ISSN 0917-0537

SCIENTIFIC REPORTS OF CETACEAN RESEARCH

Number 1

September 1990

The Institute of Cetacean Research
Tokyo Japan

*Sci. Rep. Cetacean
Res., No.1*

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OF
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Editiorial Board

Tokyo Suisan Build., 4-18 Toyomi-cho, Chuo-ku, Tokyo, 104 Japan
Printed in Japan by Kenkyusha Printing Co., Ltd.
7-14-8, Nobidome, Niiza-shi, Saitama, Japan

Price: ¥5,000

SCIENTIFIC REPORTS OF CETACEAN RESEARCH

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COMPARISON OF SONGS OF HUMPBACK WHALES (*MEGAPTERA NOVAEANGLIAE*) RECORDED IN JAPAN, HAWAII, AND MEXICO DURING THE WINTER OF 1989

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AND PAUL H. FORESTELL[3]

ABSTRACT

Recordings of humpback whale (*Megaptera novaeangliae*) song were obtained between 10 March and 14 April 1989 from the Bonin Islands and the Ryukyuan Islands of Japan, the Hawaiian Islands, and the southeastern Baja Peninsula of Mexico. Through analyses of the song samples obtained, seven "themes" were identified in Hawaiian and in Bonin song and six in Mexican song. Theme similarities across these three regions arranged themselves hierarchically: Hawaii and Mexico shared five themes in common, and did not share three ; Hawaii and Bonin shared four themes and did not share three; and Mexico and Bonin shared three themes and did not share six. Three themes appeared in all three regions. The song samples from Ryukyu were all of short duration and were likely an incomplete record of the entire song repertoire. Nevertheless, of the three themes identified in the Ryukyuan samples, two appeared in Bonin song and none in Mexican and Hawaiian song. Overall, the thematic data suggested that there is acoustic contact during some portion of the migratory cycle among the whales wintering in Mexico, Hawaii, and the Bonin Islands.

Key words: humpback whale, acoustic communication, stock identity, song dialects

INTRODUCTION

Humpback whales (*Megaptera novaeangliae*) migrate annually between high-latitude summer grounds where feeding occurs and low-latitude winter grounds. The behavior of the whales on the winter grounds (e.g., Herman, Forestell and

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Antinoja, 1980; Tyack, 1981; Darling, Gibson and Silber, 1983; Glockner and Venus, 1983; Baker and Herman, 1984) and their reproductive physiology during the winter months (Chittleborough, 1955, 1958, 1965) suggest that reproductive activities are predominant during the winter season.

Humpback whales produce a complex vocalization first characterized as "song" by Payne and McVay (1971). Singing peaks during the winter months (Winn and Winn, 1978; Thompson and Friedl, 1982; Helweg, 1989), although it has been reported occasionally late in the fall on the feeding grounds (Matilla, Guinee and Mayo, 1987; McSweeney, Chu, Dolphin and Guinee, 1989) and along migratory pathways (Tyack and Whitehead, 1983; Kaufman and Jenkins, 1985). The singing whales that have been sexed have proven to be male (Winn, Bischoff and Taruski, 1973; Glockner, 1983). The correlation of song production and seasonal gonadal activity suggests that song plays a role in the mating system, although that role is not yet established (cf. Tyack, 1981, 1983; Baker and Herman, 1984; Mobley, Herman and Frankel, 1988).

Humpback song is dynamic; songs in a given geographical region change during the course of each winter season, yet at any given time singers within the region appear to converge on the same or nearly the same rendition (Winn and Winn, 1978; Guinee, Chu and Dorsey, 1983; Payne, Tyack and Payne, 1983; Payne and Payne, 1985). The function of the seasonal changes in song and of the convergence of most singers on the current rendition remain speculative (cf. Winn and Winn, 1978; Frumhoff, 1983; Payne and Guinee, 1983; Payne *et al.*, 1983; Payne and Payne, 1985; Chu and Harcourt, 1986).

Previous studies have found substantial song differences between geographically isolated stocks of humpbacks in separate oceans: in particular, the North Atlantic, North Pacific, and South Pacific Oceans (Winn, Thompson, Cummings, Hains, Hudnall, Hays and Steiner, 1981; Payne and Guinee, 1983; Kaufman and Jenkins, 1985). Similarities in the songs of whales in different wintering areas within an ocean have also been found (Winn and Winn, 1978; Payne and Guinee, 1983). These authors have suggested that whales in different wintering areas singing the same rendition of song must be in acoustic contact during some portion of their annual cycle when song is produced. Contact may occur in the summer feeding grounds, during migration, through visits to more than one wintering ground during a season by some whales, and through visits to different wintering grounds in different seasons by some whales.

Payne and Guinee (1983) found that humpback songs recorded at about the same time near Maui in the Hawaiian Isalands and at Isla Socorro off the west coast of Mexico were similar to each other, suggesting that the whales in these two areas may constitute one stock. In this paper, we extend the North Pacific analysis by comparing songs recorded at about the same time in Hawaii, Mexico, and Japan.

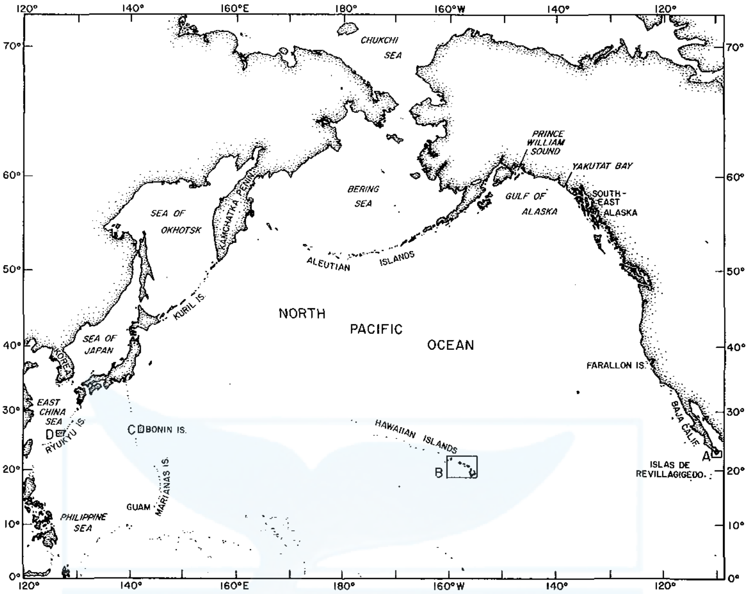

Fig. 1. The North Pacific Ocean, showing documented summer feeding sites for humpback whales from the western Gulf of Alaska through to southeast Alaska and the Farallon Islands (see text). Additionally shown are the locations of the four wintering areas from which songs were obtained in Mexico, the Hawaiian Islands, the Bonin Islands, and the Ryukyuan Islands.

The stocks of humpbacks in the North Pacific Ocean

Fig. 1 shows areas of seasonal aggregations of humpback whales in the North Pacific Ocean and neighboring waters. Five summer feeding sites have been documented in the central and eastern North Pacific (Baker, Herman, Perry, Lawton, Straley, Wolman, Kaufman, Winn, Hall, Reinke and Ostman, 1986): the Farallon Islands, southeast Alaska, Yakutat Bay, Prince William Sound, and the western Gulf of Alaska. Photographic identifications have revealed that individual whales tend to return to the same feeding site each year (Darling and Jurasz, 1983; Darling and McSweeney, 1985; Baker *et al.*, 1986), resulting in an apparent segregation of feeding stocks. The historical feeding range of humpback whales extended beyond the western Gulf of Alaska through the Aleutian Islands and northward into the Bering and Chukchi Seas, as well as into the Okhotsk Sea and along the Kamchatka Peninsula (Kellogg, 1929; Nishiwaki, 1966; Tomilin, 1967; Nikulin, 1969; Nemoto, 1978; Rice, 1978). The degree of current use of these areas is not known.

Three primary winter aggregations have been identified. One is located in Mexican waters around the Baja Peninsula, Gulf of California, and Islas de Revillagigedo (Urban and Aguayo, 1987). A second, reportedly larger, aggregation forms around the waters of the main Hawaiian Islands (Herman and

Antinoja, 1977; Herman *et al.*, 1980; Baker and Herman, 1981; Darling and Jurasz, 1983). A third wintering ground was traditionally located south of Japan, among the Bonin, Ryukyuan, and Marianas Islands (Townsend, 1935; Dawbin, 1966; Nishiwaki, 1959, 1960, 1962, 1966; Tomilin, 1967; Nikulin, 1969). The western population was greatly reduced by commercial whaling (Tomilin, 1967), and was unaccounted for as late as 1984 (Johnson and Wolman, 1984). Recent sightings indicate, however, that humpback whales are returning to the Bonin and Ryukyuan winter grounds.

Exchange among the wintering grounds *between* seasons has been documented for Hawaiian and Mexican whales, although it appears to be a relatively rare occurrence (Baker *et al.*, 1986; Darling and Jurasz, 1983; Darling and McSweeney, 1985). Travel between Mexico and Hawaii *within* a season has been reported only once thus far, using photographic data from several laboratories and the archival laser disc records of the National Marine Mammal Laboratory.[1] There are, as yet, few photographic records of humpback whales from Japanese waters, but it seems likely that the between- or within-season exchange between Hawaii and Japan would be no more frequent than that observed between Hawaii and Mexico.

Humpback whale song

Payne and McVay (1971) contended that the long, complex, vocalizations of the humpback whale in or near the winter grounds could be classified as "song" according to a definition of song as a series of sounds repeated in a recognizable sequence or pattern in time (Broughton, 1963). Payne and McVay (1971) and Payne *et al.* (1983) further described the hierarchical organization of humpback whale song: at the lowest level were discrete notes, or units, defined as "the shortest sounds in the song which seem continuous to the human ear" (Payne *et al.*, 1983, p. 15); small repeated groups of units were organized into phrases, often consisting of two subphrases, each containing repeated sounds; groups of phrases made up a theme; and, finally, the song itself was "a series of different themes given in a predictable order" (Payne *et al.*, 1983, p. 17). A song typically may last for perhaps 8 to 12 minutes. Successive songs sung without pause constituted a song session.

Transitional phrases may occur at the junction between themes (Payne, *et al.*, 1983). These transitions are often composed of the first subphrase of the preceding phrase and the second subphrase of the following phrase (Frumhoff,

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[1] *Identification of a single humpback whale traversing from Mexico to Hawaii during the 1986 winter season was made by the National Marine Mammal Laboratory, Seattle, using their computer photographic identification system and photographic records from Mexico in 1986 supplied by the Universidad Autonoma de Mexico, and records from Hawaii for that same year, supplied by the Pacific Whale Foundation. Additionally, the same whale was photo-identified in previous years in Hawaii by the Kewalo Basin Mammal Laboratory, by the Center for Whale Studies, and by the West Coast Whale Research Foundation.*

1983). Phrases within a theme may vary in the repetition rate of the subphrases or of the units (Payne and McVay, 1971; Payne, 1978).

The singing whale is most often alone (Winn and Winn, 1978; Tyack, 1981). The whale may remain submerged in a particular small area for long periods, surfacing at intervals of perhaps 8 to 15 min and then diving again after a short respiratory bout. Swimming while singing has been reported occasionally, as has singing in the company of other whales (Tyack, 1981; Baker and Herman, 1984; Frankel, Clark, Herman, Gabriele, Hoffhines, Freeman and Patterson, 1989). During some years of our observations in Hawaii, surfacing could be predicted by a series of "ratcheting" sounds, apparently similar to those described by Winn and Winn (1978) as preceding surfacing of North Atlantic humpback whales in the winter grounds near Puerto Rico. The ratchet sounds we have observed during 1987 to 1989 had a creaking, staccato character, and were usually followed by one or more short, higher frequency "whines". There is commonly a marked attenuation of sound prior to and during surfacing.

Source levels for humpback song are relatively loud, on the order of 155 dB (re 1 μPa at 1 m) (Levenson, 1972). Payne and Guinee (1983) argued, however, that humpback song can probably be heard by other whales only at distances of less than 20 km, based on the model of sound propagation developed by Payne and Webb (1971). Winn and Winn (1978) reported hearing humpback whale song on listening hydrophones at a distance as great as 32 km and Frankel *et al.*, (1989), using a three-element hydrophone array, have located some singing whales at distances estimated as 20 km. These various theories and data suggest that acoustic contact between humpback whales, for song vocalizations, is probably limited to relatively short ranges of, say, less than 40 km.

MATERIALS AND METHODS

Because humpback whale song may change to varying degrees over the course of a winter season, we chose to compare songs obtained at roughly comparable points in time from the different geographic regions. Table 1 lists the locations and dates within the Mexican, Hawaiian and Japanese regions from which our 1989 song samples were obtained, and gives the duration of each sample. Fig. 2 provides detailed maps of the specific location from which song samples were obtained within each region. Song samples were obtained in Mexico on March 10 and 11; in Hawaii on March 12 and 15, and on April 4; in the Ryukyuan Islands on March 19, 22 and 23 March; and in the Bonin Islands on April 14. Thus, with the exception of the Bonin songs and one Hawaii song, samples of song were available within the 3-week interval from March 10 to March 24. Earlier (1979) comparisons of Mexican and Hawaiian song (Payne and Guinee, 1983) were similarly based on recordings made in the month of March. The

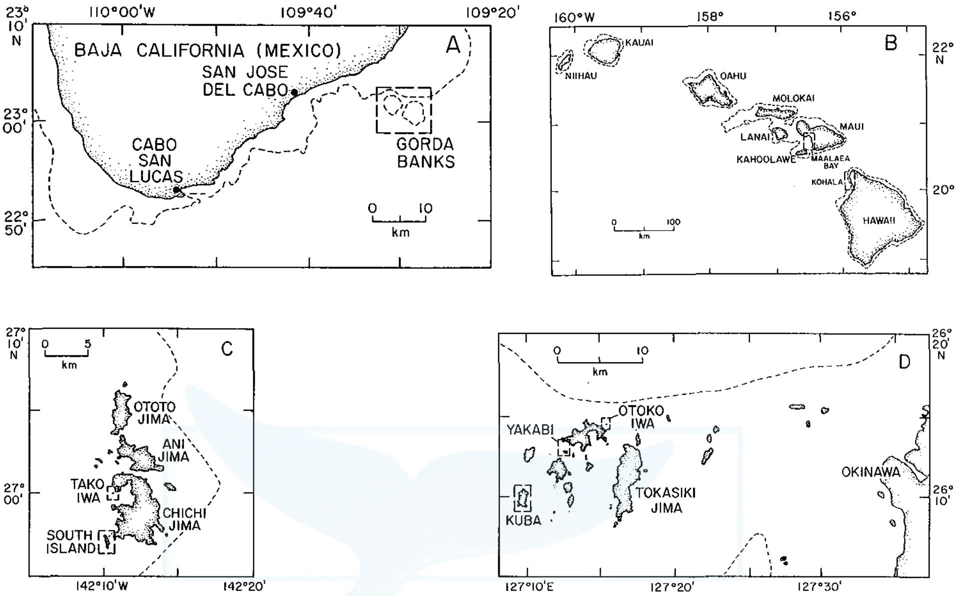

Fig. 2. Details of the study regions from which recordings were made. Each corresponds to an inset box on Fig. 1 but is not identical to the area delimited by the box in Fig. 1. The specific recording sites are shown in boxes and correspond to the locations given in Table 1. The dotted lines indicate the 200m isobath.

TABLE 1. DATES, LOCATIONS AND DURATIONS OF 1989 HUMPBACK WHALE SONG SAMPLES, AND THE RESEARCH GROUP PROVIDING EACH SAMPLE.

Date	Region (location)	Duration (min:sec)	Code	Group
10 March	Mexico (Gorda Bank)	5:13	MEX310A	CWR; UNA
10 March	Mexico (Gorda Bank)	20:20	MEX310B	CWR; UNA
11 March	Mexico (Gorda Bank)	27:05	MEX311	CWR; UNA
12 March	Hawaii (South Kohala)	30:00	HI312	KBMML
15 March	Hawaii (South Kohala)	26:24	HI315	KBMML
4 April	Hawaii (Maalaea)	31:20	HI404	PWF
19 March	Ryukyu (Otoko Iwa)	4:57	RYU319	TA; TN
22 March	Ryukyu (Kuba)	2:23	RYU322	TA; TN
23 March	Ryukyu (Yakabi)	2:56	RYU323	TA; TN
14 April	Bonin (South Island)	32:09	BON414A	PWF
14 April	Bonin (Takojima)	18:00	BON414B	PWF

Group codes: CWR = Center for Whale Research; UNA = Universidad Nacional Autononoma de Mexico; KBMML = Kewalo Basin Marine Mammal Laboratory; PWF = Pacific Whale Foundation; TA = Toba Aquarium; TN = Tsuneo Nakamura (Volvox).

hydrophones and recording equipment used by the various research groups to obtain the 1989 songs varied, but reportedly all systems had frequency responses flat from 50 Hz to at least 10,000 Hz.

The samples from Hawaii and the Bonin Islands contain full songs without interruption. Although the Mexican song samples were interrupted at several points when the research group pursued fluke photography as the singers surfaced, two of the song sessions are long enough (*ca.* 20 to 27 min) to make it likely that all sounds made by the whales are represented in the song samples (K. Balcomb, pers. comm.). The three samples from Ryukyu were all of short duration, but one (RYU319) does contain a cycle of themes that returns beyond the "starting" theme.

Sonograms of representative phrases from each theme, as well as of "atypical" transitional phrases, were made on a Kay (Series 7800) SonoGraph. Previously published sonograms of humpback song have typically limited the upper frequency to 2.0 kHz (Payne and McVay, 1971), or 2.5 kHz, and have provided tracings only of the fundamental frequency (e.g., Frumhoff, 1983; McSweeney *et al.*, 1989; Payne and Guinee, 1983; Payne *et al.*, 1983). We chose instead an upper frequency limit of 4 kHz (using an effective bandwidth of 150 Hz) because several subphrases had fundamental frequencies close to or above 2.5 kHz, and a great deal of sound energy lay in harmonics. The harmonic structure of the songs proved helpful in discriminating similarities and differences between phrases.

The obtained sonograms were used to identify units, subphrases, phrases and themes. There was some variation in the repetition rate of subphrases within phrases, and phrases within themes, but this variation occurred both within and between songs. The variation was ascribed to idiosyncrasies of particular whales rather than to a group characteristic and was not taken into consideration in the analyses of similarties and differences across regions.

Using HI315 (Table 1) as the reference song, the first theme following the surface ratchet was labelled A. This is the same criterion as used by Winn and Winn (1978) in their song analyses. Successive themes were labelled B, C, D... etc. The ratcheting sound appeared in the songs from the island of Hawaii (HI312 and HI315) and in the Bonin songs, but not in the Mexican or Ryukyuan song, nor the Hawaiian sample from Maui (HI404). The A theme was then searched for in the songs from Mexico and succeeding themes from that region were identified according to the labels used for HI315, or were given new labels if they did not appear in the Hawaii song. The Bonin themes were then analyzed using the labels identified in the Hawaiian and Mexican songs, with new labels added as needed. Finally, the Ryukyuan themes were analyzed using the labels available from the previous three regions, with one new label necessary in this last step. These procedures allowed for a comparison of theme sequences as well as theme differences.

TABLE 2. SHARED AND UNIQUE SONG THEMES

Theme	Hawaii	Mexico	Bonin	Ryukyu
A	X	X	X	
B	X	X		
C	X			
D	X	X	X	
E	X	X	X	
F1)	X		X	
G	X	X		
H		X		
I			X	X
J			X	X
K			X	
L				X

1) Ratchet sound.

RESULTS

Comparison of themes across regions

Themes from all of the song samples available in a region (Table 1) were combined to identify the themes present in that region, as shown in Table 2. A total of 12 different themes (A-L) were identified across the four regions. Hawaiian and Bonin song each contained seven themes and Mexican song six. Ryukyuan song contained only three themes but, as was noted, all song samples were of short duration.

The data yielded a hierarchy of theme similarities across regions: Hawaii and Mexico shared five themes and did not share three; Hawaii and Bonin shared four and did not share three; Mexico and Bonin shared three and did not share six; and Bonin and Ryukyu shared two and did not share six. The themes present in Ryukyuan song did not overlap with any present in Hawaiian or Mexican song. Three themes (A, D, and E) were common to Hawaiian, Mexican and Bonin song; those three are referred to here as "pan-Pacific" themes.

Fig. 3 shows sonographic records of these three pan-Pacific themes. The versions from the various regions appear very similar. Frumhoff (1983, p.83) defined "fundamental" themes as those "present in all songs of a least 90% of the song sessions recorded in both that season and at least one contiguous season." Whether the pan-Pacific themes can be termed "fundamental" in Frumhoff's sense must await data from additional seasons and from additional recordings.

The finding that no Ryukyuan theme appeared in the Hawaiian or Mexican samples, and vice-versa, suggests that the whales visiting the Ryukyuan Islands may be acoustically isolated from those visiting Hawaii or Mexico. At the same time, the very short and likely incomplete song records from the Ryukyuan Islands, the presence of two of three Ryukyuan themes in Bonin song, and the

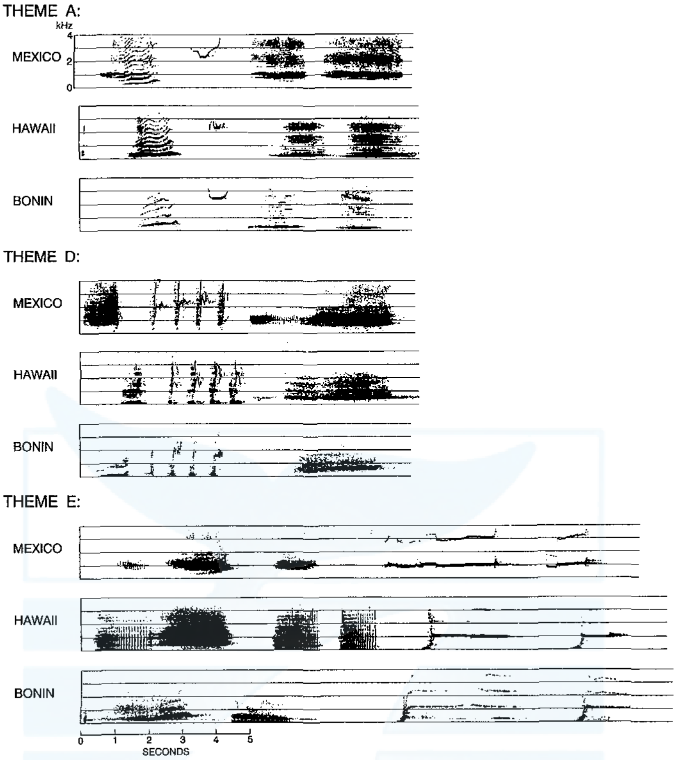

Fig. 3. Comparison of sonograms of "pan-Pacific" themes shared by song recorded in Japan, Hawaii and Mexico. Component subphrases of each theme are shown once in the figure although some may be repeated within any given phrase. Effective filter bandwidth of Kay SonoGraph was 150 Hz. Vertical scale is in 1000 Hz increments. Time is shown on horizontal axis.

partial overlap of Bonin with Hawaiian and Mexican song, weakens any case for acoustic isolation.

Fig. 4 shows sonographic records of the four themes (B, C, G and H) present in Hawaiian and/or Mexican song, but not in songs from the western Pacific. Hawaiian and Mexican song share two of these themes (B and G). Mexican song contains the unique theme H and Hawaiian song the unique theme C.

Fig. 5 shows theme F, the surface-ratchet sound, present in Hawaiian and Bonin song but not in Mexican or Ryukyuan song. As we noted earlier, the ratchet sound reliably predicted the surfacing of a singing whale in the Hawaiian songs of 1989, as well as in songs of 1988. A ratcheting sound was also reported by Winn and Winn (1978) as preceding surfacing of singing whales in the Puerto Rico Silver Bank region. Sonograms available in Winn and Winn (1978) suggest a similarity of the North Atlantic ratchet to the North Pacific sound, but it is

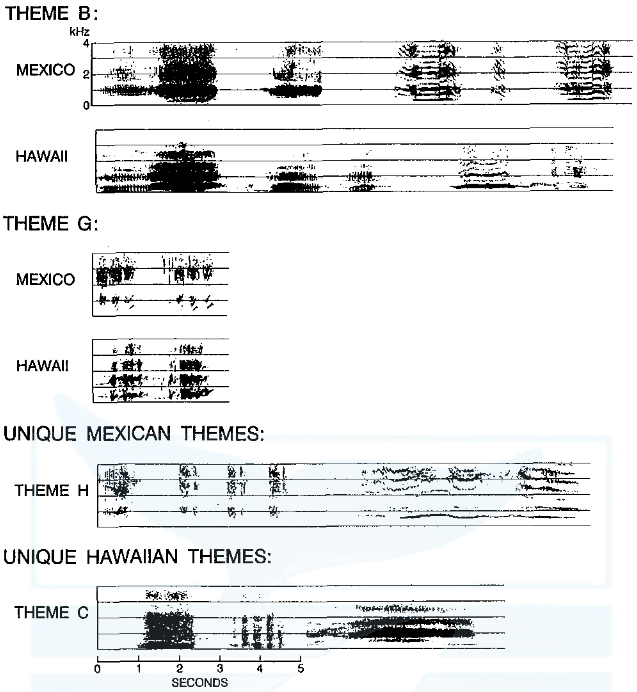

Fig. 4. Sonograms of themes found in Mexican or Hawaiian song, or both, but not present in song from Japan, prepared as in Fig. 3.

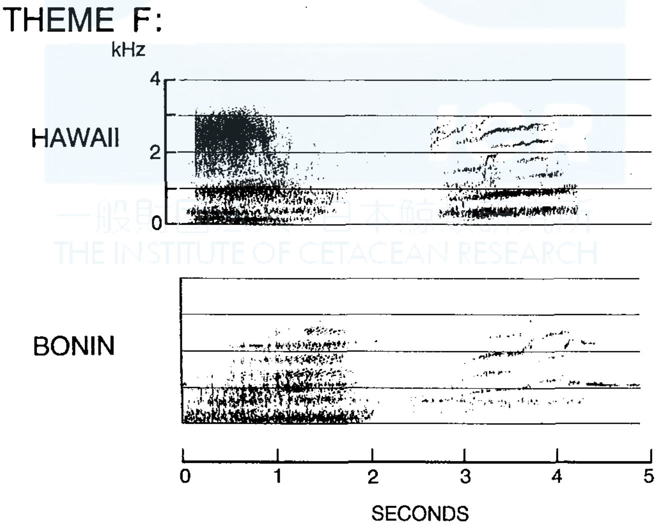

Fig. 5. Sonograms of theme F, the "surface ratchet," common to Hawaiian and Bonin song, but not present in song from Mexico or Ryukyu, prepared as in Fig. 3.

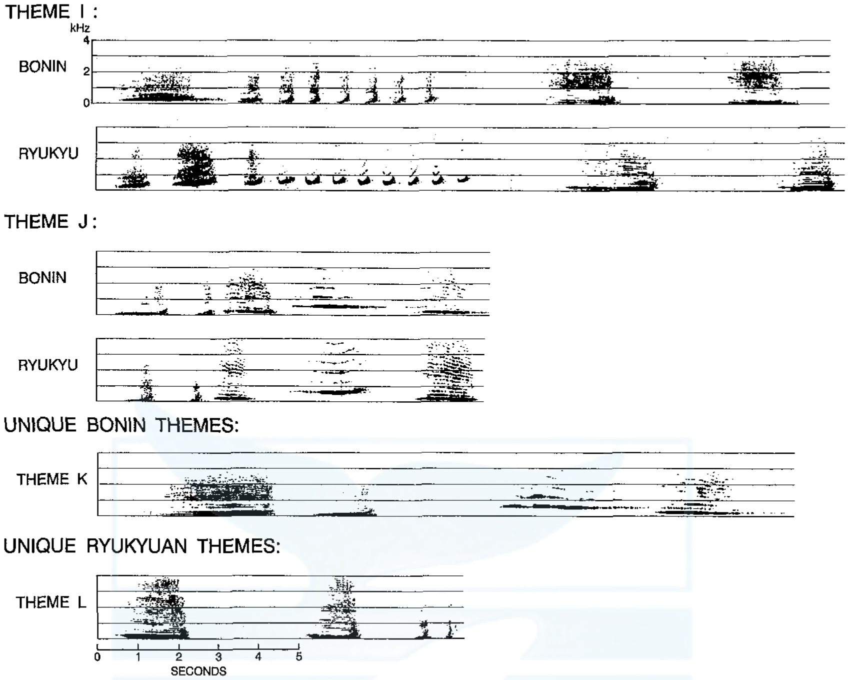

Fig. 6. Sonograms of themes found in Ryukyuan or Bonin song, or both, but not present in song from Hawaii or Mexico, prepared as in Fig. 3.

difficult to make a firm judgment from the quality of the available sonograms.

Fig. 6 describes four themes (I, J, K and L) present in Ryukyuan and/or Bonin song, but not present in Hawaiian or Mexican song. Ryukyan and Bonin song shared themes I and J. Additionally, Bonin song contains one unique theme (K). Ryukyuan theme L was not present in RYU322 or RYU323, and was produced only once in RYU319.

Comparisons of theme sequences within regions

Table 3 shows the sequence of themes in each song sample. The sequences are arranged to highlight corresponding theme sequences across the different recordings within each region. In Hawaii, the sequence DEFAB appears in the song of HI312 and of HI315. HI404 shares the sequence BCDE with HI315. The short sequences BD and DE are shared by all three samples.

The Mexican song samples show an apparent lesser degree of correspondence across song samples. The longest shared sequence is BED, found in MEX310B and MEX311. The two-theme sequence AB is found in all three samples. Again, however, the short duration of MEX310A limits this type of analysis.

TABLE 3. THEME SEQUENCES OF EACH SAMPLE OF SONG FROM EACH REGION. IDENTICAL THEMES OR THEME SEQUENCES WITHIN EACH REGION ARE ALIGNED TO HIGHLIGHT SIMILARITIES.

HI312				B		D	E		D	G	B	D	E	F	A	B						
HI315	B	F	A	B	C	D	E					D	E	F	A	B	D					
HI404				B	C	D	E				B	D										
MEX310A						A	B															
MEX310B						A	B	E	D//				B	E	D	E	D					
MEX311	B	E	D	H	G	A	B//		D	H	G	A	B	E	D				H	G	A	
BON414A									K	F	A	D	E	I	J	K	F	A	D	E	I	
BON414B	E	D	E	F	A	D	E	D		F	A	D	E	I	J		F	A	D	E	I	J
RYU319			I	L	J	I	J															
RYU322						I	J															
RYU323							J															

Note: Gaps between themes do not represent gaps in taping.
Actual breaks in taping are indicated by "//"

The two Bonin samples share a six-theme sequence FADEIJ. The shorter sequence FADE was found twice in BON414A and three times in BON414B. The Ryukyuan song samples are short and generalizations are difficult. Nevertheless, similarities are seen across samples in the sequence IJ, shared by two song samples.

It is apparent that longer sequences (three or more themes) are not shared across the different regions, but several two-theme sequences are. Hawaii, Mexico and Bonin song all share the sequences DE and the inversion ED. Additionally Hawaii and Mexico share the sequence AB. Finally, Bonin and Ryukyu share the sequence IJ.

Inverted theme sequences are rare. Payne *et al.* (1983) found only five theme inversions among 1196 two-theme sequences recorded during the 1976-77 winter season in Hawaii. In our *within*-region data, inversion of DE and ED is relatively rare. Thus, in the Hawaiian songs, DE appears five times and ED twice. Similarly, in Bonin song DE appears six times and ED twice. In Mexican song, a reverse trend occurs: ED is the more common theme, appearing five times while DE appears only once.

Fig. 7 graphs the two-theme transitions from Hawaii, Mexico and Bonin for those song sessions having the greatest number of theme sequences: HI315, MEX311 and BON414B, respectively. The graphs reveal the general orderliness in which themes are sequenced, especially for MEX311. Additionally, the figures show the inversions of themes E and D in songs of individual whales from Hawaii and Bonin and theme omissions by these same whales. Theme omissions, e.g., singing the sequence BD rather than BCD, are not unusual (Payne *et al.* 1983, Fig. 2) although omission of a fundamental theme is considered aberrant (Frumhoff, 1983).

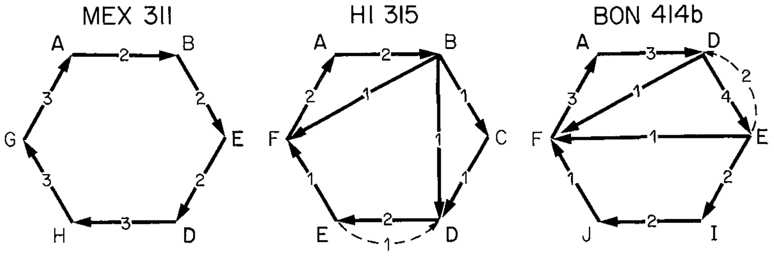

Fig. 7. Theme transitions of selected samples from Mexico, Hawaii and Bonin regions, based on data in Table 3. Frequency of transition is indicated within each arrow. Solid lines indicate usual transition order; theme reversals are indicated by dashed lines.

Unique sound units

Despite the great variability of sounds produced during a singing session, the introduction of new or unusual sounds is rare (Frumhoff, 1983). The basic "library" of sounds available to singers appears to remain relatively constant. Variability and progressive change occur mainly by recombination of basic units or phrases. Novel sounds tend to become incorporated rapidly into the songs of whales in a common wintering ground (Payne *et al.*, 1983). The presence of a few sound units in one wintering ground that do not appear in another wintering ground, while at the same time the remaining sound units are shared, may indicate that those novel sounds were developed in the winter grounds themselves when whales are acoustically isolated (because of the great distances involved) from whales in other wintering grounds.

We found only three instances of sound units unique to a given wintering ground in our song samples from Mexico, Hawaii and the Bonin Islands. The Bonin song sample coded BON414A contains a unit in Theme I that appears to be unique to this region. The unit is shown in Fig. 8a and can be described as a "pulsive scream" with a highly variable frequency structure. Furthermore, theme I contains a subphrase that is composed of a unit not found in either Mexican or Hawaiian song. This is the series of J-shaped units shown in Fig. 8b which, together, comprise the central subphrase of theme I.

The sample of Mexican song coded as MEX311 contains a complex unit, shown in Fig. 8c, that appears to be unique to the singers in Mexican waters. This unit is found in theme H and is distinguished by a rapid change of harmonic structure between the initial and subsequent subunits, as well as by a rapid traverse of frequency.

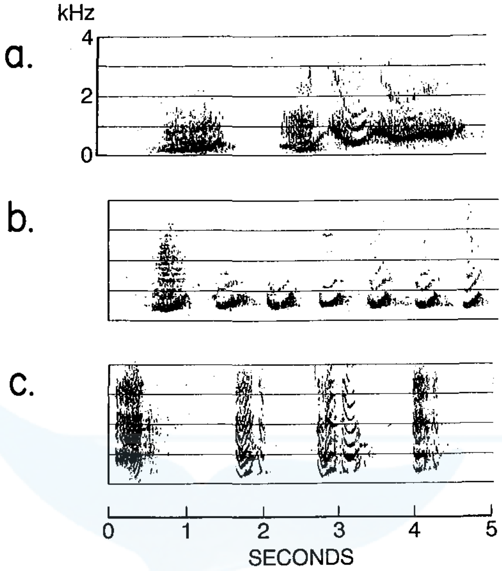

Fig. 8. Unique sound units in different wintering areas. *a*. The "pulsive scream" from Bonin theme I that is unique to the Bonin song samples. *b*. The J-shaped units that may comprise the central subphrase of theme I in Bonin song. *c*. The complex unit from Mexican theme H that is unique to the Mexican song samples.

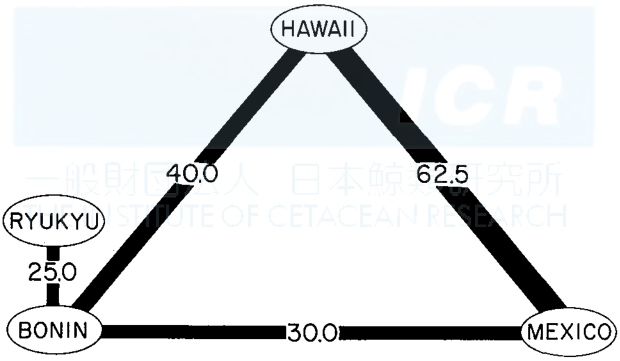

Fig. 9. The percentage of overlap of song themes from the five wintering areas, based on the data of Table 2. The width of the lines connecting paired regions is proportional to the percentage of overlap.

DISCUSSION

The comparison of themes across the different regions revealed varying degrees of theme overlap. Using the theme structure shown in Table 2, the percentage of overlap of two regions can be calculated as the number of shared themes divided by the total number of shared and unshared themes across the two regions, multiplied by 100. Fig. 9 illustrates the results obtained with this measure for each pair of regions. The largest overlap occurred for Hawaiian and Mexican song, then Hawaiian and Bonin song, then Mexican and Bonin song, and finally Bonin and Ryukyuan song. There was no overlap of Ryukyuan song with song from Hawaii or Mexico.

As we noted earlier, the Ryukyuan song samples we obtained were of very short duration, and it is probable that had longer samples been available more themes would have been found. Hence, at this time no firm conclusions are possible about the relationship between Ryukyuan song and songs from Hawaii or Mexico. The relationship between Ryukyuan song and Bonin song is probably closer than suggested by the low percentge of overlap shown in Fig. 9. Of the three Ryukyuan themes identified, two were also found in Bonin song. Ryukyu may not be a true winter terminus for humpback whales but only a temporary way-station along the migration route to the Bonin Islands or to points south, as was implied by Nishiwaki's (1959, 1960, 1962, 1966) data. In the future, further, detailed analysis of longer samples of Bonin song can help to answer questions about the degree to which whales visiting the Ryukyuan islands are affiliated with whales visiting the Bonin Islands.

The relatively large overlap of Hawaiian and Mexican song confirms earlier reports of Winn *et al.* (1981) and of Payne and Guinee (1983) of considerable song similarity across these regions. Spectrograms published in Payne and Guinee (1983) show that the seven themes found in 1979 Mexican song overlapped totally the seven found in Hawaiian song in that same year. This result is similar to our findings that five of six Mexican themes were found among the seven Hawaiian themes. Comparisons of the 1979 sonograms published by Payne and Guinee (1983) with those available here do not show any obvious similarity of themes, indicating that the song evolved considerably over the 10-year interval. This degree of change is not unexpected based on other analyses of progressive song change over years. (Payne *et al.*, 1983; Payne and Payne, 1985).

The overlap between Bonin and Hawaiian song and between Bonin and Mexican song, especially the presence of the three pan-Pacific themes in the songs of all three regions, suggests that whales in these wintering grounds are in acoustic contact during some portion of their migratory cycle. The percentage of overlap of pairings of Mexico, Hawaii and Bonin song, as shown in Fig. 9, varies directly with the distance between these locations: approximately 3,160 km from Mexico to Hawaii, 3,940 km from Hawaii to Bonin, and 7,056 km from

Mexico to Bonin. The data thus suggest a decreasing degree of acoustic contact of the whales in these separated areas as a function of distance. The distance separating the winter grounds may not be the major variable determining song similarities and differences, however, and the data on the limitation in propagation distances of song (Frankel *et al.*, 1989; Payne and Guinee, 1983; Winn and Winn, 1978) make it unreasonable to assume that whales in one winter ground could be listening to whales in another winter ground. More important variables may be the degree of spatial separation of whales in the summer feeding grounds, the spatial separation of the migration routes taken by whales journeying to the different winter grounds, and the degree to which migratory interchange occurs between summer grounds and between winter grounds.

Whales visiting Hawaii and Mexico are known to appear in some of the same feeding sites in the summer, the western Gulf of Alaska, including Prince William Sound, and southeast Alaska, in particular (Baker *et al.*, 1986; Darling and Jurasz, 1983), allowing for song exchange during the late Fall months when some singing is heard (Matilla *et al.*, 1987; McSweeney *et al.*, 1989). Additionally, whales from the feeding grounds in Prince William Sound, the western Gulf of Alaska, and southeast Alaska may share portions of their migration routes during a journey to Hawaii or Mexico, allowing for song exchange during a time when singing has been heard (Tyack and Whitehead, 1983; Kaufman and Jenkins, 1985). Also, there is some dispersion of whales from a common feeding site to the different winter grounds of Hawaii and Mexico (Baker *et al.*, 1986; Perry, Mobley, Baker and Herman, 1988), so that a common late Fall song heard in a given feeding ground could appear in different winter grounds; additionally, some convergence of song could occur after return of whales from different winter grounds to the common feeding grounds, which would manifest itself in song similarity during the subsequent winter season. Finally, although apparently rare, visits between the Mexican and Hawaiian winter regions by indivisual whales during contiguous winter seasons has also been documented (Baker *et al.*, 1986; Darling and Jurasz, 1983; Darling and McSweeney, 1985), providing a further mechanism for song exchange, provided the song has not drifted too far during the intervening year. We also noted earlier the one case reported thus far of a whale visiting both Mexico and Hawaii in a single winter season.

It seems less likely that whales visiting the western Pacific winter grounds share a migration route with whales visiting the central or eastern Pacific grounds. Contact of Mexican/Hawaiian whales with Bonin whales may take place in the summer feeding grounds, however. Nishiwaki (1966) reported the recovery of six Discovery tags in the Ryukyuan Islands from humpback whales marked in the eastern end of the Aleutian chain. This feeding region may be close enough to the western Gulf of Alaska, a documented site to which some whales return from Hawaii (Baker *et al.*, 1986), to allow for acoustic contact.

Thus at least three mechanisms—contact in the feeding grounds, common migration routes, and interchange between winter sites by individuals—seem available for song exchange between Hawaii and Mexico. In the least, the first mechanism listed may also be available for song exchange between whales visiting Hawaii and the Bonin Islands. Our findings that the songs across the three regions are not identical, that some themes are not shared, and that some unique sound units occur in Mexican and Bonin song, suggest that acoustic contact across these three principal regions—Hawaii, Mexico and the Bonin Islands—is not complete, at least during the portion of the season when we sampled song.

A final consideration is the extent to which song similarity is correlated with genetic distance, and may therefore be an indicator of the separation of stocks. Baker, Palumbi, Lambertsen, Weinrich, Calambokidis and O'Brien (1990) examined mitochondrial DNA differences among humpback whales in the Farallon Islands near central California, the Hawaiian Islands, and southeast Alaska in the North Pacific, and the Gulf of Maine in the North Atlantic. They found the greatest genetic distance between the Gulf of Maine whales and those of the North Pacific, and considerably less disparity within regions of the North Pacific. Particularly, there was virtually no difference between the Hawaiian and southeast Alaska whales. It is interesting that photographic matches have shown that a majority of the photo-identified whales from southeast Alaska winter in Hawaii (Baker *et al.*, 1986; Darling and Jurasz, 1983; Darling and McSweeney, 1985; Perry *et al.*, 1988). The genetic distance between the whales of the Farallon Islands and those from Hawaii was greater than that between Hawaii and southeast Alaska but less than that between the North Atlantic and any region of the North Pacific. Photo-identification data suggests that whales from the Farallon Islands tend to winter in Mexico primarily (Calambokidis, Steiger, Cubbage, Balcomb, Bloedel and Bockus, 1989). The analyses of song differences in this paper, as well as earlier analyses by Payne *et al.* (1983) and Winn *et al.* (1981), reveal large song differences between North Atlantic and Mexican/Hawaiian whales and, in this paper, some differences between Hawaii and Mexico whales. Thus, genetic distance and song difference appear to be positively correlated, giving some support to the thesis of Payne and Guinee (1983) that song differences may be an indicator of separate stocks. If their thesis is correct, one would expect that mitochondrial DNA analyses of whales in Japanese waters would reveal a genetic distance from Hawaiian whales at least as great as that found between Hawaiian whales and those in the Farallon Islands. Efforts to obtain miotochondrial DNA data from whales in Japanese waters should thus prove fruitful for further understanding of stock separation and the relation of song differences to stocks. Additionally illuminating would be more extensive photographic analyses of whales in Japanese waters to search for individuals that might have appeared in other years in winter grounds to the east or in summer grounds shared with whales visiting Hawaii or Mexico.

ACKNOWLEDGMENTS

We wish to thank the following people and organizations for their contribution of recordings of song: Tsuneo Nakamura and the Toba Aquairum for all samples of Ryukyuan song; Ken Balcomb and Diane Claridge of the Center for Whale Research, and Jorge Urban of Universidad Autonoma de Baja California Sur for all samples of Mexican song: the Kewalo Basin Marine Mammal Laboratory for the two samples of Hawaiian song obtained at South Kohala on the island of Hawaii; and the Pacific Whale Foundation for the samples of Bonin song and the sample of Hawaii song obtained in Maui. Recordings of Bonin song were made possible through the cooperation and support of TV-12 Tokyo, NHK Tokyo, and the Ogasawara Village Assembly. Songs recorded at South Kohala and at Mexico were supported by grants from the Center for Field Research (Earthwatch) to L.M. Herman and A. Frankel of the Kewalo Basin Marine Mammal Laboratory and to K. Balcomb of the Center for Whale Research. Sonograms were made through the cooperation of Dr V. Condax of the Department of Linguistics of the University of Hawaii.

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EXTERNAL MEASUREMENTS AND ALLOMETRY OF SOUTHERN SEI WHALE FOETUSES

AKITO KAWAMURA[1)]

ABSTRACT

External measurements and allometry of a total of 89 southern sei whale foetuses 64.0-366.0 cm in length are reported. The animals were collected during the Antarctic whaling season of 1967/68. This study was conducted to obtain numerical data on sei whale foetuses and some of their allometric features. The number of ventral grooves increased gradually after attaining *ca.* 100 cm long, and their average numbers in the largest size groups were 57.7 (♀) and 58.8 (♂). The *a*- and *b*-values as determined by the allometry formula were 0.02-9.8 and 0.93-1.18, respectively. Various growth data indicated the possibility of a monophasic-like development, with significant evenness. However, due to the limited number and size coverage of the animals, it is difficult to conclude whether the southern sei whale foetus actually shows monophasic allometry. The body proportions of the sei whale foetus showed isometric characteristics similar to those observed in the adult animal.

Key words: allometry, sei whale, foetus, Antarctic

INTRODUCTION

Exploitation of southern sei whales (*Balaenoptera borealis*) began in 1906 (Horwood, 1986, 1987), and the total number of sei whales caught in the Antarctic finally reached 171,000 (Horwood, 1986). In contrast to the other large rorqual species, heavy exploitation of the sei whale is considered to have taken place within a relatively short period, although the total catch was actually quite large.

Matthews (1938) reported body proportions of adults and foetuses of southern sei whales mainly from South Georgian waters, for a total of 55 specimens. Compared with fin whale foetuses (e.g. Ohsumi, 1960), little information is available on the growth of southern sei whale foetuses.

During the Antarctic whaling season of 1967/68, the author measured body proportions of sei whale foetuses. Since only sporadic observation was possible,

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the data for specimen number and body length are somewhat inadequate. However, the data here should facilitate biological study of the sei whale since only mean values for body proportions of sei whale foetuses are available in the literature (e.g. Matthews, 1938). This study was conducted to determine allometric features of southern sei whale foetuses and provide additional data on body measurements.

MATERIALS AND METHODS

The animals were caught by catcher boats associated with the whaling factory ship *Nisshin Maru* of Taiyo Gyogyo K.K. During the 1967-68 season, whaling was conducted in the western half of the Indian Ocean sector of the Antarctic, particularly in the quadrant including Crozet, Kerguelen and Heard Islands (see Kawamura 1974, Fig. 4).

The data for the foetuses are given in Table 1. Body lengths ranged from 64.0 to 366.0 cm. *Whale Numbers* given in Appendices II-III correspond to numbers registered in the catch logs compiled by the Fisheries Agency, Ministry of Agriculture, Forestry and Fisheries, Government of Japan.

The foetuses were measured using a handy flexible rule as long as 2.0 m. This might have caused a slight curve in scaling along the body arc for some long measurements, but no corrections were made. The measurement numbers in Appendices II-III agree with those by Mackintosh and Wheeler (1929), and some minor additions are indicated under the alphabetical headings (Fig. 1 and Appendices I-III). Ventral groove number was counted at the line connecting the anterior base of both flippers. In smaller foetuses, however, the ventral grooves were sometimes obscure or even completely absent.

TABLE 1. DATA ON SEI WHALE FOETUSES OBTAINED DURING THE ANTARCTIC SEASON OF 1967/68.

		Male	Female
Period of data		15/xii/1967 ~ 10/iii/1968	18/xii/1967 ~ 6/iii/1968
Range of body lengths (cm)		64 ~ 355	100 ~ 366
Mean body length (cm)		193.7	208.7
No. of animals measured per size group	100 cm	3	1
	101 ~ 200 cm	20	24
	201 ~ 300 cm	13	17
	301 ~ 400 cm	3	8
Total		39	50

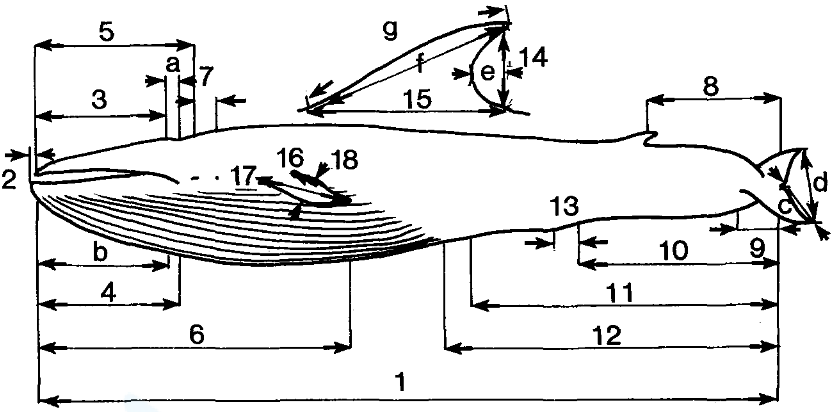

Fig. 1. Positions of external measurements of southern sei whale foetuses. For numbers see Appendix I.

RESULTS AND DISCUSSION

The number of ventral grooves increased with increased body length. In a 64.0 cm long foetus a conspicuous furrow-like structure was observed near the anterior base of the flippers. These furrows were clearly separated from the main system of ventral grooves, and became clearer in a 87.0 cm long animal. Six to ten such furrows were counted on both sides of the body. Since the ventral grooves in fin whale foetuses develop at 60.0 cm long (Ohsumi, 1960), the above-mentioned furrows may eventually develop into ventral grooves as the animal grows. The number of ventral grooves of the main system varied among individuals, but it generally increased gradually as the foetus grew (Table 2). The average numbers of ventral grooves in the 300-400 cm size group were 57.7 (male) and 58.8 (female), but the averages in fully mature adults are 47 (male) and 49 (female) (Matthews, 1938, Table XII). The difference between grown animals (Matthews, 1938) and foetuses of the present study is presumably due to the counting methods used, for instance if a different criterion was applied for counting the furrow-like structures.

The increase in the number of ventral grooves becomes gradual after the animal attains a body length of about 100 cm. In fin whale foetuses, Ohsumi (1960) reported 115 cm as the length at which development of ventral grooves may be complete. This finding, along with the above averages of 57.7 and 58.8 in 300-400 cm long sei whale foetuses, indicate increase in number of ventral grooves is nearly at the end of development.

TABLE 2. NUMBERS OF VENTRAL GROOVES IN SEI WHALE FOETUSES.1) AVERAGES APPEAR IN PARENTHESES.

Body length (cm)	Male	Female
~ 100	31 2)	No data
101 ~ 200	41 - 63 (51.8)	38 - 58 (50.0)
201 ~ 300	43 - 58 (52.2)	46 - 66 (55.8)
301 ~ 400	54 - 60 (57.7)	50 - 63 (58.8)

1) Faint furrows similar to ventral grooves at the anterior base of flippers were excluded.
2) Data for one animal.

TABLE 3. *a*- AND *b*-VALUES AS DETERMINED FROM $y = a \cdot x^b$ FOR PRINCIPAL MEASUREMENTS IN MALES OF SEI WHALE FOETUSES. FEMALES GENERALLY SHOWED A PLOT DISTRIBUTION SIMILAR TO MALES, AND ONLY THE VALUES FOR MEASUREMENT NOS 10 AND 12 ARE GIVEN FOR FEMALES.

No. of proportion measurement1)	*a*	*b*	Correlation coefficient	Total number of measurements
Male				
3	0.082	1.052	0.9912	38
4	0.169	1.023	0.9946	35
5	0.176	1.004	0.9930	36
6	0.422	1.006	0.9973	38
8	0.209	1.042	0.9939	38
9	0.136	0.968	0.9530	39
d	0.207	0.995	0.9542	37
10	0.231	1.025	0.9937	39
11	0.432	1.009	0.9957	38
12	0.886	0.931	0.9904	37
13	0.072	0.990	0.9846	37
14	9.395	1.186	0.9412	36
15	0.022	1.154	0.9497	30
17	0.079	1.083	0.9941	37
Female2)				
10	0.212	1.039	0.9911	50
12	0.928	0.925	0.9924	49

1) For measurments see Fig. 1 and Appendix I.
2) Females showed slight difference from males in these two measurements.

Measurements of relative growth of the sei whale foetuses are shown in Fig. 2, and the related data are given in Table 3. Comparing the present results on sei whale foetuses with those of Matthews (1938, Table V) for post-natal sei whales, the maximum difference in terms of percent proportions ranged −4.04 ~ +3.1 in males and −3.25 ~ +2.91 in females, while most were within the range of −1.76 ~ +1.61.

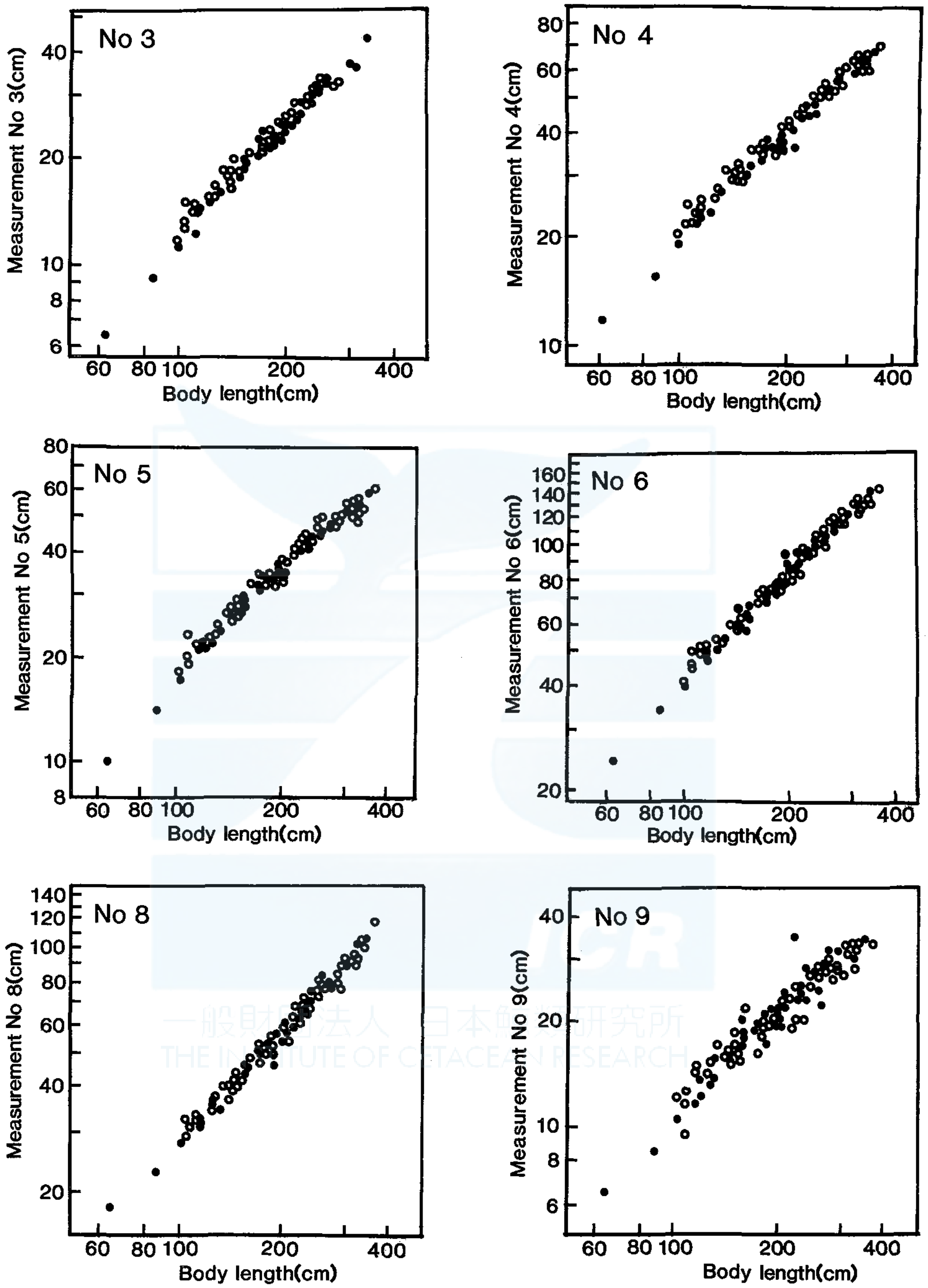

Fig. 2. Scatter plots of external measurements on body length for southern sei whale foetuses. No allometric phase was apparent within the size ranges examined. Closed circle indicates male, and open circle female. For measurements see Fig. 1 and Appendix I.

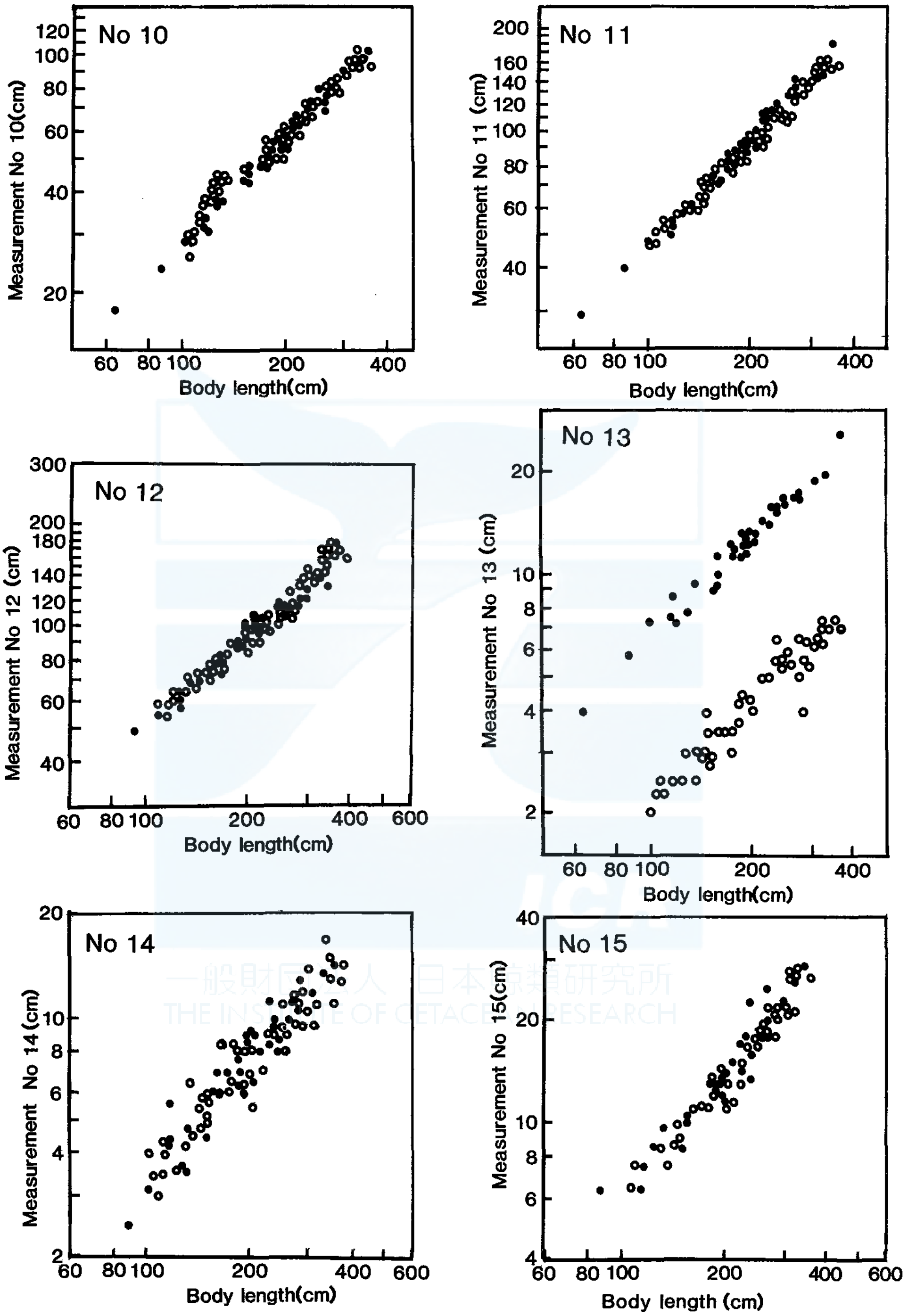

Fig. 2. (Continued)

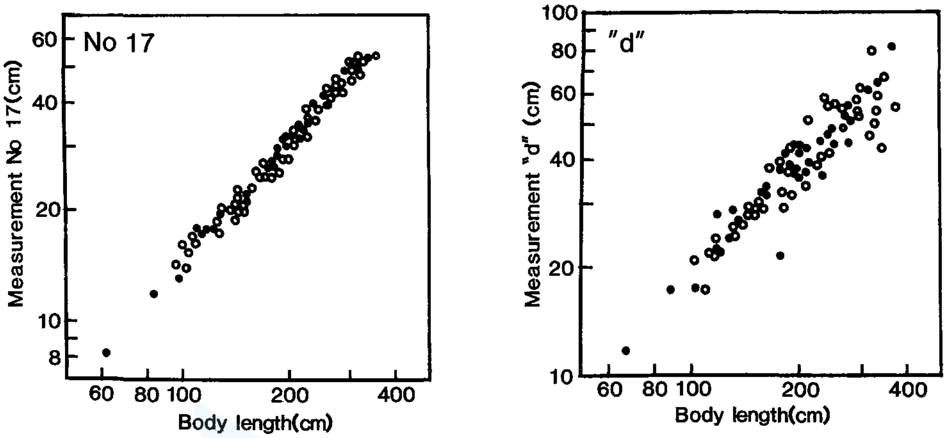

Fig. 2. (Continued)

The scatter in Fig. 2 demonstrates extremely similar or even the same functional patterns in both males and females. Although some signs suggesting possible change in the allometric phase at a length somewhere around 100 cm can be observed in Fig. 2 (e.g. Nos 4, 8, 9, 10, 13, 14 and 17), the signs for recognizing the allometric phase are obscure. The correlation coefficients for measurements No. 3 through No. 15 in male sei whale foetuses (Fig. 2) were within the range of 0.94-0.99, with high significance ($p<0.001$). In measurements No. 10 and No. 12 in females, in which greater but still small differences from males were evident, the correlation coefficients were significant, with values of 0.991 and 0.992, respectively ($p<0.001$). Monophasic-like characteristics in the allometry of sei whale foetuses are thus indicated at the size range of *ca.* 60-400 cm. Vikingsson (1988) found a relatively isometric growth for adult sei whales caught in Icelandic waters.

The a- and b-values of the allometric formula, $y = ax^b$, were in the range of 0.02-9.40 and 0.93-1.19, respectively (Table 3). In foetuses of the southern fin whale, Ohsumi (1960) found diphasic allometry in many cases, with a-values (α in Ohsumi, 1960) of 0.82-1.20 as determined by the allometry formula, and critical points mainly at body lengths of *ca.* 100-120 cm.

Due to the limited data for sei whale foetuses shorter than 100 cm and longer than 400 cm, it was difficult to determine whether the allometric phase actually occurs during the prenatal period. So far as the present results are concerned, southern sei whale foetuses appeared to exhibit monophasic allometry. However, the results cannot be considered conclusive. Matthews (1938) concluded that in the sei whale, growth is "much more evenly distributed throughout the body", and a "marked differential growth in favour of the anterior region does not occur to anything like the extent that it does in the larger whales".

ACKNOWLEDGMENTS

The author is grateful to Drs S. Ohsumi and T. Kasuya of the National Research Institute of Far Seas Fisheries, Fisheries Agency, for helpful comments and criticisms on this paper. Thanks are also due to Dr H. Kato and Mr T. Miyashita of the same institute for assistance in the data compilation.

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Appendix I. External body measurements.

1. Total length (mm)
2. Lower jaw, projection beyond tip of snout
3. Tip of snout to anterior margin of blow hole
    a. Length of blow hole
4. Tip of snout to angle of gape
    b. Tip of snout to angle of gape, inside
5. Tip of snout to center of eye
6. Tip of snout to tip of flipper
7. Center of eye to center of ear
8. Notch of flukes to posterior emargination of dorsal fin
9. Width of flukes at insertion
    c. Tail flukes, notch to tip
    d. Spread of tail flukes, tip to tip
10. Notch of flukes to center of anus
11. Notch of flukes to umbilicus
12. Notch of flukes to end of ventral grooves
13. Center of anus to center of reproductive aperture
14. Vertical height of dorsal fin
15. Length of base of dorsal fin
    e. Dorsal fin, posterior depression
    f. Anterior base to tip of dorsal fin, straight
    g. Anterior base to tip of dorsal fin along emargination
16. Flipper, tip to axilla
17. Anterior end of lower border to tip of flipper
18. Greatest width of flipper
19. Diameter of umbilical cord at base
20. Length of penis

Appendix II. External measurements and percent body proportions for the foetuses of male sei whale. December 15, 1967-March 10, 1968. Antarctic. For measurements see Fig. 1 and Appendix I.[1]

Whale number	261	1330	320	990	316	559	1029
Date of catch	25xii67	18ii68	29xii67	2ii68	28xii67	13i68	2ii68
Body length(m)	16.5	15.2	15.6	14.7	15.3	15.4	15.6
No. of Ventral grooves[2]	–	31	41	51	47	53	49
Measurements							
1.	640	870	1,004	1,155	1,165	1,170	1,270
2.	–	–	7	–	–	–	–
	–	–	0.7	–	–	–	–
3.	65	92	116	142	142	148	152
	10.2	10.6	11.6	12.3	12.2	12.6	12.0
a.	–	15	–	27	–	29	33
	–	1.7	–	2.3	–	2.5	2.6
4.	120	160	198	230	237	240	240
	18.8	18.4	19.7	19.9	20.3	20.5	18.9
b.	–	135	–	208	–	–	225
	–	15.5	–	18.0	–	–	17.7
5.	103	143	177	215	215	228	225
	16.1	16.4	17.6	18.6	18.5	19.5	17.7
6.	269	370	433	510	532	543	547
	42.0	42.5	43.1	44.2	45.7	46.4	43.0
7.	–	59	–	86	–	–	87
	–	6.8	–	7.4	–	–	6.9
8.	185	230	280	327	313	315	360
	28.9	26.4	27.9	28.3	26.9	26.9	28.3
9.	65	85	104	115	137	120	130
	10.0	9.8	10.4	10.0	11.8	10.3	10.2
c.	–	95	–	–	–	–	–
	–	10.9	–	–	–	–	–
d.	120	175	175	225	282	220	240
	18.8	20.1	17.4	19.5	24.2	18.8	18·9
10.	175	230	280	305	323	300	370
	27.3	26.4	27.9	26.4	27.7	25.6	29.1
11.	290	400	483	513	548	525	585
	45.3	45.9	48.1	44.4	47.0	44.8	46.1
12.	–	500	575	622	655	595	700
	–	57.5	57.3	53.9	56.2	50.9	55.1
13.	40	58	73	75	87	73	78
	6.3	6.7	7.3	6.5	7.5	6.2	6.1
14.	–	25	32	57	44	43	37
	–	2.9	3.2	4.9	3.8	3.7	2.9
15.	–	65	–	64	–	75	85
	–	7.5	–	5.5	–	6.4	6.7
e.	–	–	–	–	–	–	10
	–	–	–	–	–	–	0.8
f.	–	55	63	64	82	78	70
	–	6.3	6.3	5.5	7.0	6.7	5.5
g.	–	55	–	78	–	90	82
	–	6.3	–	6.8	–	7.7	6.5
16.	–	100	–	–	–	–	–
	–	11.5	–	–	–	–	–
17.	83	120	133	180	174	180	180
	13.0	13.8	13.3	15.6	14.9	15.4	14.2
18.	20	27	32	36	38	40	39
	3.1	3.2	3.2	3.1	3.3	3.4	3.1
19.	–	–	–	–	–	–	30
	–	–	–	–	–	–	2.4
20.	–	35	43	56	–	55	58
	–	4.0	4.3	4.8	–	4.7	4.6

(Continued)

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1) Bar indicates no datum

2) Number at anterior base of flipper

Appendix II. (Continued)

19	764	1052	423	1207	126	607	123	239	1539
15xii67	26i68	3ii68	5i68	10ii68	20xii67	15i68	20xii67	23xii67	25ii68
15.2	15.2	14.8	15.9	15.2	15.4	16.1	15.2	15.0	14.7
–	50	51	53	49	53	53	51	54	58
1,290	1,320	1,510	1,545	1,570	1,570	1,710	1,710	1,790	1,840
–	–	–	13	–	–	–	–	–	16
–	–	–	0.8	–	–	–	–	–	0.9
–	165	180	197	195	200	208	230	245	215
–	12.5	11.9	12.8	12.4	12.7	12.2	13.5	13.7	11.7
–	34	40	44	50	–	48	–	–	55
–	2.6	2.6	2.8	3.2	–	2.8	–	–	3.0
–	275	–	310	325	330	345	368	390	360
–	20.8	–	20.1	20.7	21.0	20.2	21.5	21.8	19.6
–	–	–	–	270	–	–	–	–	300
–	–	–	–	17.2	–	–	–	–	16.3
–	240	275	293	280	300	318	335	350	325
–	18.2	18.2	19.0	17.8	19.1	18.6	19.6	19.6	17.7
–	594	635	693	690	725	780	773	795	790
–	45.0	42.1	44.9	43.9	46.2	45.6	45.2	44.4	42.9
–	103	95	112	103	–	122	–	–	120
–	7.8	6.3	7.2	6.6	–	7.1	–	–	6.5
384	372	455	448	465	470	497	500	530	520
29.8	28.2	30.1	29.0	29.6	29.9	29.1	29.2	29.6	28.3
132	154	170	188	180	200	195	180	200	170
10.2	11.7	11.3	12.0	11.5	12.7	11.4	10.5	11.1	9.2
–	–	–	–	–	–	–	–	–	200
–	–	–	–	–	–	–	–	–	10.9
290	273	330	–	340	320	235	380	420	390
22.5	20.7	21.9	–	21.7	20.4	13.7	22.2	23.5	21.2
360	375	425	420	450	475	470	470	500	530
27.9	28.4	28.1	27.2	28.7	30.3	27.5	27.5	27.9	28.8
–	615	710	707	740	735	815	785	800	890
–	46.6	47.0	45.8	47.1	46.8	47.7	45.9	44.7	48.4
–	720	810	775	850	835	923	895	890	950
–	54.5	53.6	50.2	54.1	53.2	54.0	52.3	49.7	51.6
–	95	90	94	100	115	122	115	120	115
–	7.2	6.0	6.1	6.4	7.3	7.1	6.7	6.7	6.3
38	48	45	61	60	70	69	–	–	56
2.9	3.6	3.0	3.9	3.8	4.5	4.0	–	–	3.0
–	98	85	100	105	–	–	–	–	130
–	7.2	5.6	6.5	6.7	–	–	–	–	7.1
–	–	–	–	23	–	–	–	–	20
–	–	–	–	1.5	–	–	–	–	1.1
–	94	95	103	115	120	125	–	–	117
–	7.1	6.3	6.9	7.3	7.6	7.3	–	–	6.4
99	104	110	120	125	–	147	–	–	128
7.7	7.9	7.3	7.8	8.0	–	8.6	–	–	7.0
–	–	140	–	175	–	–	–	–	195
–	–	9.3	–	11.1	–	–	–	–	10.6
–	200	200	–	227	230	270	245	260	260
–	15.2	13.3	–	14.5	14.6	15.8	14.3	14.5	14.1
–	43	47	–	50	56	54	55	58	56
–	3.3	3.1	–	3.2	3.6	3.2	3.2	3.2	3.6
–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–
–	62	65	70	80	80	70	92	–	85
–	4.7	4.3	4.5	5.1	5.1	4.1	5.4	–	4.6

(Continued)

Appendix II. (Continued)

845	1075	948	303	1533	485	1133	986	995	758	1516
28i68	5ii68	31i68	28xii67	25ii68	9i68	8ii68	1ii68	1ii68	26i68	24ii68
14.3	15.2	16.1	16.0	15.0	15.9	14.4	14.2	14.3	15.8	16.3
49	49	52	49	60	63	55	43	62	53	59
1,880	1,880	1,910	1,918	1,950	1,975	2,020	2,030	2,120	2,260	2,290
22	–	–	14	–	18	–	–	–	–	–
1.2	–	–	0.7	–	0.9	–	–	–	–	–
224	225	237	231	230	252	245	260	255	262	295
11.9	12.0	12.4	12.0	11.8	12.8	12.1	12.8	12.0	11.6	12.9
57	57	46	–	62	55	75	65	68	65	75
3.0	3.0	2.4	–	3.2	2.8	3.7	3.2	3.2	2.9	3.3
370	370	393	385	390	405	420	420	385	445	490
19.7	19.7	20.6	20.1	20.0	20.5	20.8	20.7	18.2	19.7	21.4
–	310	348	–	330	–	350	380	375	–	410
–	16.5	18.2	–	16.9	–	17.3	18.7	17.7	–	17.9
335	335	350	358	340	367	360	370	–	407	430
17.8	17.8	18.3	18.7	17.4	18.6	17·8	18.2	–	18.0	18.8
840	820	835	858	850	882	920	950	920	965	1,030
44.7	43.6	43.7	44.7	43.6	44.7	45.5	46.8	43.4	42.7	45.0
128	123	145	–	120	130	130	145	140	150	150
6.8	6.5	7.6	–	6.2	6.6	6.4	7.1	6.6	6.7	6.6
–	460	545	575	560	545	610	570	595	635	650
–	24.5	28.5	30.0	28.7	27.6	30.2	28.1	28.1	28.1	28.4
215	193	190	220	200	204	240	225	350	225	240
11.4	10.4	9.9	11.5	10.3	10.3	11.9	11.1	11.1	10.0	10.5
–	–	–	–	230	–	–	–	–	–	270
–	–	–	–	11.8	–	–	–	–	–	11.8
375	440	375	425	440	360	430	375	395	460	360
19.9	23.4	19.6	22.2	22.6	18.4	21.3	18.5	18.6	20.4	15.7
553	550	530	528	550	575	545	525	600	615	640
29.4	29.3	27.7	27.5	28.2	29.1	27.0	25.9	28.3	27.2	27.9
890	910	880	905	895	900	920	900	1,010	1,105	1,090
47.3	48.4	46.1	47.2	45.9	45.6	45.5	44.3	47.6	48.9	47.6
1,010	1,030	995	1,022	980	1,069	1,050	1,000	1,090	1,210	1,190
53.7	54.8	52.1	53.3	50.3	53.9	52.0	49.3	51.4	53.5	52.0
122	135	115	130	135	123	135	125	145	140	160
6.5	7.2	6.0	6.8	6.9	6.2	6.7	6.2	6.8	6.2	7.0
70	65	60	87	90	90	90	65	80	115	85
3.7	3.5	3.1	4.5	4.6	4.6	4.5	3.2	3.8	5.1	3.7
125	130	120	–	130	135	140	112	150	175	140
6.6	6.9	6.3	–	6.7	6.8	6.9	5.5	7.0	7.7	6.1
–	25	30	–	30	–	–	40	35	–	35
–	1.3	1.6	–	1.5	–	–	2.0	1.7	–	1.5
130	140	130	162	145	160	155	135	165	170	175
6.9	7.4	6.8	8.4	7.4	8.1	7.7	6.7	7.8	7.5	7.6
145	155	160	–	170	–	170	180	180	188	195
7.7	8.2	8.4	–	8.7	–	8.4	8.9	8.5	8.3	8.5
–	197	–	–	200	–	225	–	–	–	240
–	10.5	–	–	10.3	–	11.1	–	–	–	10.5
268	274	277	286	300	307	320	308	310	328	350
14.3	14.6	14.5	14.9	15.4	15.5	15.8	15.2	14.6	14.5	15.3
61	55	58	64	63	59	65	67	70	72	75
3.2	2.9	3.0	3.3	3.2	3.0	3.2	3.3	3.3	3.2	3.3
–	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–
90	–	73	95	87	85	105	–	105	100	90
4.8	–	3.8	5.0	4.5	4.3	5.2	–	5.0	4.4	3.9

(Continued)

Appendix II. (Continued)

1018	759	892	950	1734	1488	1050	1446	1399	1699	1749
2ii68	26i68	30i68	31i68	7iii68	23ii68	3ii68	22ii68	21ii68	6iii68	10iii68
14.5	14.8	16.5	15.1	15.8	14.5	14.6	14.9	15.9	16.8	15.6
52	46	58	50	–	56	45	47	60	54	59
2,320	2,350	2,430	2,440	2,630	2,660	2,740	2,770	3,030	3,260	3,550
–	–	–	–	–	–	30	22	–	–	–
–	–	–	–	–	–	1.1	0.8	–	–	–
275	287	302	290	320	310	325	345	380	370	450
11.9	12.2	12.4	11.9	12.2	11.7	11.9	12.5	12.5	11.3	12.7
73	76	80	62	80	80	87	80	85	110	110
3.1	3.2	3.3	2.7	3.0	3.0	3.2	2.9	2.8	3.4	3.1
–	460	490	465	540	–	550	570	600	660	690
–	19.6	20.2	19.1	20.5	–	20.1	20.6	19.8	20.2	19.4
–	–	–	400	460	–	490	470	520	560	600
–	–	–	16.4	17.5	–	17.9	17.0	17.2	17.2	16.9
420	425	458	–	470	460	495	480	530	555	600
18.1	18.1	18.8	–	17.9	17.3	18.1	17.3	17.5	16.9	16.9
1,030	1,036	1,105	1,090	1,170	1,140	1,240	1,180	1,340	1,420	1,520
44.4	44.1	45.5	44.7	44.5	42.9	45.3	42.6	44.2	43.6	42.8
157	155	164	162	173	165	175	175	183	205	210
6.8	6.6	6.7	6.6	6.6	6.2	6.4	6.3	6.0	6.3	5.9
670	660	710	740	830	750	800	790	890	1,010	1,050
28.9	28.1	29.2	30.3	31.6	35.7	29.2	28.5	29.4	31.0	29.6
250	230	280	270	240	220	290	320	310	300	340
10.8	9.8	11.5	11.1	9.1	8.3	10.6	11.6	10.2	9.2	9.6
–	–	–	–	315	300	–	250	370	390	440
–	–	–	–	12.0	11.3	–	9.0	12.2	12.0	12.4
–	470	450	480	560	530	440	510	620	650	820
–	20.0	18.5	19.7	21.3	19.9	16.1	18.4	20.5	19.9	23.1
660	690	675	710	690	720	800	760	895	830	1,090
28.4	29.4	27.8	29.1	26.2	27.1	29.2	27.4	29.5	25.5	30.7
1,120	1,110	1,110	1,145	1,190	1,210	1,320	1,230	1,430	1,360	1,800
48.3	47.2	45.7	46.9	45.2	45.5	48.2	44.4	47.2	41.7	50.7
1,280	1,240	1,240	1,255	1,260	1,440	1,530	1,340	1,590	1,510	1,940
55.2	52.8	51.0	51.4	47.9	54.1	55.8	48.4	52.5	46.3	54.6
155	160	170	165	170	–	165	175	190	200	260
6.7	6.9	7.0	6.8	6.5	–	6.0	6.3	6.3	6.1	7.3
97	100	87	80	100	115	130	105	120	135	147
4.2	4.3	3.6	3.3	3.8	4.3	4.7	3.8	4.0	4.1	4.1
180	230	160	135	180	180	250	200	230	260	290
7.8	9.8	6.5	5.5	6.8	6.8	9.1	7.2	7.6	8.0	8.2
–	–	–	–	50	40	40	55	65	60	75
–	–	–	–	1.7	1.5	1.5	2.0	2.1	1.8	2.1
190	205	163	164	190	200	240	193	250	275	280
8.2	8.7	6.7	6.7	7.2	7.5	8.8	7.0	8.3	8.4	7.9
–	–	170	192	210	220	250	210	290	315	315
–	–	7.0	7.9	8.0	8.3	9.1	7.6	9.6	9.7	8.9
–	–	–	–	280	280	320	270	330	360	380
–	–	–	–	10.6	10.5	11.7	9.7	10.9	11.0	10.7
345	359	388	390	390	390	427	400	500	505	540
14.9	15.3	16.0	16.0	14.8	14.7	15.6	14.4	16.5	15.5	15.2
77	75	79	78	85	185	88	82	103	110	118
3.3	3.2	3.3	3.2	3.2	3.2	3.2	3.0	3.4	3.4	3.3
–	–	–	–	–	–	–	–	–	70	80
–	–	–	–	–	–	–	–	–	2.1	2.3
–	85	–	92	100	110	106	115	105	115	–
–	3.6	–	3.7	3.8	4.1	3.9	4.2	3.5	3.5	–

Appendix III. External measurements and percent body proportions for the foetuses of female sei whales. December 18, 1967-March 6, 1968. Antarctic. For measurements see Table 1 and Appendix I.[1]

Whale number	121	465	240	416	173	163	150
Date of catch	20xii67	7i68	23xii67	5i68	21xii67	21xii67	21xii67
Body length(m)	15.8	15.8	15.4	15.1	15.8	14.8	15.2
No. of Ventral grooves[2]	49	38	–	–	48	48	41
Measurements							
1.	1,000	1,053	1,070	1,080	1,130	1,170	1,230
2.	–	7	25	0	–	–	–
	–	0.7	2.3	0.0	–	–	–
3.	120	137	155	134	150	140	155
	12.0	13.0	14.5	12.4	13.3	12.0	12.6
a.	–	25	–	26	–	–	–
	–	2.4	–	2.4	–	–	–
4.	210	225	255	225	245	250	265
	21.0	21.4	23.8	20.8	21.7	21.4	21.5
b.	–	–	–	–	–	–	–
	–	–	–	–	–	–	–
5.	185	205	235	195	220	215	230
	18.5	19.5	22.0	18.1	19.5	18.4	18.7
6.	435	480	545	490	535	540	550
	43.5	45.6	50.9	45.4	47.3	46.2	44.7
7.	–	–	–	–	–	–	–
	–	–	–	–	–	–	–
8.	–	297	330	305	335	330	350
	–	28.2	30.8	28.2	29.6	28.2	28.5
9.	120	113	95	125	140	145	140
	12.0	10.7	8.9	11.6	12.4	12.4	11.4
c.	–	–	–	–	–	–	–
	–	–	–	–	–	–	–
d.	210	95 ?	–	175	240	220	220
	21.0	9.5?	–	16.2	21.2	18.8	17.9
10.	280	290	250	298	320	335	360
	28.0	27.5	23.4	27.6	28.3	28.6	29.3
11.	475	477	–	510	525	550	590
	47.5	45.3	–	47.2	46.5	47.0	48.0
12.	600	564	–	605	650	635	675
	60.0	53.6	–	56.0	57.5	54.3	54.9
13.	20	23	25	23	–	25	25
	2.0	2.2	2.3	2.1	–	2.1	2.0
14.	40	35	30	35	45	40	38
	4.0	3.3	2.8	3.2	4.0	3.4	3.1
15.	–	65	–	75	–	–	–
	–	6.2	–	6.9	–	–	–
e.	–	–	–	–	–	–	–
	–	–	–	–	–	–	–
f.	68	67	70	69	75	80	75
	6.8	6.4	6.5	6.4	6.6	6.8	6.1
g.	78	–	–	–	85	93	91
	7.8	–	–	–	7.5	7.9	7.7
16.	–	–	–	–	–	–	–
	–	–	–	–	–	–	–
17.	144	162	140	158	165	175	–
	14.4	15.4	13.1	14.6	14.6	15.0	–
18.	33	34	34	35	38	36	–
	3.3	3.2	3.2	3.2	3.4	3.1	–

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[1] Bar indicates no datum

[2] Number at anterior base of flipper

(Continued)

Appendix III. (Continued)

1083	166	1081	260	354	104	222	1442	148	508
5ii68	21xii67	5ii68	25xii67	2i68	18xii67	23xii67	22ii68	21xii67	11i68
15.6	15.3	14.9	15.0	15.3	14.4	15.9	14.6	16.3	14.4
46	52	45	44	50	49	58	53	58	52
1,290	1,300	1,370	1,400	1,405	1,430	1,460	1,470	1,470	1,475
–	–	–	–	10	–	–	–	–	4
–	–	–	–	0.7	–	–	–	–	0.3
157	170	190	185	182	165	175	185	185	205
12.2	13.1	13.9	13.2	13.0	11.5	12.0	12.6	12.6	13.9
34	–	40	–	–	–	–	33	–	37
2.6	–	2.9	–	–	–	–	2.2	–	2.5
265	280	320	300	308	300	300	300	310	325
20.5	21.5	23.4	21.4	21.9	21.0	20.5	20.4	21.1	22.0
215	–	265	–	–	–	–	255	–	–
16.7	–	19.3	–	–	–	–	17.3	–	–
235	250	275	273	280	260	270	260	275	295
18.2	19.2	20.1	19.5	19.9	18.2	18.5	17.7	18.7	20.0
580	585	650	635	657	615	660	620	635	690
45.0	45.0	47.4	45.4	46.8	43.0	45.2	42.2	43.2	46.8
–	–	105	–	107	–	–	100	–	–
–	–	7.7	–	7.6	–	–	6.8	–	–
380	–	410	415	368	400	425	400	440	423
29.5	–	29.9	29.6	27.6	28.0	29.1	27.2	29.9	28.7
150	170	155	160	150	155	160	160	185	170
11.6	13.1	11.3	11.4	10.7	10.8	11.0	10.9	12.6	11.5
–	–	–	–	–	–	–	170	–	–
–	–	–	–	–	–	–	11.6	–	–
245	260	260	280	280	290	290	300	–	295
19.0	20.0	19.0	20.0	19.9	20.3	19.9	20.4	–	20.0
365	365	375	390	390	420	420	425	440	438
28.3	28.1	27.4	27.9	27.8	29.4	28.8	28.9	29.9	29.7
605	600	590	635	625	655	690	695	720	700
46.9	46.2	43.1	45.4	44.5	45.8	47.3	47.3	49.0	47.5
710	690	720	750	705	790	780	780	820	775
55.0	53.1	52.6	53.6	50.2	55.2	53.4	53.1	55.8	52.5
30	–	25	30	29	30	40	28	35	28
2.3	–	1.8	2.1	2.1	2.1	2.7	1.9	2.4	1.9
43	65	47	55	48	58	60	50	53	58
3.3	5.0	3.4	3.9	3.4	4.1	4.1	3.4	3.6	3.9
85	–	75	–	87	–	–	100	–	90
6.6	–	5.5	–	6.2	–	–	6.8	–	6.1
20	–	20	–	–	–	–	20	–	–
1.6	–	1.5	–	–	–	1.4	–	–	–
80	105	100	85	96	95	110	103	105	102
6.2	8.1	7.3	6.1	6.8	6.6	7.5	7.0	7.1	6.9
90	105	110	100	110	102	–	125	130	128
7.0	8.1	8.0	7.1	7.8	7.1	–	8.5	8.8	8.7
130	–	150	–	–	–	–	160	–	–
10.1	–	10.9	–	–	–	–	10.9	–	–
180	190	205	200	216	195	220	210	200	228
14.0	14.6	15.0	14.3	15.4	13.6	15.1	14.3	13.6	15.5
43	40	44	40	44	45	50	40	45	47
3.3	3.0	3.2	2.9	3.1	3.1	3.4	2.7	3.1	3.2

(Continued)

Appendix III. (Continued)

156	1403	1291	944	110	1178	893	469	1112	1082	1242
21xii67	21ii68	16ii68	31i68	19xii68	9ii68	30i68	7i68	7ii68	5ii68	12ii68
14.8	15.0	14.4	13.4	15.6	14.8	15.7	17.6	14.0	14.5	15.7
52	43	52	52	61	57	53	48	49	46	58
1,620	1,710	1,750	1,750	1,805	1,830	1,840	1,965	2,010	2,010	2,160
–	–	–	–	–	–	5	18	–	15	15
–	–	–	–	–	–	0.3	0.9	–	0.7	0.7
215	210	215	220	225	225	245	258	250	255	280
13.3	12.3	12.3	12.6	12.5	12.3	13.3	13.1	12.4	12.7	13.0
–	55	54	50	–	55	47	57	50	55	65
–	3.2	3.1	2.9	–	3.0	2.5	2.9	2.5	2.7	3.0
365	380	370	370	360	380	–	423	420	440	460
22.5	22.2	21.1	21.1	19.9	20.8	–	21.5	20.9	21.9	21.3
–	315	310	340	–	320	327	–	360	360	380
–	18.4	17.7	19.4	–	17.5	17.8	–	17.9	17.9	17.6
330	330	325	340	330	330	348	377	377	–	400
20.4	19.3	18.6	19.4	18.3	18.0	18.9	19.2	18.8	–	18.5
745	790	770	790	800	800	830	887	885	930	975
46.0	46.2	44.0	45.1	44.3	43.7	45.1	45.1	44.0	46.3	45.1
–	123	113	123	–	130	134	–	135	142	146
–	7.2	6.5	7.0	–	7.1	7.3	–	6.7	7.1	6.8
490	490	530	505	565	500	530	558	600	550	640
30.2	28.7	30.3	28.9	31.3	27.3	28.8	28.4	29.9	27.4	29.6
215	160	190	180	200	195	200	–	230	230	190
13.3	9.4	10.9	10.3	11.1	10.7	10.9	–	11.4	11.4	8.8
–	200	180	–	–	–	–	210	–	–	–
–	11.7	10.3	–	–	–	–	10.7	–	–	–
390	390	330	295	320	440	380	–	340	510	390
24.1	22.8	18.9	16.9	17.7	24.0	20.7	–	16.9	25.4	18.1
465	490	525	485	545	490	490	575	605	560	580
28.7	28.7	30.0	27.7	30.2	26.8	26.6	29.3	30.1	27.9	26.9
770	800	820	790	875	820	815	935	940	930	980
47.5	46.8	46.9	45.1	48.5	44.8	44.3	47.6	46.8	46.3	45.4
870	910	920	880	980	930	910	1,065	1,060	1,040	1,110
53.7	53.2	52.6	50.3	54.3	50.8	49.5	54.2	52.7	51.7	51.4
35	35	35	30	43	37	44	43	–	40	50
2.2	2.0	2.0	1.7	2.4	2.0	2.4	2.2	–	2.0	2.3
85	60	65	84	80	65	80	68	55	80	70
5.2	3.5	3.7	4.8	4.4	3.6	4.3	3.5	2.7	4.0	3.2
–	110	110	110	–	130	120	140	110	130	140
–	6.4	6.3	6.3	–	7.1	6.5	7.1	5.5	6.5	6.5
–	20	30	–	–	35	–	–	30	–	40
–	1.2	1.7	–	–	1.9	–	–	1.5	–	1.9
120	120	130	147	133	140	148	149	130	160	165
7.4	7.0	7.4	8.4	7.4	7.7	8.0	7.6	6.5	8.0	7.6
130	130	145	167	–	160	–	–	150	200	195
8.0	7.6	8.3	9.5	–	8.7	–	–	7.5	10.0	9.0
–	190	185	–	–	185	–	–	210	230	230
–	11.1	10.6	–	–	10.1	–	–	10.4	11.4	10.6
235	250	260	260	265	262	276	282	280	315	330
14.5	14.6	14.9	14.9	14.7	14.3	15.0	14.4	13.9	15.7	15.3
53	55	54	61	59	60	61	63	61	65	70
3.3	3.2	3.1	3.5	3.3	3.3	3.3	3.2	3.0	3.2	3.2

(Continued)

Appendix III. (Continued)

1487	1059	1545	1547	998	1216	996	952	1019	1248	1076
23ii68	4ii68	26ii68	26ii68	1ii68	10ii68	1ii68	31i68	2ii68	13ii68	5ii68
15.8	14.9	15.4	13.7	13.8	15.0	14.5	15.1	14.7	15.0	16.0
56	66	–	51	–	60	64	51	–	63	50
2,250	2,260	2,300	2,370	2,440	2,450	2,510	2,640	2,670	2,730	2,810
–	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–
290	275	–	290	–	300	330	333	350	335	330
12.9	12.3	–	12.2	–	12.2	13.1	12.6	13.1	12.3	11.7
70	72	–	74	–	90	90	85	88	90	85
3.1	3.2	–	3.1	–	3.7	3.6	3.2	3.3	3.3	3.0
480	470	–	515	510	500	540	550	550	560	560
21.3	21.0	–	21.7	20.9	20.4	21.5	20.8	20.6	20.5	19.9
410	405	–	445	440	420	460	500	480	460	470
18.2	18.1	–	18.8	18.0	17.1	18.3	18.9	18.0	16.8	16.7
430	415	–	460	467	440	475	505	505	485	495
19.1	18.5	–	19.4	19.1	18.0	18.9	19.1	18.9	17.8	17.6
1,010	1,020	–	1,090	1,110	1,080	1,135	1,200	1,245	1,230	1,240
44.9	45.5	–	46.0	45.5	44.1	45.2	45.5	46.6	45.1	44.1
150	150	–	155	167	160	175	154	180	180	175
6.7	6.7	–	6.5	6.8	6.5	7.0	5.8	6.7	6.6	6.2
690	620	710	670	670	720	750	780	810	790	780
30.7	27.7	30.9	28.3	27.5	29.4	29.9	29.5	30.3	28.9	27.8
200	250	200	215	270	260	270	290	280	300	290
8.9	11.1	8.7	9.1	11.1	10.6	10.8	11.6	10.5	11.0	10.3
275	–	240	270	–	–	–	390	–	–	–
12.2	–	10.4	11.4	–	–	–	14.8	–	–	–
400	590	–	420	570	570	550	–	–	490	580
17.8	26.3	–	17.7	23.4	23.3	21.9	–	–	17.9	20.6
575	640	720	675	670	700	700	720	805	800	830
25.6	28.4	31.3	28.5	27.5	28.6	27.9	27.3	30.1	29.3	29.5
930	1,040	1,110	1,110	1,130	1,120	1,190	1,160	1,305	1,250	1,380
41.3	46.4	47.8	46.4	46.3	45.7	47.4	43.9	48.9	45.8	49.1
1,060	1,100	1,200	1,240	1,250	1,240	1,315	1,340	1,430	1,440	1,480
47.1	49.1	52.2	52.3	51.2	50.6	52.4	50.8	53.6	52.7	52.7
–	50	65	55	55	55	60	55	65	50	55
–	2.2	2.8	2.3	2.3	2.2	2.4	2.1	2.4	1.8	2.0
90	90	–	80	95	110	90	115	90	110	140
4.0	4.0	–	3.4	3.9	4.5	3.6	4.4	3.4	4.0	5.0
130	150	–	170	180	170	185	190	180	220	200
5.8	6.7	–	7.2	7.4	6.9	7.3	7.2	6.7	8.1	7.1
40	–	–	50	40	35	–	–	–	60	40
1.8	–	–	2.1	1.6	1.4	–	–	–	2.2	1.4
165	185	–	195	180	205	210	220	205	240	235
7.3	8.3	–	8.2	7.4	8.4	8.4	8.3	7.7	8.8	8.4
190	220	–	215	195	230	240	–	235	280	250
8.4	9.8	–	9.1	8.0	9.4	9.6	–	8.8	10.3	8.9
240	235	–	265	–	270	–	–	–	330	280
10.7	10.5	–	11.2	–	11.0	–	–	–	12.1	10.0
345	330	–	370	380	360	395	420	455	450	430
15.3	14.7	–	15.6	15.6	14.7	15.7	15.9	17.0	16.5	15.3
77	65	–	79	82	80	85	88	92	95	90
3.4	2.9	–	3.3	3.4	3.3	3.4	3.3	3.4	3.5	3.2

(Continued)

Appendix III. (Continued)

1400	1251	1293	1549	1209	1246	1107	1484	1537	1483	1697
21ii68	13ii68	16ii68	26ii68	10ii68	13ii68	6ii68	23ii68	25ii68	23ii68	6iii68
15.8	15.9	15.4	16.0	15.4	15.3	15.3	15.8	15.1	16.4	14.9
58	62	47	50	58	63	63	63	60	55	58
2,810	2,870	2,890	3,080	3,100	3,170	3,200	3,220	3,270	3,380	3,660
13	25	–	17	15	–	–	–	–	25	–
0.5	0.9	–	0.6	0.5	–	–	–	–	0.7	–
350	350	360	385	350	370	380	405	400	380	420
12.5	12.2	12.5	12.5	11.3	11.7	11.9	12.6	12.2	11.2	11.5
95	87	95	105	105	110	95	100	95	90	120
3.4	3.0	3.3	3.4	3.4	3.5	3.0	3.1	2.9	2.7	3.3
610	570	610	650	600	620	670	660	660	640	710
21.7	19.9	21.1	21.1	19.4	19.6	20.9	20.5	20.2	18.9	19.4
520	490	520	560	510	530	550	580	560	540	600
18.5	17.1	18.0	18.2	16.5	16.7	17.2	18.0	17.1	16.0	16.4
530	510	530	560	530	565	580	590	575	560	620
18.9	17.8	18.3	18.2	17.1	17.8	18.1	18.3	17.6	16.6	16.9
1,290	1,260	1,310	1,415	1,320	1,390	1,400	1,460	1,400	1,430	1,540
45.9	43.9	45.3	45.9	42.6	43.8	43.8	45.3	42.8	42.3	42.1
175	183	186	200	207	195	200	205	210	197	218
6.2	6.4	6.4	6.5	6.7	6.2	6.3	6.4	6.4	5.8	6.0
800	850	820	940	950	910	930	930	1,030	1,020	1,200
28.5	29.6	28.4	30.5	30.6	28.7	29.1	28.9	31.5	30.2	32.8
260	280	270	270	310	330	330	280	310	330	330
9.3	9.8	9.3	8.8	10.0	10.4	10.3	8.7	9.5	9.8	9.0
330	–	–	340	–	–	–	420	320	460	350
11.7	–	–	11.0	–	–	–	13.0	9.8	13.6	9.6
550	520	630	470	800	500	550	600	430	680	560
19.6	18.1	21.8	15.3	25.8	15.8	17.2	18.6	13.1	20.1	15.3
800	850	790	870	930	960	940	920	1,050	980	910
28.5	29.6	27.3	28.2	30.0	30.3	29.4	28.6	32.1	29.0	24.9
1,280	1,370	1,260	1,420	1,480	1,570	1,570	1,540	1,570	1,570	1,525
45.6	47.7	43.6	46.1	47.7	49.5	49.1	47.8	48.0	46.4	41.7
1,440	1,410	1,420	1,550	1,600	1,690	1,780	1,670	1,750	1,780	1,620
51.2	49.1	49.1	50.3	51.6	53.3	55.6	51.9	53.5	52.7	44.3
40	65	55	65	60	65	75	70	70	75	70
1.4	2.3	1.9	2.1	1.9	2.1	2.3	2.2	2.1	2.2	1.9
93	120	105	95	110	170	150	130	110	145	130
3.3	4.2	3.6	3.1	3.5	5.4	4.7	4.0	3.4	4.3	3.6
180	220	210	210	220	270	280	270	210	280	270
6.4	7.7	7.3	6.8	7.1	8.5	8.8	8.4	6.4	8.3	7.4
55	60	45	65	40	45	50	75	40	60	80
2.0	2.1	1.6	2.1	1.3	1.4	1.6	2.3	1.2	1.8	2.2
220	230	210	225	225	280	270	310	230	290	280
7.8	8.0	7.3	7.3	7.3	8.8	8.4	9.6	7.0	8.6	7.6
255	260	230	320	240	300	300	370	250	310	315
9.1	9.1	8.0	10.4	7.7	9.5	9.4	11.5	7.6	9.2	8.6
310	310	330	360	330	360	350	330	340	360	375
11.0	10.8	11.4	11.7	10.6	11.4	10.9	10.2	10.4	10.7	10.2
450	430	470	510	470	500	515	515	480	520	550
16.0	15.0	16.3	16.6	15.2	15.8	16.1	16.0	14.7	15.4	15.0
88	95	105	104	102	108	105	100	100	108	115
3.1	3.3	3.6	3.4	3.3	3.4	3.2	3.1	3.1	3.2	3.1

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THE RELATIONSHIP BETWEEN DEVELOPMENT OF THE BONY FALX AND BONY TENTORIUM IN CETACEANS AND THEIR DIETS

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ABSTRACT

The correlation between food habits and ossification in the falx cerebri (FC) and tentorium cerebelli (TC) of cetaceans is considered.

I have observed the bony falx (BF) and bony tentorium (BT) in a variety of mammals, including cetaceans, and have classified them into the carnivore type and the dolphin type based on their developmental pattern. The carnivore type develops as part of the skull bones during the fetal period, and these, attaining shapes closely similar to those of adults, are already completed at birth. The dolphin type, on the other hand, is formed by ossification in the FC and TC during the course of aging.

Among cetaceans, the dolphin type BF and BT are seen only in delphinids and phocoenids. The carnivore type BF and BT are present in all the Ziphiidae, and in the sperm whale (*Physeter catodon*). In the other cetaceans observed, neither the BF nor BT was seen at all.

I have reviewed many reports on food habits of cetaceans and noted that the cetaceans which possess the dolphin type BF and BT are fish-eaters (ichthyophagi). Many fishes contain a large amount of vitamin D which promotes ossification of bones, while squid and zooplankton, other main food of toothed whales and the main food of baleen whales, respectively, contain no vitamin D.

It appears likely that formation of the dolphin type BF and BT in delphinids and phocoenids is due to their continual intake of large amounts of fish high in vitamin D.

Although this approach to assessing the food habits of cetaceans is indirect, it provides consistent results. The general trend of their food habits throughout life appears to be reflected in the degree of ossification in the FC and TC, much as the growth layers formed in teeth and ear plugs of cetaceans indicate their ages.

Key words: bony falx, bony tentorium, ossification, vitamin D

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Sci. Rep. Cetacean Res.,
No. 1, 1990, 39–61

INTRODUCTION

The brain of mammals is surrounded by three membranes, or meninges: the dura mater, the arachnoid mater and the pia mater. The dura mater is a dense, strong fibrous membrane, and is conventionally described as two layers: the outer (endosteal) and inner (meningeal) layers. The outer layer is the periosteum covering the inner surface of the skull bones. The inner layer is the dura mater proper, and sends four partitions inward, which divide up the cranial cavity into freely communicating spaces lodging the subdivisions of the brain. These partitions operate to restrict the rotatory displacement of the brain.

The falx cerebri (FC) is a vertical partition that lies in the longitudinal fissure between the cerebral hemispheres. The tentorium cerebelli (TC) is a partition that inserts between the upper surface of the cerebellum and the occipital lobes of the cerebral hemispheres, and forms a floor supporting the latter (Plate I, Fig. 2). In most mammals, both the FC and TC are composed of only the folded dura mater. In other mammals, a bony plate, developed to varying degrees, is present in the FC and/or TC. The plate in the FC is the bony falx (BF) and that in the TC is the bony tentorium (BT).

There are few studies on the BF and BT of any mammals. I have examined the skulls of 189 species in 54 families from 15 orders (but not Scandentia, Dermoptera, Hyracoidea, Tubulidentata and Macroscelidea) in the class Mammalia (following Corbet and Hill, 1986).

The BT and/or BF were observed in almost all species of Carnivora and in many species of Odontoceti (Cetacea), but were seen only in a few species belonging to orders such as Perissodactyla (Equidae), Sirenia, Primates (Cebidae, genus *Ateles*) and Marsupialia.

Based on their developmental pattern, I have classified the BF and BT of mammals into two types: the carnivore type and the dolphin type (Nojima, 1988).

The BF and BT of the carnivore type develop as part of the skull bones (the parietal bone and/or occipital bone) during the fetal period, and these attain shapes very similar to those of adults by the time of birth in almost all carnivores (BT, and also the BF in all pinnipeds) and in horses (BT), phalangers (Phalangeridae) (BT), kangaroos (Macropopidae) (BT), sperm whales (Physeteridae) (BF), beaked and bottlenose whales (Ziphiidae) (BF & BT) and sirenians (BF). Morphological characteristics of the BT and BF are useful in the classification of Carnivora (Nojima, 1990a).

On the other hand, the BF and BT of the dolphin type, for example those of spotted dolphins (*Stenella attenuata*), are not seen in the newborn or juvenile at all, but are gradually formed by ossification in the FC and TC as the animal grows older (Nojima, 1988, 1989). Among cetaceans, clearly formed dolphin type BF and BT are seen only in the Delphinidae and Phocoenidae. The BT of spider monkeys is also assigned to this type (Nojima, 1990b).

The differences between the two types are not merely due to the difference in timing of onset of their development. In mammals which possess the carnivore type BT and/or BF, the membranous portions of the TC and FC in which the BT and BF are absent, do not ossify throughout life (Nojima, 1990a). The functional significance of the carnivore type BT and BF is unknown.

In previous studies (Nojima, 1988, 1989), I have suggested that ossification in the FC and TC of delphinids and phocoenids may be due to the continual intake of a large amount of fish high in vitamin D and calcium.

Vitamins D_2 (ergocalciferol) and D_3 (cholecalciferol) operate to maintain calcium homeostasis in mammals after being converted to 25-hydroxyvitamin D. Both are obtained from food. Vitamin D_3 is also obtained from exposure of skin sterols to ultraviolet radiation. Deficiencies are more likely to become a problem for housed animals which are not exposed to direct sunlight (Doyle, 1987). Vitamin D deficiencies affect bone development (rickets) in young, growing animals and cause osteomalacia in adults (see for example Coburn, Hartenbower and Norman, 1974; Delucca, 1974; Fraser, 1975; Doyle, 1987).

On the other hand, hypercalcemia, which causes hyperplasia of bones and extensive calcium deposition in soft tissue, especially kidneys and arteries, results from excessive use of the vitamin and calcium in the treatment of humans for rickets (Kure and Sakamoto, 1966; Ishii, 1973; Coburn *et al.*, 1974; Delucca, 1974; Fraser, 1975; Nakayama, 1975; Kobayashi, 1989). According to Schultze and Lubosch (1935), the dura mater of humans may be ossified, although it is unknown whether the condition is caused by hypercalcemia.

Most mammalian food in nature do not contain enough vitamin D to cause toxicity. In fish-eating mammals such as certain pinnipeds and cetaceans, however, there is a danger that excessive intake of vitamin D could produce levels known to be toxic for many terrestrial mammals (Bouillon, Vankerkhove and De Moor, 1976; Keiver, Draper and Ronald, 1988a). Fish contain large amounts of vitamin D, especially in the liver, and are the only source of the vitamin for cetaceans.

Food habits of cetaceans have been studied mainly by the examination of stomach contents. However, with the exception of larger whales whose food habits have been studied extensively using samples obtained from the commercial whaling industry, sufficient data for most toothed whales are not available.

Among cetaceans, clearly ossified BF and BT in the FC and TC, respectively, are seen only in the Delphinidae and Phocoenidae which have been reported to ingest a large amount of fish. On the other hand, little or no ossification occurs in the FC and TC of other cetaceans reported to feed mainly on squid, zooplankton or other invertebrates that lack vitamin D.

RESULTS

The dolphin type BF and BT were observed in all the Delphinidae and Phocoenidae, and are probably present in the Monodontidae. The carnivore type BF and BT were observed in all the Ziphiidae. The carnivore type BF was also observed in the sperm whale (*Physeter catodon*). In other cetaceans studied, neither the BF nor BT was seen at all.

All cetacean species and the number of skulls studied, their main food, and the BF and BT types are given in Table 1.

TABLE 1. LIST OF CETACEANS EXAMINED, TYPE OF BF AND BT, AND MAJOR FOOD ITEMS[1].

Family and species (Sample number in parentheses)	Carnivore type	Dolphin type	Main food
Platanistidae			
Pontoporia blainvillei (2)	—	—	crustaceans, molluscs, and fish (low vitamin D content)
Inia geoffrensis (1)	—	—	
Platanista gangetica (3)	—	—	
Delphinidae			
Steno bredanensis (4)	—	BF & BT	fish & squid
Sousa teuszii (1)	—	BF & BT	fish & squid
Stenella attenuata (35)	—	BF & BT	fish
Stenella coeruleoalba (12)	—	BF & BT	fish
Stenella longirostris (3)	—	BF & BT	fish
Delphinus delphis (4)	—	BF & BT	fish & squid
Tursiops truncatus (6)	—	BF & BT	fish & squid
Lissodelphis borealis (2)	—	BF & BT	fish & squid
Lagenorhynchus obliquidens (4)	—	BF & BT	fish & squid
Lagenorhynchus albirostris (2)	—	BF & BT	fish & squid
Lagenorhynchus obscurus (1)	—	BF & BT	fish & squid
Lagenodelphis hosei (1)	—	BF & BT	fish & squid
Peponocephala electra (5)	—	BF & BT	squid & fish
Pseudorca crassidens (2)	—	BF & BT	squid & fish
Orcinus orca (2)	—	BF & BT	fish & squid
Grampus griseus (3)	—	BF & BT (tiny)	squid
Globicephala macrorhynchus (4)	—	BF & BT	squid & fish
Feresa attenuata (4)	—	BF & BT	squid & fish
Phocoenidae			
Phocoena phocoena (6)	—	BF & BT	fish & squid
Phocoenoides dalli (9)	—	BF & BT	fish & squid
Neophocaena phocaenoides (2)	—	BF & BT (tiny)	squid, shrimp, fish
Monodontidae			
Monodon monoceros (1)	—	BF & BT (tiny)	squid & fish
Physeteridae			
Physeter catodon (2)	BF	—	squid
Kogia breviceps (2)	—	—	squid
Kogia simus (3)	—	—	squid

Ziphiidae			
Berardius bairdii (4)	BF & BT	—	squid
Ziphius cavirostris (7)	BF & BT	—	squid
Mesoplodon ginkgodens (2)	BF & BT	—	squid
Mesoplodon stejnegeri (2)	BF & BT	—	squid
Mesoplodon densirostris (1)	BF & BT	—	squid
Hyperoodon ampullatus (1)	BF & BT	—	squid
Balaenidae			
Balaena glacialis (1)	—	—	zooplankton
Eschrichtiidae			
Eschrichtius robustus (1)	—	—	amphipods
Balaenopteridae			
Balaenoptera borealis (1)	—	—	zooplankton
Balaenoptera edeni (1)	—	—	zooplankton
Balaenoptera acutorostrata (2)	—	—	zooplankton
Megaptera novaeangliae (1)	—	—	zooplankton

1) Classification of cetaceans is basded on Corbet and Hill (1986). The skulls of cetaceans belonging to the collections of Department of Zoology, National Science Museum, Tokyo, were mainly studied. In many species, both adult and juvenile specimens were studied for comparison of the degree of development of the BF and BT. The growth stages (adult or juvenile) and other biological data in the text were copied from museum records. Besides these, a sperm whale of the Whale Museum, Ayukawa, Miyagi, a right whale of the Whale House, Kumomi, Shizuoka. Twenty-seven spotted dolphins including fetuses, five striped dolphins, and three bottlenose dolphins including a newborn are from my own collection.

Main food of each species is based on published reports. "fish & squid" or "squid & fish", respectively, means that the former appears to be more important than the latter.

Delphinidae

The BF and BT, which had been formed in varying degrees in the FC and TC, were observed in most delphinids. In most of the juvenile animals observed, the BF and BT had not been completed as a continuous bony plate (Plate II), but in some other juveniles, only a small bony process was seen to project from the portion corresponding to the internal occipital protuberance. The BF and BT were not seen at all in fetal or juvenile spotted dolphins (Plate II), or in a newborn bottlenose dolphin (*Tursiops truncatus*).

The Risso's dolphin (*Grampus griseus*) was a peculiar species. Even in adult specimens, only a small ossified process projected from the portion corresponding to the internal occipital protuberance.

In the skulls of adult spotted dolphins, in which the BF and BT had been completed (Plate I), the inner surface of the calvaria had been made rough by many laminations formed by ossification in the dura mater (Plate III).

As an example of a delphinid pattern, the order of ossification in the FC and TC of spotted dolphins is shown diagrammatically in Fig. 1.

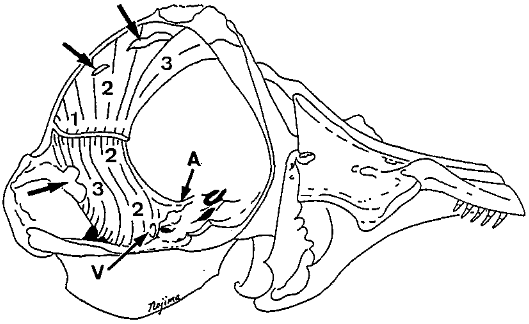

Fig. 1. The order of ossification in the FC and TC of the spotted dolphin. The cranium has been cut along a line slightly lateral and parallel to the midline and the right half has been removed. The BT of the right side has also been cut along the same side of the midline, and the BF and the inferior surface of the left BT are shown.

During 6 months to 1 year of age, ossification begins at the attachment of the FC and TC to the internal occipital protuberance (1), and advances forward along the junction of the FC and TC. Then ossification spreads toward the back part of the FC and toward the anterior portion of the TC (2). At the same time, ossification occurring in the attachment of the TC to the base of the skull also advances upward in the anterior portion of the TC (2), and fuses with the above developing plate to form the anterior half of the BT. From this, ossification spreads backward in the TC (3). At the same time, ossification in the FC advances forward and completes the free margin of the BF (3). Finally, by about 9-11 years of age, the BF and BT are completed in the shape of the entire FC and TC, except for the passage of blood vessels (black arrows) and nerves (V). The most anterior portion of the free margin of the TC is ossified to form a small bony arch above the base of the skull (A). A shallow groove for the continuations of the spinal meningeal artery to the ophthalmic retial complex runs under the arch (see Plate I). The passage of the trigeminal nerve, which occurs at the most medial and inferior portion of the TC, is completed as a foramen on the BT in older specimens (V), but remains as a round notch at the free margin of the BT in younger specimens.

Phocoenidae

In both habor and Dall's porpoises (*Phocoena phocoena* and *Phocoenoides dalli*), the BT had not been completed as a continuous bony plate to the base of the skull in any specimens. The BF was well developed in older specimens, and a round opening for the passage of the trigeminal nerve, which in the spotted dolphin is completed late during the process of ossification in the FC and TC (see Fig. 1), occurred at the partial BT projecting from the base of the skull. The BF and BT of adult porpoises observed appear to have been damaged during preparation of the skulls. In all young specimens, both the BF and BT were poorly developed.

Even in adult specimens of the finless porpoise (*Neophocaena phocaenoides*), only a small bony process projected from the portion which corresponded to the internal occipital protuberance.

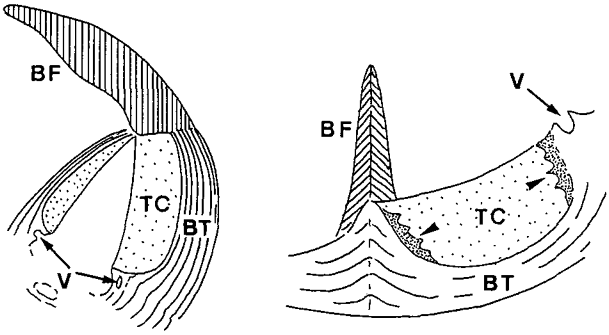

Fig. 2. Schematic drawings of the BF, BT and TC of Ziphiidae; seen from left side slightly anteriorly, and from below (right side).
BF: bony falx, BT: bony tentorium, TC: tentorium cerebelli, V: the passage of the trigeminal nerve, which occurs as a foramen or a notch. Attachments of the TC of *Mesoplodon* spp. are slightly ossified (black arrows).

Monodontidae

Only one specimen of adult male narwhal (*Monodon monoceros*) was examined. The BF and BT were not seen in the skull; however, the portion corresponding to the internal occipital protuberance was rough, probably reflecting damage to the ossified process.

Physeteridae

Owen (1866) reported the partial BF projecting from the supraoccipital bone into the back part of the FC in an advanced fetal sperm whale. I also observed the partial BF in both young and adult sperm whales (12.19 m and 16.90 m in body length) at the site corresponding to Owen's descriptions. The BT was absent. The partial BF of sperm whales is assigned to the carnivore type.

Ziphiidae

The BF, which appears to have the shape of the entire FC, and the partial BT which inserts into the posterior half of the TC, were seen in all the Ziphiidae, including both young and juvenile specimens (Fig. 2, left side). In the median sagittal section of an adult skull of Baird's beaked whale (*Berardius bairdii*), it was obvious that the element of the BF and BT was derived from the occipital bone (the supraoccipital bone). The BF and BT of Ziphiidae are assigned to the carnivore type, and characterize the skull of those animals.

In all the *Mesoplodon* species observed, the attachments of the TC were partially ossified (Fig. 2, right side), but not considered to be ossified in the entire shape of the TC.

DISCUSSION

Among prey items for wild mammals, some species of fish contain an exceptionally large amount of vitamin D concentrated in the liver. According to Kagawa (1989), vitamin D value in fish meat is fairly high on migratory fishes but is low in most bottom-dwelling fishes and freshwater fishes. Holmes, Tripp and Satterfield (1941) and Inagaki (1970) reported vitamin D value (IU/gram) in fish liver oil of some species (bluefin tuna *Thunnus thynnuis*, 27,000～70,000 IU; skipjack *Euthynnus pelamis*, 20,000 IU; mackerel *Scomber japonicus*, 5,400 IU; swordfish *Tetrapturus audax*, 1,550～25,000 IU; halibut *Hippoglossus hippoglossus*, 550～20,000 IU). Although available data on vitamin D content in fish liver oil are scarce, this can estimate from the vitamin value in the meat. Vitamin D content in the liver oil tends to increase in parallel with the increase of the vitamin value in the meat. For example, the meat of dogfish *Squalus acanthias* and blue shark *Prionace glauca* contain no vitamin D, and liver oil made from these fishes only contain the vitamin of 0～100 IU per gram. While the meat of bluefin tuna and skipjack, above species respectrively, contains about 600 IU and 420 IU per 100g.

On the other hand, squid, zooplankton and the other aquatic invertebrates contain no vitamin D (Hirano, 1982; Kagawa, 1989).

In the following sections, the correlation between degree of ossification in the FC and TC and prey items of each group of cetaceans are discussed.

Mysticeti

Although the minke whale (*Balaenoptera acutorostrata*), sei whale (*B.borealis*), Bryde's whale (*B.edeni*) and humpack whale (*Megaptera novaeangliae*) have been reported to ingest considerable amounts of fishes such as sardine, saury and mackerel (Mizue, 1951; Nemoto, 1957, 1959; Mitchell, 1975), in many areas the main food of these cetaceans is zooplankton such as euphausiids and copepods (Nemoto, 1957, 1959, 1962; Nemoto and Nasu, 1958; Nemoto and Yoo, 1970; Kawamura, 1970, 1973, 1977, 1980, 1982). The percentage of fish found in the stomachs of minke and sei whales caught south of 40°S was 0% and 0.1%, respectively (Horwood, 1987), and those of sei and Bryde's whales caught in the North Pacific was 3.4% and 11.1%, respectively (Nemoto and Kawamura, 1977).

The gray whale (*Eschrichtius robustus*) feeds primarily on benthic amphipods, especially gammaridean amphipods (Pike, 1962; Nerini, 1984; Wolman 1989).

North Pacific right whale (*Balaena glacialis*) feeds primarily on copepods such as *Calanus cristatus* and *C.plumchrus* (Omura, 1958; Omura, Ohsumi, Nemoto, Nasu and Kasuya, 1969).

No ossification in the FC and TC occurs in any baleen whales that are feeding mainly upon zooplankton with no vitamin D.

Physeteridae

Many reports on the food of sperm whales have been presented (Pike, 1950; Mizue, 1951; Rice, 1963; Okutami and Nemoto, 1964; Roe, 1969; Kawakami, 1976; Clarke, 1980). Clarke (1956) examined a considerable number of stomachs of sperm whales in the Azores, and found eight species of squid which predominated in the stomachs and a small though not insignificant amount of fish. Kawakami (1980) reviewed the published reports on the food of sperm whales taken from different localities of the world. According to this, the percentage of squid and fish found in the stomachs obviously show that the sperm whales are primarily squid-eaters although in some localities their stomachs contained fairly high percentages of fish.

The pygmy sperm whale (*Kogia breviceps*) feeds mostly on cephalopods (Hale, 1947; Raun, Hoese and Moseley, 1970; Clarke, 1986; Pinedo, 1987). Stomachs of the dwarf sperm whale (*Kogia simus*) contained large amounts of cephalopods (Ross, 1978; Jones, 1981). Nagorsen and Stewart (1983) also found cephalopod beaks and shrimp in the stomach. On the other hand, Fitch and Brownell (1968) observed otoliths of many fish species (*Ichthyococcus* sp., Macrouridae, Moridae, *Lampadena* etc.) besides cephalopod beaks and crustacean remains in the stomachs of three pygmy sperm whales (?, scientific name given in the article is *Kogia simus*). However, only small amounts of fish appear to be eaten by the species.

In the sperm whale, pygmy sperm whale and dwarf sperm whale, all of which feed mainly on squid with no vitamin D, ossification in the FC and TC does not occur at all, although the carnivore type BF is present in the sperm whale.

Ziphiidae

According to reviews on the food of the Ziphiidae by Gaskin (1976), Evans (1987), Balcomb (1989), Heyning (1989) and Mead (1989a,b), the Ziphiidae on the whole appear to be squid-eaters. Heyning (1989) listed many species of cephalopods found in the stomachs of Cuvier's beaked whales (*Ziphius cavirostris*). Baird's beaked whale (*Berardius bairdii*) and Cuvier's beaked whale also eat somewhat a considerable amount of deep-sea fishes (Rice, 1963; Nishiwaki and Oguro, 1971). Almost all deep-sea fishes, however, are distinctly low in vitamin D content.

Ross (1984) found 21 fish otoliths identified as species of the genera *Cepola*? (1), *Scopelogadus* (1) and *Lampanyctus* (19) in the stomach of a female adult Blainville's beaked whale (*Mesoplodon densirostris*) from southern Africa. Mead (1989b) found trace quantities of squid beaks from three Blainville's beaked whales and two Stejneger's beaked whales (*M.stejnegeri*) but no fish remains were found in the stomachs. Concerning the ginkgo-toothed beaked whale (*M.ginkgodens*), another *Mesoplodon* species observed in the present study, no information on their food habits appears to be available.

A small amount of ossification in the attachments of the TC was seen in all the *Mesoplodon* species observed. Because of the scarcity of published data on the food habits of *Mesoplodon* spp., it is unknown whether these whales feed on a larger proportion of fish than do the Baird's beaked whale and Cuvier's beaked whales, in which ossification in the TC does not occur at all. Mead (1989b) supposes that *Mesoplodon* species prefer mesopelagic squid and fish.

Benjaminsen and Christensen (1979) examined the stomach contents of 46 bottlenose whales (*Hyperoodon ampullatus*) caught off Iceland and 108 caught off Labrador. They found that squid was the main food. Fishes such as cusk (*Brosmius brosme*), lumpsucker (*Cyclopterus lumpus*), redfish (*Sebastes* sp.) and halibut (*Reinhardtius hippoglossoides*) were also eaten by nearly 10% of the animals off Iceland and about 50% off Labrador, respectively. However, fish represented a small proportion of the total volume of stomach contents.

The conditions of the BT and BF of all the Ziphiidae observed indicate that these whales are primarily squid-eaters, though there remains a problem of some ossification in the attachments of the TC of the *Mesoplodon* species.

Platanistidae

Reeves and Brownell (1989) reviewed feeding habits of the susu (*Platanista*). Among prey items found in the stomachs of susus, prawns, clams, catfishes (*Wallago attu* and *Macrones aor*), carp (*Catla buchanami*) and goby (*Glossogobius giuris*) appear to be their main food. In the close species to above fishes, the meat of carp (*Cyprinus carpio*) and catfish (*Silurus asotus*) contain no viamin D, and that of goby (*Acanthogobius flavimanus*) only contains the vitamin of 10 IU per 100g (Kagawa, 1989).

Boto (*Inia geoffrensis*) is known to feed on over 43 species of fish, especially on sciaenids, cichlids and characins (Best and da Silva, 1989). Leatherwood and Reeves (1983) and Evans (1987) mentioned that the dolphin also feeds on armored catfish, and perhaps molluscs and crustaceans. The boto observed in this study had been kept at a aquarium for two years and had been fed exclusively on the Japanese horse mackerel (*Trachrus japonicus*) (Tobayama and Kamiya, 1989) with low vitamin D content (Kagawa, 1989). Ossification in the FC and TC probably does not occur either in the wild botos that are feeding on prey items low in vitamin D content.

According to Brownell's (1989) review on prey items of franciscana (*Pontoporia blainvellei*), the dolphins feed on many species of fish and some species of squid and shrimp. Among a wide variety of fishes as food for the dolphins, the most important species was *Cynoscion striatus* (Sciaenidae) in the studies examined in southern Brazilian and northern Uruguayan waters. Penaeid shrimp of three species were found in the stomachs of dolphin. Squid beaks, *Loligo sanpaulensis*, were commonly found in the stomachs of dolphins, and the squid was one of the most important prey item for the dolphin in Bahia Samboromdon. The importance of squis as food for the dolphin appears to remain an open question. Although the vitamin D content in most species of sciaenids including the important species, *C.striatus*, and other bottom-dwelling fishes listed in the review are unknown, bottom-dwelling fishes on the whole are of low vitamin D content. The vitamin is not contained at all in fish meat of *Ammodytes personatus, Platycephalus indicus, Paraplagusia japonica, Salangichthys microdon, Lampetra mitsukurii, Trachurus japonicus* and *Conger myriaster*, and is contained only 8～20 IU per 100g in fish meat of *Acanthopagrus schlegeli, Acanthogobius flavimanus* and *Sillago japonica* (Kagawa, 1989).

Monodontidae

According to a review of prey items on narwhals (*Monodon monoceros*) by Hay and Mansfield (1989), the narwhal mainly feeds on the Arctic cod (*Boreogadus saida*), the polar cod (*Arctogadus glacialis*), the Greenland halibut (*Reinhardtius hippoglossoides*), the squid (*Gonatus fabricii*) and the shrimps (*Pasiphaea tarda* and *Hymenodora glacialis*). Finley and Gibb (1982) found abundant squid beakes besides a number of cod (above spp.) in the stomachs of 73 narwhals.

Among the fishes eaten by narwhals, the liver oil of halibut (*Hippoglossus hippoglossus*) contains a large amount of vitamin D, although the value vary according to seasons (550～20,000 IU/g). It is unknown whether the poorly ossified process (might be present) in the animal observed was caused by ingested halibuts.

Delphinidae

The genus *Stenella* feeds mainly on a wide variety of epipelagic and mesopelagic fishes and a substantial amount of squid (Gaskin, 1982; Evans, 1987). Among fish species, myctophids predominated in stomachs of *S.longirostris* (Fitch and Brownell, 1968), *S.coeruleoalba* (Wilke, Taniwaki and Kuroda, 1953; Miyazaki, Kusaka and Nishiwaki, 1973) and *S.clymene* (Perrin, Mitchell, Mead, Caldwell and van Bree, 1981), and they were also important to *S.graffmani* (Fitch and Brownell, 1968). *S.attenuata* mainly feeds on epipelagic fishes such as flying fish (Mitchell, 1975).

In the skulls of elderly spotted dolphins, in which the BF and BT are complete, the inner surface of the calvaria is roughened by many laminations formed by ossification in the dura mater. This is considered to be caused by hyperplasia of the bones.

According to Evans (1987) and Mitchell (1975), the genera *Delphinus,* *Steno, Tursiops, Lagenorhynchus, Sousa, Lissodelphis* and *Lagenodelphis* feed on a wide variety of epipelagic and mesopelagic fishes as well as squid and other molluscs.

The percentage of fish and squid in the stomachs of bottlenose dolphins and Pacific white-sided dolphins (*Lagenorhynclus obliquidens*) caught in waters adjacent to Kyushu, Japan, during 1968-1969, were reported by the Research Department Fisheries Agency, Japan (1969). Although stomach contents of catches varied a little according to different localities and different seasons, these dolphins had fed mainly on epipelagic and bottom-dwelling fishes, and the percentage of squid was only 15-30% in the bottlenose dolphin and less than 40% in the white-side dolphin.

According to Baker (1981), Torres and Aguayo (1979) found 1,261 lantern fish otoliths and 46 squid beaks in the stomach of one southern right whale dolphin (*Lissodelphis peronii*).

Nishiwaki and Handa (1958) reviewed the published reports of the stomach contents of 567 killer whales (*Orcinus orca*) caught in the coastal waters off Japan from 1948 to 1957. Although the killer whale eats other warm-blooded animals, most stomachs of the animals contained a large amount of fishes such as cod, flatfish, sardine, salmon and tuna as well as squid. In the younger animals, the intake ratio of fish was higher than those of adults. Macintyre (1934) described that the killer whale is an important predator of the salmon.

Nishiwaki (1965) described that the captive Risso's dolphin showed little interest in any food except squid. According to Evans (1987), squid and octopus are main foods of the Risso's dolphin, but fish is occasionally taken. No fish was found in any Risso's dolphins in a study in Washington State (Stroud, 1968). Poorly ossified BF and BT of the Risso's dolphins observed also suggest that this species is primarily a squid-eater.

On the whole, the correlation between the degrees of ossification in the FC and TC and known food items of cetaceans agrees with the hypothesis in this study. However, there are several species in which the data do not support the hypothesis, although the details of their feeding habits are not well known.

Pilot whale generally prefer squid. Sergeant (1962) observed the long-finned pilot whale (*Globicephala melaena*) feeding on short-finned squid (*Illex illecebrosus*) almost exclusively during the July-October interval at Trinity Bay, Newfoundland; cod was only taken when squid was scarce. He pointed out a close relationship between the distribution of the pilot whale population off the east coast of Newfoundland and that of the squid. He also quoted Kritzler's (1952) observations that a young captive short-finned pilot whale (*Globicephala macrorhynchus*) had refused to feed on fish at first, although it eventually learned to take them. Sergeant (1962) concluded that squid is the preferred food of pilot whales, with fish as an alternative.

Keiver, Ronald and Draper (1988b) showed that plasma levels of 25-OHD, 24,25-$(OH)_2D$ and calcium in the long-finned pilot whales (stranded, place and season are not mentioned) were similar to those of nonmarine mammals, while in the white whale (*Delphinapterus leucas*) and bottlenose dolphin (feeding mainly on fish), levels of 25-OHD and 24,25-$(OH)_2D$ were extremely high. The results suggest that the long-finned pilot whale had fed mainly on squid (at least during the time immediately preceding the stranding) and indicate high plasma levels of vitamin D in fish-eating dolphins.

In this study, the long-finned pilot whale was not studied. If the animals are truly squid-eaters, both the BF and BT should be absent according to my hypothesis. However, the BF and BT of the short-finned pilot whale, another *Globicephala* species, and those of the false killer whale (*Pseudorca crassidens*) and pygmy killer whale (*Feresa attenuata*), were ossified in the shape of the entire FC and TC. The stomach of a false killer whale caught off western Japan contained 12 common sea basses *Lateolabrax japonicus* (about 60 cm in length) as well as many squid beaks (the Research Department Fisheries Agency, Japan, 1969). These whales may ingest much larger amounts of fish than is generally believed.

Phocoenidae

In the finless porpoise which feeds on small squid, cuttlefish and shrimp but also takes small sandeels and other fishes (Mitchell *et al.*, 1975), ossification in the FC and TC (even in a lactating adult) has occurred much less frequently than in other phocoenids. Poorly developed BF and BT in these porpoises suggest that they feed mainly on crustaceans and molluscs or that fishes eaten have a low vitamin D content. The meat of sandeel *Ammodytes personatus* contains no vitamin D (Kagawa, 1989).

The harbor and Dall's porpoises feed on a large number of fish species. Rae (1965) reviewed food habits of the harbor porpoise reported in an earlier time in the North Sea, and more recently in the Baltic Sea (Lindroth, 1962), off eastern Canada (Sergeant and Fisher, 1957) and off Scotland by Rae himself. The stomach contents showed that the harbor porpoise feeds mainly on fishes such as clupeoids, gadoids and pleuronectids such as herring, whiting and mackerel, but squid were occasionally found in the stomachs in some quantity. Smith and Gaskin (1974) examined stomach contents of *P.phocoena* taken from coastal waters of New Brunswick, Nova Scotia, and Prince Edward Island during 1969-1972. The animals fed mainly on fishes such as herring, gadoids and mackerel, but squid was occasionally taken. Wilke and Nicholson (1958) examined the stomachs of 86 *truei*-type and seven *dalli*-type Dall's porpoises (*Phocoenoides dalli*) collected off Japan, March to June 1952. Various myctophids formed 70%, by volume, of the stomach contents in the True's porpoises and 73% in the Dall's porpoises; the percentages of squid were 11 and

5%, respectively. Wilke *et al.* (1953) found that squid formed 98%, by volume, of the stomach contents in four Dall's porpoises taken from March to May off northern Japan. This result contradicts Cowan's (1944) statement that Dall's porpoise feeds exclusively on herring in the northern North Pacific.

In a previous study (Nojima, 1988) of the BF and BT of spotted dolphins, I prepared the skulls very carefully so as not to damage the BF and BT. When ossification of the BF and BT has not been completed, these are very fragile, especially the BT. It is likely that the BF and BT of all harbor and Dall's porpoises observed had been damaged during preparation of the skulls. I observed no specimen in which the BT was complete, but the BF was relatively well developed and the passage of the trigeminal nerve occurred as a round foramen in most older specimens.

These porpoises probably ingest a large amount of fish, as has been reported.

Consumption of Vitamin D by Fish-eating Dolphins

In the following section, the amounts of vitamin D that are taken by fish-eating dolphins are estimated.

Sergeant (1969) examined feeding rates in captivity of nine dolphin species. He estimated that of bottlenose dolphins to be 4.2% body weight. Nakajima (1973) also reported the average volume of daily food of a 300 kg captive bottlenose dolphin as about 15 kg (mackerel *Scomber japonicus*).

The liver of a 410 g mackerel (*Scomber japonicus*) weighs about 10 g. If a 10 g mackerel liver is estimated conservatively to yield 1 g liver-oil (the average liver-oil content of cod liver is more than 50%, by weight: Omura, Matsuura and Miyazaki, 1942; although the values for fish vary according to season: Pugsley, 1939), total vitamin D in 15 kg of mackerel can be estimated as at least 230,000 IU. This amount corresponds to about 120 times the recommended daily dose for a human in weight-specific intake. With the exception of 1α-OH-D and 1α, 25-$(OH)_2D$, the active form of vitamin D used to treat humans for vitamin deficiencies, toxicity rarely results from an excessive intake of vitamins D_2 and D_3 contained in food. However, a repeated intake of more than 100,000 IU per day of these vitamins may cause toxicity in humans (Krupp and Chatton, 1977; Kobayashi, 1989). Although the estimated vitamin D values taken by the dolphin do not approach the above dangerous level for humans in weight-specific intake, such large values cannot be ignored. Further consideration is needed to extend this calculation to the wild dolphins, because of uncertainties in the feeding rate (probably higher in the wild) and the consumption of variable food items with lower vitamin D values such as squids and many fish species other than mackerel.

Keiver *et al.* (1988a) studied vitamin D metabolism in hooded seals (*Cystophora cristata*), which ingest large amounts of fish, as do dolphins of the genus

Stenella. They concluded that rapid conversion of vitamin D and a high capacity for vitamin D storage in the large blubber mass appear to be factors in the resistance of seals to vitamin D toxicity. It is unknown whether similar factors operate in the fish-eating cetaceans.

Concluding Remarks

Besides delphinids and phocoenids, I have observed the dolphin type BT only in spider monkeys (*Ateles geoffroyi* and *A.paniscus*) among all mammals studied, and in those species the BF was absent although the FC was identical with the TC histologically. The factors involved in ossification only in the TC are unknown. Most of the animals studied had been born and bred in a zoo and they had been fed the usual diets, with no special items high in vitamin D. Formation of the dolphin type BT in spider monkeys cannot be related to their diet (Nojima, 1990b), and it obviously differs from those of delphinids and phocoenids in which ossification occurs in both the FC and TC.

Although I have not systematically examined hyperplasia of bones and calcium deposition in soft tissue (which may occur in the fish-eating mammals), the degree of ossification in the FC and TC of cetaceans obviously proceeds in parallel with the increased proportion of fish in the diet.

Stomach contents provide direct evidence of the food eaten by an animal. However, they do not necessarily reveal much about its longterm diet.

Although many cetaceans have been described as opportunistic feeders, the degree of ossification in their FC and TC appears to reflect the general trend of their food habits throughout life in the same way that the growth layers formed in the teeth and ear plugs of cetaceans indicate their ages. A comparison of the degrees of ossification in the FC and TC between captive dolphins fed mainly squid and others fed mainly fish would provide a further test of this hypothesis.

Recommended Preparation Procedures

As already mentioned in the text, the BF and BT of delphinids and phocoenids are fragile during preparation, especially when ossification has not been completed in the shape of the entire FC and TC. Therefore, close attention should be paid to preparation of the skulls. Boiling the skull is not recommended because the incomplete BF and BT are often fractured owing to strong contraction of the FC and TC by heat. Furthermore, the BF and BT are easily damaged when the brain and its membranes are extracted through the foramen magnum. In order to keep the BF and BT complete during preparation of the skulls, it is best to ensure that the head (after removing the soft tissue as completely as possible) is submerged in fresh water for several months, or until the brain and its membranes have completely rotted and can be washed away.

ACKNOWLEDGMENTS

I wish to express sincere gratitude to Dr N. Miyazaki and Dr M. Yoshiyuki, Department of Zoology, National Science Museum, Tokyo, for giving me access to the valuable collections, and to Dr M. Nakajima, Izu-Mito Sea Paradise, Shizuoka, who supplied me with materials and useful information. My sincere thanks are also due to Dr K. Shigemasa, Department of Anatomy, Nihon University School of Dentistry, Tokyo, who kindly helped me to collect references. I particulary thank Dr T. Kasuya and two anonymous reviewers for their comments on the manuscript. One of the two reviewers is greatly acknowledged for his kindly check of English style and grammar. I want to add a few words of gratitude to my wife Miwa for her help in all respects throughout this study.

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EXPLANATIONS OF PLATES

PLATE I.

Lateral view of the skull and head of adult spotted dolphins.

Fig. 1. BF: bony falx, BT: bony tentorium, U_1: unossified portion for the passage of the cerebral veins into the dorsal sagittal sinus, U_2: unossified portion for the passage of the continuation of the spinal meningeal artery (SMA), G: groove for the continuation of SMA.

Fig. 2. FC: falx cerebri, TC: tentorium cerebelli, SMA: continuation of the SMA (intradural).

PLATE II.

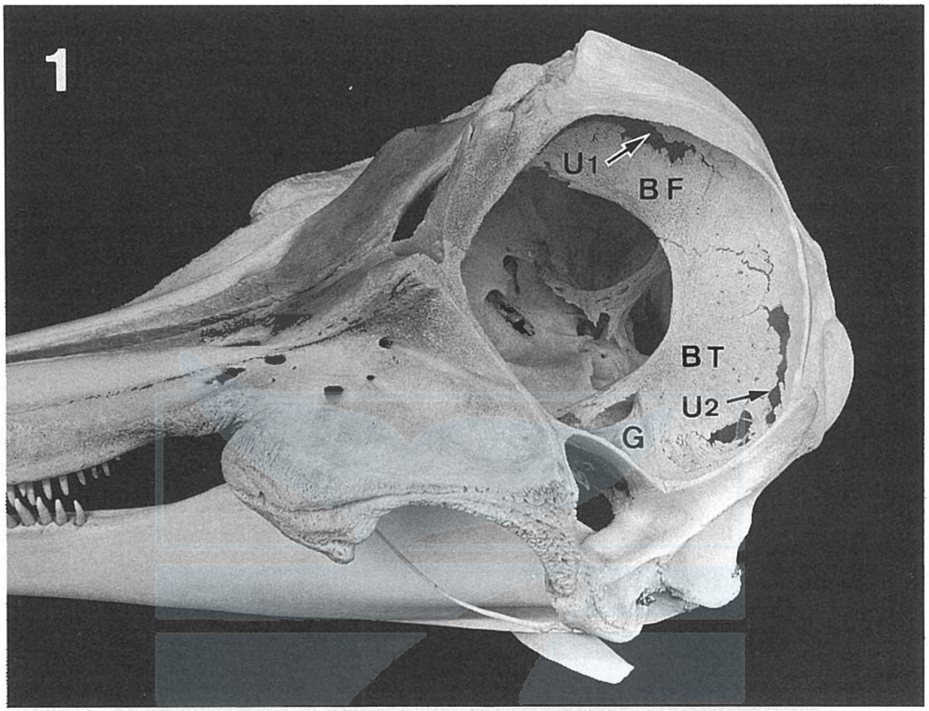
Fig. 1. Inner surface of the cranial cavity of a juvenile spotted dolphin. DSS: dorsal sagittal sulcus.

Fig. 2. Lateral view of the skull of a young striped dolphin. The BF and BT have not been completed as a continuous bony plate. Black arrows point to the edges of developing BT.

PLATE III.

Interior of the posterior half of the cranial cavity of an elderly spotted dolphin. Arrows indicate ossified laminations. FM: foramen magnum.

PLATE I.



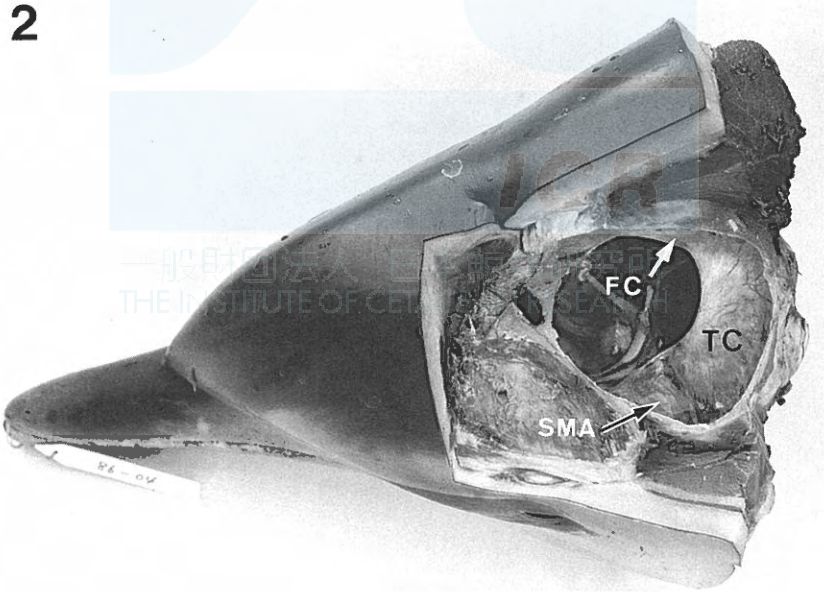
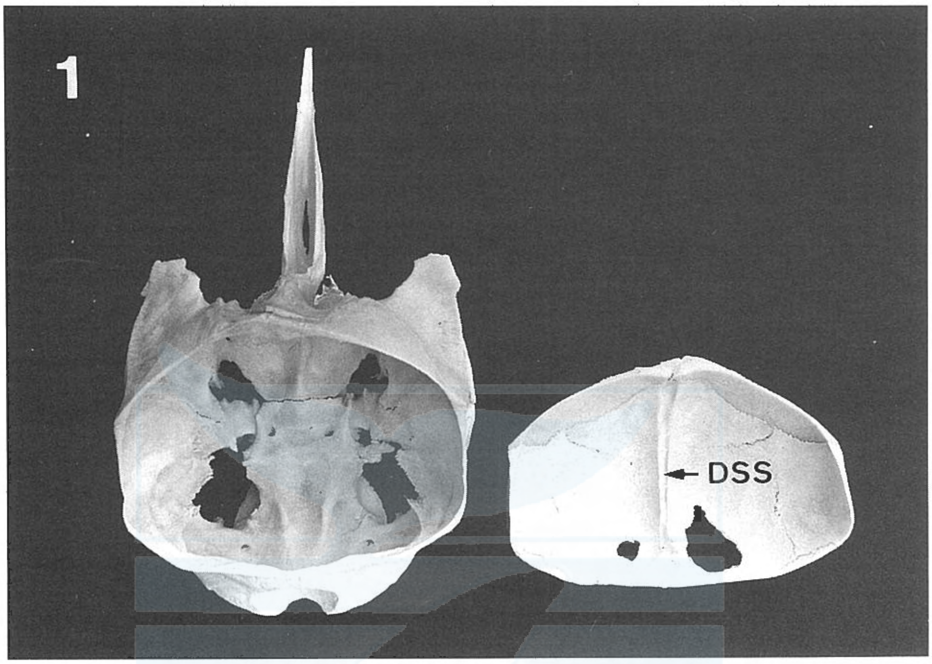


PLATE II.



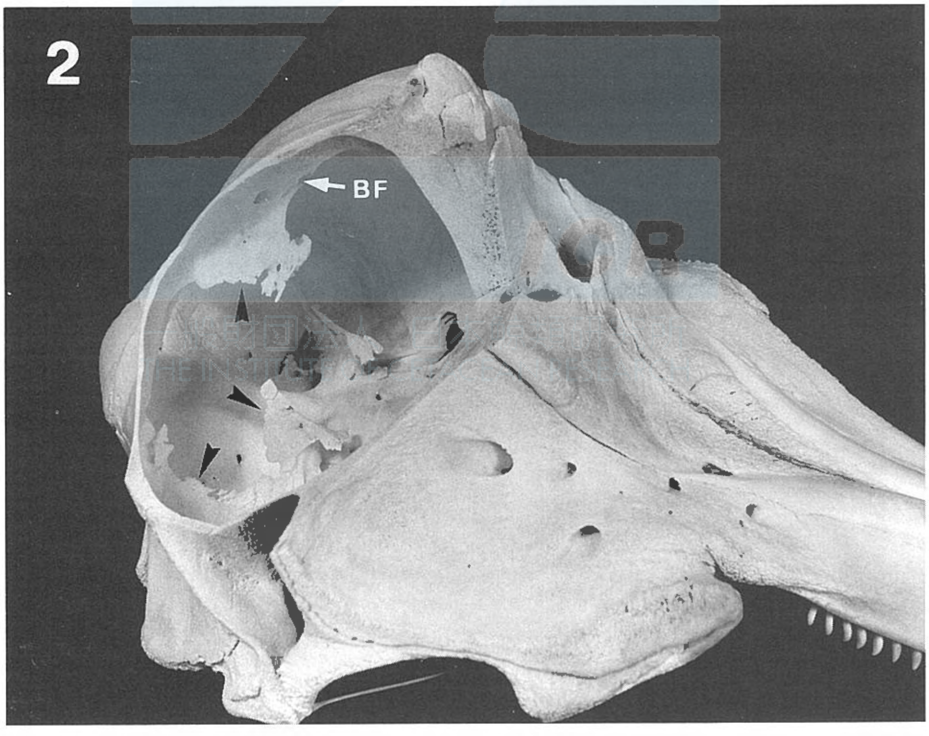
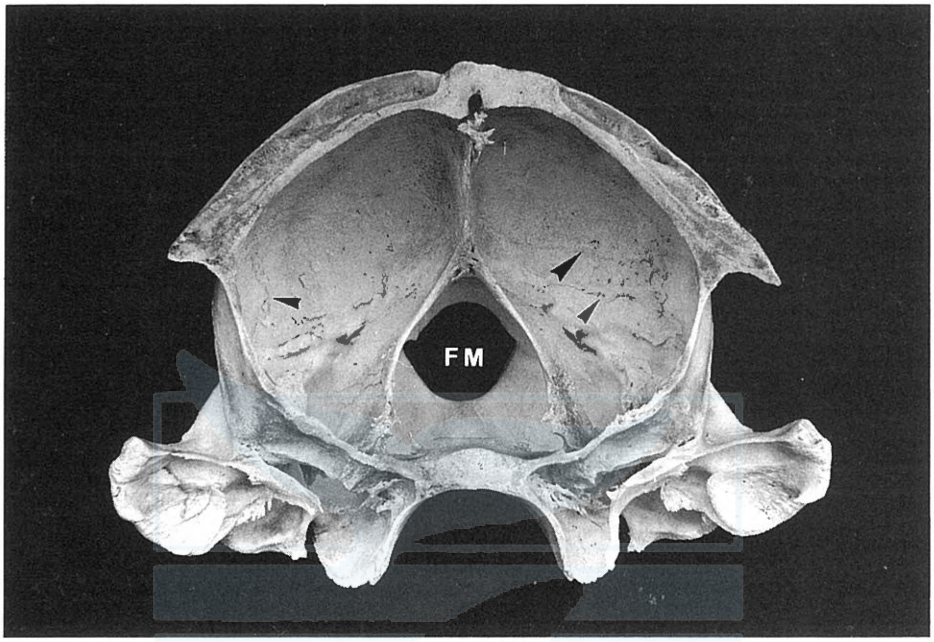


PLATE III.



ICR

RECORDS OF BEAKED WHALES IN QUEENSLAND

ROBERT A. PATERSON[1] AND STEPHEN VAN DYCK[1]

ABSTRACT

Beaked whale records in the Queensland Museum are confined to eleven specimens representing four species. They include the holotype of *Indopacetus pacificus* (Longman, 1926) and specimens of *Mesoplodon densirostris* (de Blainville, 1817) (5), *M. layardii* (Gray, 1865) (3) and *Ziphius cavirostris* (Cuvier, 1823) (2). Dental/mandibular relationships are demonstrated by radiographic methods in specimens of *M. densirostris* and *M. layardii*. Temperatures in Queensland waters are influenced by the warm East Australian Current and the composition of the collection reflects known distributions of the relevant species.

Key words: Ziphiidae, beaked whales, Queensland

INTRODUCTION

The Queensland coast borders the north-eastern aspect of the Australian continent and lies between latitudes 10°S and 28°S (Fig. 1). In contrast to the diversity of beaked whale species (Ziphiidae) recorded from the cooler waters of the southern hemisphere (Baker, 1983; Ross, 1984; Lichter, 1986), the collection in the Queensland Museum is limited to four species represented by eleven specimens.

Lichter (1986) described records of beaked whales from the Atlantic coast of South America and referred to isolation and climatic extremes among difficulties preventing examination of some fresh specimens. Goodall (1978) collected small cetacean specimens (including beaked whales) from Tierra del Fuego and also referred to the lack of early reports of strandings from that isolated and rugged region. Coastal Queensland is not subject to the isolation and climatic extremes of Patagonia and Tierra del Fuego but late reports of stranded or beach-cast specimens have resulted in the loss of important material even in recent years when cetaceans, including non-commercial species, have been accorded a high public profile (Anderson, 1985).

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Sci. Rep. Cetacean Res.,
No. 1, 1990, 63–77

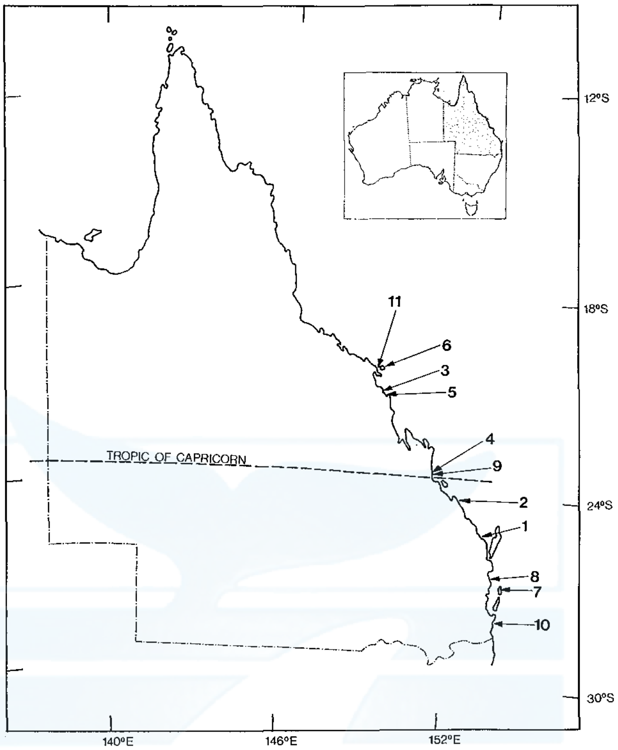

Fig. 1. Queensland coast showing collection sites of beaked whales referred to in Table 1.

SPECIES ACCOUNTS

The data are summarised in Table 1 and stranding locations are shown numerically in Fig. 1.

Ziphius cavirostris (Cuvier, 1823)
J3262 and JM5264 are illustrated in Fig. 2. Longman (1919) referred to a single tooth of J3262 when describing it as an immature female but the tooth has since been lost. JM5264 is from a whale which stranded at a popular, but secluded, camping site during the 1985 summer holidays. A photograph taken soon after stranding showed that colouration was pale grey dorsally and white ventrally. The decaying carcass was hacked and burned by campers in attempts to destroy it, and the success of those attempts can be judged by the extensive axe and fire damage to the skull. Sufficient material survived to demonstrate extensive posterior meso-rostral ossification which, together with the deep pre-narial basin, indicates that the specimen is that of an adult male (Hale, 1931).

TABLE 1. BEAKED WHALES IN THE QUEENSLAND MUSEUM

Map reference	Registration number	Date of stranding	Location	Sex and maturity	Length	Material	Reference
Ziphius cavirostris (CUVIER, 1823)							
1	J3262	December 1918	Nikenbah (25°19′S, 152°48′E)	F Immature	–	skull and mandible	Longman (1919)
2	JM5264	December 1985	Agnes Water (24°10′S, 151°53′E)	M Adult	–	skull	–
Indopacetus pacificus (LONGMAN, 1926)							
3	J2106	–	Mackay (21°01′S, 149°11′E)	M Adult	–	skull and mandible	Longman (1926)
Mesoplodon densirostris (DE BLAINVILLE, 1817)							
4	J4056	–	Yeppoon (23°08′S, 150°44′E)	M Adult	–	skull	Longman (1926)
5	J5330	–	Sarina (21°24′S, 149°19′E)	F Immature	–	skull and mandible	Paterson (1986a)
6	J13600	–	Whitsunday Group (20°10′S, 149°05′E)	M Adult	–	skull and mandible	〃 〃
7	JM4399	–	Moreton Island (27°12′S, 153°22′E)	M Adult	–	skull	〃 〃
8	JM6460	June 1986	Noosa (26°25′S, 153°07′E)	M Adult	4.01 m	almost complete skeleton	–
Mesoplodon layardii (GRAY, 1865)							
9	J2105	–	Emu Park (23°16′S, 150°50′E)	M Adult	–	skull, mandible and cervical vert.	Jaggard (1884)
10	J3280	December 1884	Southport (28°00′S, 153°26′E)	F Adult	3.7 m	incomplete vertebral column	De Vis (1884)
11	JM6198	August 1986	Whitsunday Passage (20°20′S, 148°50′E)	M Immature	4.7 m	complete skeleton	–

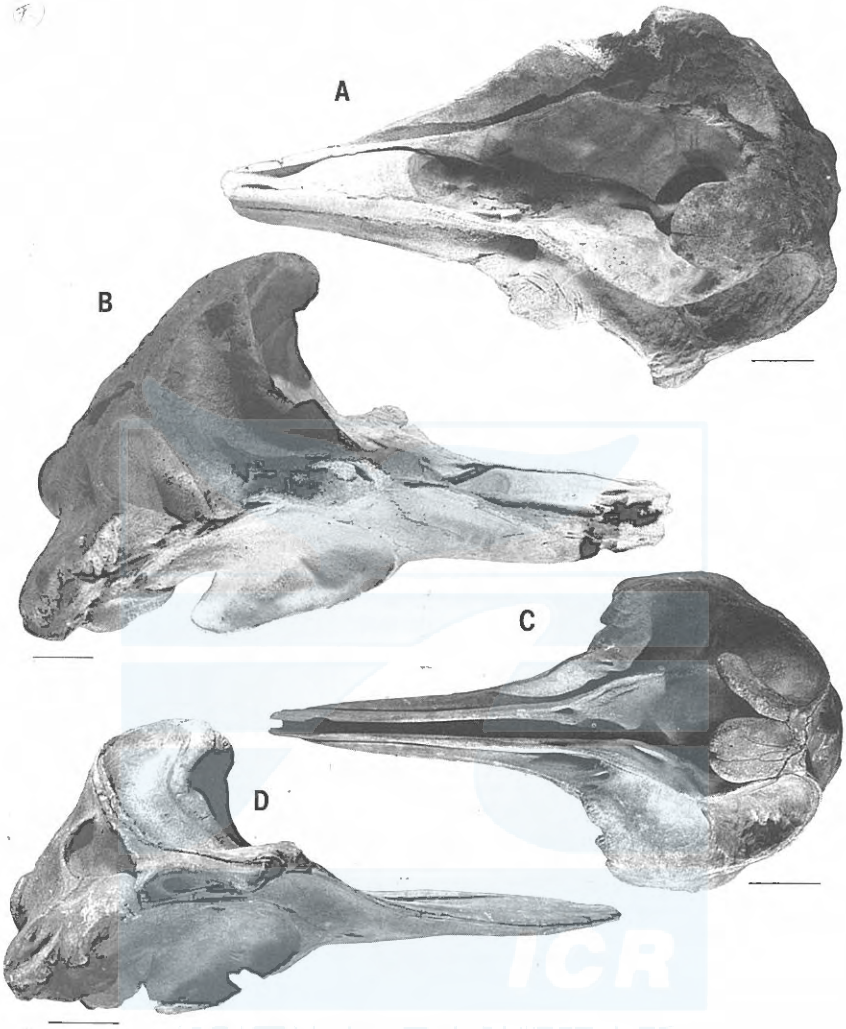

Fig. 2 *Ziphius cavirostris*.
Skull of JM 5264. A. Dorsal view.
B. Lateral view.
Skull of J3262. C. Dorsal view.
D. Lateral view.
(Scale in each case represents 10 cm)

Indopacetus pacificus (Longman, 1926)
The type specimen (J2106), a skull and mandible with the teeth missing, discovered at Mackay in 1882, was described by Heber A. Longman, a former director of the Queensland Museum. He named it *Mesoplodon pacificus*. Its status was confirmed by Moore (1968) who considered it to be an adult male and renamed it *Indopacetus pacificus* on

左右 11 cm

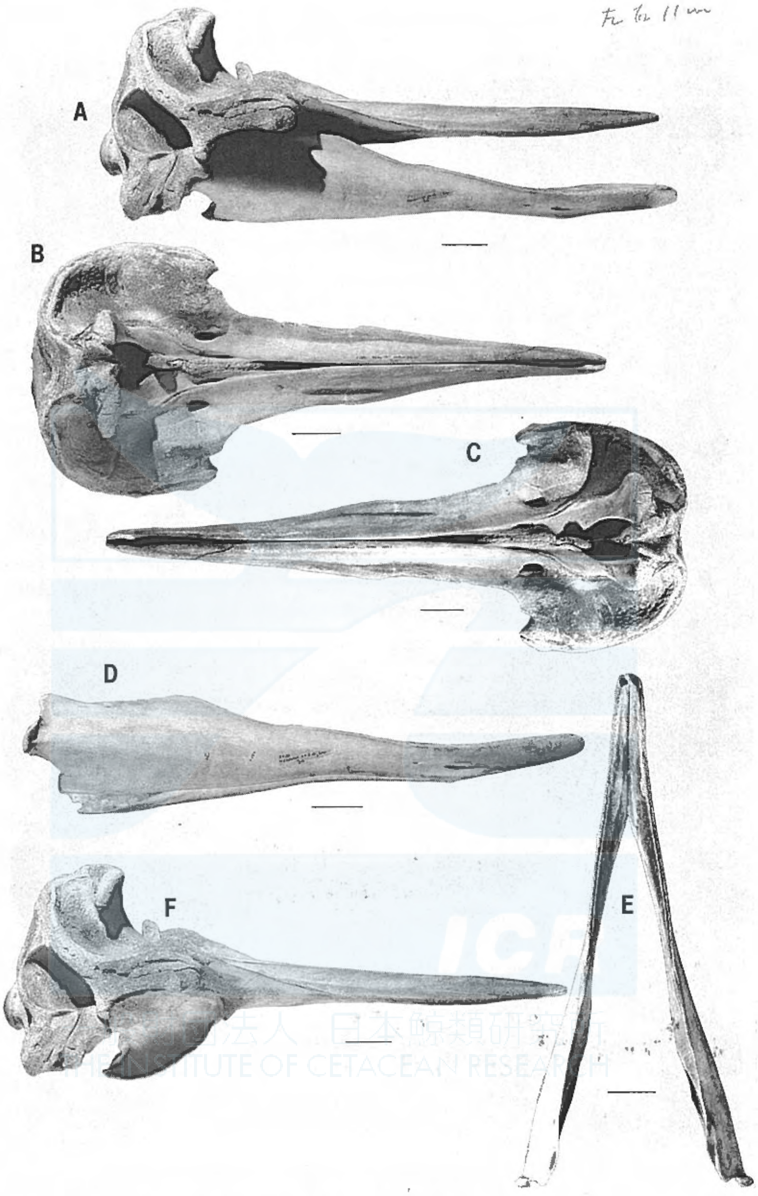

Fig. 3. *Indopacetus pacificus*, holotype, J2106.
A. Lateral view, skull and mandible.
B. Dorsal view, skull.
C. Additional dorsal view of skull, angled to show narial relationships.
D. Lateral view, mandible.
E. Dorsal view, mandible.
F. Lateral view, skull.
(Scale in each case represents 10 cm)

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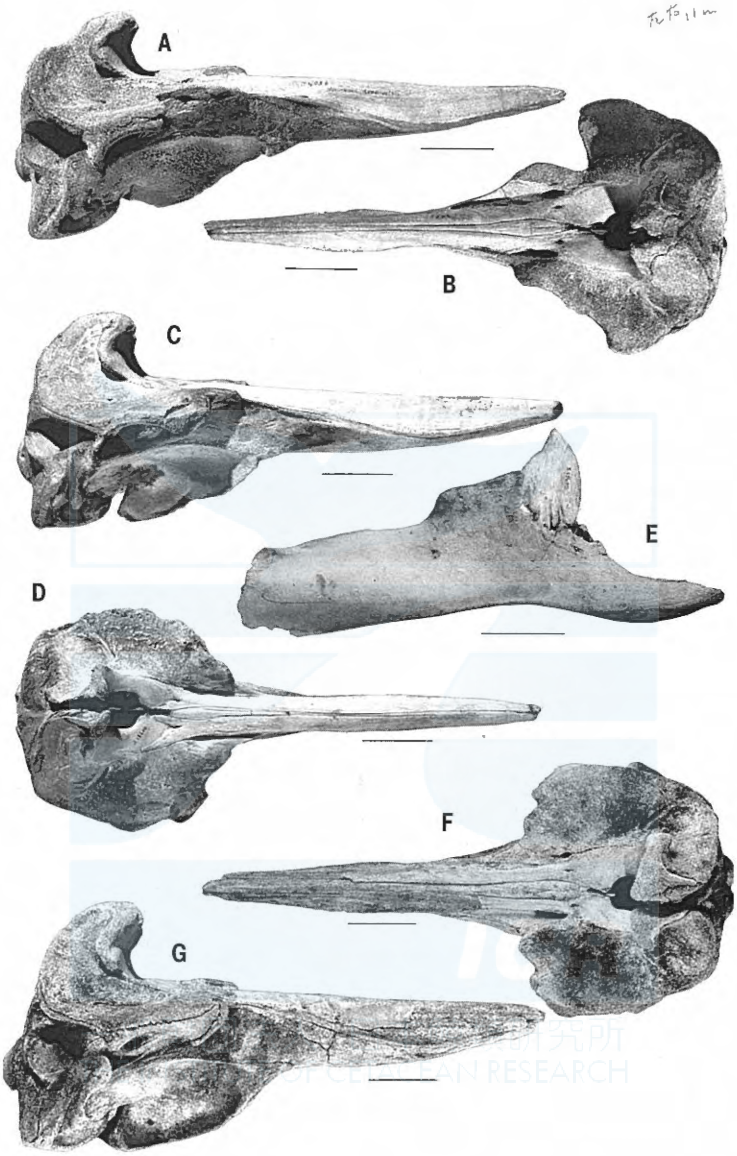

Fig. 4. *Mesoplodon densirostris*
Skull of J4056. A. Lateral view.
B. Dorsal view.
Skull and mandible of J13600. C. Lateral view.
D. Dorsal view.
E. Lateral view, mandible.
Skull of JM4399. F. Dorsal view.
G. Lateral view.
(Scale in each case represents 10 cm)

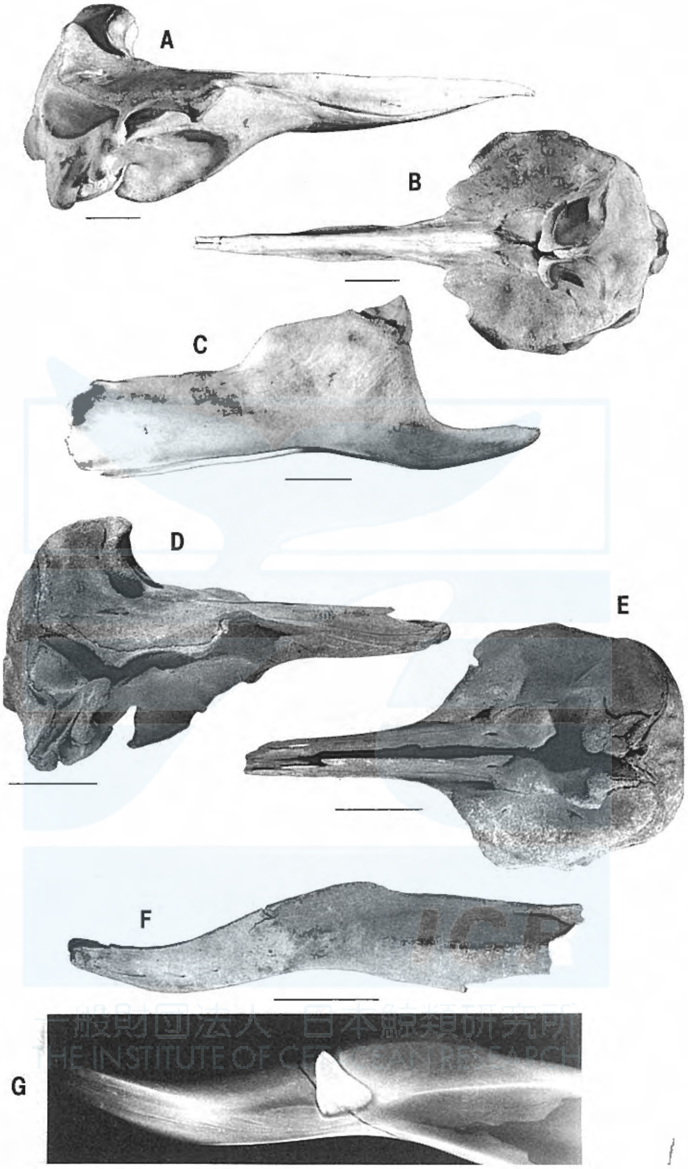

Fig. 5. *Mesoplodon densirostris*
Skull and mandible of JM6460. A. Lateral view, skull.
B. Dorsal view, skull.
C. Lateral view, mandible.
Skull and mandible of J5330. D. Lateral view, skull.
E. Dorsal view, skull.
F. Lateral view, mandible.
G. Lateral radiograph, mandible.
(Scale in each case represents 10 cm)

the basis of the deep horizontal grooving of the maxillary bone above the orbit, the short posterior processes on the premaxillary crest, and the lack of projection and poor indentation of the nasal bones. A second specimen, also a skull and mandible, discovered at Danane in Somalia was described by Azzaroli (1968). Moore (1972) considered this latter specimen to be immature as compared with the type specimen which is illustrated in Fig. 3.

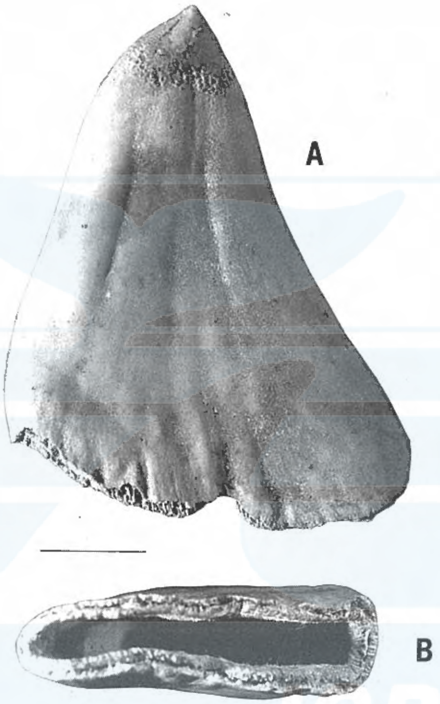

Fig. 6. *Mesoplodon densirostris*.
Right tooth of J5330. A. Lateral view.
B. Ventral view.
(Scale in each case represents 10mm)

Mesoplodon densirostris (de Blainville, 1817)
Skulls and mandibles of J4056, J13600, JM4399, J5330 and JM6460 are illustrated in Figs 4 and 5.

The skull and mandible of J5330 are damaged. The dental/mandibular relationship is demonstrated radiographically. The shape of the unerupted left tooth (Fig. 5G) is typically female (Raven, 1942) and the complete lack of pulp space filling demon-

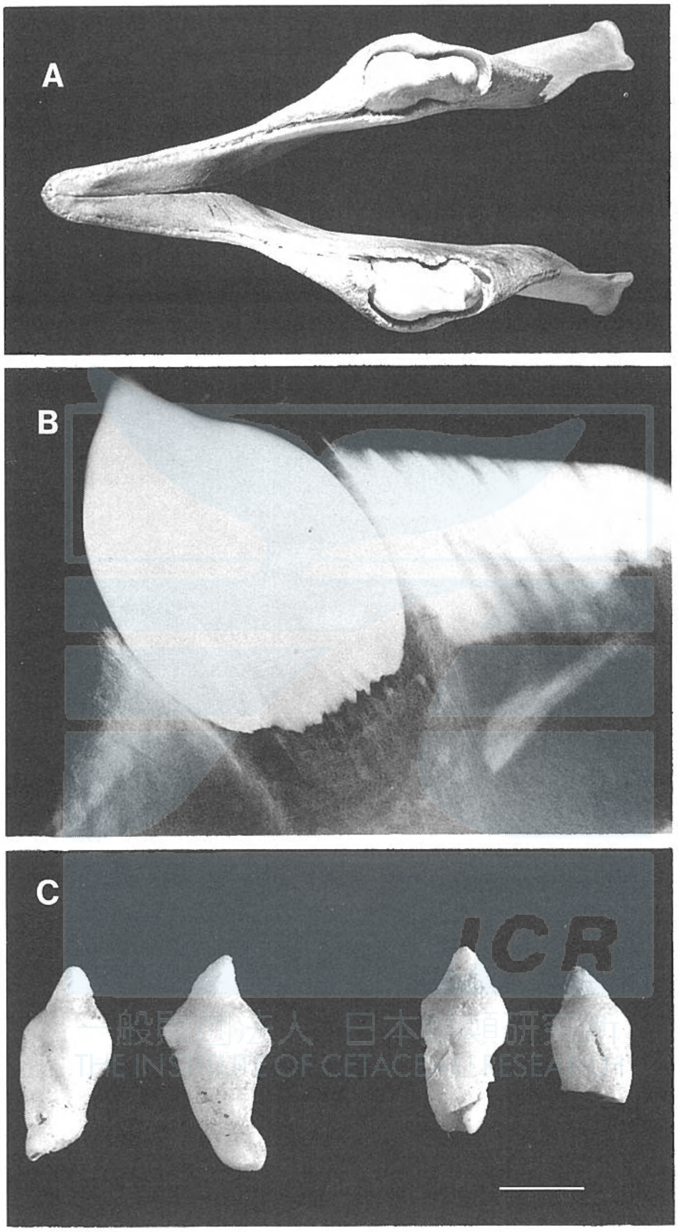

Fig. 7. *Mesoplodon densirostris.*
Mandible and teeth of JM6460.
A. Angled dorsal view, mandible.
B. Lateral radiograph showing tooth in situ (the anterior aspect of the mandible is to the left of the radiograph).
C. Rudimentary teeth (scale represents 5mm).

strated in its right counterpart (Fig. 6) indicates that the specimen is immature. The right tooth measures 50 mm in height, 39 mm in length and 12 mm in maximum width. Besharse (1971) noted that the teeth of adult and subadult female specimens of *Mesoplodon densirostris* from Midway Atoll measured 59 mm and 57 mm in height, respectively. The damaged state of J5330 precludes comparison with all the Midway data but the dental evidence alone indicates that the Queensland specimen is less mature than the Midway subadult.

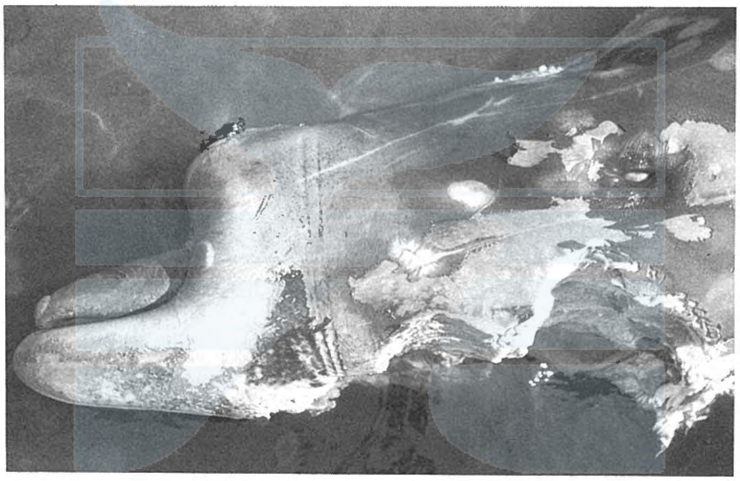

Fig. 8. Mauled head and upper body of *Mesoplodon densirostris* JM6460.

With the exception of J5330, the Queensland specimens are considered to be those of mature males. JM6460 was the only specimen examined in the fresh state. It measured 4.01 m in length. Colouration was blue-grey dorsally and light grey ventrally. Prominent oval scars, which coalesced ventrally, were similar to those described by Ross (1984). Mead, Walker and Houck (1982) discuss in detail the possible aetiologies of these scars. When the soft tissues anterior to the pair of erupted mandibular teeth were being cleaned, two rudimentary teeth were found in relation to each of them (Fig. 7). The rudimentary teeth had no mandibular attachment. Although primitive in form, they show greater differentiation than those found on occasions in the upper jaws of *Mesoplodon grayi* (Hale, 1932; Delhon, Crespo and Pagnoni, 1987) and *Ziphius cavirostris*

(Watson, 1981). Stalked barnacles identified as *Conchoderma auritum* (Linnaeus, 1767) were attached to the tip of each erupted tooth. Pringle (1963) noted a mass of seaweed about 6″ to 10″ [15 to 25 cm] in length attached to the tip of each tooth in a specimen of *Mesoplodon densirostris* from South Africa. Mead (1989) considered that the "seaweed" was *Conchoderma*. The erupted teeth of *M. densirostris* are non-occlusal and Clarke (1956) noted that attachment of *C. auritum* in sperm whales is also confined to teeth which do not occlude with their corresponding maxillary sockets because of the extreme anterior position of those teeth or, more uncommonly, mandibular deformity.

The vertebral formula for JM6460 is C.7; T.10; L.9; Cd.17 = 43. The first three cervical vertebrae are fused. Raven (1942) noted that such fusion did not involve the transverse processes. However, in JM6460 the transverse processes of C.1 and 2 are fused. It is likely that the smallest caudal vertebrae are absent as a result of mauling by sharks. This is supported by the fact that the posterior portion of C.17 is severed. Extensive post-mortem mauling of JM6460 also accounted for the destruction of abdominal and cranial soft tissues (Fig. 8).

Mesoplodon layardii (Gray, 1865)

Apart from some cervical, thoracic and lumbar vertebrae (all exhibiting complete epiphyseal fusion), the skeleton of J3280 has been lost. The skulls and mandibles of J2105 and JM6198 are illustrated in Fig. 9. The posterior inclination of the tooth, unerupted in the immature specimen (JM6198), is illustrated radiographically in Fig. 9G. Moore (1968) noted that the lateral position of the denticle at the apex of the tooth was characteristic of the species and those findings were confirmed in this specimen (Fig. 10).

The carcasss of JM6198 was decomposed when collected but it was identified as a male. The central epiphyses of the thoracic and lumbar vertebrae are unfused. The vertebral formula is C.7; T.9; L.10; Cd.19 = 45.

DISCUSSION

Temperatures in Queensland coastal waters are influenced by the warm East Australian Current and maximum and minimum temperatures occur during January/February and July/August, respectively. Annual maximum and minimum sea surface temperatures recorded by shark fishing contractors on the central Queensland coast were 28°C and 19°C, respectively (Paterson, 1986b). The two Queensland *Ziphius cavirostris* strandings occurred during summer, one *Mesoplodon layardii* stranded during summer and another during winter and one *Mesoplodon densirostris* stranded during winter.

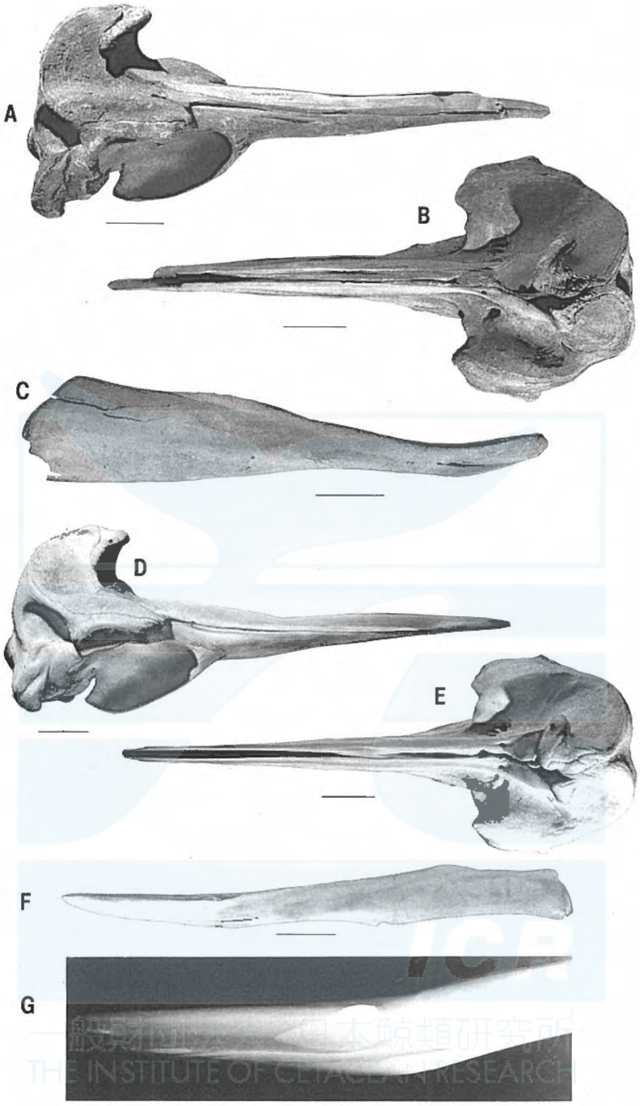

Fig. 9. *Mesoplodon layardii*
Skull and mandible of J2105. A. Lateral view, skull.
B. Dorsal view, skull.
C. Lateral view, mandible.
Skull and mandible of JM6198. D. Lateral view, skull.
E. Dorsal view, skull.
F. Lateral view, mandible.
G. Lateral radiograph, mandible (the anterior aspect of the mandible is to the left of the radiograph).
(Scale in each case represents 10 cm)

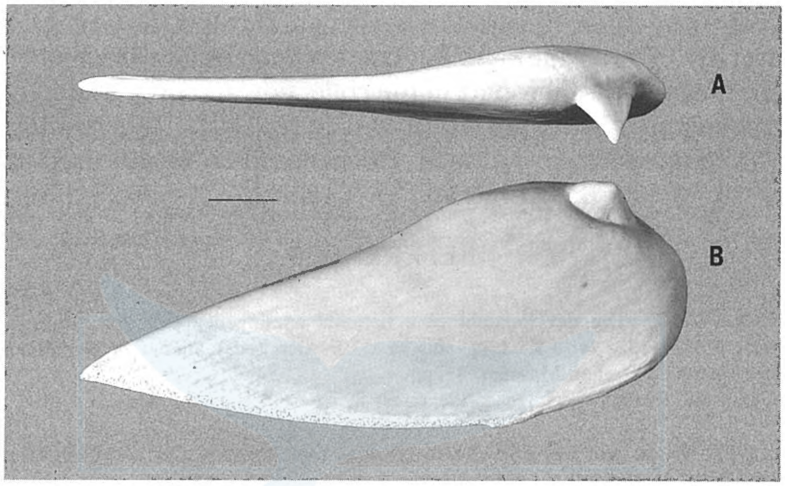

Fig. 10. *Mesoplodon layardii*.
Left tooth of JM6198. A. Dorsal view.
B. Lateral view.
(Scale in each case represents 10mm)

Ziphiids in the Queensland Museum reflect known distributions of the relevant species in Australian waters (Ross, 1989). Although the southernmost record of *Mesoplodon densirostris* is from Marrawah, latitude 40°50′S, in Tasmania (Guiler, 1966), the five specimens from Queensland indicate preference of the species for warm waters. *Mesoplodon layardii* is more commonly reported from cooler waters of the southern hemisphere (Dixon, 1980) and the southernmost record is from Heard Island, latitude 53°S (Guiler, Burton and Gales, 1987). However, the Queensland records indicate that the range of the species extends to latitudes lower than the Tropic of Capricorn.

Radiographic methods are useful to demonstrate dental/mandibular relationships in beaked whales.

Mead and Payne (1975) radiographically demonstrated the unerupted anterior pair of teeth in a female specimen of *Tasmacetus shepherdi*. Radiographic examination is of particular value in female and immature male specimens, where the teeth are unerupted.

ACKNOWLEDGMENTS

The assistance of Queensland Boating and Fisheries Patrol Officers (Munna Point) Messrs R. Grimley, C. Butler and C. Andrews is gratefully acknowledged in regard to the collection of specimen JM6460. Drs H. Marsh (James Cook University, Townsville) and P. Arnold (Queensland Museum, Townsville Branch) are thanked for their part in the collection and preparation of specimen JM6198. Radiographs were generously taken by Dr I. Robertson and Miss S. Kupis of the Jindalee Medical Centre, Brisbane. Photographs used in this paper were taken by Messrs B. Cowell and G. Cranitch (Queensland Museum).

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MASS STRANDING OF *PEPONOCEPHALA ELECTRA* (CETACEA, GLOBICEPHALINAE) ON PIRACANGA BEACH, BAHIA, NORTHEASTERN BRAZIL

LILIANE LODI[1], SALVATORE SICILIANO[2] AND LILIAN CAPISTRANO[3]

ABSTRACT

On 16 April 1987 a pod of over 240 melon-headed whales, *Peponoce phala electra* (Gray, 1846), stranded on Piracanga Beach, Bahia, northeastern Brazil (14°14'S, 39°00'W). A total of 182 whales were examined 8 days after the stranding period had started. Data on body length and/or sex ratio from 123 specimens were collected. The group of animals examined included 81 females and 44 males; 57 individuals could not be sexed due to decomposition and damage caused by vulture feeding.

Key words: *Peponocephala electra*, mass stranding, northeastern Brazil

INTRODUCTION

On 16 April 1987 a group of melon-headed whales, *Peponocephala electra*, was observed stranding on Piracanga Beach (14°14'S, 39°00'W), Itacaré County, approximately 423 km south of Salvador, State of Bahia, Brazil. Because of the remoteness of the stranding site, news of the event took several days to reach the authors. Although melon-headed whales have a world-wide distribution in tropical and subtropical seas (Leatherwood and Reeves, 1983), we here report on the first known mass stranding of the melon-headed whale, for the Atlantic Ocean. This species has only recently been recorded for the Brazilian coast, based on a skull collected at Caravelas, southern Bahia, in July 1985 (Siciliano, Fiori, Lodi and Borobia, 1987).

THE STRANDING

Piracanga is a 14.5 km sandy beach, with widths varying from 11 and 18.5 m.

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Two rivers flow into the ocean, the Piracanga and Aibim de Melo, which are lined with mangrove swamps.

For three days preceeding the stranding, winds from the south and southeast with speeds varying between Beaufort scale 1 and 6 were recorded. Such winds were coupled with heavy rain and air temperatures averaging 26°C. During the stranding, the rains continued and winds generally from the south, varied between Beaufort scale 1 and 3 (National Institute of Meteorology, VI District, Station 83348, Ilhéus, Bahia). The stranding occurred during a full moon period.

Information on the circumstances of the stranding was obtained from local fishermen. The whales stranded on the beach in groups, starting on 16 April and continuing until 19 April, when the last group came ashore. Local people tried unsuccessfully to push some of the whales back into the water. Certain individuals arrived bleeding, probably after being injured by the coral reef off Piracanga Beach. Some females reportedly aborted on the beach, although we found no foetuses on the beach upon our arrival. The actual number of whales stranded was probably higher than that reported here since some of them were removed and consumed by local people. In this case smaller animals were selected as they were easier to transport. Other whales were observed washing away with the tide. On 23 April we counted 240 whales, however during the period from 24 to 27 April, due to continued high tides, we were able to examine only 182 specimens. Most of the carcasses were in a state of advanced decomposition and heavily damaged due to feeding by vultures (*Coragys atratus*). Photographs, data on stomach contents, internal parasites (da Silva, Thatcher and Capistrano, 1987), skulls and complete skeletons were collected for further studies.

DISCUSSION

Our findings refer to the second mass stranding of cetaceans reported for the Brazilian coast. On 1 December 1972 a herd of 33 sperm whales, *Physeter macrocephalus*, stranded on Bojurú Beach, State of Rio Grande do Sul (Castello and Piñero, 1974). Large areas of the Brazilian coast are sparsely inhabited, and interest in reporting and recording strandings is very low. It is only in the last 10 years that the situation has begun to change as researchers have increased their efforts to study marine mammals in Brazil.

During the stranding reported here, whales were found within a 5 km section of the beach (Figs 1 and 2). We divided the 5 km stretch of beach into 3 sections for collecting data: section I, the portion of the beach on the south side of the Piracanga River (46 animals); section II, along the Piracanga River (18 animals); and section III, the portion of the beach on the north side of the Piracanga River (118 animals) (Fig. 3).

Of the 125 animals that could be sexed, 81 (64.8%) were females and

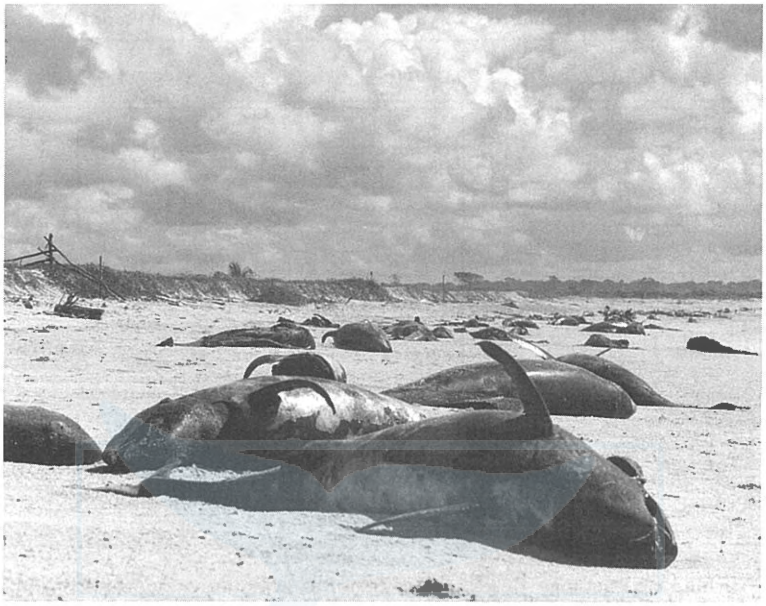

Fig. 1. Stranded melon-headed whales on Piracanga Beach, April 1987. Photo by S. Siciliano.

Fig. 2. Head of a melon-headed whale showing its coloration a few days after death. Photo by S. Siciliano.

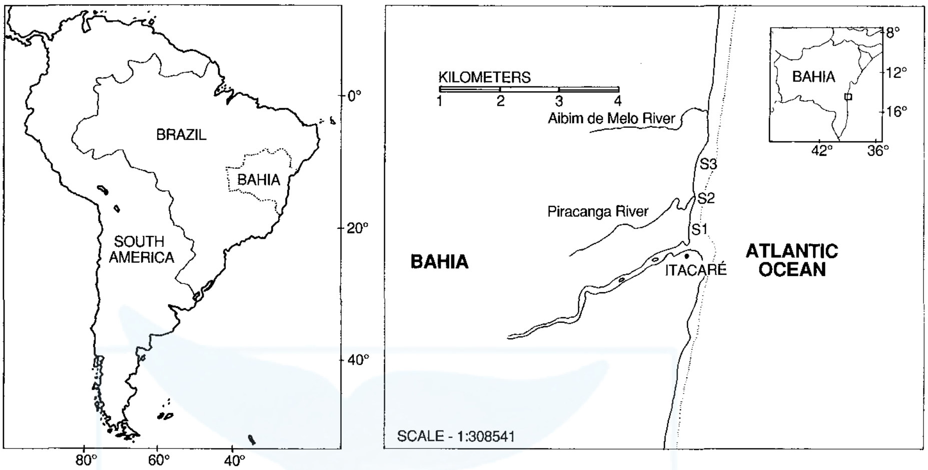

Fig. 3. Map of Piracanga Beach, Bahia State, showing the stranding site and the sections of beach where the melon-headed whales were collected.

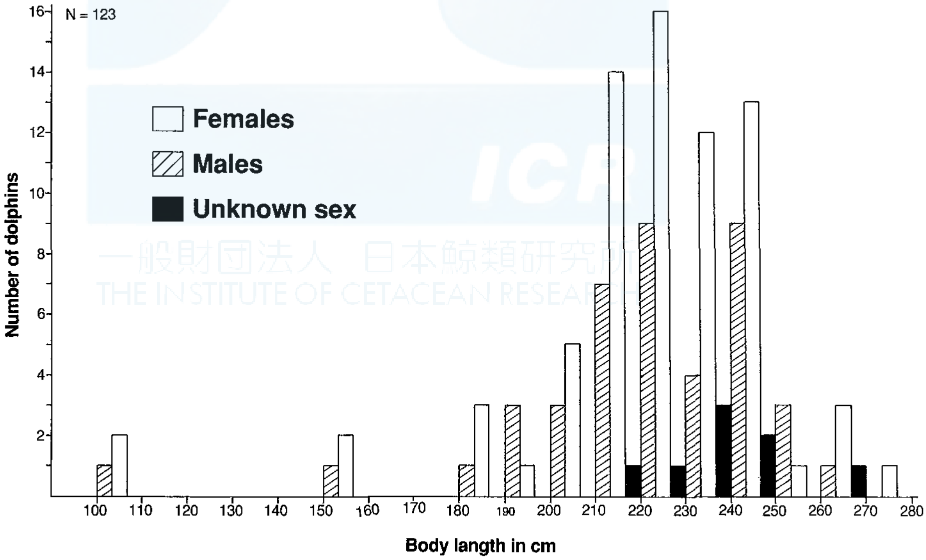

Fig. 4. Body-length frequency distribution for 123 melon-headed whales, *Peponocephala electra*, mass stranded on Piracanga Beach, Bahia, Brazil.
□Females (n = 73), ▨males (n = 42), ■unknown sex (n = 8).

TABLE 1. MASS STRANDINGS OF *PEPONOCEPHALA ELECTRA* KNOWN TO DATE

Date	Locality	Remarks	Number of animals	Reference
April 1987	Piracanga Beach, Itacaré, Bahia, Brazil		240+	Present paper
November 1972	Malékoula Is., Vanuatu, Melanesia		231	Rancurel, 1974
October 1976	Tambor Village, Costa Rica	Approx. 2,000 animals observed in Ballenas Bay before the stranding	180	James G. Mead, pers. comm. 1987
January 1982	Aoshima, Miyazaki Prefecture, Japan		160	Miyazaki, 1983
August 1958	Crowdy Heads, Australia	Large herd observed off Port Macquarie a day before the stranding	150-250	Dawbin *et al.*, 1970
August 1976	Moreton Is., Australia	Approx. 300 sighted near the stranding area	53	Bryden *et al.*, 1977

44(35.2%) were males, for a sex ratio of approximately 2:1. This agrees with results for a mass stranding of this species on Moreton Island, Australia, where 35 females and 16 males were found (Bryden, Harrison and Lear, 1977) and for a mass stranding in Costa Rica (Pacific coast) where the ratio was approximately two to one (J. Mead, pers. comm., Dec. 1987).

Body-length frequencies were computed based on sexed and/or measured animals (n = 123) and are shown in Fig. 4. Frequency distribution for both sexes indicate that a wide range of size classes were involuved in the stranding. The longest animal, a female, was 275 cm, and the shortest, also a female, 106 cm; 21.4% of the males and 21.9% of the females were between 221 and 230 cm long. The longest and the shortest males were 261 and 110 cm long, respectively. Females in the Pacific Ocean have been reported to reach sexual maturity at somewhere between 225 and 257 cm (Bryden *et al.*, 1977), and males between 248 (Best and Shaughnessy, 1981) and 268 cm (Bryden *et al.*, 1977).

Mass strandings of melon-headed whales have been reported to involve from 53 to 250 individuals (Table 1). Sightings (van Bree and Cadenat, 1968; Dawbin, Hoble and Fraser, 1970; Bryden *et al.*, 1977; Miyazaki and Wada, 1978; Pilleri, 1982) and observations in conjunction with captures (Nishiwaki and Norris, 1966) show that *P. electra* is highly gregarious and occurs in large groups.

The reasons for this mass stranding could not be determined.

ACKNOWLEDGMENTS

We would like to thank Vera M.F. da Silva and William F. Perrin for reviewing the manuscript. We also thank Everaldo Lima de Queiroz (Federal University of Bahia – UFBA), the former Fisheries Development Agency (SUDEPE-Bahia branch), the Center of Environmental Studies (CRA), Government of Bahia State and the Prefecture of Itacaré for logistical support which made the field work at Piracanga possible.

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THE MORPHOLOGY OF THE CETACEAN DIATOM GENUS *PLUMOSIGMA* NEMOTO

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AND
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ABSTRACT

This report concerns the morphology of the cetacean diatom genus *Plumosigma* which may be obligately associated with sperm whales (*Physeter catodon*). Diatom colonies on sperm whales collected off the Pacific coast of Hokkaido, Japan and off San Francisco, U.S.A. were cleaned using sulfuric acid/potassium permanganate/oxalic acid. The cleaned materials were examined with a light microscope, a scanning electron microscope and a transmission electron microscope. The morphology of the colonies was described as well as the valve morphology of *P. hustedti* and *P. rimosum*, although it was impossible to observe internal valve structure of the latter due to lack of specimens. Additional material of *P. rimosum* needs to be examined to characterize its morphology and ultrastructure.

Key words: cetacean diatom, *Plumosigma*, valve morphology, sperm whale

INTRODUCTION

Diatoms observed on the skin of cetaceans have been studied by Bennett (1920), Hart (1935), Karcher (1940), Usachev (1940), Omura (1950), Hustedt (1952), Okuno (1954), Nemoto (1956, 1958), Kliashtorin (1962), Best (1969), Nemoto, Brownell and Ishimaru (1977), Nemoto, Best, Ishimaru and Takano (1980) and Holmes (1985). Except for some planktonic species found on the skin, which may have been attached accidentally, genuine cetacean diatoms are few and comprise only 4 genera, *Bennettella, Epipellis, Stauroneis, Plumosigma,* and a small number of species.

Cocconeis ceticola, which Nelson described and named in Bennett's (1920)

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No. 1, 1990, 85–91

paper, was recently transferred to the new genus *Bennettella* after careful examination of diatoms assigned to the genus *Cocconeis* (Holmes, 1985). *Bennettella* includes 3 species (Holmes, 1985). *Epipellis*, a monotypic genus, was established to accommodate the invalid *Cocconeis orcii* Kliashtorin (Holmes, 1985). We report here morphological studies on *Plumosigma* Nemoto, a group not examined since Nemoto established this genus and its two species (*P. hustedti* and *P. rimosum*) in 1956.

MATERIALS AND METHODS

Diatoms examined in this study came from two sources:

1) Skin samples of sperm whales (*Physeter catodon*) with diatom patches collected by T. Nemoto off the Pacific coast of Hokkaido, Japan in 1957.

2) Skin samples of sperm whales with diatom colonies collected west of San Francisco in 1970 by Dr Judith Hansen.

All samples were rinsed in distilled water, treated with sulfuric acid-potassium permanganate and decolorized with oxalic acid. The cleaned material was mounted in Naphrax for light microscopic examination. SEM mounts were prepared by air-drying cleaned material directly on stubs or on cover glasses, affixing the cover glasses to aluminium stubs, and coating the material with gold or gold/palladium. Three different scanning electron microscopes were used: a Hitachi S-415A at University of California, Santa Barbara; a JSM-35 at Ocean Research Institute, University of Tokyo; and a JSM-25 at Otsuchi Marine Research Center, University of Tokyo. For TEM, aqueous suspensions of cleaned cells were air-dried on formvar-coated copper grids. A JEM-100CX located at the Ocean Research Institute, University of Tokyo, was used for transmission electron microscopy.

RESULTS

Plumosigma typically forms circular patches of varying dimensions on the skin of sperm whales. Individual diatoms within the patches attach adnately to the skin (Plate I, Fig. 1). This taxon usually co-occurred with *Stauroneis aleutica, S. olympica, Bennettella ceticola* and *B. constricta* (Plate I, Fig. 2). Although the first three of these diatoms also occur on the Dall's porpoise *Phocoenoides dalli* (Holmes, unpublished) only one specimen of *Plumosigma* has been observed in the many hundreds of Dall's porpoise diatom colonies examined by us. Provisionally, we conclude that *Plumosigma* is obligately associated with sperm whales.

In the samples examined by us, *P. hustedti* (Plate I, Figs 3, 4, 5, 7 and 8; Plate II, Fig. 3) was much more abundant than *P. rimosum* (Plate I, Fig. 6; Plate II, Figs 1 and 2). Nemoto (1956) reported that in his study *P. rimosum* was more abundant than *P. hustedti*. We remain uncertain of the significance of these contradictory observations.

The external valve surface of *Plumosigma* is concave. The raphe rises above the basal siliceous layer forming what appears to be a ridge separating the two halves of the valve face. The valve outline is slightly sigmoid (Plate I, Figs 5, 6, 7 and 8; Plate II, Figs 1 and 3). The central raphe endings terminate in a hyaline area which differs in outline in the two species (Plate I, Figs 5, 6, 7, 8 and 9; Plate II, Fig. 1). The valve mantle is easily deformed and often missing in our photos (Plate I, Figs 7 and 8; Plate II, Figs 1, 6 and 7). Anomalous valves indicated by the presence of two raphes and overlapped puncta were found in our material (Plate II, Fig. 3). Valves somewhat similar to these valves were also illustrated by Nemoto (1956).

The external distal raphe fissures at the poles are curved in opposite directions (Plate I, Figs 5 and 6). These distal raphe endings terminate in the interior of the valve in a thickened U-shaped helictoglossa in *P. hustedti* (Plate I, Fig. 4; Plate II, 5 and 6). The region between the central raphe endings in the interior of the valve is thickened (Plate II, Fig. 5). The exterior surface of the valve mantle is shown in Plate II, Fig. 4.

Nemoto's (1956) illustrations suggest that the puncta of the striae are mostly round in *P. hustedti*. By contrast, those close to the raphe and margin of the valve are long and narrow in *P. rimosum*, although a few rows of round puncta are sometimes present. Our observations confirm this morphology.

Morphometric data on the two species of *Plumosigma* have been published (Nemoto, 1956). Combining Nemoto's morphometric data with our own measurements, the following characteristics may be summarized for *P. hustedti*: length 11-22 μm, width 4.6-7.5 μm, length/width ratio 2.4-3.8, striae in the central region of the valve 31-40 in 10 μm, striae at the valve margin near the valve ends 40-55 in 10 μm, puncta in the central region of the valve 23-30 in 10 μm, puncta at the margin of the valve near the valve ends 30-42 in 10 μm.

We do not have similar data on *P. rimosum* because of the limited number of this species in our samples. According to Nemoto (1956), the striae of *P. rimosum* are denser than those of *P. hustedti*.

DISCUSSION

We have obtained additional information on the valve morphology of *Plumosigma hustedti* using SEM and TEM. We have not found girdle views of frustules nor carried out examination of the internal structure of *P. rimosum*.

The distal raphe endings of *P. hustedti* have an unusual internal structure, which looks rather like an anchor (Plate II, Figs 5 and 6). Unfortunately, it was impossible to observe internal valve structure of *P. rimosum* due to lack of specimens.

We were unable to document the structure of hymenate pore occlusions in either taxon. These occlusions are very delicate and were absent in the sperm whale samples examined, but one specimen of *P. rimosum* found in the sediments of Otsuchi Bay retained hymenate pore occlusions (Nagasawa, Holmes and Nemoto, 1989). The absence of hymenate pore occlusions in the present material and the scarcity of specimens of *P. rimosum* have made it difficult to describe the morphology of this species with any degree of certainty. However, transmission electron microscope photographs of the three valves of *P. rimosum* available for observations suggest the possibility that this taxon represents a stage in the dissolution of the siliceous valve structure of *P. hustedti*. The admixture of circular and elongate puncta along the axial area of *P. rimosum* and the irregular inner margin of the elongate puncta suggest the possibility that the walls between puncta have dissolved, producting "elongate" puncta (Plate II, Figs 1 and 2). On the other hand, the central area is quite different from that of *P. hustedti*. What appear to be very small poroids occur with some frequency along the inter-striae in one of our photographs of *P. rimosum* (Plate II, Fig. 2). Such poroids have not been observed in *P. hustedti*. Clearly, additional material of *P. rimosum* needs to be examined to characterize its morphology and ultrastructure in more detail.

ACKNOWLEDGMENTS

We thank the staff of Otsuchi Marine Research Center, University of Tokyo, for the use of their laboratory facilities and scanning electron microscope during our visit. This study was supported by the Japan Society for Promotion of Science, National Science Foundation and the Nissan Science Foundation.

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EXPLANATIONS OF PLATES

PLATE I

Each scale bar indicates 1 μm.

Fig. 1. A colony of *Plumosigma* on the skin of a sperm whale, source 2, SEM.
Fig. 2. Co-occurrence of *Plumosigma* with *Stauroneis* sp. and *Bennettella ceticola* on the skin of sperm whales, source 1, SEM.
Fig. 3. Exterior of *P. hustedti*, source 1, LM.
Fig. 4. Interior of *P. hustedti*, source 1, LM.
Fig. 5. Frustule of *P. hustedti*, source 1, SEM.
Fig. 6. Frustule of *P. rimosum*, source 1, SEM.
Fig. 7. Three valves of *P. hustedti* without girdle bands, source 1, TEM.
Fig. 8. Another valve of *P. hustedti* without girdle bands, source 1, TEM.

PLATE II

Each scale bar indicates 1 μm.

Fig. 1. Valve of *P. rimosum*, source 1, TEM.
Fig. 2. Central area of *P. rimosum*, source 1, TEM.
Fig. 3. Double valves of *P. hustedti*, source 1, TEM.
Fig. 4. Exterior of *P. hustedti* with valve mantle, source 1, SEM.
Fig. 5. Interior of *P. hustedti*, source 1, SEM.
Fig. 6. End of interior valve of *P. hustedti*, source 1, SEM.
Fig. 7. Detached interior valve mantle of *P. hustedti*, source 1, SEM.

PLATE I

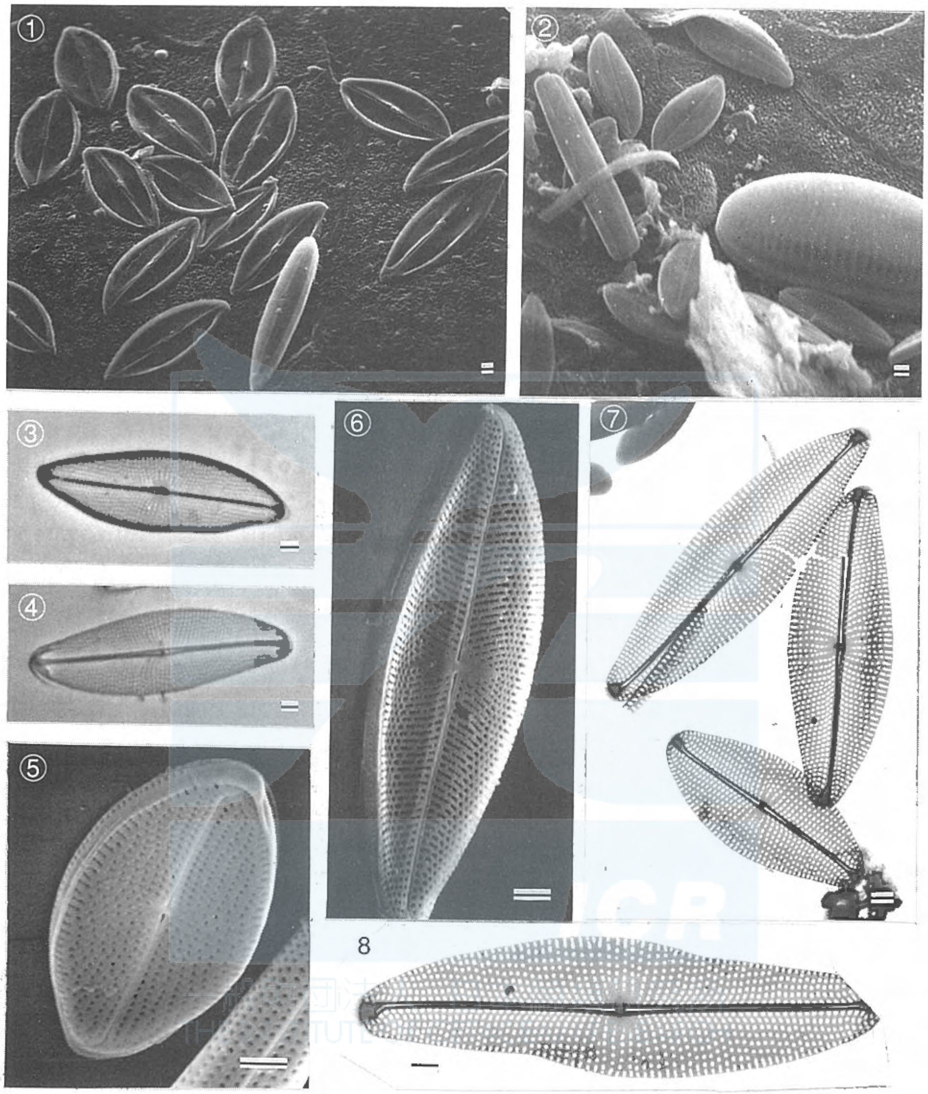
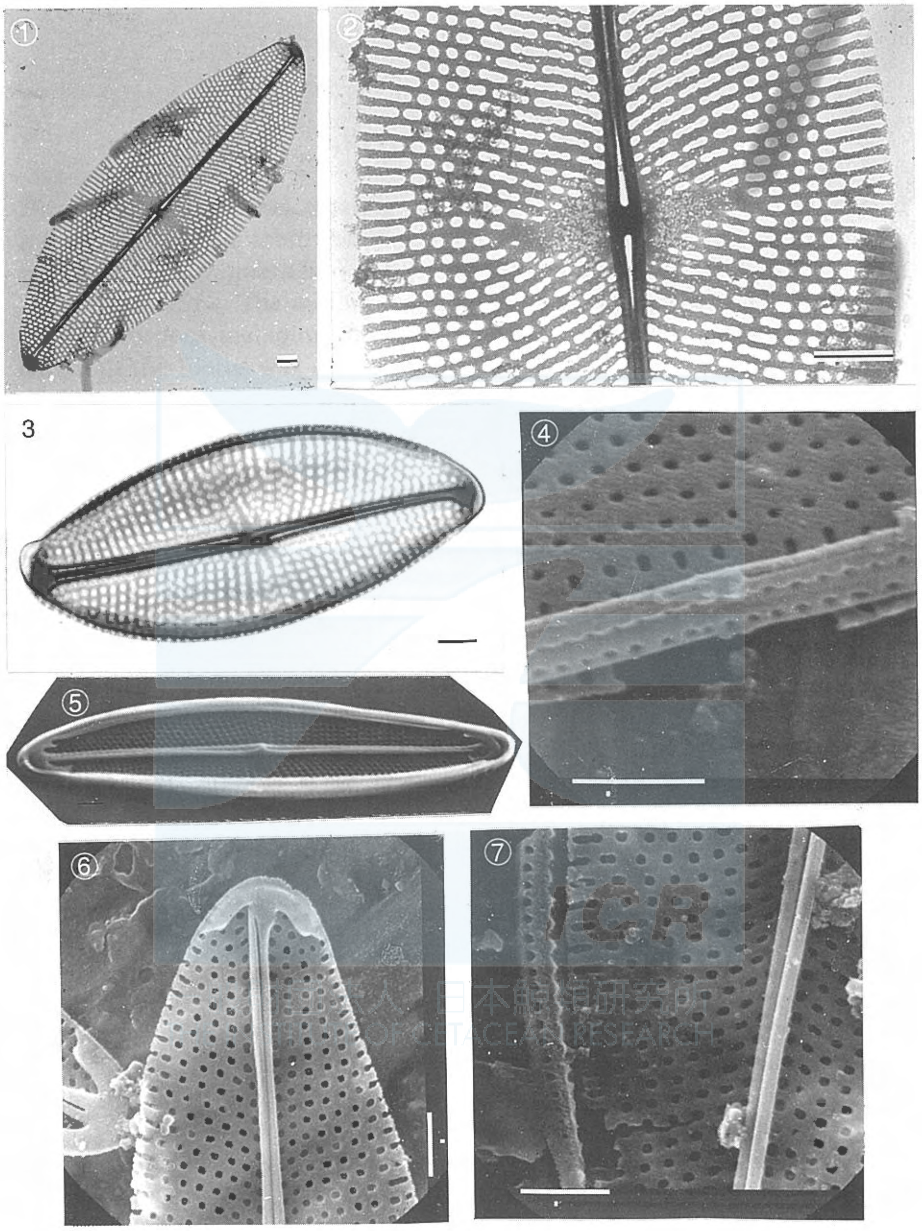


PLATE II

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A MALFORMED FOETUS OF A SOUTHERN SEI WHALE

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During the Antarctic whaling season of 1967/68, a badly malformed 230 cm long female foetus was found on the F/F Nisshin Maru. It was from a sei whale (*Balaenoptera borealis*) (No. 1545) caught at 57° 35′ S, 84° 54′ E on 26 February 1968. The mother was 15.4 m long and 11-years old, with seven ovarian corpora including the corpus luteum of this pregnancy. The total length of the foetus was measured from the most anteriorly protruding part of the premaxilla to the notch between the flukes. It was recorded in the catch log as 218 cm long. The foetus showed a harelip-like malformation due to grotesque development of the head region. The premaxilla was greatly deformed, resulting in a downward curve. A deep depression was evident on the lower mandible (Fig. 1). Although the animal was not dissected, the entire head appeared poorly developed as far as the region of the maxillae. This region appeared shorter than the premaxillae region. The tail flukes sloped considerably, causing the entire fluke spread to be very narrow. Essentially the same characteristic was reported by Ohsumi (1959) for a deformed fin whale (*B. physalus*) foetus. Measurements for the right flipper: 1) Tip to axilla, 2) anterior end of lower border to tip of flipper, and 3) greatest width of flipper, were 27.0, 38.0, and 8.3 cm, respectively. These measurements are the same as those of a 244-245 cm long, normally developed foetus. The foetus was placed in formalin solution and transferred from the Whales Research Institute to the Institute of Cetacean Research in Tokyo.

The upper jaw of the present foetus was clearly deformed. Although one instance of an upwardly bent upper jaw has been reported in *Stenella coeruleoalba* (Tobayama and Uchida, 1964), Nakamura (1968) stated, after surveying the occurrence of deformed lower jaws in postnatal sperm whales (*Physeter catodon*), that malformation of the upper jaw rarely occurs in cetaceans. Two examples similar to the present case have been reported for fin whale foetuses (Nishiwaki, 1957; Ohsumi, 1959), and siamese twins of the humpback whale (*Megaptera novaeangliae*) had upper jaw deformation to some extent (Zemsky and Budylenko, 1970, Figs 3 and 4). However, deformation appears to occur only rarely in postnatal baleen whales. Extensive head and mouth region malformation in whale neonates probably causes difficulty in sucking or later feeding, thus greatly lessening the chances of survival.

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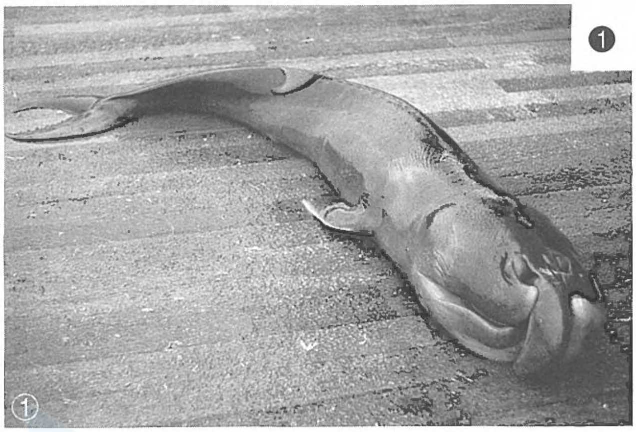
Fig. 1. A 230 cm malformed female foetus of a southern sei whale found on 26 February 1968. Whale number indicated as 1545 in the catch log of the Nisshin Maru fleet in 1967/68 season.

① Entire body of the foetus.

② Head of the foetus showing the blowholes in an extremely forward position, malformed development of the maxillae and premaxillae regions, and upwardly curved tip of the lower jaw. The eye is shown by the arrow.

③ Opened mouth showing oral cavity, palatal ridge, tongue and extremely depressed lower jaw.



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日本鯨類研究所研究報告
編集委員会

印刷・発行　平成２(1990)年９月30日
発行　財団法人　日本鯨類研究所
東京都中央区豊海町４番18号　東京水産ビル
電　話　03－536－6521
ＦＡＸ　03－536－6522
印刷　研究社印刷株式会社
埼玉県新座市野火止　7－14－8

定価　5,000 円（本体価格　4,855円）