was calculated by the least squares methods during the period from 10.5 years to 45.5 years.

vertebral epiphyses of 19 specimens deposited in the National Science Museum (Miyazaki, 1986). Physical mature males are defined as animals having all epiphyses completely fused. Physically mature animals ranged from 247 to 264 cm in males, and from 231 to 252 cm in females. The oldest physically immature and the youngest physically mature animals were a male of 13.5 (M23739) and a female of 13.5 years old (M23738), respectively. All animals of over 17 years were physically mature. These suggest that the age when 50% of the melon-headed whales attains physical maturity is between 13.5 and 17.5 years old (Table 1).

Internal parasites

During dissection, we examined the parasites around the tympanic cavity of 20 melon-headed whales and counted the number of *Nasitrema gondo* as exactly as possible (Table 1). This species was identified from histological examination by Morimitsu (Morimitsu *et al.*, 1986). *N. gondo* was found in the tympanic cavity of all animals examined, including the youngest one of 2.5 years (M23727). Although the numbers showed a considerable individual variation ranging from 6 to 352, there appears to be a tendency of their numbers increasing with age.

Discussion

Lodi *et al.* (1990) reported that in several mass strandings of *Peponocephala electra* including their own data, the sex ratio (females/males) was approximately 2 : 1. This ratio is different from the figure of 2 : 3 in the mass stranding reported here. The sex ratio in mass-stranded animals is one of the important clues to school composition and might reflect a behavioral segregation of sexes, as suggested by Perryman *et al.*(1994). In the present mass stranding, the sex ratio among the 53 sexually mature animals of over 15 years old was about 1 : 1. The rate of sexual maturity was 87.2% for females and 70% for males. The number of sexually active mature males with a testis of 500 g or more was 18 (72% of mature males), and the number of non-pregnant mature females was 23 (70.6% of mature females). This composition is close to that of a school of *Stenella coeruleoalba* in breeding condition (Miyazaki & Nishiwaki, 1978), suggesting that most of present animals too were in breeding condition.

There are only sporadic data on life history parameters in *P. electra*. The smallest sexually mature female has been reported to be 230 cm long (Mead *et al.* unpublished data cited from Perryman *et al.*, 1994), which is slightly smaller than our smallest sexually mature female of 234.3 cm. Best & Shaughnessy (1981) reported that a male of 248 cm was sexually mature. This falls within the range (244–264 cm) of the possibly sexually mature males in the present study.

On the ventral side of the melon-headed whales studied by us the typical white color was found in the throat chevron, midventral streak and genital patch, with some individual variation in shape and size (Figs. 6–8 and 11). A similar coloration has also been observed in fresh specimens of *Globicephala macroryhnchus*, *Globicephala melas*, *Orcinus orca*, *Pseudorca crassidens*, *Feresa attenuata*, *Grampus griseus* (Sergeant, 1962; Nishiwaki *et al.*, 1965; Mitchell, 1970; Best & Shallowness, 1981). Ontogenetic changes in the coloration of the present melon-headed whales suggest that the black color is not formed in the throat chevron, midventral streak and genital patch in their life.

The proportional dimensions of melon-headed whales change with growth, indicating that the thoracic and caudal regions become relatively larger after birth, whereas in the head this is the reverse. This tendency has commonly been observed in dolphins such as *G. melas* (Sergeant, 1962), *S. coeruleoalba* (Miyazaki, 1972) and *Stenella attenuata* (Perrin, 1975). This change of proportions appears to correspond to the development of capacity for locomotion with growth.

Comparison of the vertebral formula of a melon-headed whale from South Africa (Best & Shallowness; 1981) and the present 19 individuals indicates that the number of vertebrae of the South African animal falls within the range of those of the Japanese animals. Coalescence of the first four cervical vertebrae was found in the specimen from South Africa (Best & Shallowness, 1981), which is different from the fused first three cervical vertebrae in the present sample. As it is well known that coalescence of the cervical vertabrae in small cetaceans shows some individual variation, this difference probably is individual.

Although Perryman *et al.* (1994) reported that there is no indication of sexual dimorphism in overall length of melon-headed whales, judging from the data collected by many scientists, in the present study we did find sexual dimorphism in body length as well as in the following six external characters: (1) length of flipper, (2) shape of dorsal fin, (3) shape of tail flukes, (4) anal girth, (5) development of keel, and (6) shape of the anterior part of the head. In melon-headed whales from South Africa, Best & Shallowness (1981) reported an identical sexual dimorphism in the above characters except head shape. The melon-headed whale shows sexual dimorphism in external appearance as well as in body weight, but not in condylobasal length. The sexual dimorphism observed in *P. electra* is intermediate between that in *Lagenorhynchus obliquidens* regarding the shape of the dorsal fin, but not body length, body weight and condylobasal length (Miyazaki & Shikano, 1997), and that in *G. macrorhynchus* and *O. orca* regarding the shape of the dorsal fin, body length, body weight and skull morphology (Nishiwaki, 1972; Miyazaki, 1983; Kasuya & Matsui, 1984; Matkin & Leatherwood, 1986; Kishiro, *et al.*, 1990; Miyazaki & Amano, 1994).

The factors that may be instrumental in mass strandings have been related to such various factors as coastal configuration, rough weather and sea conditions, chasing by killer whales or large sharks, geomagnetic disturbance, disruption of equilibrium function by parasites, morbillivirus infection, range expansion due to an increasing population, etc. (Geraci, 1978; Sergeant, 1982; Klinowska *et al.*, 1985; Duigman, *et al.*, 1995). As we had no indication of the presence of killer whales or large sharks off Aoshima before the present mass stranding, nor of a severe debilitation of the animals by morbillivirus infection, a significant population increase or the occurence of geomagnetic disturbance, the main cause of the present mass stranding is discussed considering the following three aspects; (1) parasitogenic octavus neuropathy (Morimitsu *et al.*, 1986), (2) concentration of PCBs, DDTs (DDT and its metabolites) and HCHs in the tissues (Tanabe *et al.*, 1983), and (3) coastal configuration and weather and sea conditions (Miyazaki, 1983 a).

As to the first possibility, Morimitsu *et al.* (1986) reported severe damage to the octavus nerve caused by the parasite *N. gondo*, based on examination of the inner ear of one male, and supposed that acute octavus neuropathy could disrupt equilibrium functions in cetaceans and eventually lead to stranding. However, their idea seems to be unconvincing because sample size is small. Still more, even if *N. gondo* were to be found around the inner ear of many stranded animals as was the case in the present school, the parasite would not necessarily be a direct cause of the mass stranding, because *Nasitrema* sp. were found in the most (85.6%) of common dolphins, *Delphinus delphis*, captured in tuna seine nets (Walker & Cowan, 1981) and in 90% or more of

Dall's porpoises, *Phocoenoides dalli*, captured by hand harpoons (Miyazaki, unpublished). Thus, there is no evidence that parasitogenic octavus neuropathy has been a direct cause of the present mass stranding.

Next, we considered the possibility of high concentrations of PCBs (15–19 μg/g), DDTs (22–29 μg/g) and HCHs (0.04–0.19 μg/g) accumulated in the adult males (BL: 247–264 cm) (Tanabe *et al.*, 1983). However, during our investigation we could not find any abnormality in external appearance, internal organs and skeleton, which could have been caused by a morbillivirus infection. In addition to this, the concentrations of PCBs, DDTs and HCHs were very similar to those of free-ranging *S. coeruleoalba* in Japanese waters (Tanabe *et al.*, 1983). Thus, these high concentrations of organochlorine compounds are unlikely to have accounted for the present mass stranding.

As the third possibility, the coastal configuration at Aoshima and the rough weather conditions on 5 January 1982 were considered. According to Director K. Kouno of the Fisheries Research Institute of Miyazaki Prefecture, Aoshima Island shows the following characteristics in coastal configuration: (1) the coast is simple, (2) the coast directly faces the ocean, (3) the coastal area forms a gently sloping beach till 40 m depth at about 30 nautical miles from the coast. In addition to this, 4 January was a day with heavy rain and high waves of weak transparence, and this condition with noise continued during the following day of 5 January. Thus, combined effect of rough weather and/or sea conditions with the shallow coastal configuration might have triggered the present mass stranding of this oceanic species.

Finally, as the other point of view, we should consider the school behavior of small cetaceans. In *S. coeruleoalba*, which used to be driven into the harbor on the east coast of Izu Peninsula, Japan, the senior author often observed the following typical types of behavior during these drive-fishery operations (Miyazaki & Nishiwaki, 1978): (1) when some members of the school became stranded on the coast outside harbor for unknown reason, all the other members followed them in disorder and panic, and (2) when some supposed leaders of the school entered the harbor without becoming stranded on the coast outside harbor, all the other members followed them without trouble. In the former case, although fishermen tried to return them to the sea, the animals were stranded again in apparent panic. Thus, although no definite conclusion can be drawn in the present mass stranding of melon-headed whales, the more realistic possibility would seem that the incidental stranding of one or some animals caused by the rough weather and/or sea conditions with noise and the typical coastal configuration, described above, may have led to panic among the other members of the present school, so that all animals became stranded, widely scattered and in disorder.

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