

DWARF MINKE WHALES: MORPHOLOGY, GROWTH AND LIFE HISTORY BASED ON SAMPLES COLLECTED FROM THE HIGHER LATITUDES IN THE SOUTHERN HEMISPHERE

Hidehiro KATO^{1,2*}, Yoshihiro FUJISE², Gen NAKAMURA¹,
Takashi HAKAMADA², Luis A. PASTENE^{2,3} and Peter B. BEST^{4†}

¹ Tokyo University of Marine Science and Technology, 5-7-1 Konan, Minato-ku, Tokyo 108-8477, Japan

² Institute of Cetacean Research, 4-5 Toyomi-cho, Chuo-ku, Tokyo 104-0055, Japan

³ Project Microbiome as Bioindicators of the Aquatic Ecosystem Health in Chilean Patagonia, Centro de Estudios del Cuaternario de Fuego-Patagonia y Antártica (CEQUA), Punta Arenas, Chile

⁴ Mammal Research Institute, University of Pretoria, c/o Iziko South Africa Museum,
P. O. Box 61, Cape Town, 8000 South Africa

† deceased on April 22, 2015.

*Corresponding author: katohide@kaiyodai.ac.jp

Abstract

This study examined the morphology, growth and life history of dwarf minke whales to identify and confirm any differences from other minke whale species and subspecies. The study was based on biological samples and data obtained from 16 whales (3 males and 13 females) collected through the 1987/88 to 1992/93 austral summer seasons by the Japanese Whale Research Program under Special Permit in the Antarctic (JARPA). The whales were collected between latitudes 58°23'S and 65°04'S in the Antarctic area between 90°E and 180°. Mean body length at physical maturity was estimated to be 7.16 m for females, approximately 1.5 m to 2.0 m smaller than equivalent values of Antarctic minke whales and North Pacific common minke whales. The characteristic feature of a white shoulder/flipper patch was confirmed and some variations in the overall color pattern was found. Skeletal observations confirmed the previously reported characteristic features on the vertex of the skull. In addition, this study found a longer rostrum, deeply curved mandible, and narrower nasal bone in dwarf minke whales in comparison with other minke whales. All pregnant females had conceived in mid-austral winter (middle of June to early August). Females are likely to attain sexual maturation at 6–6.5 m and at around 7–10 years of age. Stomach contents indicated that dwarf minke whales mainly fed on lantern fishes around the Antarctic Convergence in summer. Analyses by ANCOV revealed significant differences in both external body and skull morphology among different species and subspecies. Furthermore, cluster analyses on the skull morphology revealed differentiation between dwarf minke whales and other common minke whales but they are more closely related to North Atlantic common minke whales. These analyses concurred with previous genetic analyses results. The results of this study provided support for the proposed subspecific status of dwarf minke whales.

Key words: dwarf minke whale, diminutive minke whale, minke whale clade, morphology, life history parameters.

Introduction

Early reports suggested the existence of a different form of minke whale from the typical southern

minke whale (now known as the Antarctic minke whale, *Balaenoptera bonaerensis*) in the Southern Hemisphere (Kasuya and Ichihara, 1965; Gaskin, 1976; Wada and Numachi, 1979; Best, 1982; Baker, 1983; Singrajah, 1983). Subsequently, Best (1985) described two morphological forms of southern minke whale as being the ordinary and the small (diminutive) forms based on material collected from both the South African coast and the Antarctic. He also documented differences in shoulder/flipper coloration, type of baleen as well as other differing external morphological features between the two forms: the smaller ('dwarf' or diminutive) and the larger ordinary (*B. bonaerensis*) forms.

Arnold *et al.* (1987) further examined the morphology of the small form of minke whales in the Australian coastal area which he called 'diminutive' minke whales. They conducted some preliminary osteological examination and found some characteristic skull features and distinctive pigmentation which were additional to those reported in Best (1985). However, their sample sizes were too small and geographically restricted to reach any definitive conclusions on their taxonomic status. Subsequently some additional studies were conducted on the Australian diminutive form e.g., Arnold *et al.* (2005).

The Japanese Whale Research Program under Special Permit (JARPA) started in the 1987/88 austral summer season and continued until the 2004/05 season. The target species for the sampling was the southern 'ordinary' minke whale. However, at the end of the first survey in 1987/88, a minke whale, having a noticeably clear white patch on the shoulder (Fig. 1) was sampled on 23 March 1988. Fifteen additional whales with a similar characteristic were sampled in subsequent JARPA surveys until the 1992/93 season. Those whales were associated with the dwarf minke whales reported by Best (1985) and Arnold *et al.* (1987). The total 16 dwarf minke whales were examined by two of the authors (Kato and Fujise) on the deck of the research base vessel. Materials from these dwarf minke whales were first reported by Kato and Fujise (2000), and some of the biological data from their report was used in Perrin and Brownell (2002, 2009) for their description of different types of minke whales.

Wada *et al.* (1991) and Pastene *et al.* (1994) conducted the first genetic analyses of dwarf minke whales sampled by the JARPA, based on mitochondrial DNA. They found substantial differences among southern 'ordinary,' North Pacific and dwarf minke whales. Their phylogenetic analyses suggested that dwarf minke whales were closer to the North Pacific minke whale than to the southern ordinary minke whale. North Atlantic minke whale samples were not available for genetic analysis at that time and the authors recommended additional genetic and non-genetic analyses to elucidate the taxonomy of the minke whale. Based on the genetic and non-genetic studies summarized above and the recompilation of Rice (1998), the Committee of Taxonomy of the Society for Marine Mammalogy (SMM, marinemammalscience.org) listed the following species and subspecies of minke whale:

Antarctic minke whale, *Balaenoptera bonaerensis* Burmeister, 1867 also known as ordinary southern minke whale, Southern Hemisphere minke whale, ordinary form of minke whale, dark shoulder



Fig. 1. A dwarf minke whale (88/89-013) sampled under the JARPA program in the Antarctic, in the 1988/89 season.

form of minke whale.

Common minke whale, *B. acutorostrata* Lacépède, 1804 having three separate subspecies as below:

North Atlantic minke whale, *B. a. acutorostrata* Lacépède, 1804.

North Pacific minke whale, *B. a. scammoni*, Deméré, 1986.

Dwarf minke whale, *B. a. un-named* subsp. [Rice, 1998] also known as diminutive minke whale, dwarf form of minke whale.

More recent genetic analyses using samples of minke whale worldwide provided further evidence for the separation of the two species, and at least three subspecies of the common minke whale using mtDNA sequences (Pastene *et al.*, 2007, 2010) and microsatellite DNA (Glover *et al.*, 2013). These studies indicated that dwarf minke whales are more closely related to the North Atlantic common minke whale (see also relevant sections in Murase *et al.*, 2020).

The biological samples and data of dwarf minke whales taken by the JARPA were further analyzed in the present study following the initial analyses conducted by Kato and Fujise (2000) while it is still a small sample size. The aim of the study is to compare the biological features, including external and skeletal morphologies, with those of other species and sub-species of minke whales in an attempt to elucidate the taxonomic status of the dwarf minke whale. Also, the study provided an opportunity to test the hypothesis derived from recent genetic studies that dwarf minke whales are more closely related to the North Atlantic common minke whale.

Materials and methods

The present paper examined biological features of the dwarf minke whales taken by the Japanese Whale Research Program under Special Permit in the Antarctic (JARPA). Preliminary results of the previous analyses of these samples were presented to the IWC Scientific Committee meeting in 2000 (Kato and Fujise, 2000). The biological features, including external and skeletal morphologies, were compared in the present study with those of other species and sub-species of minke whales in an attempt to elucidate the taxonomic status of the dwarf minke whale.

Biological materials

The present study primarily used biological samples and information collected from the 16 dwarf minke whales (3 males and 13 females) sampled under JARPA through 1987/88 to 1992/93, at which time the dwarf minke whale was not recognized as a different taxon from the Antarctic minke whale, at least at the species level. No dwarf minke whales were sampled after the seasons of 1992/1993. Table 1 summarizes primary biological information used in the present study. The following data were collected onboard the research base vessel according to the field and laboratory protocols provided in Kato *et al.* (1989): body length to the nearest cm, sex, number and length of fetus, testes weight, number of corpora in both ovaries, thickness of blubber, and stomach contents.

Sexual maturity was examined by standard methods based on ovary and testis examination. Females were determined as sexually mature animals by the presence of at least one *corpus albicans* or a *corpus luteum* in both ovaries.

Sexual maturity in males was determined by histological examination of the testis. Tissues were collected from the center of the heavier testis by cutting out a 5 mm square sample. After fixation with 10% neutral buffered formalin solution, the tissues were sliced to a thickness of 3 μ m. Subsequently they were stained by Eosin Hematoxylin solution and examined under a light microscope with 400 \times magnification scale. Taking account of the timing of samplings, which were conducted outside of the likely breeding season, sexual maturity was determined by the presence of spermatids in addition to sperm. If there were neither sperm nor spermatids in the seminiferous tubules, size of the open lumen (minor axis) in the seminiferous tubules was considered, as in other studies for balaenopterids (North

Table 1. Primary biological information of the sixteen dwarf minke whales which were examined in the present study, listed by order of their body lengths.

Sample No.	Body length (m)	Body weight (t)	Sex	Stomach contents*			Foetus Length (cm)	Age and at its transition phase (Tp)**)		Testis wt. (g)		no. ovulation, corpus luteum (CL) and albicans (CA)	Sexual status after present examination	Blubber thickness at lateral side below dorsal fin (cm)	Girth at umbilicus (cm)		
				Type	Volume	Size		no.	Sex	Age	Tp					Left	Right
92/93-108	3.53	0.65	Female	—	0	—	0	1	—	0	0	0	Immature	3.3	92		
90/91-002	3.83	0.7	Female	Eu	1	S	0	1	—	0	0	0	Immature	3.1	114		
89/90-002	4.29	0.85	Female	Fish	1	—	0	3	—	—	—	—	Immature	3	115		
88/89-005	4.45	1	Female	—	0	—	0	—	—	0	0	0	Immature	3.3	126		
88/89-070	5.94	2.25	Female	Fish	1	—	0	7	—	0	0	0	Immature	2.4	150		
90/91-014	6.61	4.3	Female	Fish	1	—	1	F	19	9	10	10	Mature	4.1	204		
90/91-118	6.82	5.05	Female	Fish	1	—	1	F	22	5	6	6	Mature	4.6	214		
88/89-013	6.99	4.2	Female	Fish	1	—	1	M	23	11	—	—	Mature	3.7	203		
88/89-227	7.02	4	Female	Fish	1	—	—	Lost***	10	4	—	—	Mature	5.6	192		
92/93-107	7.04	3.79	Female	—	0	—	1	F	17	9	—	—	Mature	4	178		
89/90-215	7.07	4.55	Female	Fish	2	—	1	M	—	—	1	10	Mature	3.6	196		
92/93-330	7.17	5.5	Female	Fish	1	—	1	F	19	6	4	4	Mature	5.4	214		
90/91-012	7.47	4.45	Female	Fish	1	—	1	M	26	6	13	13	Mature	3.1	189		
89/90-199	5.41	2.05	Male	Fish	1	—	—	—	—	57	53	—	Immature	3.3	153		
88/89-014	6.6	2.95	Male	Fish	2	—	—	10	—	195	182	—	Mature	3.6	165		
87/88-273	7.01	4.66	Male	Fish	1	—	—	21	11	540	530	—	Mature	3.7	201		

*: Recorded according to BIWS (Bureau of International Whaling Statistics) format. Eu: Euphasiids.

** : Tp represents age at sexual maturity.

***: Left ovary and foetus lost by harpoon.

****: Ovaries and foetus partly damaged by harpoon.

Pacific sei whale, Masaki, 1976; Antarctic minke whale, Kato, 1986; Inoue *et al.*, 2014). The measurements on the minor axis of the respective seminiferous tubules using the ocular micrometer were taken by randomly choosing 25 tubules from the respective samples.

Age was determined by counting growth layers on the bisected core surfaces in earplugs under a stereoscopic microscope, as detailed by Lockyer (1984), under the assumption that one growth layer (a pair of pale and dark laminae) was deposited per year, as well as establishing the position of a transition phase in the earplug (Locker, 1972; Kato, 1985).

In addition, external measurements (76 points), were obtained according to the protocol of Kato *et al.* (1992), and comparison of sexually mature individuals was carried out among 10 dwarf minke, 704 Antarctic minke and 161 North Pacific common minke whales (from the ICR data base for JARPA and the Japanese Whale Research Program under Special Permit in the North Pacific (JARPN)).

Skeletal measurements were compared among dwarf, Antarctic minke and North Pacific common minke whales. Skeletal measurements (21 points) from eight dwarf minke whales and five Antarctic minke whales were made based on the protocol of Omura (1975). For North Pacific common minke whales, skeletal measurements from Nakamura (2012), which followed the same principal method of Omura (1975), were used.

To compare biological aspects of the dwarf minke whales with other minke whale species and sub-species, published biological information with equivalent quality was used. Details are given in the relevant sections.

Sighting information of sampled whales

While sighting information was available from 1987/88 onwards under the JARPA program, for the present study, only sightings of the dwarf minke whales sampled from 1987/88 to 1992/93 were used. All dwarf minke whales sighted and recorded during the shipboard surveys were identified from their characteristic white shoulder/flipper patches, which could be easily observed during closing mode surveys (also see Kato *et al.*, *in press*).

Table 2. Sighting information of the dwarf minke whales used in the present study.

Year/Month/ Date sighted	School ID no.	Sighting time	Location						School size	Estimated B.L. at sea	Sample no.
			Latitude			Longitude					
1988/3/23	5002	14.47	58	23	S	111	26	E	2	6.8, 6.0	87/88-273
1989/1/13	8014	14.24	55	22	S	178	10	E	1	5.5	88/89-005
1989/1/17	5001	10.27	62	4	S	177	28	E	1	6.2	88/89-013
1989/1/17	8003	11.42	62	7	S	177	2	E	1	6.1	88/89-014
1989/2/4	5004	8.43	60	38	S	175	7	E	1	5.0	88/89-070
1989/3/19	1001	8.13	61	54	S	177	55	E	1	6.0	88/89-227
1989/12/6	8004	17.24	55	59	S	97	17	E	1	5.0	89/90-002
1990/1/12	1001	7.4	61	30	S	128	6	E	1	6.0	89/90-199
1990/1/15	1002	9.41	60	59	S	116	6	E	1	8.3	89/90-215
1990/12/29	1001	6.16	65	4	S	178	12	E	1	4.5	90/91-002
1991/1/3	1001	8.13	61	9	S	175	21	W	1	7.0	90/91-012
1991/1/3	5003	11.5	60	40	S	176	34	W	1	8.5	90/91-014
1991/1/26	8001	9.08	60	34	S	146	49	E	1	7.5	90/91-118
1993/1/10	1004	18.00	60	51	S	167	42	E	1	6.5	92/93-107
1993/1/11	8001	15.02	60	31	S	166	5	E	1	3.0	92/93-108
1993/3/22	8003	15.28	61	49	S	143	16	E	1	6.5	92/93-330

Results

Sighting position of sampled whales

Table 2 indicates relevant sighting information regarding the dwarf minke whales sampled during the present study.

Fig. 2 plots the 16 dwarf minke whales sampled based on locations of their sightings during the JARPA surveys from 1987/88 to 1992/93, and by reproductive category. No specific difference in location between reproductive categories was observed. In the longitudinal sector, searched between 97°17'E and 173°33'W, dwarf minke whales occurred from 48°42' to 65°04'S. Most animals (75%; n=12 animals) were seen around latitudes 60° to 62°S, but it should be noted that there was limited sighting effort north of 60°S. Therefore, this result does not necessarily mean they were rare north of 60°S. Rather, these records should be interpreted to represent the likely southern limit for dwarf minke whale distribution in summer. Within the area surveyed there were three regions of relatively high concentration: 125°–128°E, 141°–146°E, and 177°–179°E at 60–62°S. These areas were located off the concaved continental coastlines of Antarctica such as the Ross Sea.

In terms of segregation from Antarctic minke whales, it is noticeable that dwarf minke whales were distributed in more northern waters than the Antarctic minke whales in summer (Fig. 1). Sightings of Antarctic minke whales by JARPA surveys from the early 1990s to the present were distributed south of 60°S with their density much higher from 63°S to the ice edge zone (e.g., Hakamada *et al.*, 2005).

Throughout the surveys of the IDCR/SOWER¹ programmes, a total of 54 dwarf minke whales, comprised of two pairs and 50 singletons, were sighted (Kato *et al.*, in press). These sightings were only 0.13% of the total number of Antarctic minke whale (*B. bonaerensis*) sightings (41,854 individuals) made during the same searching effort.

Body size and growth

As summarized in Table 1, the 16 dwarf minke whales collected from 1987/88 to 1992/93 comprised three males and 13 females. The smallest (3.53 m) and largest (7.47 m) individuals were both females. Of the three males, two were sexually mature and their mean body length was 6.81 m. Of the

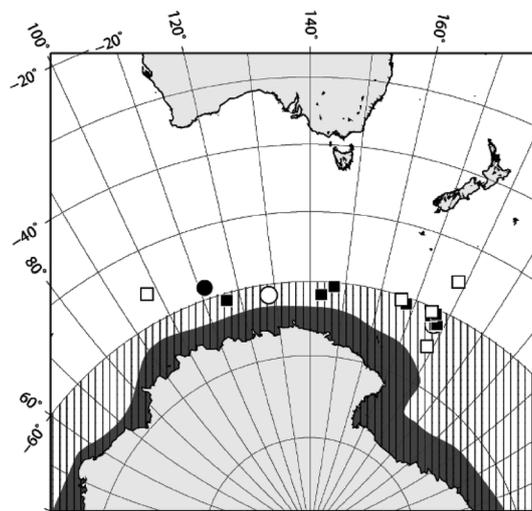


Fig. 2. Sighting locations of the dwarf minke whales sampled during JARPA surveys from 1987/88 to 1992/93 and showing the approximate range of Antarctic minke whale in summer (hatched, with darker area indicating higher sighting density). Immature male (○), mature male (●), immature female (□), mature female (■).

¹International Whaling Commission International Decade for Cetacean Research (IDCR), Southern Ocean Whale and Ecosystem Research (SOWER).

13 females, eight individuals were sexually mature with a mean body length of 7.02 m (SD: 0.249).

Of the 16 animals, the age was successfully determined for 13 (two males and 11 females). Resultant age readabilities were 0.67 (2/3) and 0.85 (11/13) for males and females, respectively. The mean growth curve of the dwarf minke whales together with that of Antarctic minke whales (Zenitani *et al.*, 1997) and North Pacific common minke whales (Maeda, 2012) are shown in Fig. 3 for both sexes. Female dwarf minke whales appeared to grow to 3.5–3.7 m at age one and then rapidly reach 6 m at age 10, with an asymptote at around 7.0 m (or slightly more) in body length at about age 20.

Fitting the von Bertalanffy growth model to the available data produced the following formula for female dwarf minke whales:

$$Lt = 7.16(1 - e^{(-0.19(t+2.69))}) \tag{1}$$

where Lt is body length in meters at age (t).

If the asymptotic length from the equation is taken as a proxy for the mean body length at physical maturity, then an interim value of 7.16 m for female dwarf minke whales is obtained. Allowing for possible errors due to the characteristics of the growth formulae used here and the limitations of the data (especially small sample size among older animals), a comparison with Antarctic minke whales (Zenitani *et al.*, 1997; Bando *et al.*, 2006) and North Pacific common minke whales (Maeda, 2012) was carried out using von Bertalanffy growth formulae as below:

$$Lt = 9.16(1 - e^{(-0.23(t+2.13)}) \text{ Antarctic minke whale - Female} \tag{2}$$

$$Lt = 8.61(1 - e^{(-0.27(t+2.00)}) \text{ Antarctic minke whale - Male} \tag{3}$$

$$Lt = 8.66(1 - e^{(-0.11(t+7.60)}) \text{ North Pacific common minke whale - Female} \tag{4}$$

$$Lt = 7.49(1 - e^{(-0.41(t+0.90)}) \text{ North Pacific common minke whale - Male} \tag{5}$$

From the above equations as well as from Fig. 3, it is concluded that dwarf minke whales are significantly smaller in body length at least in females than both Antarctic minke whales and North Pacific common minke whales throughout all age classes. The mean asymptotic lengths estimated from the growth formulae above indicated that fully grown female dwarf minkes were about 2.0 m shorter than Antarctic minke whales (Zenitani *et al.*, 1997; Bando *et al.*, 2006) and about 1.5 m shorter than North Pacific common minke whales (Maeda, 2012). Thus far, under the present analysis, those differences were statistically significant (t-test; $p < 0.001$).

Due to the small sample size in all age classes, it was not possible to estimate the mean asymptotic

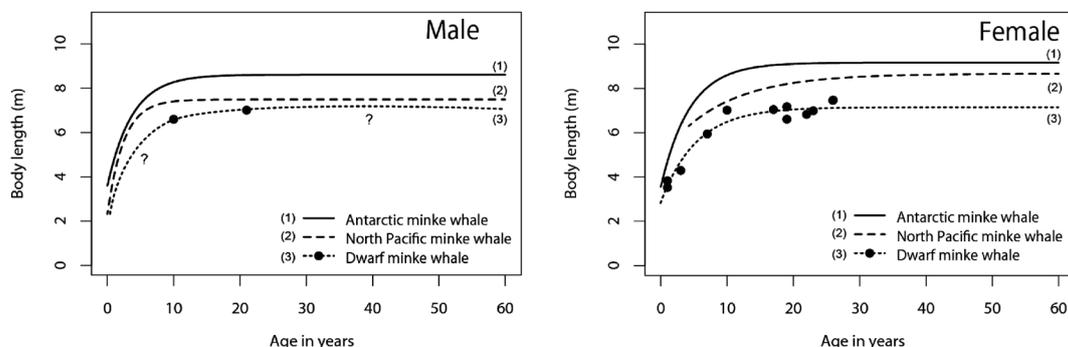


Fig. 3. Plots of body length at age and growth curves of dwarf minke whales by sex (closed circle, dotted line), in comparison with mean growth curves (length at age) of Antarctic minke whales (solid line) from Zenitani *et al.* (1997) and of North Pacific common minke whales (broken line) from Maeda (2012). All the resultant growth curves were fitted by the von Bertalanffy growth formulae.

length or the length at physical maturity of males under the present study.

Under such limitation of the data, an attempt was made to obtain the range of body length at physical maturity for males by using values from other minke whales. The ratios of asymptotic body length of males to those of females are 0.94 (8.61/9.16 m) and 0.86 (7.49/8.66 m) in the Antarctic minke whales and the North Pacific common minke whales, respectively. These ratios were applied to the dwarf minke whales using the value for females (7.16 m), and the values of 6.73 m and 6.16 m were obtained from the Antarctic minke whales and the North Pacific common minke whales, respectively. It is considered inappropriate to narrow down these values further given the limitations of the data. Thus, mean body length at physical maturity for males in the dwarf minke whales is likely to be around 6.2–6.7 m.

Body length-weight relationship

Two male and 13 female dwarf minke whales were weighed both before and after flensing (Table 3). Whole body weights before flensing varied from 0.650 tons (3.53 m) to 5.50 tons (7.47 m). For females, the relationship was examined by fitting an exponential regression of whole-body weight on body length, as follows:

$$W = 0.01235L^{3.007} \quad (r = 0.9922, n = 13) \quad (6)$$

where W is whole-body weight in tons and L is body length in meters.

The slope of the regression provides an indication of the relative fatness of the animal shape. The body weight-length relationship for female Antarctic minke whales (Fujise *et al.*, unpublished), obtained through the same procedure as the present study using whole body weight during the feeding season, was as follows:

$$W = 0.019304L^{2.792} \quad (r = 0.9741, n = 1,113) \quad (7)$$

The coefficient for the slope (2.792) was significantly smaller than that for dwarf minke whales

Table 3. Body weights of dwarf minke whales by weighing their whole body before flensing and in parts after flensing.

Sample No.	Body length (m)	Body weight* (t)	Sex	Foetus number	Blubber**		Muscle**		Bone**		Viscera**		Other**		Total**	
					(kg)	(%)	(kg)	(%)	(kg)	(%)	(kg)	(%)	(kg)	(%)	(kg)	(%)
92/93-108	3.53	0.65	F	None	146	26.3	234	42.4	94	17.0	72	13.0	7	1.3	552	100
90/91-002	3.83	0.70	F	None	174	25.7	333	49.3	92	13.7	68	10.0	9	1.3	676	100
89/90-002	4.29	0.85	F	None	212	25.8	391	47.4	112	13.7	90	11.0	17	2.1	823	100
88/89-005	4.45	1.00	F	None	225	21.2	599	56.6	133	12.6	91	8.6	10	0.9	1,057	100
88/89-070	5.94	2.25	F	None	401	19.1	1,264	60.2	277	13.2	150	7.1	6	0.3	2,098	100
90/91-014	6.61	4.30	F	1	967	23.0	2,350	55.9	447	10.6	392	9.3	45	1.1	4,201	100
90/91-118	6.82	5.05	F	1	1,054	21.7	2,816	58.0	463	9.5	495	10.2	30	0.6	4,857	100
88/89-013	6.99	4.20	F	1	950	21.9	2,505	57.8	403	9.3	401	9.3	73	1.7	4,331	100
88/89-227	7.02	4.00	F	Lost	984	24.9	2,278	57.7	411	10.4	263	6.7	13	0.3	3,948	100
92/93-107	7.04	3.79	F	1	834	22.5	2,142	57.8	435	11.8	284	7.7	10	0.3	3,705	100
89/90-215	7.07	4.55	F	1	975	22.0	2,452	55.2	478	10.8	454	10.2	84	1.9	4,442	100
92/93-330	7.17	5.50	F	1	1,149	21.3	3,073	56.9	511	9.5	517	9.6	148	2.7	5,397	100
90/91-012	7.47	4.45	F	1	957	21.9	2,378	54.4	562	12.9	409	9.4	62	1.4	4,368	100
89/90-199	5.41	2.05	M		399	20.4	1,156	59.2	211	10.8	165	8.4	22	1.1	1,952	100
88/89-014	6.60	2.95	M		662	22.6	1,652	56.5	327	11.2	234	8.0	47	1.6	2,922	100
87/88-273	7.01	—	M		960	20.5	2,897	61.9	495	10.6	306	6.5	26	0.5	4,684	100

*: Whole body weighted using a large scale before flensing.

** : Percentage figures are the proportions to the sums of all parts after flensing.

(3.007), which suggests that dwarf minke whales tended to be stockier than other minke whale types, despite both being sampled at the peak of their feeding seasons. This is also endorsed by nature in Fig. 6, which indicates proportion to body length of the dwarf minke whales is higher than of other minkes at the measurement point P17 of girth at umbilicus.

The proportion of the sum of parts to the whole-body weight before flensing ranged from 0.851 to 1.058² with a mean of 0.973, indicating an average of only 2.7% weight loss during flensing. Muscle occupies almost half or more of the sum of parts (mean: 54.58%), with the proportion being higher in the larger animals, while the proportions of blubber (mean: 22.87%) and bone (mean: 11.92%) were higher among the smaller animals.

Morphology

External appearance in terms of discriminating the dwarf minke whale from other species and subspecies of minke whales

Previous authors have reported that dwarf minke whales have distinctive external characteristics, primarily a white shoulder patch. This distinguishes dwarf minke whales from all other types of minke whales at sea (Best, 1985; Arnold *et al.*, 1987, Kato and Fujise, 2000). Additional features have been described for dwarf minke whales such as the dark throat patch and a thorax blaze (Arnold *et al.*, 2005).

From field examinations during this study, the following three points by which dwarf minke whales can be easily distinguished from other types of minke whales were identified (Fig. 4A and additional images given in Fig. 4B):

Characteristic (a): A dark throat patch usually extends ventrally as a peninsula of pigmentation on

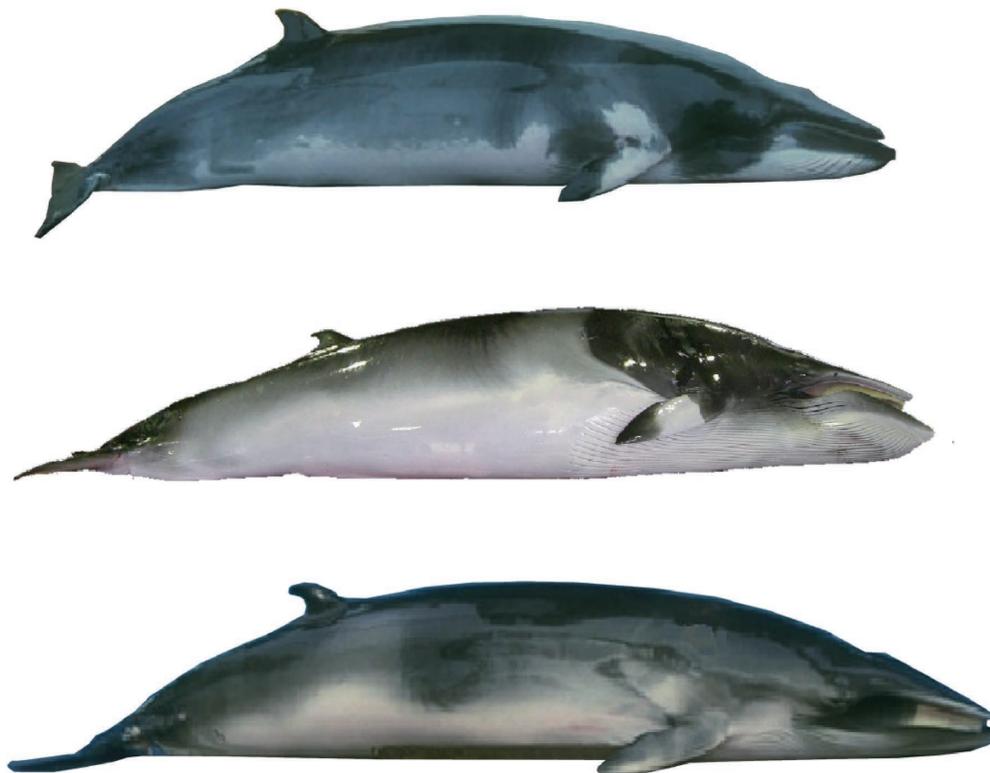


Fig. 4A. Lateral views of different types of minke whales scaled down to the same size; **upper**: dwarf minke whale (DWM); **middle**: North Pacific common minke whale (NPM); **bottom**: Antarctic minke whale (ATM). Alphabetical symbols in the upper picture correspond to the explanation of characteristics above.

²It is unlikely that the value exceeds 1.0, which may be due to logistic errors during the measurement.

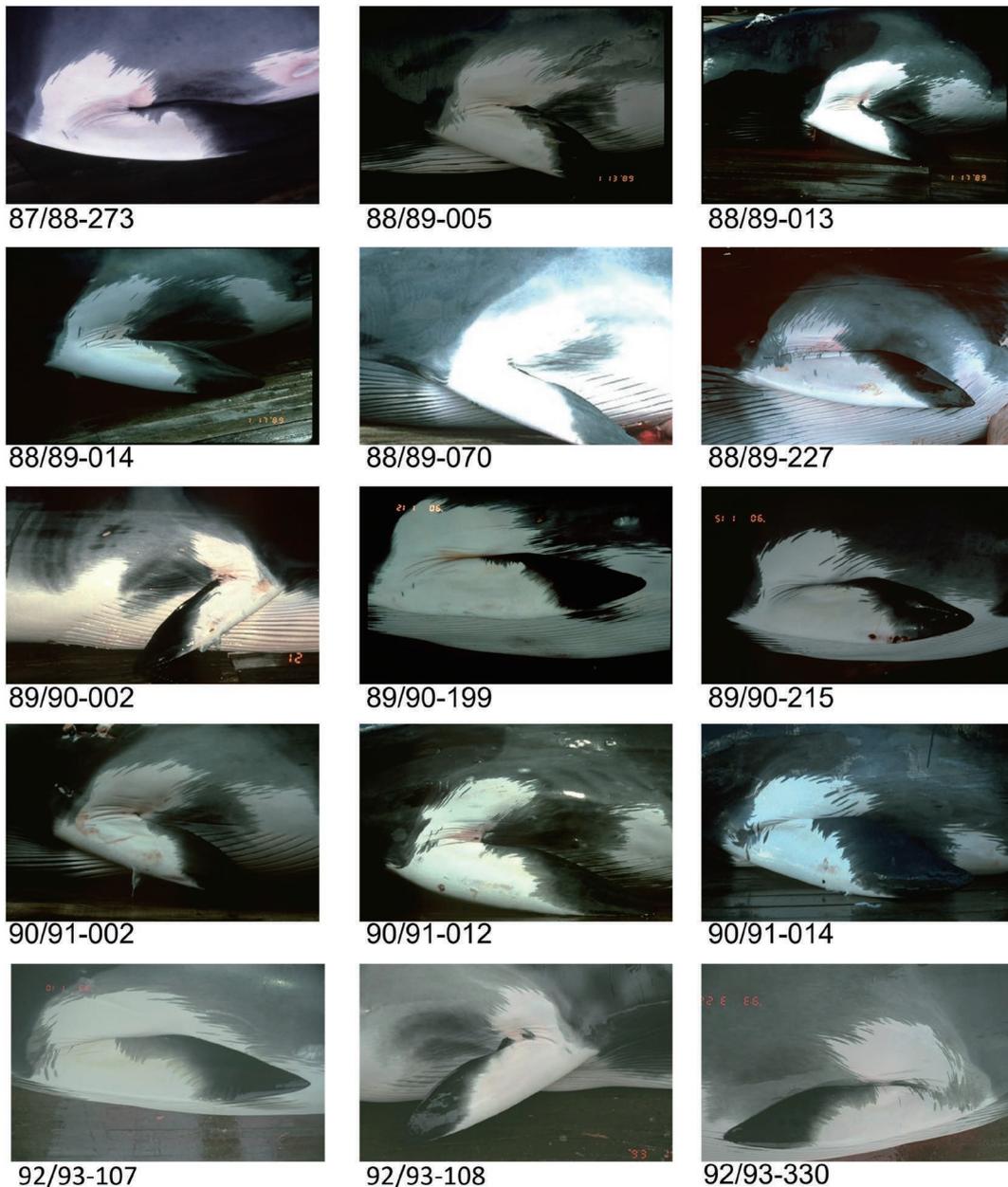


Fig. 4B. Variation of shoulder/flipper coloration on the body surface for 15 of the 16 dwarf minke whales examined in the present study. No photography was taken of 90/91–118 (see also Table 2).

the ventral grooves restricted to the region between the flipper insertion and the angle of the gape. In the samples for the present study, this dark patch was symmetrically arranged on both sides.

Characteristic (b): Fig. 4B shows the variation in shoulder/flipper pigmentation among the 16 specimens. Best (1985) reported that dwarf minke whales have an entire white patch on the shoulder/flipper regions. On the other hand, Arnold *et al.* (1987) found an elongated dark oval patch within it and hidden when the flipper is held against the body, which they called the “flipper oval.” However, there is much variation in this pattern as illustrated in Fig. 4B. The flipper ovals certainly existed in their approximate position in all specimens, but the ‘arch like white bands’ surrounding the dorsal margin of the flipper oval were sometimes incomplete so that the white patch on the shoulder region was cut into two in all but one case. Only one animal (90/91–118) had a complete white patch above the flipper oval on the shoulder region. Unfortunately, no photograph was available in Fig. 4B for this animal.

Characteristic (c): The thorax blaze/patches were principally located above the white patch on the

flippers, usually in a somewhat triangular shape. As in Fig. 4B, there were some variations in the pattern of connection between the flipper oval and the thorax blaze/patches being totally connected or separated by splashed pigmentations.

The present study confirmed the three characteristics noted above as consistent keys to distinguishing dwarf minke whales from other minke whales (Fig. 4A). In addition, the present samples provided some additional information on blowhole streaks, which Best (1985) reported in a small dwarf minke whale (about 4m) from South Africa but were not seen in any dwarf minke whales off Australia (Arnold *et al.*, 1987, 2005). In the specimens examined in the present study, the blowhole streaks were absent or obscure. However, all of the six fetuses larger than 98.6 cm listed in Table 1 had very distinctive parallel streaks in the posterior region of the blowhole. This may indicate changes in coloration with respect to age that is more distinct in younger stages, or possibly more visible in living animals or when underwater (Arnold *et al.*, 2005).

Baleen plate coloration

Fig. 5 (A and B) shows a typical baleen plate coloration of dwarf minke whales, which was shared by all the specimens in the present study. As both Best (1985) and Arnold *et al.* (1987) noted, the outside view of the baleen plate series is two-tone, being creamy white anteriorly and dark gray or brown posteriorly. The darker coloration in the posterior portion of the series is due to a thin dark outer border of the plates. As in Fig. 5(B), this baleen plate coloration is different from the other minke whales. The external view of the baleen plate series of Antarctic minke whales is predominantly black on the left side and creamy white in 1/3 of the anterior portion and black in 2/3 of the posterior portion on the right side while it is usually entirely creamy white for North Pacific common minke whales (though there are rare cases where animals have plates with a thin dark outer border in the posterior parts of the series). Thus, it is evident that the dark outer border is much wider in Antarctic minke whales than in dwarf minke whales (Best, 1985).

Kato *et al.* (1992) suggested that the occurrence of a dark outer border to the baleen had some growth-specific nature in North Pacific common minke whales, therefore the proportion of anterior creamy white plates and posterior black outer margined plate in dwarf minke whales was examined. According to similar statistics (Table 4), the length of the creamy white portion varied from 24 to 115 cm (mean: 67.29, SD: 21.15) and 28–94 cm (mean: 63.21, SD: 16.98) on right and left sides respectively, or 31–85% (mean 53, SD: 13) and 36–85% (mean: 50, SD: 12) of the total length of the baleen plate series, respectively. The ratio of right side to the left side was 1.06 (SD: 0.13), thus the creamy white portion of the right side was slightly longer than that of the left, but not significantly so. As to growth specific changes in proportion of the plates having black outer margin, the samples were not clear enough for detecting such nature.

In summary, the external view of a baleen plate series of dwarf minke whales is mostly bilaterally symmetrical in coloration with a creamy white anterior portion that extends for almost half of the en-

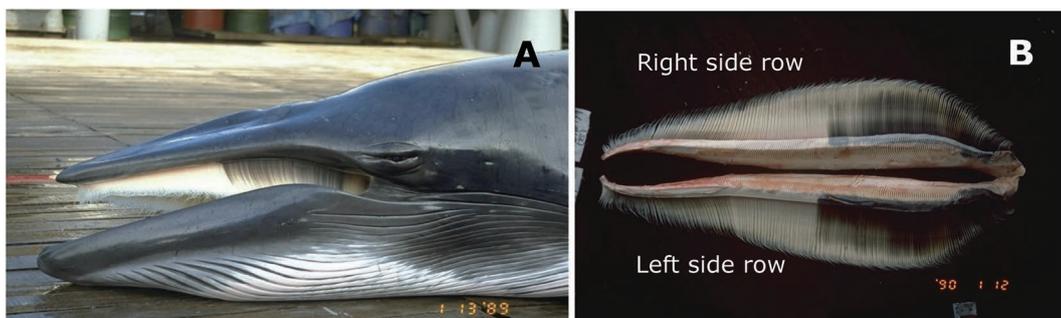


Fig. 5. **A:** Lateral view of left side of dwarf minke whale head showing baleen plates exposed in its slightly opened mouth. **B:** Labial view of the baleen plate series removed from both sides of the upper jaw.

Table 4. Baleen plate series of the dwarf minke whales having measured data, especially the proportion of baleen series of the plate with creamy white coloured outer margin to the total length of baleen. See also Fig. 5B.

Sample no.	Sampling date	Body length (cm)	Sex	Baleen plate series, length (cm) at outer margin						% of Right side of creamy white margin R (w/t)/L (w/t)
				Right side series			Left side series			
				Total	creamy white	R (w/t)*	Total	creamy white	L (w/t)*	
87/88-273	1988/3/23	701	Male	145	72	0.50	142	72	0.51	0.98
88/89-005	1989/1/13	445	Female	88	41	0.47	89	37	0.42	1.12
88/89-013	1989/1/17	699	Female	147	65	0.44	148	78	0.53	0.84
88/89-014	1989/1/17	66	Male	134	45	0.34	130	48	0.37	0.91
88/89-070	1989/2/4	594	Female	118	73	0.62	118	71	0.60	1.03
88/89-227	1989/3/19	702	Female	148	79	0.53	148	71	0.48	1.11
89/90-002	1989/12/6	429	Female	86	73	0.85	86	73	0.85	1.00
89/90-199	1990/1/12	541	Male	112	60	0.54	112	59	0.53	1.02
89/90-215	1990/1/15	707	Female	152	86	0.57	152	76	0.50	1.13
90/91-002	1990/12/29	383	Female	77	24	0.31	78	28	0.36	0.87
90/91-012	1991/1/3	747	Female	163	115	0.71	166	94	0.57	1.25
90/91-014	1991/1/3	661	Female	142	83	0.58	141	70	0.50	1.18
92/93-118	1991/1/26	682	Female	139	65	0.47	139	51	0.37	1.27
92/93-107	1993/1/10	704	Female	135	61	0.45	135	57	0.42	1.07
				Mean	67.29	0.53		63.21	0.50	1.06
				S.D.	21.15	0.13	S.D.	16.98	0.12	0.13

*: Proportion of creamy white length per total length of baleen plate row in each side.

ture length of the baleen plates. With this characteristic, they differ from both Antarctic minke whales (bilaterally asymmetric baleen coloration) and North Pacific common minke whales (usually all creamy white baleen). In comparison, dwarf minke whales have an intermediate coloration.

External body proportion

Prior to the statistical analyses, the general characteristics of the external body proportions of dwarf minke whales were examined in comparison with Antarctic minke whales (n=507) and North Pacific common minke whales (n=91). Fig. 6 shows the body proportions (expressed as a percentage of the body length from tip of snout to notch of tail flukes) for dwarf minke whales, Antarctic minke whales and North Pacific common minke whales. The rostrum of the dwarf minke whale is elongated in a V shape, typical of minke whales. On average the head (P19) comprised 22.90% (min. 21.20–max. 24.10) of the body length. The average length from the tip of snout to the center of the blowhole (P2) comprised 14.50% (12.80–15.60); to the center of the eye (P3) 17.60% (15.50–17.60); and to the external auditory meatus (P4) 22.70% (20.20–24.10) of the body length. The average length from the tip of snout to the posterior end of the ventral grooves (P6) comprised 51.00% (49.10–53.10), to the umbilicus (P7) 54.90% (53.10–56.00), the center of the genital aperture (P8) 71.00% (67.00–72.60), and to the anus (P9) 74.80% (73.80–75.70) of the body length.

The pectoral fin is also an elongated oval shape with tapering tip typical of balaenopterids and its length (P12, tip to anterior insertion) and breadth (P14) were 16.10% (15.00–17.50) and 4.10% (3.60–4.30), respectively. The dorsal fin is falcate with a tapering tip of which the height (P11) was 4.30% (3.30–4.30). The tail flukes are leaf-like in shape with a rather straight posterior margin and tapering tips at both ends, while their width (P16) was relatively broad at 28.10% (24.90–31.10) and depth (P15) was 7.00% (6.40–7.50).

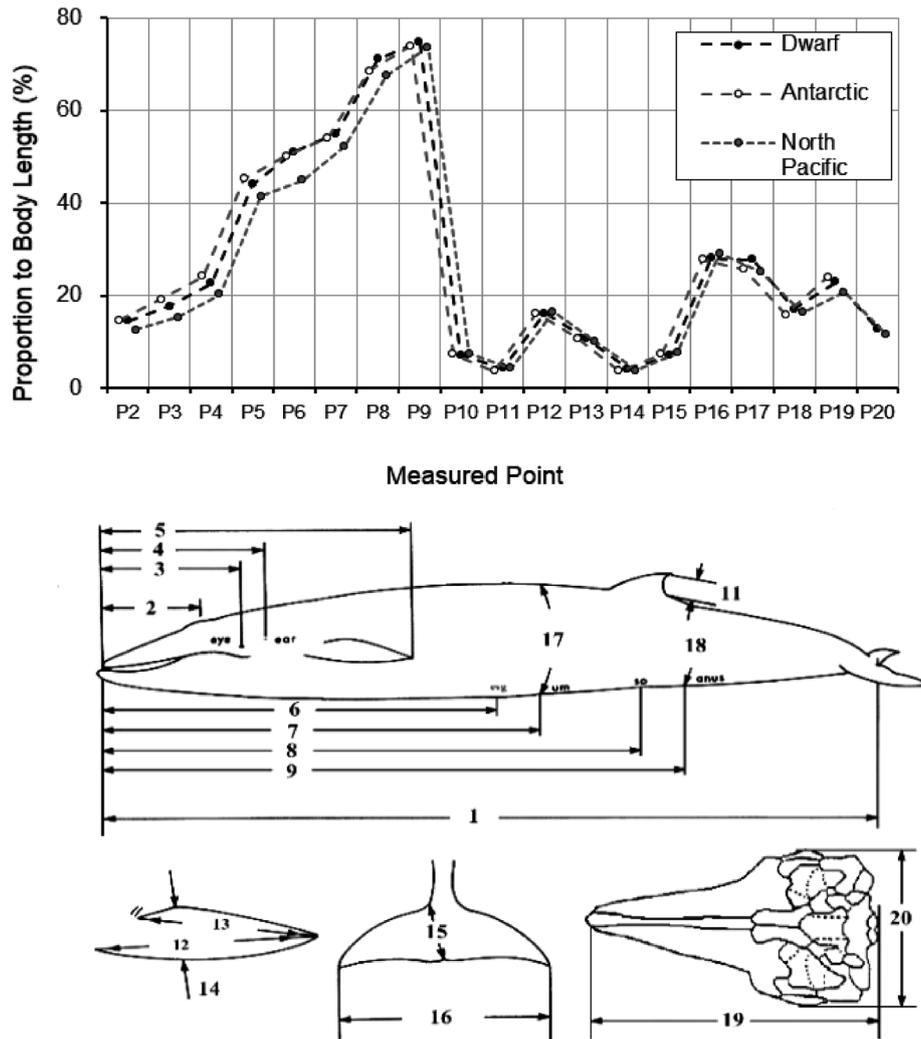


Fig. 6. Mean external measurements (P2–P20) of sexually mature dwarf (closed circle), Antarctic (open circle) and North Pacific minke whales (gray colored circle), expressed as respective proportion to the body length. Abbreviations of respective measurement points correspond to the numbered locations in the illustration.

All the body proportion measurements in the anterior half of the body were highest for Antarctic minke whales and lowest for North Pacific common minke whales, with dwarf minke whales being intermediate between the two but somewhat closer to Antarctic minke whales. On the other hand, the relative proportions of the appendages were remarkably close to each other among the three types of minke whales. Those aspects are further examined by statistical analyses in the later section.

Skeletal features

Skeletal observations were taken from all 16 animals collected, but data from eight sexually mature animals were to be the base for the present analyses especially on skull, to minimize possible growth dependent changes. Those observations were appropriately compared and verified with other type of minke whales in some cases.

1. Skull

Firstly, before the statistical analyses, general aspects of the skeleton are presented in this section. See also details of the skeleton in Appendix 1.

Fig. 7 shows the dorsal view of the skull of a dwarf minke whale as compared to those of North Pacific common minke whales and Antarctic minke whales. The diagnostic differences in skull mor-

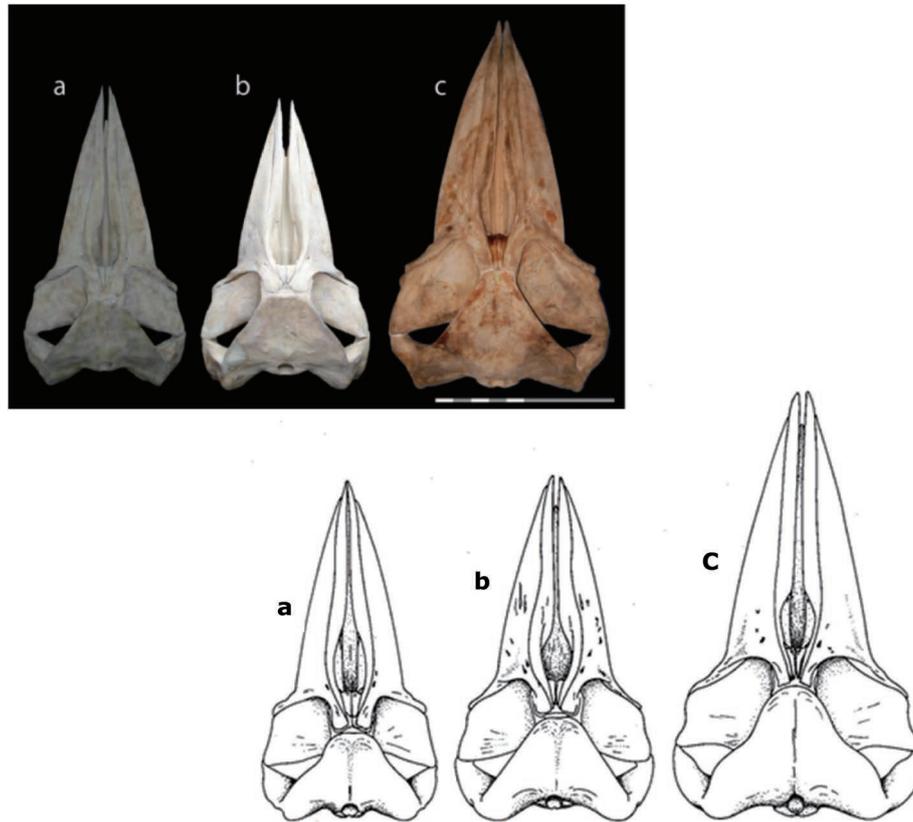


Fig. 7. Dorsal view of skulls by photographing (upper) and corresponding contour drawings (bottom) of the dwarf (**a**: 87/88-273), the North Pacific (**b**: 08NPCK-M030) and the Antarctic minke whale (**c**: 93/94-AM287) showing the principal differences in morphology among the three different types of minke whales of which were fully grown animals. The attached bar on the photos is 1.0 m long with a 10 cm scale interval.

phology can be seen among them. As an example of the skeletal specimens, multidimensional views of the entire skeleton, including skull and other skeletal parts of a male dwarf minke whale of 7.10 m in body length registered as specimen MTUM-DW273, are shown in Appendix 1. Details of the skull measurements are given in Appendix 2.

The vertex of the skull is considered an important taxonomic trait. A distinct interparietal bone was present in dwarf minke whales (Arnold *et al.*, 1987; Kato and Fujise, 2000). This characteristic has been identified in North Pacific common minke whales and in Antarctic minke whales (Nakamura, 2012). Further, the presence of the interparietal in the vertex has also been identified in North Atlantic minke whales (Fig. 8). In dwarf minke whales, the posterior end of the nasal bone and the posterior end of the premaxilla are more extended toward the vertex compared with those of North Pacific common minke whales. As a result, the nasal bone of dwarf minke whales is more elongated than in North Pacific common minke whales, resulting in a significantly larger ratio of the length of the nasal bone relative to the anterior width of the nasal bone. In dwarf minke whales, proportional length of maxilla and premaxilla to the skull were significantly larger than those in North Pacific common minke whales. On the other hand, the width of the orbit, width and height of the occipital condyle, and the length and width of the palatine relative to the skull length were all smaller than in North Pacific common minke whales.

In terms of absolute measurement values, the maximum length and maximum width of the tympanic bullae of dwarf minke whales (7.9 ± 0.3 cm and 6.1 ± 0.2 cm, respectively) were approximately 10% smaller than in North Pacific common minke whales (9.0 ± 0.4 cm and 6.9 ± 0.3 cm, respectively) and Antarctic minke whales (9.2 ± 0.6 cm and 7.1 ± 0.3 cm, respectively), whereas their maximum width was close to North Atlantic common minke whales (8.2 ± 0.2 cm).

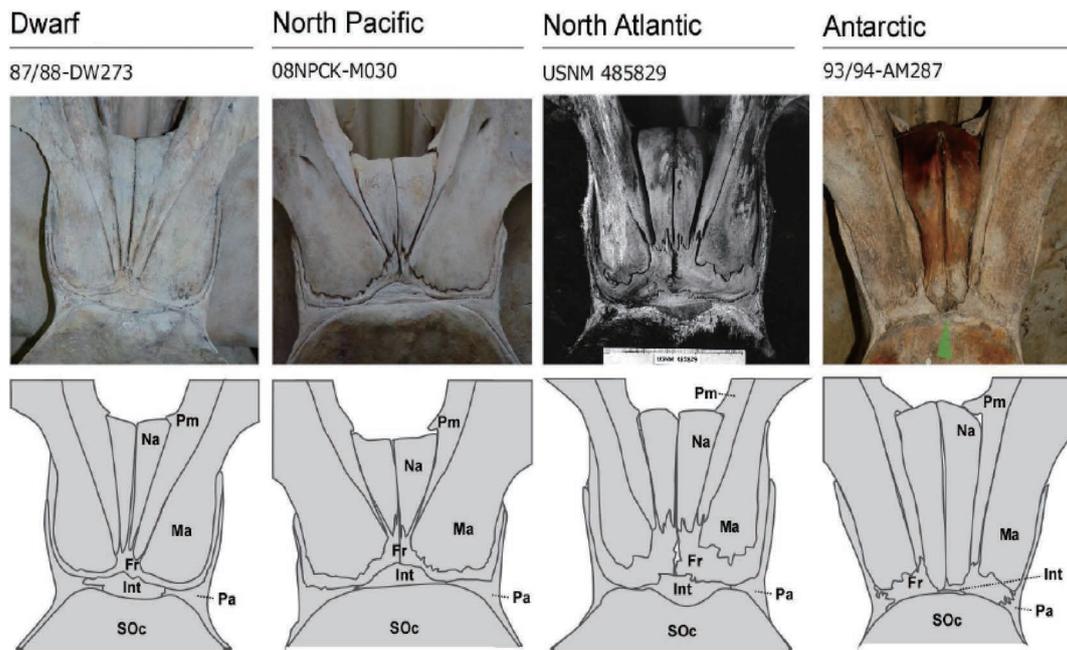


Fig. 8. Morphological comparison of the vertex region on the skulls among dwarf, North Pacific, North Atlantic common minke whales and the Antarctic minke whales. Abbreviations represent: **Fr**, frontal; **Int**, interparietal; **Ma**, ascending process of maxilla; **Na**, nasal; **Pa**, parietal; **Pm**, premaxilla.



Fig. 9. Lateral view of mounted complete skeleton of the dwarf minke whale (museum specimen No. MTUM DW273; field sample ID No. 87/88-273). The specimen was mounted under supervision by Kato and is displayed at the Museum of Marine Science, Tokyo University of Marine Science and Technology, Tokyo.

An entire lateral view of the dwarf minke whale skeleton (87/88-273) is shown in Fig. 9.

2. Vertebral number

The total number of vertebrae in the dwarf minke whales examined ranged from 47 to 50 with a mean of 48.6 (SD: 0.9). The ranges were 47–51 with a mean of 49 (SD: 0.9) and 47–51 with a mean of 48.8 (SD: 0.80) in Antarctic minke whales and North Pacific common minke whales, respectively. Thus, the total number of vertebrae is virtually identical in all three minke whale species or sub-species (Table 5).

The vertebral formula for the dwarf minke whale was $C7+D10-11+L11-14+Ca18-20=47-50$, and for the mean values $C7+D10.6+L11.7+Ca19.2=48.6$ (SD: 0.9). Again, this formation is the same, or within the known range, to those of other minke whale species and sub-species.

Table 5. Mean and range of number of vertebrae in each section of the vertebral column by different type of minke whales.

	Dwarf (n=16)	Antarctic (n=42)	North Pacific (n=200)	North Atlantic (n=1)
Cervical (C)				
Mean	7	7	7	7
SD	0	0	0	0
Range	7	7	7	7
Dorsal (D)				
Mean	10.6	10.7	10.5	11
SD	0.5	0.5	0.5	0
Range	10–11	10–12	10–11	11
Lumbar (L)				
Mean	11.7	11.8	12.1	12
SD	0.9	0.8	0.6	0
Range	11–14	10–14	11–13	12
Caudal (Ca)				
Mean	19.2	19.4	19.3	18
SD	0.8	0.9	0.8	0
Range	18–20	17–22	17–23	18
Total				
Mean	48.6	49.0	48.8	48
SD	0.9	0.9	0.8	0
Range	47–50	47–51	47–51	48

3. Number of ribs

For the dwarf minke whales examined, the ribs are relatively thin and broad, and their numbers are 10–11 on each side, with the mean number of ribs being identical on each side as 10.7 (SD: 0.48). These are slightly fewer than in the Antarctic minke whales (10–12, mean 11.1 (SD: 0.45)) and North Pacific common minke whale (10–12, mean 10.8 (SD: 0.4)), but not significantly so. No floating rib was found among the present specimens of dwarf minke whales.

4. Shape of sternum

Three types of sternum shape are observed in species and sub-species of minke whales: Y-shape (looks like a ginkgo leaf), T-shape and an intermediate shape (Fig. 10). The T-shape sternum is common among dwarf minke whales, Antarctic minke whales and North Pacific common minke whales; the manubrium parts were rather larger in the North Pacific common minke whales. The Y-shape was only confirmed in dwarf minke whales with the presence of a hole in the center of the sternum in some whales. The Y-shape sternum is likely to be rare among balaenopterids and is possibly exhibited only in dwarf minke whales and must be closely related to the shape of the associated ribs. This characteristic may suggest some differences in feeding behavior, but more samples and further examinations are required to confirm this.

Life history parameters

Females

1. Reproductive status

While ovaries were unfortunately lost from the three females, six of the 13 females of dwarf minke whales were firstly confirmed to be sexually mature and four were confirmed as immature based

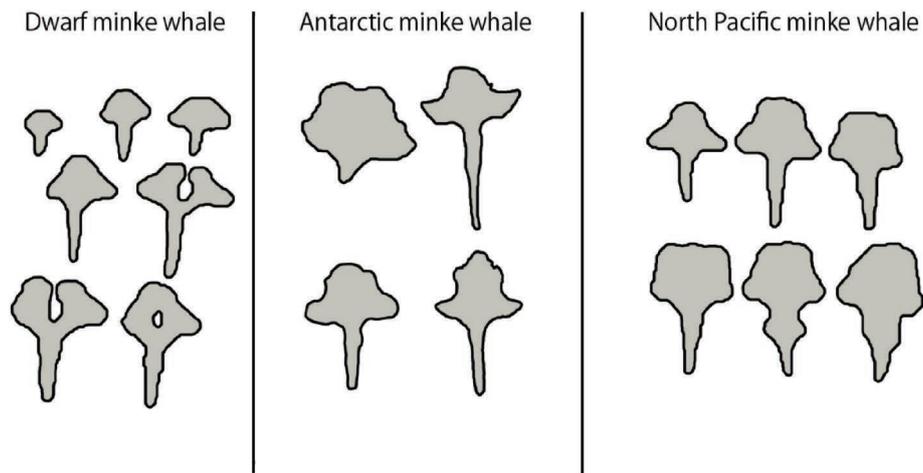


Fig. 10. Variations in shape of the sternum among dwarf, Antarctic and North Pacific common minke whales based on contours of the actual sternums in each type of minke whale.

on gonad examination. Of the remaining three females one (88/89-013) was to be mature because of having a fetus, another (88/89-227) was thought to be mature given its size (7.02 m) and age (10 years old) as well as the presence of a transition phase as a mark of attainment of sexual maturity in the ear plug, and the third (89/90-002) likely to be immature from its size (4.29 m) and age (3 years old), as summarized in Table 1. Resultant sexual status of the present samples was five sexually immature versus eight mature. All sexually mature females excepting one missing the uterine horns were confirmed to be pregnant, apparently indicating a 100% pregnancy rate. This figure should be, however, treated with caution because of the small sample size and possible segregation or timings of migration associated with reproduction.

The transition phase in the earplug was used as an indicator of age at sexual maturity while an annual rate of growth layer deposition was assumed (Lockyer, 1972; Kato, 1982). The mean annual ovulation rate after attainment of sexual maturity was estimated as follows:

$$no.corpora / (total\ age - transition\ phase) \quad (8)$$

Values from four females having both transition phase and number of corpora ranged from 0.31 to 1.00 with a mean of 0.58, which are understood to be annual ovulation rate leading to maximum value of annual pregnancy rate. This result suggests that the apparent 100% pregnancy rate might be too high as an annual pregnancy rate (true pregnancy rate) and this high value was possibly due to reproductive segregation in relation to latitude, i.e., pregnant females migrate further south as in the case of Antarctic minke whales (Masaki, 1979; Kato, 1982).

None of the mature females was lactating, but possible milk remnants consisting of transparent yellowish liquid were found in the mammary gland of one female (sample ID number: 92/93-107), suggesting this animal was sampled just after weaning her calf.

2. Fetus and breeding season

The sex ratio in the fetus samples was 3 males to 4 females, and the mean litter size was 1.0 (n=7). The lengths of the fetuses were relatively similar, ranging from 98.6 to 119 cm with one at 169.6 cm (Table 6).

To investigate the timing and duration of the breeding season, conception dates were estimated by back-calculating from fetus length and date of capture, and applying the fetal growth rate formula for Antarctic minke whales (Kato and Miyashita, 1991; Kato, 1995), as follows:

$$t = 1.622L^{0.892} + 74 \quad (9)$$

Table 6. Estimated conception date for the pregnant dwarf minke whales based on back-calculating by the fetal growth curve estimated by Kato (1995).

Season	Specimen no.	Date	Fetal length (cm)	Days after concept.	Estimated concept. date*
90/91	012	3 Jan, 1991	102.8	175	13 Jul, 1990
90/91	014	3 Jan, 1991	98.6	171	17 Jul, 1990
92/93	107	10 Jan, 1993	84.0	158	6 Aug, 1992
89/90	215	15 Jan, 1990	115.0	186	14 Jul, 1989
88/89	013	17 Jan, 1989	119.0	189	13 Jul, 1988
90/91	118	26 Jan, 1991	111.7	183	28 Jul, 1990
92/93	330	22 Mar, 1993	169.6	232	3 Aug, 1992

*: Mean=22 July.

where t is time (days) passed since conception and L is fetal body length in cm (Table 6).

Estimated conception dates were concentrated in a very narrow band from the middle of July to early August, that is, over a 25-day period. Thus, provided that southbound migration is not dependent on reproductive segregation, even with the small sample size, it appears that the breeding season of the dwarf minke whale likely occurs over a few weeks in mid-winter with a peak in middle to late July. This contrasts with the case of Antarctic minke whales where the breeding season extends over six months with a weak peak in September/October (Kato, 1995).

3. Body Length and age at sexual maturity

With the present small sample size, it was difficult to estimate lengths or ages at sexual maturity with accuracy, especially for males.

For females, the smallest mature individual was 6.61 m and the largest immature individual was 5.94 m in length (Table 1), from which body length at sexual maturity is likely to be around these values or around 6.0–6.5 m. In a separate study, Kato (1987) examined the density dependent nature of temporal changes for parameters related to sexual maturity in Antarctic minke whales and concluded that the length at sexual maturity remained constant over time, while age at sexual maturity declined with density dependence. Thus, length at sexual maturity is a reliable threshold parameter for species- or subspecies-specific sexual maturity. For other minke whales, estimates are:

North Pacific common minke whales, female, 7.1 m (Kato, 1992),

North Atlantic common minke whales, female, 7.1–7.5 m (Jonsgard, 1951; Christensen, 1981; Larsen and Kaple, 1982),

Antarctic minke whales, female, 8.1 m (Best, 1982; Kato, 1982; Zenitani *et al.*, 1997; Bando *et al.*, 2006).

In females, values for dwarf minke whales were much smaller (approximately 1.0–2.0 m smaller) than the those for Antarctic and North Pacific common minke whales.

The age of the youngest sexually mature female was 10 years and that of the oldest immature female was 7 years. Therefore, their average age at sexual maturity is likely in the range of 7–10 years (Table 1). This result is consistent with the age at sexual maturity estimated from the transition phase (Table 1), which was 4–11 years with a mean of 7.14 years (SD: 1.05).

4. Maximum life span

The oldest whale in the sample was a 26-year-old female (Table 1). This is most likely to be an under-estimate of longevity due to the small sample size. This parameter can be estimated using the equation of Ohsumi (1979) which was derived from fitting both baleen and toothed whales as below:

$$T = 31.277e^{0.05480L} \quad (10)$$

where T is maximum life span in years and L is body length at physical maturity in meters.

The above equation was applied to the estimated length at physical maturity (asymptotic length for females, 7.16 m) in the present study to estimate the approximate value of the maximum life span. The result was 47 years. This is not so different from those of other minke whale species and sub-species derived from the same equation, e.g., 50 years for the Antarctic minke whale and 48 years for the North Pacific common minke whale. It is emphasized here that this is an interim value.

Males

It was difficult to estimate any life history parameters in males because of the limited number of specimens (Table 1). It was considered that the 5.41 m dwarf minke whale with testes weighing 53 and 57 g was an immature animal. The other two whales, a 7.01 m male (age 21) with testes weighing 530 and 540 g (hereafter 87/88–273) and a 6.6 m male (age 10) with testes of 182 and 195 g (hereafter 88/89-014) were presumed to be mature animals. For these two cases, additional analyses based on histological examinations of the testes were conducted.

Histological sections for those testes are shown in Fig. 11. It was confirmed that numerous spermatocytes were present in most of the seminiferous tubules of both males, but no sperm was present in both males. The reason why there were no sperm among almost all of the seminiferous tubules is not a surprising event even for fully sexually mature males. It is thought to be due to timing of the samplings of the testes (January to March which did not overlap with the likely breeding season in July–August inferred from conception timing calculated backward from the fetus frequencies in the above section.

However, it was further noted that some spermatids existed in the seminiferous tubules of the larger male. Some examples of these are shown by the arrows in Fig. 11(B). This suggests the male was

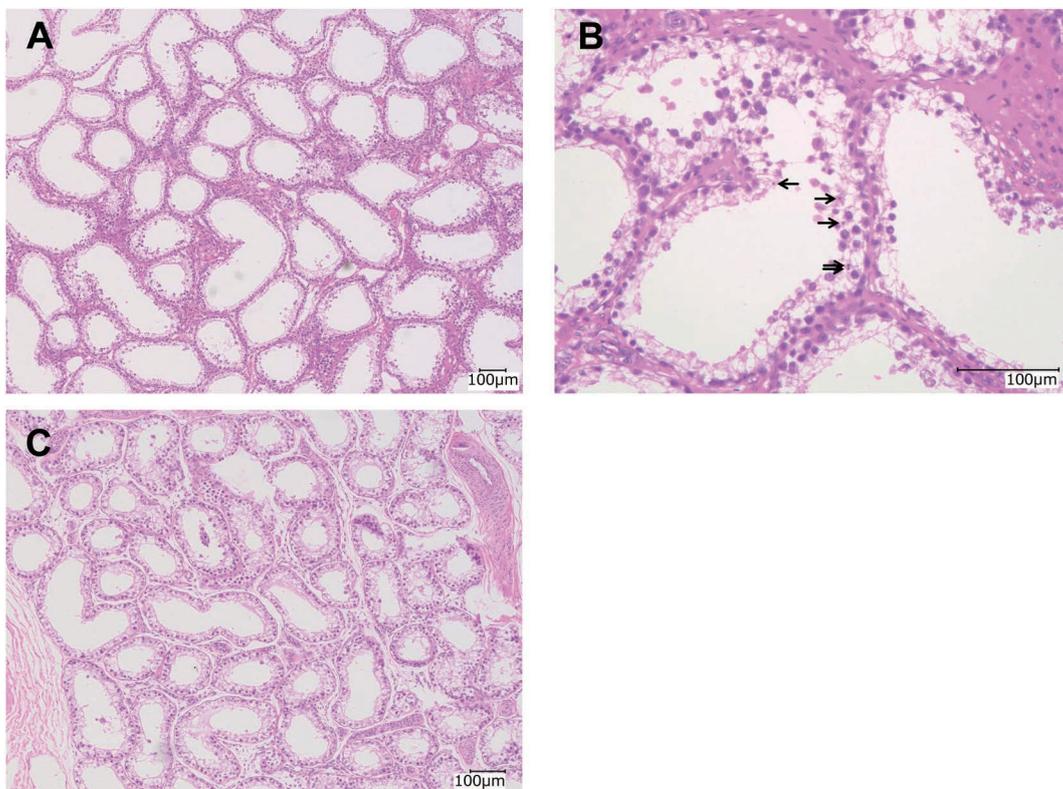


Fig. 11. Histological section images of the seminiferous tubules for the males examined. Bars in all three images represent 100 μm . **A:** large male (87/88-273), body length 7.01 m and age 21 years. **B:** magnified view of the 87/88-273 seminiferous tubules indicating spermatids with arrows. **C:** the second large male (88/89-014) whose body length was 6.60 m and age 6 years.

in a somewhat sexually active status even if out of the main breeding season. Thus, the larger male (87/88-273) was definitely a mature animal. For the second larger male (88/89-014), spermatids could not be confirmed in any of its seminiferous tubules during the present microscopic observation.

Another measure of male sexual maturity was the size of the seminiferous tubules. Masaki (1976) examined the diameter (minor axis) of seminiferous tubules in sei whales and found significant correlation in relation to sexual maturity. Kato (1986) also found a similar relationship between the diameter and sexual maturity in Antarctic minke whales. The threshold value for sexual maturity was mostly $100\mu\text{m}$. Inoue *et al.* (2018) examined the minor axis of the seminiferous tubules in North Pacific common minke whales and found that over $100\mu\text{m}$ would be enough to determine sexual maturity even when the samples were collected in the non-breeding season. According to the present measurement of seminiferous tubules, those were $177.6\mu\text{m}$ ($n=25$, SD: 29.49) and $124.4\mu\text{m}$ ($n=25$, SD: 13.71) for the larger male (87/88-273) and the second larger male (88/89-014) respectively. They were wider than the threshold value of $100\mu\text{m}$ of sexual maturity in other minke whale types even in non-breeding season. Another measure for sexual maturity in males is the presence of the open lumen within the respective seminiferous tubules. Masaki (1976) reported that the presence of the open lumen could be used as a criterion for sexual maturity in North Pacific sei whales. In our analyses, as evident in Fig. 11(B), the open lumen can be seen in the majority of the seminiferous tubules for the two males.

From the above examinations, it can be confirmed that the two large males (87/88-273, 88/89-014) were sexually mature.

Food and feeding habits

The stomach contents of 16 dwarf minke whales were examined. 13 individuals contained food, while the remainder were empty or contained only traces of food (Table 7).

Table 7. Stomach contents, weights and prey species eaten by dwarf minke whales in relation to sampling location and time.

Sample no.	Location						Sampling time	BIWS stomach record			Content weight in kg**	Prey species identified
	Latitude		Longitude		Item	Relative richness*		Size				
87/88-273	58	23	S	111	26	E	15.24	Fish	1	—	22.7	Myctophidae
88/89-005	55	22	S	178	10	E	14.55	—	0	—	4.9	
88/89-013	62	4	S	177	28	E	10.54	Fish	1	—	38.3	Myctophidae
88/89-014	62	7	S	177	2	E	12.50	Fish	2	—	33.9	Myctophidae
88/89-070	60	38	S	175	7	E	9.00	Fish	1	—	5.6	Myctophidae
88/89-227	61	54	S	177	55	E	8.40	Fish	1	—	6.8	Myctophidae
89/90-002	55	59	S	97	17	E	18.23	Fish	1	—	15.6	Myctophidae
89/90-199	61	30	S	128	6	E	9.20	Fish	1	—	14.0	Myctophidae
89/90-215	60	59	S	116	6	E	10.51	Fish	2	—	47.3	Myctophidae
90/91-002	65	4	S	178	12	E	7.29	Eu	1	small	3.4	Euphausiids
90/91-012	61	9	S	175	21	W	8.38	Fish	1	—	29.1	Myctophidae
90/91-014	60	40	S	176	34	W	12.36	Fish	1	—	20.7	Myctophidae
90/91-118	60	34	S	146	49	E	9.43	Fish	1	—	2.6	Myctophidae
92/93-107	60	51	S	167	42	E	18.26	—	0	—	0.0	
92/93-108	60	31	S	166	5	E	16.16	—	0	—	2.5	
92/93-330	61	49	S	143	16	E	15.53	Fish	1	—	35.7	<i>Krefflichthys anderssoni</i>

*: Relative richness by the BIWS format: 0, empty; 1, 25%; 2, 26–50%; 3, 51–75%; 4, 76–100%.

** : Combined value for the first (fore) and second (main) stomachs.

Stomach contents weighed between 2.6 kg and 47.3 kg ($n=13$) and the contents were partially digested. The species composition of the contents was mainly uniform within each stomach, thus the food in the stomachs would have been representative of food organisms typically consumed by dwarf minke whales.

Sampling locations were spread out latitudinally and longitudinally. Except for one sampled further north from the Antarctic Convergence (with empty stomach), the majority of dwarf minke whales were sampled in the vicinity of the Antarctic convergence (58–62°S). The species identification of food organisms was referred to Mr. Hiromasa Furuhashi (Hokkaido University) a specialist of morphology and taxonomy of myctophid fish. Observations were made by placing the photophore pattern over the fish body surface, a method which is widely used for species identification of myctophid fishes. The specialist inferred that there were remnants of myctophids, including *Krefflichthys anderssoni*. This clarified that these dwarf minke whales fed mainly on small fish in the vicinity of the Antarctic Convergence.

On the other hand, euphausiids (probably *Euphausia superba*) were found in the stomach of one dwarf minke whale sampled at 65°S, which is further south of the Antarctic Convergence and where dwarf minke whales are known not commonly occur (Kato *et al.*, in press). Euphausiids such as *E. superba* are known to be abundant in this region. Thus, it cannot be automatically determined that the dwarf minke whale is a fish-feeder. It appears that the dwarf minke whale is more of an opportunistic feeder and utilizes organisms which are available in abundance as food.

From the above, it can be summarized that dwarf minke whales feed mainly on small gregarious fish species such as myctophids in their normal summer habitat, while dwarf minke whales in lower latitudes off Brazil feed on euphausiids (Secchi *et al.*, 2003) on an opportunistic basis.

Morphometric analysis

External body proportions

A total of 21 external measurements collected from 16 dwarf minke whales were compared statistically with those from 507 Antarctic minke whales and 91 North Pacific common minke whales. All measurements were log-transformed prior to the analysis.

The morphometric comparison for the three species and sub-species of minke whales was carried out using three methods. The first was the analysis of covariance (ANCOV). This assumes that the allometric relationship between body length (V01) and each of the remaining measurements holds irrespective of age, while body length was used as a covariate to the other measurements (Jover, 1992; Tanaka and Tarumi, 1986). Secondly, measurements showing no significant regression with body length were also used for the multivariate analysis of variance (MANOVA) (Jover, 1992; Tanaka *et al.*, 1990). The third method was the canonical discriminant analysis (DA) using component scores from a principal component analysis (PCA) (Tanaka *et al.*, 1984a, 1984b; Christensen *et al.*, 1990).

To evaluate morphometric differences between males and females, 14 measurements of the dwarf minke whales were analyzed using MANOVA, and a significant difference (Wilks' $\Lambda=0.17026$, $p<0.01$) was detected. ANCOV was also carried out using 20 measurements (V02-V09, V11-V20 and V31-V32) of the dwarf minke whales with body length as a covariate. The analysis indicated no sexual difference except for one characteristic (V08: from tip of snout to sexual aperture), which is known to be sexually dimorphic.

To evaluate differences in external body proportion for dwarf minke whales, Antarctic minke whales and North Pacific common minke whales, MANOVA was carried out using the 14 measurements, and a significant difference was detected (females: Wilks' $\Lambda=0.17026$, $p<0.01$; males: Wilks' $\Lambda=0.24714$, $p<0.01$). ANCOV was conducted using 20 measurements from females. The analysis revealed that 14 of the measurements were significantly correlated with body length (Table 8) while some of the measurements differed significantly in that dwarf minke whales showed larger values in the posterior parts of the body (V08 and V09), flipper, and dorsal fin (V11 and V12). Antarctic minke

Table 8. Results of ANCOV of body proportion with body length (V01) as a covariate for three types of minke whale: dwarf (DWM), Antarctic (ATM) and North Pacific (NPM) minke whales. **Upper**, for female; **bottom** for male.

Female							
	Sample size			Result of ANCOV	Estimated value at mean covariate with 95% CF		
	DWM	ATM	NPM		DWM	ATM	NPM
	n	n	n		Mean+95%	Mean+95%	Mean+95%
V02	13	270	40	p<0.01	4.732+0.035	4.761+0.007	4.665+0.020
V03	13	270	34	p<0.01	4.940+0.031	5.024+0.006	4.847+0.018
V04	13	268	9	p<0.01	5.188+0.023	5.258+0.005	5.113+0.027
V05	13	257	40	p<0.01	5.856+0.018	5.866+0.004	5.795+0.010
V06*	13	270	33	p<0.01			
V07*	13	269	33	p<0.01			
V08	13	267	18	p<0.01	6.345+0.009	6.328+0.002	6.311+0.007
V09	13	270	43	P<0.01	6.369+0.008	6.357+0.002	6.348+0.005
V11	13	259	30	p<0.01	3.461+0.067	3.362+0.014	3.402+0.042
V12	13	264	36	p<0.01	4.850+0.051	4.732+0.011	4.681+0.029
V13*	13	267	18	p<0.01			
V14*	13	269	33	p<0.01			
V15	13	270	25	p<0.05	4.038+0.043	4.052+0.009	4.013+0.029
V16	13	266	21	p<0.01	5.405+0.039	5.384+0.008	5.440+0.029
V17*	13	270		p<0.01			
V18*	13	270	29	p<0.01			
V19	13	265	14	p<0.01	5.192+0.022	5.243+0.005	5.084+0.022
V20	13	264	17	p<0.01	4.607+0.025	4.635+0.005	4.460+0.023
V31	11	216		p<0.01	5.128+0.027	5.169+0.006	
V32	12	247		p<0.05	5.120+0.035	5.164+0.007	

Male							
	Sample size			Result of ANCOV	Estimated value at mean covariate with 95% CF		
	DWM	ATM	NPM		DWM	ATM	NPM
	n	n	n		Mean+95%	Mean+95%	Mean+95%
V02	3	236	48	p<0.01	4.723+0.082	4.725+0.009	4.654+0.021
V03	3	235	41	p<0.01	4.931+0.055	4.986+0.006	4.859+0.015
V04	3	233	15	p<0.01	5.170+0.042	5.220+0.005	5.072+0.021
V05	3	229	45	p<0.01	5.837+0.043	5.832+0.005	5.758+0.012
V06	3	237	36	p<0.01	5.969+0.041	5.955+0.005	5.857+0.012
V07*	3	237	36	p<0.01			
V08	3	237	30		6.266+0.019	6.253+0.002	6.255+0.006
V09	3	237	48	p<0.01	6.352+0.016	6.344+0.002	6.335+0.004
V11	3	229	40	p<0.05	3.525+0.134	3.370+0.015	3.411+0.038
V12	3	231	41	p<0.01	4.849+0.078	4.728+0.009	4.774+0.022
V13*	3	232	9	p<0.01			
V14	3	235	41	p<0.01	3.450+0.063	3.330+0.007	3.360+0.018
V15	3	237	40		3.973+0.075	4.012+0.008	3.994+0.022
V16	3	236	33	p<0.01	5.382+0.068	5.365+0.008	5.412+0.021
V17	3	237			5.327+0.066	5.334+0.007	
V18*	3	237	44	p<0.01			
V19	3	236	19	p<0.01	5.156+0.041	5.210+0.005	5.078+0.018
V20	3	233	20	p<0.01	4.572+0.048	4.613+0.005	4.401+0.021
V31	3	199			5.098+0.043	5.136+0.005	
V32	3	218			5.095+0.045	5.138+0.005	

*: As the results showed no correlation with body length as a covariate, a multivariate analysis of variance was adopted.

whales showed larger values in measurements related to head proportion (V03, V04, V19, V31, V32). North Pacific common minke whales showed wider flukes (V16). In spite of the small sample size, similar results were observed for males (Table 8).

The result of PCA showed that the first Principal Component (PC1) is related to growth, with a positive value observed for all variables. The PC2 seems to be correlated to body appendages such as flipper, dorsal fin, and flukes. The values were positive for girth (V11) and flukes (V15 and V16) while negative values were observed in anterior parts of the body (from V02 to V09). Principal component scores from PCA were examined using the canonical discriminant analysis (DA). Eigenvalues and eigenvectors derived from DA are shown in Table 9 by each canonical variate (CAN) with and without PC1. Plots of the first two variates are shown in Fig. 12 for both sexes. For males, irrespective of whether PC1 was included or not, the three forms are visibly separate from each other. These results indicate significant differences in external morphology among the three types of minke whale.

Skull measurements

1. ANCOV analyses

Comparative skull morphology analyses were carried out based on 76 skull measurements from 15 dwarf minke whales, 33 Antarctic minke whales, 27 North Atlantic common minke whales and 29 North Pacific common minke whales. The measurements were log-transformed prior to the analyses. Because of the small sample size, the analysis was conducted by combining data of both sexes.

The same methods of analysis as those for external morphometry were conducted: MANOVA, ANCOV, PCA, and DA. In ANCOV, condylo-premaxillary length (SK01) was used as the covariate.

Table 10 shows the results of ANCOV. Fifty-nine measurements indicated a significant regression with the SK01. Of these, 46 were significantly different among the four species and sub-species of minke whales. For five measurements (indicated by ** in Table 10) that had no significant slope in the regression line taking the SK01 as a covariate, MANOVA were applied instead of ANCOV, indicating that measurements related to rostrum (SK03, SK05, SK06, SK07, SK08, SK09, SK19, SK21) are

Table 9. Eigenvectors and eigenvalues derived from the canonical discriminant analysis using the PC scores of PCA for each sex.

Female					Male				
Principal Component	PC1-PC14		PC2-PC14		Principal Component	PC1-PC14		PC2-PC14	
	CAN1	CAN2	CAN1	CAN2		CAN1	CAN2	CAN1	CAN2
PC1	-1.0647	1.0367			PC1	1.2805	-0.7460		
PC2	5.8434	-1.8680	4.5469	3.9497	PC2	-5.8619	1.8779	5.4162	2.5298
PC3	14.1278	-0.6006	12.4648	5.6995	PC3	-13.4996	-1.0185	12.7377	0.1822
PC4	1.7539	6.3519	3.9619	-5.6118	PC4	0.7162	-6.3630	-0.3579	-6.7861
PC5	4.9272	3.2111	5.6326	-1.3752	PC5	5.3022	-2.4817	-4.8601	-3.1148
PC6	-4.7839	-4.6171	-6.0319	2.8102	PC6	8.5320	0.8708	-8.0618	0.1251
PC7	-2.0632	0.9634	-1.4914	-1.6930	PC7	-2.2883	0.1613	2.1421	0.3836
PC8	1.0791	-8.8291	-2.3480	9.0719	PC8	0.8390	9.7660	-1.2719	10.2354
PC9	15.2995	3.0035	14.8688	2.5732	PC9	-19.5342	-4.2379	18.5691	-2.6552
PC10	16.0063	28.5834	25.1179	-22.3201	PC10	-13.2718	-18.5866	13.3946	-18.3927
PC11	14.2007	13.2371	17.7122	-7.9283	PC11	-2.2114	14.2976	1.3674	15.3041
PC12	11.7966	21.5350	18.7129	-16.8394	PC12	18.7030	4.3906	-17.7983	2.8929
PC13	-13.6419	35.3312	1.0133	-39.6776	PC13	12.6217	-30.3189	-10.3333	-33.1692
PC14	-12.6909	15.0742	-5.6906	-19.3782	PC14	-14.0194	-2.3797	-13.3009	-1.2024
Eigenvalue	2.0810	0.9049	1.6351	0.5091	Eigenvalue	2.4671	0.1671	1.7534	0.1430

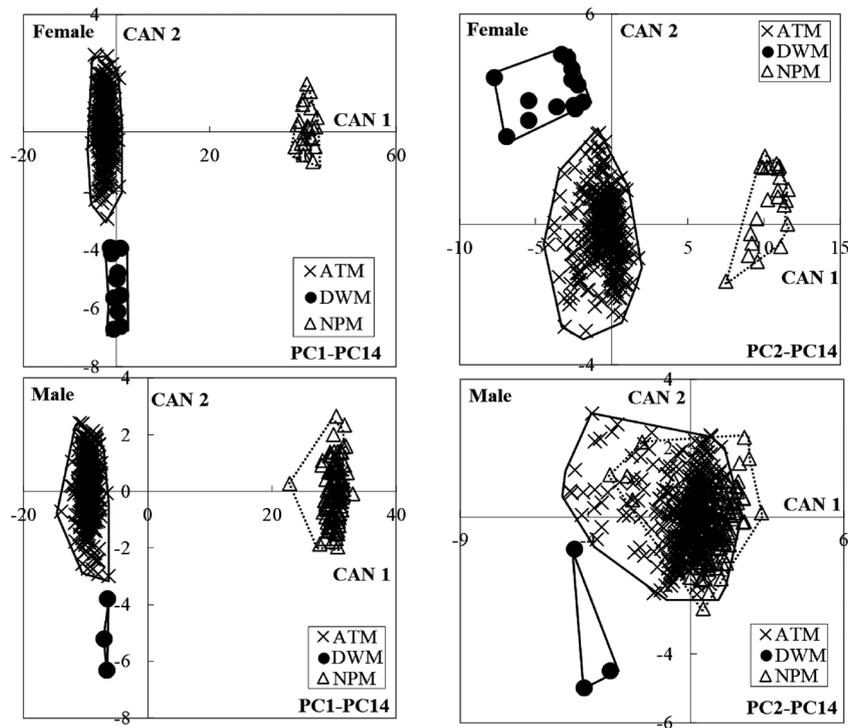


Fig. 12. Scatter plots of scores on the first and second canonical variates derived from external body proportions of dwarf minke whales (DWM), Antarctic minke whales (ATM) and North Pacific common minke whales (NPM), for females (upper) and males (lower).

smaller in Antarctic minke whales, i.e., Antarctic minke whales seem to possess a relatively shorter and narrower rostrum, and a larger mouth cavity. The analysis also shows that Antarctic minke whales have a somewhat larger occipital portion of skull (SK30, SK32, and SK63).

From the results of PCA, eigenvalues and eigenvectors were calculated using DA for each canonical covariate CAN (Table 11) with and without PC1. Plots of the first two CANs are shown in Fig. 13. Irrespective of whether PC1 was included or not, skull morphology differed among dwarf minke whales, Antarctic minke whales and North Pacific common minke whales.

CLUSTER analyses for skull morphology

Although the following analysis is not necessarily the most effective approach to advance the investigation on differences in skull morphology among taxa, cluster type analyses were carried out using skull data of sexually mature whales, comprising eight dwarf minke whales (present study), 14 North Atlantic common minke whales (present study and from Tomilin (1967)), five Antarctic minke whales (from Nakamura, 2012), and 47 North Pacific common minke whales (from Nakamura, 2012).

In earlier analyses, statistical differences were identified in 29 of 44 proportions among minke whale taxa. Furthermore, reliable measurements, which are potentially less subject to technical measuring error, were extracted. These included (1) CBL (condylobasal length), (2) length of tympanic bulla, (3) pre-maxilla length as proportion of CBL, (4) maxillary length as proportion of CBL, (5) mandible length along its outer margin as proportion of CBL, (6) occipital length as proportion of CBL.

Among the six variables chosen, (3), (4) and (5) had growth dependent changes in relative values. For this comparison, only the data obtained from sexually mature animals or those from animals with a CBL >145 cm, which were known to be independent of growth dependent changes, were used. The values of the respective variants are given in Appendix 2.

In the next step to evaluate degree of similarity among the different taxa, the parameter S was esti-

Table 10. Results of ANCOV of skull measurements with skull length (SK01) as a covariate for minke whales in four types: dwarf form (DWM), North Atlantic (NA), North Pacific (NPM) and Antarctic (ATM) minke whales.

Item	Sample size				Result of ANCOV	Estimated value at mean covariate with SE			
	DWM	NA	NPM	ATM		DWM	NA	NPM	ATM
	n	n	n	n		Mean+SE	Mean+SE	Mean+SE	Mean+SE
SK02	15	5	29	32	0.450	4.715+0.009	4.703+0.014	4.700+0.006	4.696+0.007
SK03	13	8	25	31	0.000	4.845+0.008	4.845+0.009	4.831+0.005	4.785+0.006
SK04	13	1	26	31	0.000	4.857+0.008	4.835+0.026	4.842+0.006	4.797+0.006
SK05	12	5	25	28	0.000	4.802+0.008	4.818+0.012	4.793+0.005	4.748+0.006
SK06	12	2	24	26	0.000	4.804+0.080	4.814+0.019	4.795+0.005	4.749+0.007
SK07	13	1	27	25	0.000	4.851+0.009	4.876+0.027	4.841+0.006	4.799+0.007
SK08	13	1	27	25	0.000	4.857+0.009	4.891+0.026	4.844+0.006	4.796+0.007
SK09	14	1	29	28	0.000	4.872+0.008	4.908+0.024	4.865+0.005	4.810+0.006
SK10	15	7	29	29					
SK11	12	1	23	25	0.048	2.098+0.047	2.370+0.135	2.204+0.032	2.127+0.037
SK12	12	1	23	24	0.000	2.152+0.043	2.551+0.122	2.236+0.028	2.079+0.034
SK13	15	4	28	32	0.041	4.204+0.017	4.163+0.029	4.233+0.012	4.194+0.013
SK14*	13	27	28	29					
SK15*	15	1	26	30					
SK16*	14	5	26	29					
SK17*	15	9	28	32					
SK18	14	5	25	29	0.045	4.432+0.028	4.439+0.038	4.412+0.019	4.333+0.022
SK19	15	11	28	33	0.000	4.110+0.017	4.033+0.017	4.052+0.011	3.975+0.013
SK20*	15	11	28	32					
SK21	14	—	25	25	0.000	2.727+0.068		2.838+0.044	2.271+0.056
SK22	13	—	11	27	0.527	2.211+0.055		2.284+0.054	2.235+0.040
SK23*	13	8	25	28					
SK24	14	3	24	28	0.967	2.728+0.030	2.750+0.054	2.731+0.020	2.743+0.023
SK25	13	—	20	24	0.244	0.991+0.150		0.987+0.107	0.678+0.122
SK26*	13	5	27	32					
SK27	13	5	28	32	0.000	2.815+0.028	3.025+0.042	2.851+0.018	2.917+0.021
SK28*	14	3	27	31					
SK29*	14	—	28	30					
SK30	14	—	28	30	0.000	2.328+0.019		2.421+0.013	2.479+0.015
SK31	13	3	28	31	0.009	2.834+0.051	2.679+0.101	2.650+0.033	2.633+0.039
SK32	15	4	27	29	0.000	3.695+0.017	3.842+0.030	3.763+0.012	3.830+0.014
SK33	14	—	28	30	0.000	2.085+0.026		2.148+0.018	1.913+0.021
SK34*	14	—	28	28					
SK35	11	1	20	26	0.000	2.096+0.019	2.181+0.051	2.239+0.014	2.200+0.015
SK36**	11	1	22	26	0.000	1.793+0.017	1.758+0.057	1.945+0.012	1.965+0.011
SK37**	10	1	20	26	0.000	2.040+0.018	2.140+0.057	2.220+0.013	2.235+0.011
SK38**	10	1	19	26	0.000	1.808+0.016	1.705+0.049	1.952+0.011	1.973+0.010
SK39**	10	1	19	26	0.000	1.808+0.016	1.705+0.049	1.952+0.011	1.973+0.010
SK40**	14	6	28	27	0.004	3.316+0.070	3.056+0.106	3.325+0.049	3.475+0.050
SK41	12	2	23	28	0.001	2.595+0.039	2.736+0.078	2.581+0.026	2.767+0.029
SK42	14	—	26	26	0.000	4.967+0.005		4.946+0.003	4.966+0.004
SK43	14	—	24	24	0.000	4.926+0.005		4.908+0.003	4.927+0.004
SK44*	14	2	26	25					
SK45	14	—	25	22	0.000	4.927+0.006		4.900+0.004	4.919+0.005
SK46	13	—	24	23	0.000	4.637+0.010		4.571+0.006	4.640+0.008
SK47	13	—	24	24	0.000	4.640+0.010		4.582+0.006	4.650+0.008
SK48	14	21	28	26	0.159	3.692+0.069	3.525+0.058	3.658+0.046	3.667+0.061
SK49*	14	21	28	26					
SK50*	13	3	28	30					
SK51*	13	3	21	26					
SK52	14	2	29	27	0.000	4.696+0.008	4.698+0.018	4.655+0.005	4.712+0.007
SK53	13	2	25	24	0.000	4.702+0.008	4.711+0.016	4.653+0.005	4.706+0.006
SK54	13	4	26	30	0.010	4.991+0.006	5.006+0.009	4.978+0.004	4.990+0.004
SK55	12	4	21	27	0.010	4.994+0.005	5.010+0.007	4.980+0.003	4.991+0.004
SK56*	15	2	29	30					

Table 10. Continued.

Item	Sample size				Result of ANCOV	Estimated value at mean covariate with SE			
	DWM	NA	NPM	ATM		DWM	NA	NPM	ATM
	n	n	n	n		Mean+SE	Mean+SE	Mean+SE	Mean+SE
SK57	14		28	28	0.224	2.899+0.044		2.871+0.029	2.788+0.036
SK58	14	4	28	32	0.050	3.018+0.040	3.032+0.070	3.028+0.027	2.894+0.032
SK59	15	6	27	32	0.000	5.179+0.011	5.215+0.015	5.150+0.008	5.143+0.009
SK60	15	3	28	32	0.095	5.164+0.019	5.238+0.040	5.147+0.013	5.120+0.015
SK61	15	5	27	32	0.011	5.125+0.010	5.148+0.015	5.111+0.007	5.091+0.008
SK62	15	3	28	32	0.093	5.111+0.015	5.168+0.031	5.107+0.010	5.076+0.012
SK63	14	2	28	31	0.000	3.129+0.015	3.170+0.037	3.103+0.010	3.195+0.012
SK64	14	6	29	30	0.000	3.131+0.015	3.117+0.021	3.103+0.010	3.184+0.012
SK65	14	2	29	31	0.708	2.821+0.026	2.770+0.062	2.802+0.017	2.828+0.021
SK66	14	5	28	31	0.576	2.829+0.026	2.810+0.040	2.793+0.018	2.819+0.021
SK67	8	—	27	22	0.027	2.571+0.038		2.589+0.020	2.481+0.028
SK68	8	—	25	22	0.035	2.551+0.040		2.586+0.021	2.482+0.029
SK69	6	—	23	24	0.002	2.506+0.084		2.750+0.045	2.927+0.050
SK70	6	—	25	24	0.006	2.573+0.071		2.759+0.037	2.890+0.043
SK71	6	—	25	25	0.000	1.870+0.072		2.186+0.037	2.031+0.043
SK72	6	—	26	25	0.000	1.883+0.061		2.177+0.031	2.036+0.037
SK73	7	—	26	26	0.004	3.039+0.032		3.044+0.015	2.946+0.018
SK74	7	—	24	26	0.009	3.057+0.033		3.051+0.016	2.960+0.019
SK75	6	—	26	25	0.136	0.957+0.076		0.931+0.034	1.052+0.042
SK76	6	—	25	25	0.058	0.952+0.075		0.928+0.033	1.071+0.040

*: Parallel test indicated no significance.

**: As the result showed no correlation with skull length as a covariate, a multivariate analysis of variance was adopted.

Table 11. Eigenvectors and eigenvalues derived from the canonical discriminant analysis using the PC scores of PCA.

Principal Component	PC1-PC5		PC2-PC5	
	CAN1	CAN2	CAN1	CAN2
PC1	-1.5129	0.4102		
PC2	1.1734	0.7607	1.2413	0.3346
PC3	-0.0517	0.8427	0.5924	-0.6666
PC4	0.6007	-0.3278	0.1062	0.7068
PC5	0.0859	-0.3668	-0.1870	0.5102
Eigenvalue	3.2417	0.7854	1.0365	0.3831

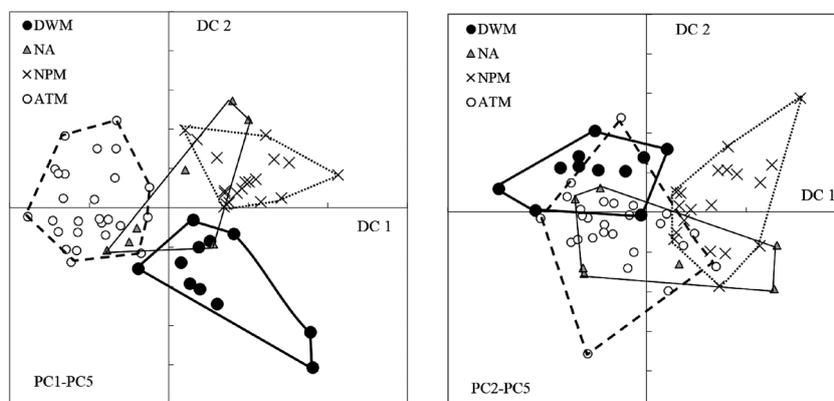


Fig. 13. Scatter plots of scores on the first and second canonical variates derived from skull measurements of dwarf (DWM), North Atlantic (NA), North Pacific (NPM) and Antarctic minke whales (ATM).

Table 12. Estimated value of correction coefficient r and degree of similarity S in the cluster analysis on the skull between different types of minke whales.

Type	Estimated (r/S)			
	Antarctic	North Pacific	Dwarf	North Atlantic
Antarctic				
North Pacific	0.9922 0.0078			
Dwarf	0.9833 0.0167	0.9983 0.0017		
North Atlantic	0.9825 0.0175	0.9972 0.0028	0.9983 0.0017	

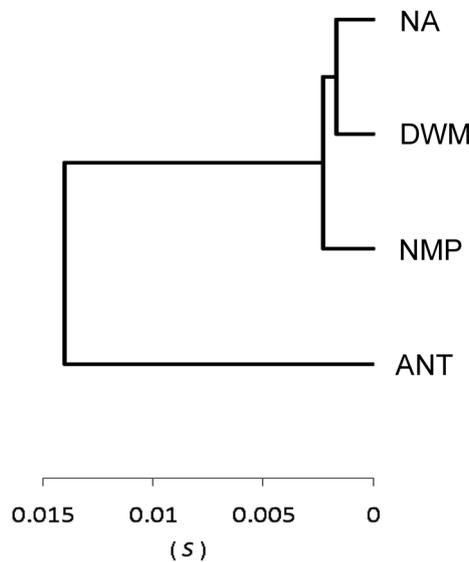


Fig. 14. Dendrogram showing the degree of similarity among the minke whale clade based on cluster analyses on the skull morphology. ANT, Antarctic minke whale; NPM, North Pacific common minke whale; NA, North Atlantic common minke whale; DWM, dwarf minke whale. S , see below.

mated as defined below:

$$S = 1 - r \tag{11}$$

where S represents the degree of similarity, r being the correlation coefficient on the variants between different types of minke whales.

Table 12 gives the estimated values for correlation coefficient and degree of similarity for each pairwise comparison. A dendrogram was produced through cluster analyses using the values from the group average method. These represent the interrelationships in different minke whale taxa by weighing the degree of similarity (Fig. 14). From this dendrogram it was clear that the Antarctic minke whales were most distant, and secondly, the North Pacific common minke whales were relatively distant from the North Atlantic common minke whales and dwarf minke whales. In conclusion, in the present cluster analysis, the dwarf minke whales were closest morphologically to the North Atlantic common minke whales. This was also genetically supported by the previous analyses such as Pastene *et al.* (2007).

Discussion

First of all, throughout this study, the scarcity of available samples has become an issue, however, as it is almost impossible to obtain further samples of the same quality, we had to proceed with the analyses, bearing in mind this sample limitation. Thus, the shortage of an adequate number of samples should be recognized as a potential problem in all analyses during this study.

There are currently many reports on the occurrence of dwarf minke whales from coastal waters in low and middle latitudes in the Southern Hemisphere, mainly Brazil and Australia (Zerbini *et al.*, 1996; Acevedo *et al.*, 2006; Meirells *et al.*, 2011, etc.). In higher latitudes, data on dwarf minke whales has only been from sightings (Kato and Fujise, 2000, Acevedo *et al.*, 2011, Kato *et al.* in press). Until the present study there was no information on the biology of dwarf minke whales in higher latitudes. Arnold *et al.* (1987) reported a considerable number of the dwarf minke whale strandings and sporadic sightings in the austral winter. The 80% of sightings were in the waters off Queensland, Australia, in June and July (Arnold, 1997), which would be consistent with the north-south seasonal movements exhibited by other austral balaenopterids. However, there have also been mid-summer strandings of dwarf minke whales on the southeast coast of Australia (Arnold *et al.*, 1987; Zerbini *et al.*, 1996; Kemper, pers. comm.) and sightings off Brazil (at 23°S) during the month of January (Hassel *et al.*, 2003). Therefore, it is possible that migrations are dispersed seasonally but not undertaken by all individuals.

The relative distributions of dwarf minke whales and Antarctic minke whales in winter are not well known, although dwarf minke whales were found closer inshore than Antarctic minke whales in the waters off both Brazil as well as the east coast of South Africa (Best, 1985; Zerbini *et al.*, 1996). Published information (Arnold, 1997; Arnold *et al.*, 2005) suggested that a large proportion of dwarf minke whales remain in lower to mid-latitudes during summer, even though they can be found as far south as the Antarctic Convergence. Kato *et al.* (in press) examined all of dwarf minke whale sightings made during the 1994/95 to 2003/04 IDCR/SOWER cruises and reached almost the same conclusion as the present study in terms of sighting distribution. Further sighting information, combined with experiments such as photo-identifications, will provide a clearer understanding on their distributions and movements.

The migration of dwarf minke whales as far south as the Antarctic Convergence in summer is latitudinally of a much wider range than generally expected, as dwarf minke whales are thought to prefer coastal zones in low and middle latitudes. However, this may not be unnatural when considered as an adaptive radiation process of the minke whale clade.

In both hemispheres, minke whales are widely distributed from the ice edge to tropical waters while developing or dividing into closely related species or subspecies. In this interpretation, they might further adapt this cline along the allopatric speciation. The minke whale is one of the most cosmopolitan groups and has a clear morphological cline from North Pacific or North Atlantic common minke whales to Antarctic minke whales. Dwarf minke whales may have evolved in an ecological niche between Northern Hemisphere common minke whales and Antarctic minke whales. Inferring from this relationship, it can be said that the same interpretation is also true morphologically and perhaps behaviorally for food and feeding habits. Those of the dwarf minke whales are somewhere between North Pacific or North Atlantic common minke whales and Antarctic minke whales. Both Best (1985) and Arnold *et al.* (1987) indicated dwarf minke whales have distinct morphological features and they bear a closer morphological resemblance to Northern Hemisphere common minke whales rather than to Antarctic minke whales. The present study also identified these characteristics in-depth with a larger sample size and the use of morphometric analyses.

Pastene *et al.* (2007) provided mtDNA sequence evidence for the separation of the two species, the Antarctic minke whale and the common minke whale, and at least three sub-species of the common minke whale. They hypothesized that the two species diverged in the Southern Hemisphere less than

5 million years ago, and that the current subspecies of the common minke whale diverged after the Pliocene some 1.5 million years ago. Furthermore, Pastene *et al.* (2010) provided mtDNA sequence evidence for the genetic separation of the dwarf minke whale in the Southern Hemisphere. The study used samples from JARPA in the western South Pacific sector of the Antarctic, Tonga and New Zealand (western South Pacific: WSP), as well as from Brazil, Chilean Patagonia and Antarctic Peninsula (western South Atlantic: WSA). They found phylogenetic differences between dwarf minke whales in the WSP and WSA, with dwarf minke whales from the WSA being closer to North Atlantic common minke whales than to dwarf minke whales from the WSP. Glover *et al.* (2013) provided microsatellite DNA evidence for the separation of the two species and three subspecies of the common minke whale. These genetic analyses used the dwarf minke whale specimens from this study.

Nakamura *et al.*, (2018) showed that there were clear morphological differences in the white patch of the flipper between North Pacific and North Atlantic common minke whales, which have been recently recognized as two distinctively separate subspecies. Further, the length between the tip of flipper to the proximal border of white patch relative to the total flipper length was significantly larger in the North Atlantic (74.31%) as compared to the North Pacific (63.62%) common minke whales. Also, the mean angle between the proximal boundary line of the white patch and the longitudinal axis of the flipper was significantly different between the North Atlantic (70.05 degrees) and the North Pacific (92.29 degrees) common minke whales. Therefore, a numerical comparison of the white patch on the flipper/shoulder should be conducted in the future for the three sub-species of common minke whales.

Morphometric analyses on both the body proportion and the skull revealed at least three types of common minke whale clade can be distinguished. Also, the flipper/shoulder portion is a consistent and reliable characteristic for distinguishing the three types. As examined by Nakamura *et al.* (2018), the white patch of the flipper/shoulder portion is wider in the following order; dwarf minke whale > North Atlantic common minke whale > North Pacific common minke whale. This is an additional indication that the dwarf minke whale is closer to the North Atlantic common minke whale. While it is still inconclusive due to small sample size, the cluster analyses on body proportion and skull morphometry (Fig. 12) in the present study supports this hypothesis. Before reaching the final conclusion on the taxonomic status of dwarf minke whales, there are some outstanding issues to be pursued. Numerical comparison of the white patch between the dwarf minke whale and the North Atlantic common minke whale needs to be conducted. In addition, in light of the genetic differences suggested by several studies, morphological and morphometric comparative analyses among dwarf minke whales from different locations of the Southern Hemisphere should be carried out.

However, there is little doubt that the dwarf minke whales have diverged from other common minke whales, at least at the subspecies level. Morphometric comparison in both external body and skull proportions in the present study provided reliable evidence to identify and confirm the differences among the minke whale clade. The separation of dwarf minke whales from other common minke whale sub-species is further supported by genetic evidence. Based on such convincing evidence, dwarf minke whales from the Indo-Pacific sector of the Antarctic examined in this study should be formally described as an independent sub-species or species from other common minke whales.

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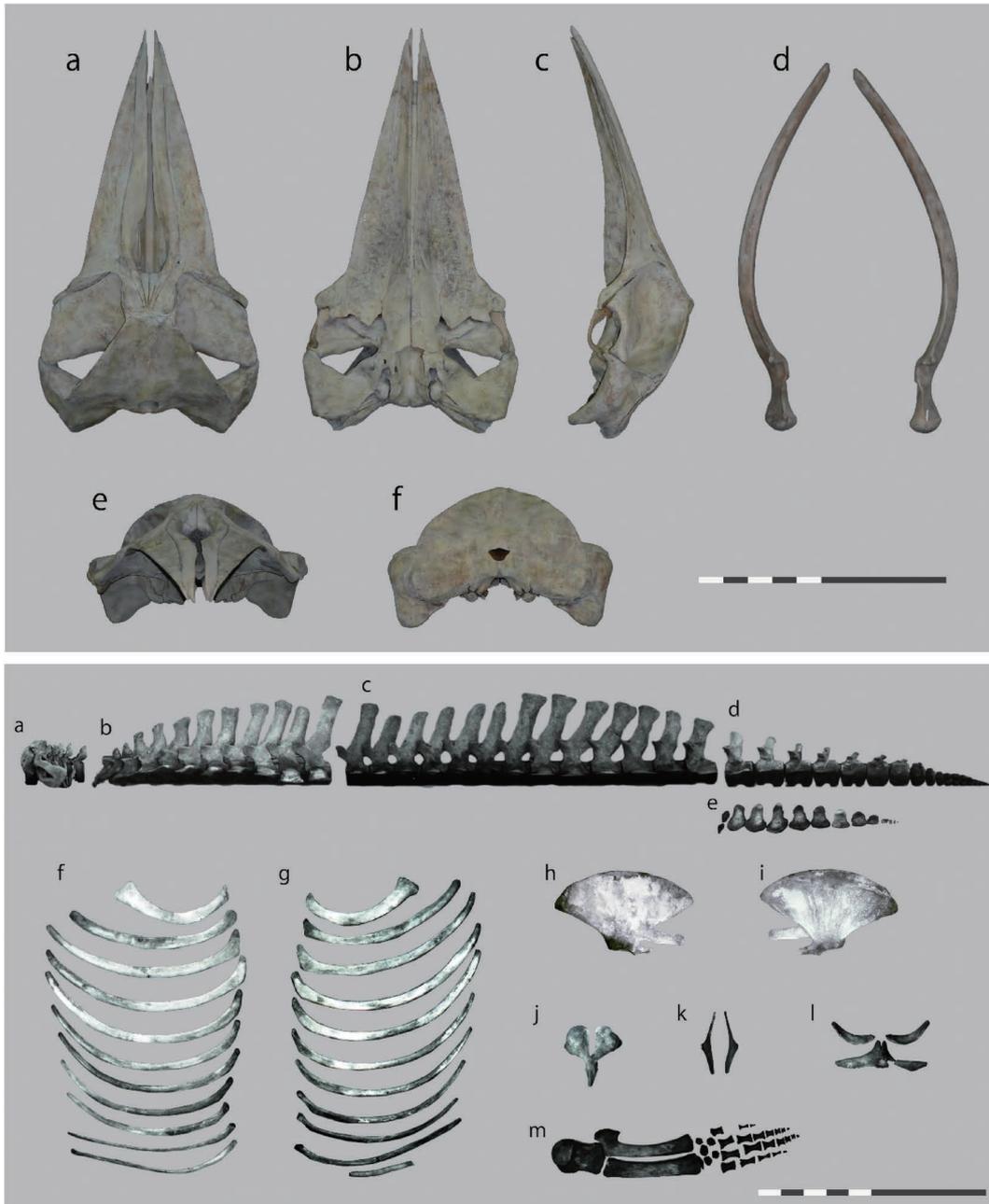
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Appendices

Appendix 1. Upper: Skull and mandible of the dwarf minke whale (MTUM-DW273); **a)** skull dorsal view, **b)** skull ventral view, **c)** skull lateral view, **d)** mandibles dorsal view, **e)** skull frontal view, **f)** backward view. **Bottom:** other bones of the same skeleton; **a)** cervical, **b)** dorsal, **c)** lumbar, **d)** caudal vertebrae, **e)** chevron, **f, g)** left and right ribs with lateral surface and **h, i)** coastal surface of right and left scapula, **j)** sternum, **k)** pelvic bone, **l)** hyoid, **m)** humerus, radius, ulna and manus on the left flipper. Scale bars are 1.00 m size marked with 0.1 m intervals.



Appendix 2. List of skeletal measurements by the standard measuring method for all dwarf minke whales examined in the present skeletal analysis.

Measurement points	87/88 273		88/89 013		88/89 014		88/89 070		89/90 199		88/89 227		89/90 215		92/93 330	
	7.01		6.99		6.6		5.94		5.41		7.02		7.07		7.17	
	M	%	F	%	M	%	F	%	M	%	F	%	F	%	F	%
Condylobasal length	159.7	163.4	149.0	133.1	122.3	164.7	169.2	156.1								
Length of rostrum	101.4	63.5	106.0	64.9	81.6	111.0	67.4	112.0	66.2	106.8	68.4	65.7±1.94				
Length of premaxillary (L)	119.3	74.7	119.4	73.1	109.8	73.7	97.9	73.6	120.0	72.9	122.8	72.6	119.8	76.7	73.9±1.44	
Length of premaxillary (R)	120.0	75.1	121.3	74.2	109.3	73.4	98.5	74.0	92.0	75.2	120.8	72.3	120.2	77.0	74.3±1.44	
Length of maxillary (L)	117.2	73.4	114.3	70.0	105.5	70.8	94.3	70.8	115.2	69.9	119.3	70.5	111.4	71.4	71.1±1.18	
Length of maxillary (R)	117.3	73.5	114.8	70.3	105.0	70.5	94.1	70.7	115.4	70.1	119.3	70.5	112.8	72.3	71.1±1.26	
Tip of premaxillary to tip of maxillary (L)	4.5	2.8	8.4	5.1	8.3	5.6	8.7	6.5	10.7	6.5	9.6	5.7	10.3	6.6	5.5±1.33	
Tip of premaxillary to tip of maxillary (R)	4.9	3.1	9.8	6.0	9.2	6.2	5.7	4.3	10.7	6.5	8.3	4.9	10.5	6.7	5.4±1.34	
Tip of premaxillary to nares, anterior	109.0	68.3	106.2	65.0	96.8	65.0	85.9	64.5	82.2	67.2	109.1	66.2	110.4	65.2	104.2	66.8
Tip of premaxillary to vertex	123.7	77.5	126.5	77.4	116.0	77.9	103.7	77.9	96.3	78.7	128.3	77.9	131.7	77.8	125.5	80.4
Tip of premaxillary to palatine, anterior (L)	99.5	62.3	102.3	62.6	97.8	65.6	85.8	64.5	108.2	65.7	108.0	63.8	100.2	64.2	64.1±1.33	
Tip of premaxillary to palatine, anterior (R)	99.8	62.5	105.2	64.4	97.8	65.6	86.9	65.3	78.7	64.3	107.6	65.3	108.3	64.0	100.1	64.1
Tip of premaxillary to palatine, posterior (L)	134.5	84.2	137.4	84.1	128.1	86.0	111.7	83.9	142.2	86.3	145.3	85.9	135.2	86.6	85.3±1.16	
Tip of premaxillary to palatine, posterior (R)	134.5	84.2	139.2	85.2	127.6	85.6	111.7	83.9	102.8	84.1	141.3	85.8	143.2	84.6	135.5	86.8
Tip of premaxillary to pterygoid process (L)	144.0	90.2	146.3	89.5	134.6	90.3	119.7	89.9	150.3	91.3	153.8	90.9	143.1	91.7	90.5±0.76	
Tip of premaxillary to pterygoid process (R)	143.8	90.0			134.8	90.5	119.3	89.6	108.4	88.6			152.3	90.0	143.3	91.8
Tip of premaxilla to posterior edge of occipital bone (L)	170.0	106.4	165.7	101.4	156.8	105.2	139.1	104.5	173.4	105.3	177.8	105.1	165.3	105.9	104.8±1.63	
Tip of premaxilla to posterior edge of occipital bone (R)	169.4	106.1	166.1	101.7	155.9	104.6	138.7	104.2	127.4	104.2	172.0	104.4	176.8	104.5	165.3	105.9
Tip of premaxilla to posterior edge of temporal bone (L)	164.2	102.8	168.7	103.2	153.5	103.0	136.5	102.6	169.4	102.9	172.2	101.8	162.7	104.2	102.9±0.74	
Tip of premaxilla to posterior edge of temporal bone (R)	164.8	103.2	171.2	104.8	152.2	102.1	136.5	102.6	124.0	101.4	168.2	102.1	170.7	100.9	162.7	104.2
Breadth of maxillary, posterior edge	19.0	11.9	14.2	8.7	14.3	9.6	14.0	10.5	11.6	9.5	19.0	11.5	15.3	9.0	17.9	11.5
Breadth of premaxillary, posterior edge	3.0	1.9	3.4	2.1	3.2	2.1	2.1	1.6	1.3	1.1	4.8	2.9	3.2	1.9	3.0	1.9
Tip of premaxillary to anterior end of vomer, median	21.2	13.3	17.7	10.8	18.3	12.3	19.3	14.5	17.9	14.6	21.7	13.2	18.5	10.9	16.3	10.4
Length of vomer	122.4	76.6	131.3	80.4	116.2	78.0	107.0	80.4	93.7	76.6	127.6	77.5	136.5	80.7	126.1	80.8
Breadth of rostrum at base	55.1	34.5	50.7	31.0	51.2	34.4	49.2	37.0	43.8	35.8	53.8	32.7	59.3	35.0	58.2	37.3
Breadth of premaxillary at base	17.3	10.8	15.4	9.4	12.8	8.6	11.7	8.8	11.3	9.2	13.7	8.3	12.8	7.6	13.2	8.5
Breadth of rostrum at middle	31.4	19.7	30.7	18.8	30.5	20.5	28.7	21.6	23.7	19.4	34.2	20.8	36.4	21.5	34.8	22.3
Breadth of premaxillary at middle	12.6	7.9	12.7	7.8	12.7	8.5	11.8	8.9	9.8	8.0	15.2	9.2	16.5	9.8	15.4	9.9
Greatest breadth of premaxillary	22.2	13.9	20.2	12.4	19.2	12.9	17.4	13.1	15.9	13.0	22.3	13.5	22.0	13.0	22.8	14.6
Breadth of cranium, maxillaries	79.1	49.5	76.0	46.5	73.8	49.5	65.9	49.5	57.6	47.1	78.7	47.8	82.8	48.9	80.5	51.6

Appendix 2. (Continued.)

Measurement points	87/88 273		88/89 013		88/89 014		88/89 070		89/90 199		88/89 227		89/90 215		92/93 330		Mean±S.D. %
	Specimen ID		Body length (m)		Sex		F		M		F		F		F		
	cm	%	cm	%	cm	%	cm	%	cm	%	cm	%	cm	%	cm	%	
Breadth of cranium, anterior edge of zygomatic process	89.1	55.8	84.5	51.7	80.8	54.2	72.8	54.7	64.7	52.9	86.3	52.4	91.5	54.1	89.4	57.3	54.1±1.82
Breadth of cranium, middle of orbital foramen	80.1	50.2	77.5	47.4	72.3	48.5	66.7	50.1	58.6	47.9	77.7	47.2	83.0	49.1	80.4	51.5	49±1.51
Breadth of occipital bone	69.5	43.5	63.3	38.7	59.3	39.8	51.2	38.5	49.4	40.4	66.4	40.3	62.6	37.0	61.7	39.5	39.7±1.9
Breadth of cranium, middle of zygomatic process	89.3	55.9	82.1	50.2	79.4	53.3	71.8	53.9	64.6	52.8	85.3	51.8	88.5	52.3	87.7	56.2	53.3±2.01
Length from upper ridge of foramen magnum to superior part of occipital bone	40.4	25.3	40.4	24.7	36.4	24.4	31.4	23.6	27.7	22.6	40.2	24.4	43.2	25.5	37.3	23.9	24.3±0.93
Greatest breadth of palatine	24.8	15.5	23.3	14.3	23.8	16.0	21.8	16.4	18.5	15.1	22.7	13.8	26.5	15.7	25.3	16.2	15.4±0.93
Length of palatine (L)	36.8	23.0	37.4	22.9	32.3	21.7	28.3	21.3	26.6	21.7	36.2	22.0	37.8	22.3	37.7	24.2	22.4±0.94
Length of palatine (R)	37.1	23.2	36.1	22.1	32.3	21.7	27.3	20.5	27.0	22.1	35.8	21.7	36.4	21.5	37.1	23.8	22.1±1.02
Breadth of palatine, posterior	25.3	15.8	22.8	14.0	23.1	15.5	21.3	16.0	21.7	17.7	27.3	16.6	27.7	16.4	26.7	17.1	16.1±1.14
Breadth across hamular processes of pterygoid	12.9	8.1	12.7	7.8	11.7	7.9	11.3	8.5	11.6	9.5	13.8	8.4	14.4	8.5	12.8	8.2	8.3±0.54
Length of orbit (L)	17.0	10.6	15.0	9.2	16.5	11.1	15.5	11.6	14.5	11.9	16.5	10.0	16.5	9.8	16.5	10.6	10.6±0.92
Length of orbit (R)	16.5	10.3	16.0	9.8	15.5	10.4	15.5	11.6	14.0	11.4	17.0	10.3	16.0	9.5	16.5	10.6	10.5±0.74
Height of cranium	50.0	30.6	45.1	30.3	34.3	25.8	34.3	25.8	37.2	30.4	49.4	30.0	51.5	30.4	53.4	34.2	30.2±2.45
Length of nasals	14.9	9.3	16.3	10.0	14.5	9.7	14.0	10.5	10.8	8.8	17.8	10.8	18.7	11.1	17.8	11.4	10.2±0.89
Breadth of nasal, posterior	1.1	0.7	2.0	1.2	1.3	0.9	1.1	0.8	0.8	0.7	2.6	1.6	1.2	0.7	1.9	1.2	1±0.33
Breadth of nasal at middle	4.4	2.8	5.8	3.5	4.9	3.3	4.5	3.4	3.3	2.7	7.1	4.3	6.5	3.8	5.3	3.4	3.4±0.53
Minimum breadth of parietal bones	18.5	11.6	16.4	10.0	15.3	10.3	16.5	12.4	12.8	10.5	20.1	12.2	19.4	11.5	20.0	12.8	11.4±1.05
Height of foramen magnum	6.4	4.0	5.9	3.6	7.3	4.9	6.6	5.0	6.3	5.2	6.3	3.8	6.3	3.7	6.7	4.3	4.3±0.61
Breadth of foramen magnum	8.2	5.1	7.8	4.8	6.0	4.0	7.3	5.5	7.4	6.1	7.1	4.3	6.5	3.8	7.3	4.7	4.8±0.75
Breadth across occipital condyles	17.0	10.6	16.7	10.2	15.7	10.5	15.8	11.9	13.3	10.9	14.3	8.7	16.8	9.9	17.2	11.0	10.5±0.93
Breadth of occipital condyle (L)	6.8	4.3	7.0	4.3	6.2	4.2	6.6	5.0	5.3	4.3	6.8	4.1	6.7	4.0	6.3	4.0	4.3±0.31
Breadth of occipital condyle (R)	6.9	4.3	7.0	4.3	6.5	4.4	6.2	4.7	5.3	4.3	6.3	3.8	6.5	3.8	6.8	4.4	4.2±0.28
Height of occipital condyle (L)	10.9	6.8	9.8	6.0	10.1	6.8	9.2	6.9	8.6	7.0	8.8	5.3	10.0	5.9	9.8	6.3	6.4±0.6
Height of occipital condyle (R)	11.1	7.0	10.0	6.1	10.0	6.7	9.2	6.9	8.4	6.9	8.9	5.4	10.0	5.9	9.8	6.3	6.4±0.56
Length of tympanic bulla (L)	8.3	5.2	8.2	5.0	7.9	5.3	8.2	6.2	7.3	6.0	7.7	4.7	8.3	4.9	7.6	4.9	5.3±0.53
Minimum breadth of tympanic bulla (L)	4.8	3.0	5.1	3.1	4.9	3.3	5.2	3.9	4.5	3.7	5.1	3.1	4.8	3.1	4.8	3.1	3.3±0.35
Greatest breadth of tympanic bulla (L)	6.1	3.8	6.3	3.9	6.1	4.1	6.2	4.7	5.7	4.7	5.9	3.6	5.9	3.8	5.9	3.8	4.1±0.43
Thickness of tympanic bulla at middle (L)					4.3	2.9	4.5	3.4	3.8	3.1	4.3	2.6	4.2	2.5	4.0	2.6	2.8±0.35
Skull height					50.0	30.6	45.1	30.3	34.3	25.8	37.2	30.4	49.4	30.0	51.5	36.1	30.5±3.01
Minimum width of the skull at squamous temporal					17.4	10.6	15.8	10.6	14.9	11.2	17.1	10.4	14.8	8.7	17.2	11.0	10.5±0.84

Appendix 2. (Continued.)

Measurement points	87/88 273		88/89 013		88/89 014		88/89 070		89/90 199		88/89 227		89/90 215		92/93 330		Mean±S.D. %
	cm	%	cm	%	cm	%											
Specimen ID	87/88 273		88/89 013		88/89 014		88/89 070		89/90 199		88/89 227		89/90 215		92/93 330		
Body length (m)	7.01		6.99		6.6		5.94		5.41		7.02		7.07		7.17		
Sex	M		F		M		F		M		F		F		F		
	cm	%	cm	%	cm	%											
Occipital bone width at jugal process			36.8	22.5	36.2	24.3	36.2	27.2	21.7	17.7	46.6	28.3	43.3	25.6	41.3	26.5	24.6±3.56
Length of mandible, straight (L)	164.5	103.0	167.0	102.2	155.0	104.0	140.0	105.2	127.0	103.8	170.8	103.7			165.0	105.7	104±1.2
Length of mandible, straight (R)	155.4	97.3	157.4	96.3	146.0	98.0	133.5	100.3	120.7	98.7	161.0	97.8			154.8	99.2	98.2±1.3
Length of mandible, curved (L)	156.2	97.8	158.0	96.7	145.8	97.9	133.5	100.3	121.5	99.3	162.0	98.4	167.0	98.7	154.5	99.0	98.5±1.1
Length of mandible, curved (R)	164.5	103.0	166.4	101.8	154.0	103.4	139.9	105.1	126.0	103.0	170.8	103.7	167.5	99.0	165.5	106.0	103.1±2.12
Breadth of mandible at middle (L)	7.0	4.4	6.8	4.2	6.4	4.3	6.0	4.5	4.7	3.8	7.5	4.6	6.8	4.0	6.8	4.4	4.3±0.24
Breadth of mandible at middle (R)	7.0	4.4	7.1	4.3	6.5	4.4	6.2	4.7	4.7	3.8	7.3	4.4	6.8	4.0	7.0	4.5	4.3±0.26
Height of mandible at middle (L)	10.4	6.5	10.0	6.1	9.8	6.6	9.7	7.3	7.6	6.2	11.1	6.7	11.8	7.0	10.6	6.8	6.7±0.38
Height of mandible at middle (R)	10.5	6.6	10.3	6.3	10.2	6.8	9.5	7.1	7.7	6.3	11.2	6.8	12.0	7.1	10.7	6.9	6.7±0.32
Height of mandible at coronoid process (L)	21.5	13.5	21.0	12.9	19.3	13.0	18.4	13.8	16.0	13.1	23.3	14.1	23.2	13.7	21.4	13.7	13.5±0.46
Height of mandible at coronoid process (R)	21.4	13.4	21.2	13.0	19.4	13.0	18.5	13.9	16.3	13.3	23.2	14.1	23.7	14.0	21.6	13.8	13.6±0.44
Height of mandible at coronoid (L)	16.8	10.5	16.1	9.9	14.3	9.6	14.4	10.8	12.1	9.9	18.3	11.1	17.3	10.2	17.7	11.3	10.4±0.63
Height of mandible at coronoid (R)	16.4	10.3	16.1	9.9	14.8	9.9	14.4	10.8	12.3	10.1	18.5	11.2	18.3	10.8	17.3	11.1	10.5±0.54
Breadth of mandible at coronoid (L)	10.2	6.4	10.0	6.1	9.4	6.3	9.3	7.0	7.7	6.3	10.7	6.5	11.5	6.8	11.7	7.5	6.6±0.46
Breadth of mandible at coronoid (R)	11.0	6.9	9.9	6.1	9.3	6.2	9.1	6.8	8.0	6.5	10.7	6.5	11.3	6.7	11.2	7.2	6.6±0.36