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FOOD HABITS OF THE BRYDE'S WHALES TAKEN IN THE SOUTH PACIFIC AND INDIAN OCEANS*

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ABSTRACT

A total of 459 Bryde's whales were taken in the Coral Sea, South Pacific and Indian oceans during the seasons of 1976/77–1978/79 under the scheme of scientific permit. As one of research items on the least known baleen whale species, food habits of the caught animals were studied on the carcasses in the field, and some 234 stomach samples out of 252 animals of filled stomach were closely examined in the laboratory. On the whole 55% or 252 animals out of 459 were found to be retaining stomach contents with varying fulness. Analysis on stomach samples suggested that the Bryde's whales in pelagic waters of the southern hemisphere largely prey upon the euphausiid crustaceans in stead of the fish. These evidences clearly suggest the locally abundant distributions of food organisms. The southern Bryde's whales may be considered to live substantially on euphausiids such as *Euphausia diomedeae*, *E. recurva*, and *Thysanoessa gregaria* widely in the studied area, but both *Pseudeuphausia latifrons* and *E. sibogae* may characteristically become more important food items than the three others in the equatorial eastern Indian Ocean. Although the found evidence as a whole is the phenomenon confined to somewhat local areas, both rich fulness of stomach and monospecific composition of the prey organisms suggest that those euphausiid species may occur with fairly large biomass by forming densely aggregated swarms even in the tropical and subtropical pelagic regions. The ecological importance of euphausiid crustaceans over the warmer seas as well as those in the colder seas is discussed.

INTRODUCTION

Since Olsen (1913) studied the Bryde's whales, *Balaenoptera brydei* from the South African waters, distribution of the Bryde's whales in the southern hemisphere has long been known but this animal remained as less known balaenopterid whales due to rather sporadic information. Except several taxonomical studies on the stranded and/or occasionally taken animals, there has been no biological study of any extent. Recently, however, Best (1960, 1967, 1977) studied the Bryde's whales caught off Durban and Donkergat, South Africa and found that there occurs two allopatric forms, *i.e.* inshore and offshore forms. The main difference which separates the species into two forms was the morphological differences in the shape of

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baleen plates such as the width/length ratios in addition to the general biological characteristics by each form (Best, 1977). The exhibited character of baleen plates in both forms resulted to show a considerable different food habits among them. Best (1977) states that the inshore form feeds mainly on small gregarious fishes such as anchovy (*Engraulis capensis*) and pilchard (*Sardinops ocellata*), while the offshore form strongly prefers to feed upon the Euphausiacea such as *Euphausia lucens*. It can be said that our knowledge on the biology of the southern species of Bryde's whales has largely increased during the past two decades.

However, our knowledge having been obtained to date seems to be still confined to that from local and possibly coastal stocks of this animals. The catches at South Africa (Best, 1960), Western Australia (Chittleborough, 1959), New Zealand (Gaskin, 1972) and Chile (Aguayo, 1965) were all done by the land based whaling. On the other hand, there occurs more larger number of Bryde's whales over the vast pelagic regions of the southern hemisphere (Gambell *et al.*, 1974), but neither has been studied concerning the status of possible pelagic stocks nor the biological characteristics due to the international control measures of whaling.

It has been known that the distribution of Bryde's whales are confined largely within the temperate to tropical seas where the temperature is higher than 20°C (Omura and Nemoto, 1955). The habitat for the Bryde's whales is quite unusual when it is compared with the case in another balaenopterid whales, to which most baleen whale species may visit only for breeding.

From the viewpoints of ecological energetics, the breeding ground for the baleen whale species cannot be considered the place of any extent of feeding, *i.e.*, there is no nutritional importance at all. On the other hand, some observations strongly suggest that the feeding of balaenopterid whales may take place in the warmer seas (Gambell *et al.*, 1974; Masaki, 1979). The author too observed many Bryde's whales that swam away leaving a patch of brick red feces when they were chased during the tagging investigations in the equatorial Pacific. An estimation of the energetic budget of locomotion in balaenopterid whales suggests that even the animals under breeding migrations to the warmer seas must perhaps feed to some extent (Kawamura, 1975). The above mentioned facts strongly suggest that there must exist the aggregations of possible food organisms which are available for the baleen whales visiting those warmer waters. These, however, must be clarified by the actual observations on the collected materials and the examination of stomach conditions of whales occurring in the warmer waters.

In order to study the southern Bryde's whales (*Balaenoptera edeni*) in pelagic waters, Japanese Government granted to take specially 120 animals per fleet per season in 1976, and the programme went on next three successive seasons, 1976/77–1978/79. The special permit programme for the purpose of scientific research carried out under the supervision of the Far Seas Fisheries Research Laboratory of Fisheries Agency, and the whole programme came to an end in 1979. A total of 459 animals have been caught in the pelagic waters over the central South Pacific and Indian oceans. Although there has preliminarily been reported on earlier results by separating each fishing season (e.g. Ohsumi, 1978; Kawamura, 1977), Ohsumi (1979) finally submitted provisional report to the 31st IWC meeting, in which he dealt with the whole result throughout the past three seasons, and estimated a possible harvestable quotas by the sea regions worked out. However, the food habits of the Bryde's whales were not treated in his report since it was not the subject being treated in the fishery biology and stock management. Therefore, this report could be considered as one of the supplements relating to the Japanese catch of the southern Bryde's whales under the scheme of scientific permit.

MATERIAL AND METHOD

A total of 459 Bryde's whales were caught during the past three exploratory expedtions. It is, however, still unknown to date that to which forms, inshore or offshore, the animal belongs. The overall figures for the experimental catch are given in Table 1 and Fig. 1. Two factories, *Tonan Maru* No. 2 and *Nisshin Maru* No. 3 of Nippon Kyodo Hogei K. K. operated during 1976/77 season and each of them was granted to take 120 animals. However, during the two successive seasons, there operated only one factory, *Nisshin Maru* No. 3 and the catch reduced to about an half from that expected when programme came to an implementation in 1976, and this resulted somewhat insufficient collection of data for the general biological study.

TABLE 1. EXPLORATORY CATCHES OF THE SOUTHERN BRYDE'S WHALES DURING THE SEASONS, 1976/77-1978/79

Season	Sea area	No. of animal caught			Stomach contents		A/A+B (%)	No. of stomach sample examined
		Male	Female	Total	Present (A)	Empty (B)		
1976/77	Coral Sea	3	4	7	5	2	71.43	5
	Central S. Pacific	66	47	113	85	28	75.22	64
	SW Indian Ocean	61	44	105	49	56	46.67	52
1977/78	Central S. Pacific	72	42	114	60	54	52.63	60
1978/79	E. Indian Ocean	61	59	120	53	67	44.17	53
Total		263	196	459	252	207	54.90 (Av.)	234

The observations on the stomach condition of animals were carried out on two different basis: 1) eye observations on the carcasses in the field, and 2) more closer examinations of the food species based on a fraction of stomach materials by random samplings. The stomach contents were collected regardless the magnitudes of freshness and of the amount in a stomach. Observations in the field may provide somewhat rough evidence such as an approximate amount of stomach contents in terms of percent stomach volume by five different fulness and the kind of food species by rough systematic taxa such as Pisces, Euphausiacea, Amphipoda and Copepoda. In the case of Euphausiacea, however, the difference of body size by three size classes, viz. 'large', 'medium', and 'small' were also recorded by a personel who was skillful enough for this kind of observations. The observed records in the field were compiled into a register format, 'Catch Records of Whales' by the whaling inspectors of the Fisheries Agency. I used some data from that records especially in constructing the general catch figures and stomach conditions.

A total of 234 stomach contents were collected from 252 animals with filled stomach. The collected materials preserved in 10% formalin solution were sent to the Whales Research Institute, Tokyo, but later to Hokkaido University where the composition of food species were studied.

RESULT

a) *Catch distribution*

It has long been known that the Bryde's whales occur frequently in the tropical to subtropical waters of both hemispheres where the whaling fleet passed by every season *en route* to and from the Antarctic whaling ground. By taking account of this fact but with an uncertainty as the object of mothership operation, experimental and exploratory catch investigations were carried out by setting a possible sea regions in the South Pacific and Indian oceans. It was proved by sighting investigations that the Bryde's whales largely distribute in both South Pacific and Indian oceans, and the latitudinal range may extend over the tropical to temperate regions. During the 1976/77–1978/79 seasons the main concentrations of Bryde's whales were spotted in the Coral Sea, central South Pacific, and eastern and southwestern Indian oceans (see Ohsumi, 1978, Fig. 1).

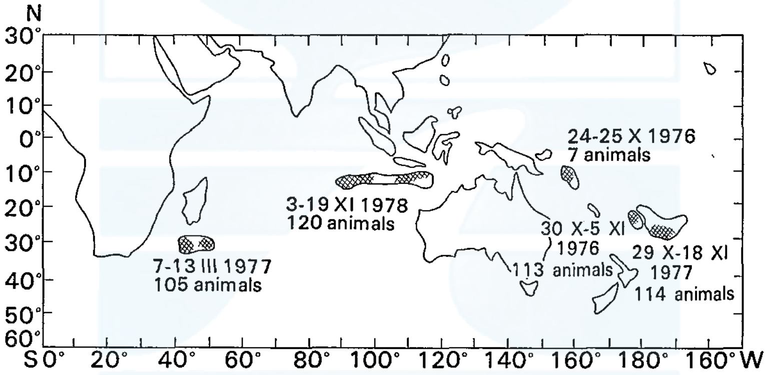


Fig. 1. Catch areas of the Bryde's whales taken by scientific permit in the South Pacific and Indian oceans during the seasons of 1976/77–1978/79. The shaded area indicates heavy concentration of catches.

Figure 1 demonstrates approximate catch areas along with related figures where a total of 459 animals was taken during the exploratory whaling. It is obvious that the catches in the central South Pacific and equatorial eastern Indian oceans were actually made being based on the sightings worked out in 1976/77 season. Except the catch in the southwestern Indian Ocean all the rest were caught in the tropical sea regions where the south equatorial current or its counter current prevails. The observed surface sea temperature ranged 20.0–30.3°C during October to November. Contrary, the region of southwest Indian Ocean was operated in March when the surface sea temperature showed 24.6–26.6°C. According to Ohsumi (1979), the averaged body length and weight of animals by catch areas was found to be 13.05 m (15.2 tons) as the largest figure in the South Pacific, while the smallest was 12.10 m (12.36 tons) in the Indian Ocean animals (Table 2).

Comparing these figures with those having been observed in the northern equatorial to temperate Pacific (e.g. Wada, 1975; Ohsumi, 1978; Masaki, 1979), it may be considered that the Bryde's whales seem to distribute with somewhat biantitropical pattern over the both hemispheres.

TABLE 2. THE AVERAGE BODY LENGTH OF SOUTHERN BRYDE'S WHALES BY THE SEA AREAS (AFTER OHSUMI, 1979, TABLE 13)

Sea area	Indian*	S. Pacific**	Total
No. of whales caught	225	235	459
Total average body length (m)	12.10	13.05	12.58
Estimated average body weight (ton)	12.36	15.12	13.66

* Boths outhwestern and eastern areas of the Indian Ocean are combined.

** Coral Sea animals are included.

TABLE 3. STOMACH CONDITIONS OF THE BRYDE'S WHALES IN THE SOUTHERN HEMISPHERE. THE QUANTITY OF FOOD IS APPROXIMATED BY THE VOLUMES OF BOTH STOMACH AND THE AMOUNT OF CONTENTS

Whaling ground	Season	Food species		Quantity less than:					Total
		Euphausiacea	Pisces	Empty	25%	50%	75%	100%	
SW Indian	1976/77	49	—	56	21	10	1	17	105
E Indian	1978/79	46	7	67	16	24	10	3	120
Coral Sea	1976/77	5	—	2	2	1	1	1	7
Central Pacific	1976/77	85	—	28	47	19	12	7	113
Central Pacific	1977/78	60	1	53	28	15	9	9	114
Total		245	8	206	114	69	33	37	459
Percent		96.8	3.2	44.9	24.8	15.0	7.2	8.1	100.0

b) *Stomach condition*

The stomach condition in general was observed in the field. The catch record shows quite high percent occurrences of the Euphausiacea (96.8%) throughout five different whaling grounds worked out. There were no biassed trends of the regional occurrence in Euphausiacea, and fish food accounted only 3.2% among all. This was really unexpected evidence from that supposed in advance to the catch of whales came to an implementation (Table 3).

The quantity of stomach contents actually found in each animal was found to be relatively abundant. Table 3 shows that 253 animals (55%) out of 459 were repleted with food under various magnitudes. It must be noted that 70 animals

(27.7%) out of 253 were found to be very abundantly (75%+100%) repleted with food. To see the similar figures by each whaling ground, the highest was found in the Coral Sea (40.0%) and/or southwestern Indian Ocean (36.7%) while the lowest was in the central South Pacific (22.4%) for the 1976/77 season. These figures may suggest that there must be comparatively abundant distributions of available food concentrations even in the so-called 'barren' tropical seas, the place of far well outside from the proper feeding ground of baleen whales in the southern oceans.

c) *Diel changes in the quantity of stomach contents*

It may be hard to believe that the baleen whale shows any local behavioral changes in their feeding activity or behavioral pattern to an appreciable extent although some locally modulated changes are expected by the composition of available food species due to their own local characteristics in the diel migratory pattern. If the whale does not change essentially their behavioral pattern of feeding, then the diel variation of the quantity of stomach contents may suggest the diel variation of feeding activity and/or its intensity.

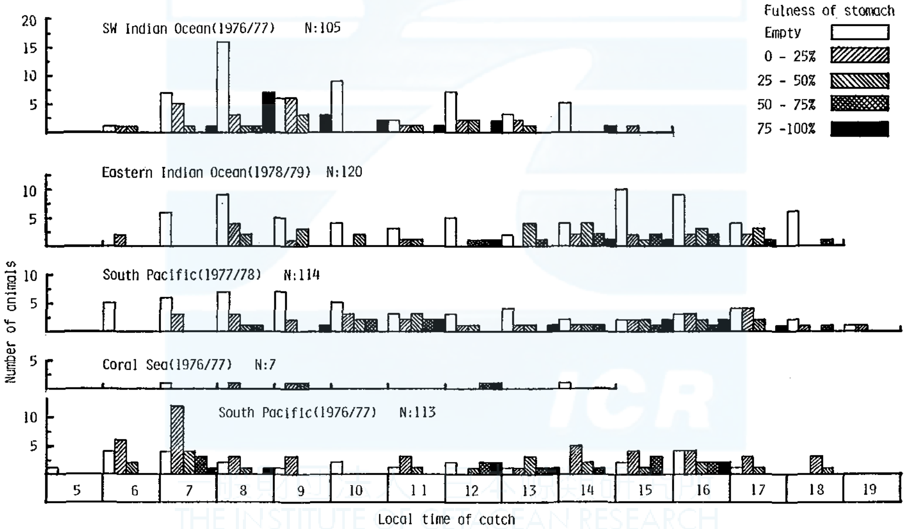


Fig. 2. Change of stomach fulness by the local time of catch in five different whaling areas.

Figure 2 demonstrates the number of animals by the five different stomach conditions against local time when the animals were caught. Among the animals with food of any magnitudes in their stomach, it is observed that the stomachs repleted 50% or more seems to occur poorly except very few examples. This may suggest that the stomachs with food are represented chiefly by rather poorly repleted animals. The occurrence of empty stomach predominated during the first half of day, and seems to reduce toward evening. The empty stomach was found largely in three examples; southwestern Indian Ocean (1976/77), equatorial eastern Indian Ocean (1978/79) and the South Pacific (1977/78). In the Coral Sea region the number of catch amounted only seven animals in all, and it is difficult to draw any general trends of feeding activity. On the other hand, feeding condition in the South Pacific region for 1976/77 season showed very high percent occurrence of well repleted animals (75.22%), while the rest ranged 44.7–52.6% (see also Table 1).

The diel changes in feeding activity can be observed over the regions in question. In the animals from southwestern Indian Ocean the occurrence of well repleted stomachs was concentrated clearly in the first half of the day, and this region must be noted of being different feeding conditions from the four others. There were no catches after 1600 hours in this region. On the other hand, the animal with well repleted stomachs in the eastern Indian Ocean, South Pacific and possibly in the Coral Sea showed dispersed occurrence over the whole daytime but somewhat biassed in the afternoon toward evening, and a possible nocternal feeding may take place in these sea regions. Although there observed quite unusual large number of animals in the morning for the 1976/77 and the 1977/78 seasons of the South Pacific, the feeding activity of whales on the whole possibly follows to a definite trends. That is, despite a great variety in the diel feeding activity of whales by season and localities, it is noteworthy that more intense feeding would take place twice a day to show a bimodal changes, once in the early morning and then toward the evening (Fig. 3). The more detailed figures relating feeding activity are given in appended tables (Appendix Tables I and II).

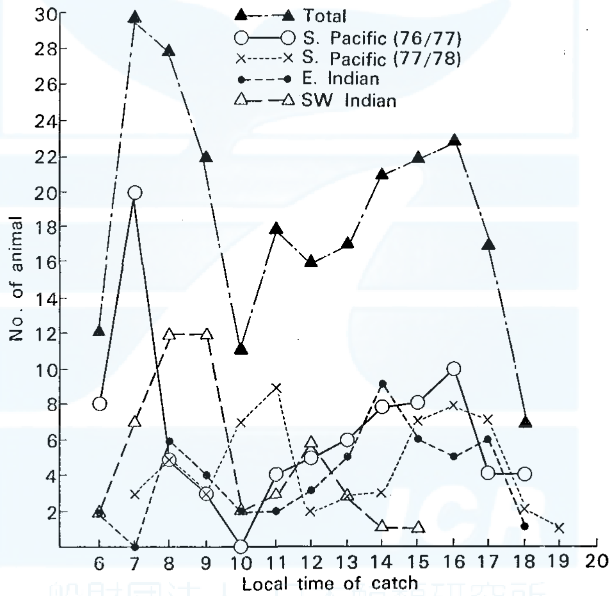


Fig. 3. Diel variation in the number of animals with filled stomach.

TABLE 4. SYSTEMATIC LIST OF THE FOOD ORGANISMS OF THE SOUTHERN BRYDE'S WHALES

Euphausiacea :
- *Euphausia recurva* Hansen
- *Euphausia diomedeae* Ortmann
- *Euphausia sibogae* Hansen
- *Pseudeuphausia latifrons* (G. O. Sars)
- *Thysanopoda tricuspidata* Milne-Edwards
- *Thysanoessa gregaria* G. O. Sars

Pisces :
- *Vinciguerria nimbaria* (Jordan & Williams)
- *Auxis thazard* (Lacépède)
- Myctophiformes*

* unidentifiable larval forms

TABLE 5. KIND OF FOOD ORGANISMS OF SOUTHERN BRYDE'S WHALES BY THE SEASON AND CATCH AREAS

Season	Date	Sea temp. (°C)	Sea area	Approx. location	Food species
1976/77	Oct. 24-25	28°	Coral Sea	9°49′-10°17′ S 157°29′-157°56′ E	*Euphausia diomedeae*
	Oct. 30-Nov. 5	20°-23°	S. Pacific	24°25′-27°59′ S 177°11′-178°34′ E	*Euphausia recurva* *Thysanoessa gregaria*
	Mar. 7-13	24.6°-26.6°	SW Indian Ocean	28°23′-31°47′ S 43°55′-51°36′ E	*Euphausia recurva* Hatchetfish*
1977/78	Oct. 29-Nov. 18	20.2°-23.4°	S. Pacific	21°15′-29°24′ S 179°45′ E-170°58′W	*Euphausia recurva* *Thysanoessa gregaria* Gonostomatid fish**
1978/79	Nov. 3-Nov. 19	25.8°-30.3°	E. Indian Ocean	9°47′-12°49′ S 92°02′-118°32′ E	*Euphausia diomedeae* *Euphausia sibogae* *Pseudeuphausia latifrons* *Thysanopoda tricuspidata* *Vinciguerria nimbaria* *Auxis thazard* Myctophiformes

* found only one specimen as a possible contaminant.
** probably *V. nimbaria*.

d) Kind of food organisms

There have been found comparatively poor composition of food species for the southern Bryde's whales in pelagic waters (Kawamura, 1977). It is clear that the Bryde's whales feed mainly upon Euphausiacea and the shoaling fish or its larval forms, and epipelagic planktonic or micronektonic organisms other than eueuphausiids were much lesser extent (Table 4).

The result actually found was that hardly been expected until the catches of Bryde's whales were implemented. Among the Euphausiacea, there found three species of the genus *Euphausia* (*E. diomedeae, E. recurva and E. sibogae*) and one species belonging to the three different genera, *i.e.*, *Thysanopoda tricuspidata*, *Thysanoessa gre-*

garia, and *Pseudeuphausia latifrons*. *T. gregaria* must be considered tentative identification due to ill conditioned specimens by digestion. The geographical occurrence of each food species is given by the whaling grounds in Table 5. It is observed that the composition of food organisms is very monotonous over the first four whaling grounds where *E. diomedeae*, *E. recurva* and/or *T. gregaria* predominated. Fish was considered to be less important by any magnitudes. The equatorial eastern Indian Ocean, on the other hand, showed relatively diversed complexity to the another four cases in the composition of stomach contents. However, there found only *P. latifrons* as the principally important food species than three another species. As for the gonostomatids, *Vinciguerria nimbaria* showed a meso-scale importance among the whole member of food species. *V. nimbaria* has been found to be of greater importance as the food of skip jack, *Katsuwonus pelamis* in the tropical Pacific (Kubota and Kawamura, 1972).

TABLE 6. OCCURRENCE OF SPERM SACS IN SIX EUPHAUSIID SPECIES FED BY THE SOUTHERN BRYDE'S WHALES

	Sperm sac present:					
	Both	Only		Absent	Unknown	Whaling ground
	Male+Female	Male	Female	Male+Female		
E. diomedeae	3	1	1			Coral Sea
E. diomedeae			6	2	2	E. Indian
E. recurva	6		28	5	11	S. Pacific (76/77)
E. recurva	2		29	5	16	SW Indian
E. recurva			3	30		S. Pacific (77/78)
T. gregaria				11	2	S. Pacific (76/77)
T. gregaria	2	1		35	2	S. Pacific (77/78)
E. sibogae		1	2		4	E. Indian
P. latifrons		1	1	29	2	E. Indian
T'da tricuspidata				1		E. Indian

The populations of six euphausiid species above mentioned are usually composed of both adult male and female in similar sex ratios though there were several cases of slightly biassed sex ratios with more numerous in the number of male than the female. Although the majority of *T. gregaria* was composed of adult forms of both sexes, there were a few cases that adolescent or juvenile forms occurred mixing with the adults. Some male and/or female individuals over several populations of above six euphausiid species carried a sperm sacs on the thelycum or ejaculatory duct but this strongly biassed to females (Table 6). *E. diomedeae* of the Coral Sea population carried the sperm sacs on both sexes, while it was only on females from the equatorial eastern Indian Ocean. Similar trends were found in *T. gregaria* but no sperm sacs were found in the South Pacific populations occurred in the 1976/77 season. Although, there found very occasional occurrence of carrying sperm sacs in *P. latifrons*, it may be reasonable to refer the species as having no associations with mating at this time of the season viz. early to mid-November. One of interests is that there were very close associations in the occurrence of possible euphausiid eggs with *P. latifrons.* The appearance of the egg was observed very similar to those of euphausiids. Therefore, it is reasonable to suppose that the egg might perhaps come from *P. latifrons* since it was the only species that possibly lost sperm sacs from all individuals occurred. *Thysanopoda tricuspidata* also did not carry sperm sacs but this species by no means occurred associating with any kind of planktonic eggs.

In summerizing the results concerning euphausiid food, it is noticed that both *E. recurva* and *T. gregaria* covered geographically wider ranges and are considered most important food species in the central South Pacific while it was only *E. recurva* in the southwestern Indian Ocean. In the equatorial eastern Indian Ocean, on other hand, the principal dietary members turn to *P. latifrons* and *E. sibogae.* Both *T'da tricuspidata* and *E. diomedeae* occurred with much lesser extent.

TABLE 7. PREY ORGANISMS FOUND FROM SOME FISH SPECIES THAT WERE FED BY THE BRYDE'S WHALES TAKEN IN THE EQUATORIAL EASTERN INDIAN OCEAN DURING 1978/79 SEASON

Fish species	Body length (mm)	Location	Date	Food items
Auxis thazard (Frigate mackerel)	215	10°14′ S 112°12′ E	Nov. 9, 1978	*Candacia pachydactyla* *Euchaeta marina?* Others*
Vinciguerria nimbaria	38–50	11°00′ S 97°12′ E 11°13′ S 95°26′ E 11°15′ S 95°32′ E 11°16′ S 95°28′ E 11°52′ S 94°12′ E	Nov. 15–17, 1978	Copepods** Fish larva Euphausiid (*P. latifrons*) -egg?
Myctophiformes	24–25	11°16′ S 97°34′ E	Nov. 15, 1978	Copepods**

* Decapoda-megalopa, large cheliped like appendages, Amphipoda-Hyperiidae, *Lucifer? Cavolinia* sp. Bivalvia larvae, and unidentifiable crustaceans due to heavy digestion.

** unidentifiable.

As for the fish diet there found three kind of shoaling fish species: the Myctophiformes, gonostomatids (*Vinciguerria nimbaria*), and possibly contaminated one specimen of frigate mackerel (*Auxis thazard*). Among these fish diet only the gonostomatid species, *V. nimbaria* was actually formed the diet of the southern Bryde's whales especially in the equatorial eastern Indian Ocean. The unidentifiable larval forms of fish belonging to the Myctophiformes was also preyed upon the animals but by far the lesser magnitudes than *V. nimbaria.* In general the occurrence of fish diet is very local phenomenon limited spacially in small area. Althouth the Myctophiformes species was found only in one stomach, and *V. nimbaria* in five stomachs in the 1978/79 catches, they occurred in the state of solely monospecific composition except one mixed example with *E. diomedeae*.

The prey organisms found from those above mentioned fishes were examined in order to compare them with the stomach contents of whales. Both frigate mackerel and the Myctophiformes were very young forms, while *V. nimbaria* was adult. Although the taxonomical details of prey organisms from these fish species are still insufficient, Table 7 demonstrates that the species composition of prey organisms in the gut from those fish species are very variable. The frigate mackerel ate at least several adult males of *Candacia pachydactyla*, *Euchaeta marina* (?) and many unidentifiable copepod species, Decapoda, Amphipoda, and very young Thecosomata of possibly belongs to *Cavolinia* sp. It is noteworthy that not withstanding the fact of greatly diversified prey items, there found to lack euphausiid species that were the main diet of the Bryde's whales. This, however, seems to be confirmed by further examinations since micronektonic fish migrants in the tropical Pacific are known to feed euphausiids by a magnitude accounting for 8% of total food ingested (Roger, 1973a). Even so the completely different gut contents of preyed fishes found from the whale stomachs suggest that these fish species were not associated with the occurrence of food euphausiids. It may be considered that those micronektonic fishes may linked with another branched off foodchain systems which are perhaps different one from the prey- predator relationships between Bryde's whales and euphausiids.

TABLE 8. NUMBER OF STOMACHS BY THE KIND OF FOOD ORGANISMS

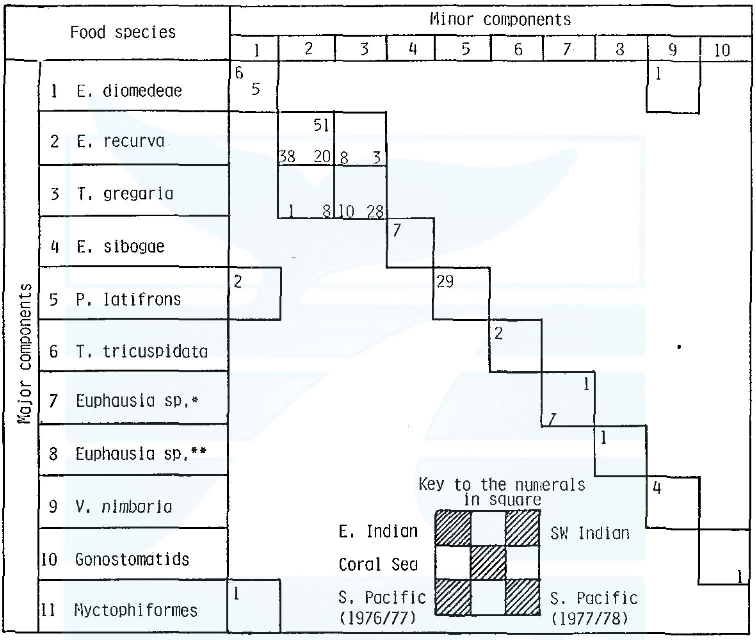
	1976/77			1977/78	1978/79	Total
	S. Pacific	Coral Sea	SW Indian	S. Pacific	E. Indian	
E. diomedeae		5			6	11
T. gregaria	10			28		38
Euphausia sp.*	7		1			8
E. recurva+*T. gregaria*	8			3		11
T. gregaria+*E. recurva*	1			8		9
E. recurva	38		51****	20		109
E. sibogae					7	7
P. latifrons					29	29
P. latifrons +*E. diomedeae*					2	2
T'da tricuspidata					2	2
Euphausia sp.**					1	1
E. diomedeae +*V. nimbaria*					1	1
Fish larva***+*E. diomedeae*					1	1
V. nimbaria					4	4
Gonostomatid fish				1		1

* Probably *E. recurva*.
** Probably *E. sibogae*.
*** Larval forms of Myctophiformes.
**** Mixture with one individual of hatchet fish is included.

e) Composition of stomach contents

The composition of stomach contents from the collected samples is given in

Table 8 by separating the catch area and the season. In order to show the characteristics of the composition of stomach contents a matrix was constructed (Fig. 4). Although a considerable diversity in the composition of forage was observed in general, it may be noticed that the principal food items were comprised of four major euphausiid species; *Euphausia diomedeae*, *E. recurva*, *Pseudoeuphausia latifrons*, and *Thysanoessa gregaria*. Both South Pacific for the 1976/77 season and southwestern Indian oceans were represented largely by *E. recurva*, where this species accounted 59.4% and 98.1% respectively in number of the stomach. Different from the previous season, however, *T. gregaria* occurred in addition to *E. recurva* as major food species by 50% of occurrence in the South Pacific for the 1977/78 season. Although the number of whale catches in the Coral Sea were seven in all, there occurred only *E. diomedeae*. In the equatorial eastern Indian Ocean *P. latifrons* occurred in great numbers, where this species accounted for 58.5% among all. *E. recurva* did not occur in this locality but *E. diomedeae* and *E. sibogae* accounted for 11.3% and 13.2% respectively. The latter two species can be refered to as a meso- scale importance as the whales food. As it is noticed in Fig. 4 one of the characteristics in the equatorial eastern Indian Ocean may be found in the diversity of species composition when it is compared with the case in four another whaling areas. It must be noted



* Probably E. recurva
** Probably E. sibogae

Fig. 4. Composition matrix for the 234 stomach analysis in the southern Bryde's whales. Numerals in the square denote the number of stomachs by the five different whaling areas.

that both *E. sibogae* and *T'da tricuspidata* by no means occurred under the mixed state in composition with another kind of food species, while *E. diomedeae*, *E. recurva*, *P. latifrons* and *T. gregaria*, the principal food items of the southern Bryde's whales in pelagic waters, occurred at times by mixture with one of each other. The stomach contents composed of the Euphausiacea seem to very similar composition over the different four whaling ground occupied through the 1976/77–1977/78 seasons while they changed notably to different food species in the equatorial eastern Indian Ocean. Except the case in *T. gregaria* and *E. recurva*, there were very few stomachs that were composed of mixture by more than two food species. Although there were several instances scattered at far from the diagonal line which indicates a single species composition, the most stomachs were found to be characteristically composed of mono-specific composition, that is, 210 (89.7%) stomachs out of 234 food contained stomachs were comprised of only one food species. The animals in the South Pacific ground for both the 1976/77 and 1977/78 seasons fed same euphausiid species and their mixture. It can be said that the general feature of the food composition was very simple and the fish was of minor importance in so far as the given localities in pelagic waters.

While laboratory examination of the stomach contents under the microscope, it was noticed that there were difference between each component species in their freshness and/or the magnitude of damages among the preserved materials of mixed composition with two or more kind of species. This may suggest a possible time-lag due to the difference in feeding time by each component species. The whale might have fed upon them from one to another, each of which might have had formed aggregations independently with a little spacing over the spacially small scaled area.

f) *Distribution of food species*

Figures 5–6 demonstrate the horizontal distribution of food organisms by species over the five whaling areas. The plot in the Fig. 5 represents all position where positive occurrence of each food species was recorded. When the stomach was composed of two species in mixed state, they were plotted separately by each species elsewhere in the chart.

In the Coral Sea there found only five stomachs of containing *E. diomedeae.* The South Pacific areas were visited twice during two successive seasons as noted in the figure. Each whaling area is located at almost same sea region with a little overlappings, but there were no notable differences in the catch periods and sea temperature in these two seasons (see Fig. 1 and Table 4).

Since the catch of whales in the Coral Sea took place in a locally biassed area, the occurrence of *E. diomedeae* was also confined to spacially small area. The central South Pacific areas, on the other hand, covered over the wide latitudinal or longitudinal ranges of magnitudes expanding for several degrees. Both *E. recurva* and *T. gregaria* occurred over the whole geographical ranges but somewhat dispersed distributions in the latter species. *E. recurva* for the 1976/77 season fairly well concentrated locally where the species occurred approximately within a la-

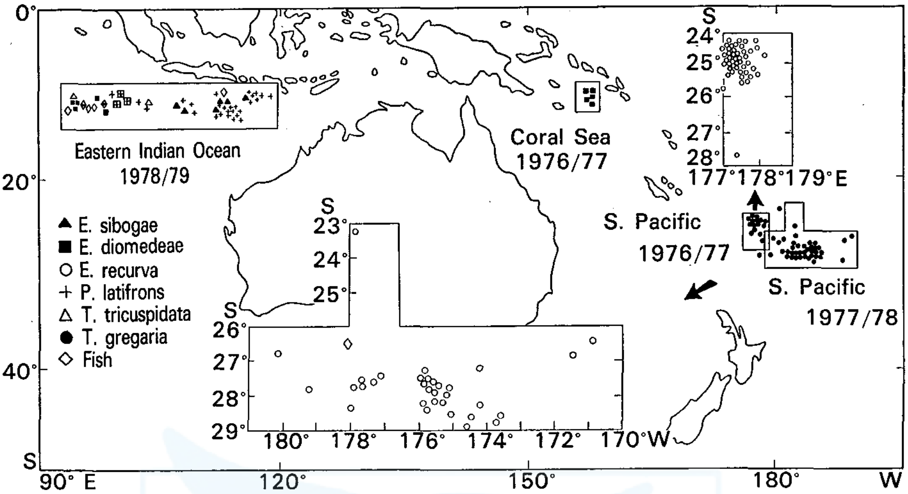


Fig. 5. Distribution of euphausiids and fish that were fed by the southern Bryde's whales.

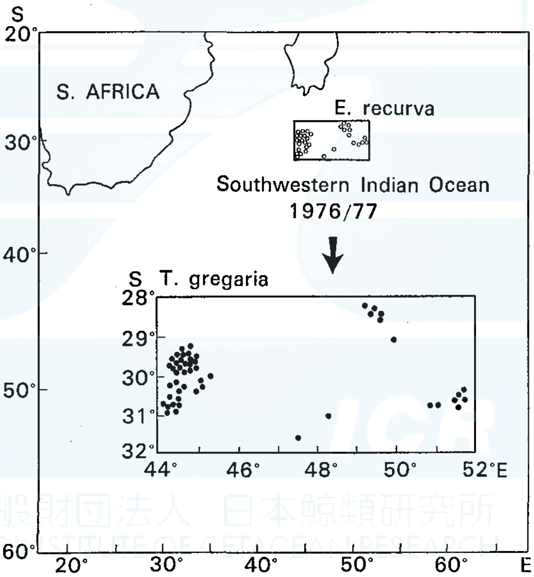


Fig. 6. Distribution of euphausiids that were fed by the southern Bryde's whales.

titudinal or longitudinal square by one-degree. Similar local concentrations were again observed in the 1977/78 season but lesser magnitude. It is, however, hard to know whether or not the horizontal distribution of *E. recurva* and *T. gregaria* was different to any appreciable magnitudes. Very similar locally biassed concentrations of food euphausiids are also observed in the southwestern Indian Ocean but the spacial expand of the whaling area was relatively larger than the formers.

In the equatorial eastern Indian Ocean the food species distributed with considerable geographical differences by each species. *P. latifrons* was the most dominant food species among three others, and occurred more frequently in the eastern half of this whaling area. Both *P. latifrons* and *E. sibogae* showed a possible very closer associations with each other in their occurrence. Although very occasional in frequency occurrence, *E. diomedeae* did not show such characteristic trends as the former two species but somewhat closer associations with the gonostomatid fish, *V. nimbaria* in the western area. *T'da tricuspidata* occurred at only two positions and hardly be known its distributional characteristics. There was the space where the food organisms distributed very sparcely in the midst of the eastern Indian Ocean area. Although the reason why food organisms distributed so sparcely is unknown at present, the region well coincides with the area where distinct discontinuity of euphausiid distributions has been demonstrated (Ponomareva, 1972).

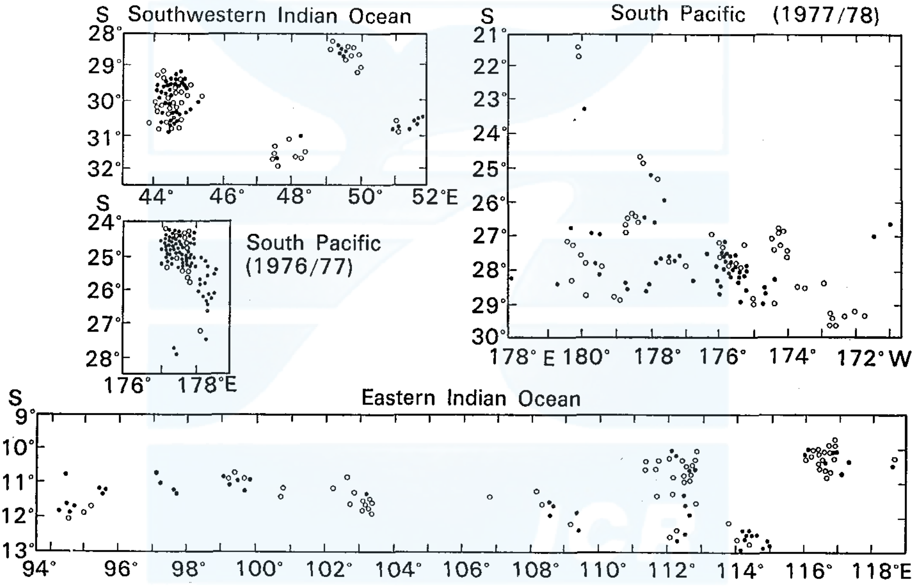


Fig. 7. Catch distribution of Bryde's whales during the seasons of 1976/77–1978/79. Filled and open circles denote the animal of filled and empty stomach respectivelly.

To summerize the overall distribution characteristics of the food species throughout the five different whaling areas, it is obvious that the main concentration area of food organisms and whales distributed unevenly with local biass over the regions worked out. From this viewpoints it may be observed that the concentration of whales occurred at very spacially small localized areas where the distribution of aggregated food organisms showed quite biassed occurrences. These therefore, can be confirmed that the animals with filled stomach concentrated in the way above mentioned while those with empty stomach having been possibly in search of food were found to show relatively scattered distribution over the whole whaling areas (see Fig. 7). This evidence may suggest that the movement of whales in the tropical and/or subtropical seas is significantly related to the presence of available foods. Where abundant food distribution is exhibited, movement of whales may become stationary for the time being.

DISCUSSION

Several past catch records of the Bryde's whales in the southern hemisphere are completely confined to the catches by the land based operations. This may represent very locally limited feeding conditions for the whales occurring in coastal to offshore regions since locally characteristic environmental conditions in near shore waters may determine the faunal distribution—the occurrence of endemic species including planktonic organisms.

There have been reported a several number of such informations as that came from the coastal whaling. In regard to food and/or feeding habits of the Bryde's whales in the southern hemisphere, Symons (1955) described only pilchards found from the Saldanha Bay animals. Examining Donkergat animals, South Africa, Olsen (1913) more earlier reported that the Bryde's whales feed upon 'fish' and he found but one occasion of the remains of euphausiid crustaceans. Best (1960) summerized some of those earlier data and reported that the catches of Bryde's whales in the southern hemisphere are largely took place around the South African coast, but there were also catch records of lesser extent in Western Australia, North Island of New Zealand, and northern Chile. The Saldanha Bay animals were found to feed upon pilchard (*Sardinops occellata*) and anchovy (*Engraulis japonicus*) (Best, 1960), but the latter was corrected to be *E. capensis* in the later study. More later, Best (1967) reported that the majority of Bryde's whales of visiting Cape Province region, South Africa feed upon both shoaling fish such as pilchard (*Sardinops occellata*) and anchovy (*Engraulis capensis*), and euphausiids, *Euphausia lucens*. Bannister and Baker (1967) also reported but one instance of *E. recurva* as the food of Bryde's whales off Durban. Best (1977, Table 5), however, gave more complete sets of dietary habits, where he reported the following food items by identifying both inshore and offshore forms of the Bryde's whales each of which demonstrates very characteristic food habits: The inshore form chiefly feeds upon shoaling fish members, *Engraulis capensis*, *Trachurus trachurus* (jack mackerel), and *Sardinops occellata*, while the offshore form feeds largely upon the Euphausiacea such as *Euphausia lucens*, *E. recurva*, *Nyctiphanes capensis* and *Thysanoessa gregaria* along with some pelagic fish species such as *Maurolicus muelleri*, *Lestidium* sp., *Scomberesox saurus* and *Scombrid* sp. He (Best, 1977) also found cephalopods, *Lycoteuthis diadema*, as the first record as whales food from the same locality. In northern waters off Point Cloates, Western Australia, *Euphausia hemigibba* and *Pseudeuphausia latifrons* were found from the humpback whales (Dall and Dunstan, 1957), and these are considered to be a possible Bryde's whales food in that locality. In the southern waters off Western Australia, the Bryde's whales are known to feed upon *Engraulis australis* and/or young mackerel, *Pneumatophorus australiasicus* (Chittleborough, 1959), while it changes to mugilid fish called 'mullet' and crustaceans at Great Barrier Island in the Hauraki Gulf, New Zealand (Gaskin, 1976). Aguayo (1965) examined first the South American 'sei' whale at Iquique, northern Chile and found the animal was identical to the so-called Bryde's whales but failed to show its food items except 'fluid' from the lst to 2nd stomachs.

All that the food items of the southern Bryde's whales having been known to date strongly suggests the animal preferable feeds upon shoaling fish of mostly commercial importance instead of planktonic organisms during their stay in the coastal or near shore waters. On the population and movements of the Bryde's whales in the New Zealand waters, Gaskin (1977) states that " . . . it is largely confined to the area between North Cape and East Cape on the eastern side of the North Island, and migratory only in the sense that groups of these whales appear to follow local movements of pelagic fish schools". However, the distinct planktivorous food habits as demonstrated by the offshore form of the Bryde's whales in the South African waters where the animal feeds largely upon euphausiids (Best, 1977) are noteworthy. The animal of offshore form is characteristic for having a short but relatively broader width of baleen plates while the inshore form is furnished with slender, a more sei whale-like baleen plates. Form the morphological or functional point of view concerning baleen plates (e.g. Nemoto, 1970), the offshore form seems to be more adapted to swallowing type of feeding which seems to be more effective to eat fish.

Although the baleen plates of the southern pelagic species caught by special permit have not been studied to date the whole filter area formed by the baleen series in the South Pacific animals caught during 1976/77 season was significantly smaller than that found in the pelagic North Pacific animals (Kawamura and Satake, 1976; Kawamura, 1978a). This may suggest the South Pacific, Coral Sea, and possibly the Indian Ocean animals to be an identical types of baleen plates to the offshore form of the South African waters. According to Kawamura and Satake (1976) the North Pacific Bryde's whales show two different types of baleen plates but each of which is similar to the forms found in the South African animals although there were considerable variations from one to the another. The baleen plates of Bryde's whales being caught in the coastal region in Japan showed generally a stronger similarity to those of offshore form while the animals in the pelagic waters were of the inshore form. The 88.9% of totaling 109 North Pacific animals from pelagic waters feed the Euphausiacea while 11.1% were the fish (Nemoto and Kawamura, 1977). On the other hand, the animal in the coastal waters around Japan feeds on variable food items by the localities but mainly focussed on both shoaling fish such as anchovy (*Engraulis japonicus*), *Trachurus japonicus*, *Myctophum asperum* and euphausiids (*E. similis*, *E. recurva* and possibly *E. pacifica*) (Nemoto, 1959). In the eastern North Pacific off Baja California, the Bryde's are reported to feed upon the red crab, *Pleuroncodes planipes* and anchovy, *Engraulis mordax* (Rice, 1977).

These above mentioned evidences may suggest that the Bryde's whales of occurring in the coastal waters of both hemispheres are considered to be a distinct ichtyophagous animals among all of the balaenopterid whales, *i.e.*, the Bryde's whale seems to feed upon whatever the organisms of greater availability or encountered frequently in the surrounding environments. In this connection such the morphological characteristics of baleen plates as found in both allopatric forms by no means determine the kind of food species, and these perhaps mean the lesser ecological functions in the food preference throughout the whole population of the Bryde's whales. An instance that ichtyophagous inshore form of Bryde's whale feeds an euphausiid, *Nyctiphanes capensis* in the South African waters (Best, 1977) suggests the animal preys upon simply due to the abundant distribution of *N. capensis* in the neritic waters (Brinton and Gopalakrishnan, 1973).

As observed in this study it was only the Euphausiacea that was taken largely by the Bryde's whales in the pelagic waters as the main dietary organisms of the Bryde's whales over the central South Pacific, Coral Sea, southwest and equatorial eastern Indian oceans. In general the food of tunas and skip jacks occurring in the Pacific equatorial regions is composed of young or larval forms of many kind of fish, cephalopods and planktonic crustaceans other than euphausiids which are of minor importance, although the larval fish feed largely on zooplankters (Shirota, 1975). These might resulted from the difference of feeding types of animals as the filterer and/or the attacker, but also came from the difference of ambient biomass of each prey organism and diel feeding activity of predators (Roger, 1973b). Even young fish of various kinds in the tropical pelagic waters by no means forms such school or aggregations of enormous biomass as usually found in euphausiid swarms. The fish usually shows more dispersed distribution than the euphausiids but may give fairly larger biomass by the individual basis (Nemoto and Kawamura, 1977). This may be more beneficial for the attack-feeder than for the filter-feeder. The baleen whales cannot but feed upon euphausian swarms, which may occur under the strongly and locally biassed conditions. Although some copepods such as *Clausocalanus arcuicornis* seems to occur numerously in the Central Pacific (Chiba and Hirakawa, 1972), and actually both *C. arcuicornis* and *C. laticeps* have been found as the food of sei whales (Best, 1967; Kawamura, 1974). Even so, there seems little possibility of occurring any kind of prey organisms except euphausiids for the baleen whales in the pelagic region of the tropical to subtropical waters where no planktivorous and school forming fish stocks hardly be exist. The possible total amount of available euphausiid food per head of animals in the tropical sea region in terms of occurrence freguency of animals was 44–75% (Table 1), and this is hardly comparable with that of 70–90% found in the feeding grounds in boreal or colder seas (e.g. Kawamura, 1978b).

The concentration or the feeding of Bryde's whales took place was spotted in some local area while the euphausiid species in general distribute widely over the whole South Pacific and Indian oceans in question (Brinton, 1962; Brinton and Gopalakrishnan, 1973). To see the distinct mono-specific composition of stomach contens, it is clear that the euphausiid species actually fed by the Bryde's whales are considered to be the swarm forming species that distribute numerously in the epipelagic and/or meso-pelagic waters.

According to Brinton (1962), *E. recurva* shows biantitropical distribution in the Pacific but somewhat scarce in the southern hemisphere. The day-night depth distribution of this species is biassed in the upper 100 m during the night but it is below 140–700 m during the day, and he (Brinton, 1962) found only daytime aggregations of furcilia larvae below 140 m. *T. gregaria*, one of another important food species of the Bryde's whales in the South Pacific may occur between 25–300 m during the night but it is below 500 m during the day. *E. diomedeae*, the only food species both in the Coral Sea and equatorial eastern Indian Ocean is found 10–140 m during the night but this species goes down to deep far below during the day. The rest euphausiid species fed by the whale may demonstrate a similar pattern of diel depth distribution or the species known as the lesser migrant such as *P. latifrons* (Brinton, 1962). The Brinton's findings suggest a scarcity of the whales food during the day. The diel changes in stomach conditions, however, strongly suggest that a possible daytime feeding of whales actually took place in all five different whaling areas (see Fig. 2). This may lead to a consideration that those food euphausiid species may come to or be stationary close to the surface layers even the daytime at least when they aggregate to form the patchy swarms. However, it is still unknown that the aggregation of euphausiid species is related to their feeding, since active feeding intensity in the shallower layer in *E. diomedeae* and *T'da tricuapidata* is concentrated during the night later than 20 hrs (Roger, 1973c). The occurrence of sperm sacs in female or in both sexes of those species might have possibly related to their aggregations at such a shallower layer as to be fed by the whales during the austral summer. Even so, it is curious that any species of the genera *Stylocheiron* and *Nematoscelis* were not fed by the whales while only these genera having been known to occur abundantly during the day in the tropical South Pacific Ocean (Roger, 1973d), and actually ichtyofauna of Gempylidae, Paralepididae, and Bramidae feed largely upon *Stylocheiron* and *Nematoscelis* (Roger, 1973b). The catches in the southwestern Indian Ocean represents only the materials collected in the austral autumn while other four collection areas are early summer. The food species found in each local and seasonal set of the catches and the magnitude of stomach fulness, were not different each other. This may lead to a consideration that there might be very few seasonal changes in the availability of food euphausiids in terms of both quality and quantity. The abundance of euphausiids in a magnitudes of ordinal biomass by no means of any importance for the baleen whales but surface swarms of several hundreds to thousnads times of biomass per unit volume of water must be expected over the study areas as the similar case found in the copepod food (Kawamura, 1974).

The complicated occurrence of euphausiid food in the equatorical eastern Indian Ocean may largely be due to the characteristics of zoogeography in the Indo-Pacific regions. The eastern Indian Ocean ground was situated within the ranges of the South Equatorial Current systems to which strong westerly current of Pacific origin may flow via the Arafura, Banda and Java seas (Wyrtki, 1973). Although the distribution of zooplankton biomass in this region varies with seasons under the influence of southwestern or northeastern monsoon, the whaling area in the eastern Indian Ocean was corresponded to relatively larger biomassed plankton rich region especially during October-November (Rao, 1973). Studying the mysids and euphausiids in the eastern Indian Ocean, Taniguchi (1974) actually found a fairely complicated faunal composition in the waters south of Java Island and pointed out that the diversity of species composition in the area is mainly due to the inflow of the Banda Sea waters. Among the euphausiids species that showed the most frequent occurrence in the region as reported by Taniguchi (1974), three food species for the Bryde's whales, *T'da tricuspidata*, *P. latifrons* and *E. diomedeae* were included. Only *E. sibogae* is reported to be of minor importance by lesser magnitudes of occurrence (Taniguchi, 1974). The lesser occurrence of the genus *Euphausia* as food of Bryed's whales in the eastern Indian Ocean agrees well to the findings by Taniguchi (1974), and this along with the ocean current systems may further related to the faunistic characters of the Euphausiacea in the Sulu Sea region (Ponomareva, 1976). Brinton and Gopalakrishnan (1973) found the abundant distribution of *P. latifrons*, that was the commonest food species in the equatorial eastern Indian Ocean during November-March and noted the region as "a typical parts of the distribution". Ponomareva (1972) also showed the eastern equatorial Indian Ocean including southern waters off Java Islands as the high biomassed and ecologically interesting region from a viewpoint of food chains. Brinton and Gopalakrishnan (1973) states "Essentially a neritic euphausiid, *P. latifrons* was nevertheless caught sporadiacally throughout the oceanic part of the tropical zone, but usually near islands". The frequencies of euphausiid occurrence as the food of Bryde's whales in the Indian Ocean was very similar to the general geographical abundance of each euphausiid species.

Despite the very much diversified communities, species composition and distribution of euphausiids in the tropical to temperate Pacific and Indian oceans (Mauchline and Fisher, 1969), there seems to be very little number of species that are actually available to the baleen whales as their primaly diet in the pelagic part of those warmer sea regions. The former studies on the diet of baleen whales made it clear that the food organisms must be the species undoubtedly aggregate densely to form the patchiness (Nemoto, 1963; Kawamura, 1974, 1978c; Brodie *et al.*, 1978). From the obvious mono-specific composition of stomach contents, *E. diomedeae*, *E. recurva*, *E. sibogae*, *P. latifrons*, and *T'da tricuspidata* may be refered to as the distinct swarm-forming species. Among these members, at least *T'da tricuspidata*, *P. latifrons* and *E. diomedeae* have been known to be the omnivorous and/or detritus feeders (Ponomareva *et al.*, 1962; Roger, 1973c, 1978; Mauchline and Fisher, 1969). The pelagic food relationships, Bryde's whale vs euphausiids, copepods vs young fish and then, young fish vs larger fish are the subject of biological interests in connection with comparing those in the coastal waters and with the case in another whale species. Both biological and ecological knowledge on the euphausiid swarms along with their food habits would be one of the key subjects in the steps of studying tropical marine ecosystems since only the genera *Stylocheiron* and *Nematoscelis* have been known as possible swarm-forming food organisms during the light hours of the day in the tropical Pacific (Roger, 1973e,f).

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APPENDIX TABLE I. NUMBER OF ANIMALS BY THE QUANTITY OF STOMACH CONTENTS AGAINST LOCAL CATCH TIME

Local time of catch	CORAL SEA (1976/77)						SOUTH PACIFIC (1976/77)						SOUTHWEST INDIAN OCEAN (1976/77)					
	Empty	Quantity less than (%)				Total with food	Empty	Quantity less than (%)				Total with food	Empty	Quantity less than (%)				Total with food
		25	50	75	100			25	50	75	100			25	50	75	100	
5							1											
6							4	6	2			8	1	1	1			2
7	1						4	12	4	3	1	20	7	5	1		1	7
8		1				1	4	3	1		1	5	16	3	1	1	7	12
9		1	1			2	1	3				3	6	6	3		3	12
10							2						9				2	2
11							1	3	1			4	2	1	1		1	3
12				1	1	2	2		1	2	2	5	7	2	2		2	6
13							1	1	3	1	1	6	3	2	1			3
14	1						1	5	2	1		8	5				1	1
15							2	4	1	3		8		1				1
16							4	4	2	2	2	10						
17							1	3	1			4						
18								3	1			4						

APPENDIX TABLE II. NUMBER OF ANIMALS BY THE QUANTITY OF STOMACH CONTENTS AGAINST LOCAL CATCH TIME

Local time of catch	SOUTH PACIFIC (1977/78)						EASTERN INDIAN OCEAN (1978/79)					
	Empty	Quantity less than (%)				Total with food	Empty	Quantity less than (%)				Total with food
		25	50	75	100			25	50	75	100	
6	5							2*				2
7	6	3*				3	6					
8	7	3	1	1		5	9	4**	2*			6
9	7	2			1	3	5	1	3			4
10	5	3	2	2		7	4		2			2
11	3	2	3	2	2	9	3	1	1			2
12	3	1	1			2	5		1	1	1*	3
13	4	1	1		1	3	2		4*	1		5
14	2	1	1	1		3	4	2	4	2	1	9
15	2	2	2	1	2	7	10	2	1	2	1	6
16	3	3	2	1	2	8	9	2*	3	2		7
17	4	4	2		1	7	4	2	3	1		6
18	2	1		1		2	6			1		1
19	1	1				1						

South Pacific (1977/78): * one stomach by fish food is included.

Eastern Indian Ocean (1978/79): * one stomach by fish food is included. ** two stomachs by fish food are included.


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MORPHOLOGICAL STUDY OF PELVIC BONES OF THE MINKE WHALE FROM THE ANTARCTIC

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ABSTRACT

In the 1978–79 Antarctic whaling season a total of 72 pairs of pelvic bone of the minke whale, 36 from males and 36 from females, were collected for morphological study. The basic forms for males and females are thought to be " drum stick " and " knife " respectively, as in the case in the North Atlantic animals. There are, however, very wide range of variation both in males and females and the individual sex can not be determined by the pelvic bone alone.

Existence of ossified remnant of femur was noted in whales exceeding one third of total whales examined, both in males and females.

INTRODUCTION

In the 1976–77 Antarctic whaling season a total of 51 pairs of pelvic bones of the minke whale, 50 from males and one from females, was collected by Japanese expeditions for morphological study. These results have suggested some doubts on sexual dimorphism of the bone, which was confirmed in whales from the North Atlantic, and the size of bones was thought to be a little smaller than those from the North Atlantic, and the presence of the ossified remnant of the femur was noted in some specimens (Omura, 1978).

In the 1978–79 season a total of 72 pairs of pelvic bones, 36 from males and 36 from females, were collected by courtesy of Mr H. Kato on board the whaling factory ship *Nisshin Maru No.* 3. He joined the southern hemisphere minke whale assessment cruise 1978–79, a program of the International Decade of Cetacean Research of the International Whaling Commission, led by Dr Peter B. Best of the South Africa, and after conclusion of the cruise he remained in the factory and carried out biological investigation of whales treated in the factory. Dr P. B. Best had also remained in the factory ship for some time and according to Kato he also helped in collection of the sample. Material thus collected are the basis of this study.

MATERIAL

The pelvic bones were collected from minke whales taken in the Antarctic during a period from 18 January to 3 March 1979, in which period the expedition moved from eastern part of the Area III eastwards to western part of the Area V. As

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shown in Table 1 bones were mostly or 75 percent of the total were collected in Area IV. In this table are also shown distribution of body length classes, separately by sexes.

When sampling the bone care was taken in order to secure the remnant of the femur, and thus much meat and other tissues were attached to the bones. These samples were kept frozen in the factory ship and then transported to WRI.

At the laboratory these bones were boiled for some hours in order to remove meat and other soft parts from the bone, each pair is being packed in a small bag made of cotton cloth. Thus all solid bones were secured, even if a very small remnant of femur was present. The bones were boiled again, after removal of all soft parts, for extraction of oil and finally they were dried by direct sun. All of these bones are shown in Plates I–VII. Date and position and other catch particulars of whales from which bones were collected are shown in Appendix Table together with measurements of each bone.

TABLE 1. NUMBER OF MINKE WHALES FROM WHICH SAMPLES OF PELVIC BONES WERE COLLECTED IN THE 1978-79 SEASON

Body length in m	Area III			Area IV			Area V			Total		
	M	F	T	M	F	T	M	F	T	M	F	T
5.5—5.9	—	—	—	—	1	1	—	—	—	—	1	1
6.0—6.4	—	—	—	—	—	—	—	—	—	—	—	—
6.5—6.9	—	—	—	1	2	3	—	—	—	1	2	3
7.0—7.4	—	—	—	—	2	2	1	—	1	1	2	3
7.5—7.9	3	1	4	6	3	9	3	1	4	12	5	17
8.0—8.4	2	2	4	15	6	21	—	1	1	17	9	26
8.5—8.9	—	1	1	5	7	12	—	1	1	5	9	14
9.0—9.4	—	2	2	—	3	3	—	—	—	—	5	5
9.5—9.9	—	—	—	—	2	2	—	—	—	—	2	2
Over 10.0	—	—	—	—	1*	1	—	—	—	—	1	1
Total	5	6	11	27	27	54	4	3	7	36	36	72

M···male, F···Female, T···Total
* 10.1 meter.

RESULTS AND DISCUSSION

According to Burmeister (1867) his whale of *Balaenoptera bonaerensis* was found dead, floating on the river Plata, near Belgrano, about ten miles from Buenos Ayres, by a fisherman, who brought the body on shore. This was a male of 32 feet (9.6 m) long and had the small bone of the pelvis, which is 7½ inches (19.1 cm) long and 1½ inch (3.8 cm) broad in the middle, and of a lanceolate form, being narrowed at both ends. Heyerdahl jr. (1973) found sexual dimorphism in pelvic bones of the minke whale from the North Atlantic, those of the female having the shape of a knife while those of the male look like drum stick. Burmeister's "lanceolate form" may possibly similar to Heyerdahl's "drum stick". In my previous work (Omura, 1978), however, there were wide range of variation in the shape of pelvic

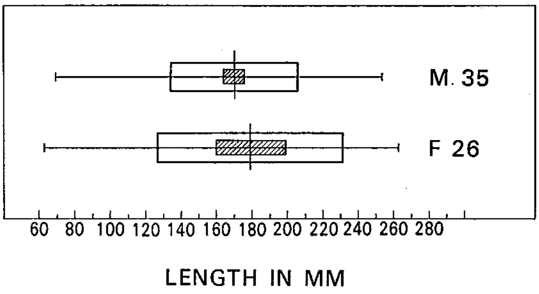

Fig. 1. Comparison of length of pelvic bones of minke whales from the Antarctic between males and females. The horizontal line represents the range; the vertical midline, the arithmetic mean; the outer and inner boxes, the standard deviation and standard error on either side of the mean respectively. The numerals in the figure are sample number of males and females.

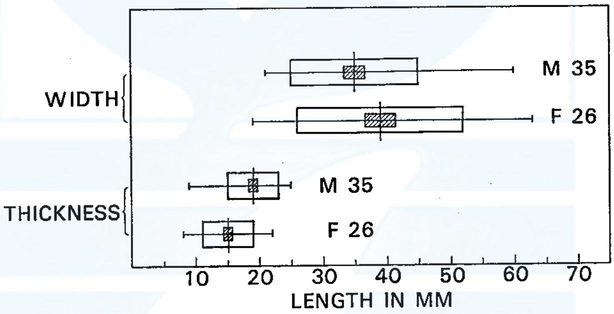

Fig. 2. Comparison of width and thickness of pelvic bones of minke whales from the Antarctic between males and females. See Fig. 1 for explanation.

bone of males, though only one sample from female showed the shape of a knife in general.

In the 1978–79 season pelvic bones were collected from 36 males and 36 females, as shown in Table 1. Photographs of these bones of males are shown in Plates I-III and Figs 1–3 of Plate VII and those of females in Plates IV-VI and Figs 4–7 of Plate VII.

In these figures typical drum stick type may be observed in pelvic bones of males, for example Figs 1, 6 and 8 of Plate I, Figs 2, 8 and 10 of Plate II, Figs 5, 6 and 11 of Plate III. Typical knife shape are observed in pelvic bones of females, for example Figs 1, 2, 6 and 7 of Plate IV, Figs 2, 4 and 7 of Plate V, and Fig. 4 of Plate VI. These two forms are thought to be the basic forms of the pelvic bones of the minke whale from the Antarctic too. There are, however, a good range of variations both in males and females, and it is very difficult or nearly impossible to identify males and females only by the shape of these bones.

In Figs 1 and 2 pelvic bones of males and females are compared of their length, width and thickness. In these cases samples are taken from whales at or above

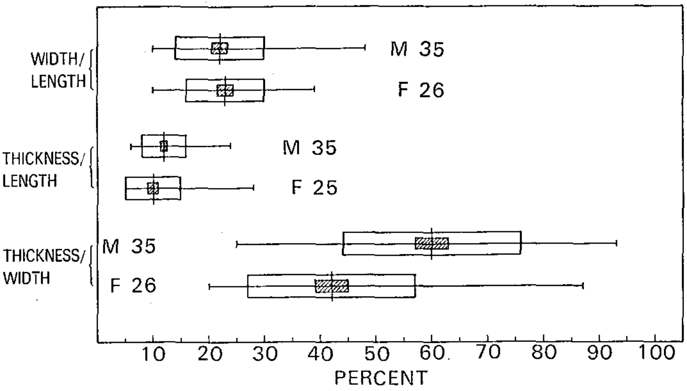

Fig. 3. Comparison of proportion Width/Length, Thickness/Length, and Thickness/Width of pelvic bone of minke whales from the Antarctic between males and females. See Fig. 1 for explanation.

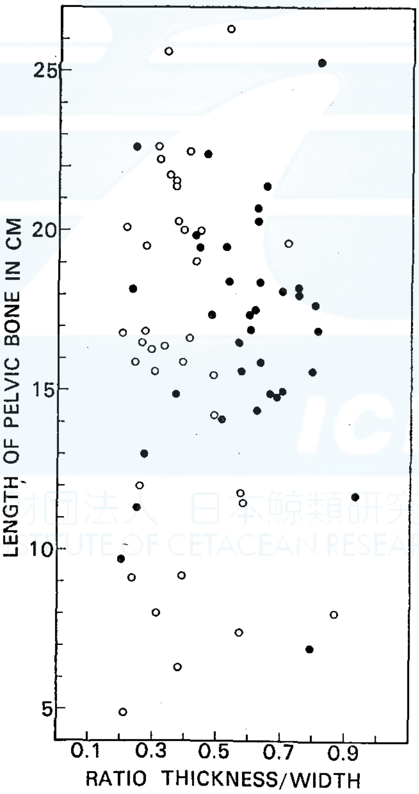

Fig. 4. Relation between length of pelvic bones and ratio Thickness/Width across the promontry in minke whales from the Antarctic. Closed circle indicates male and open circle female.

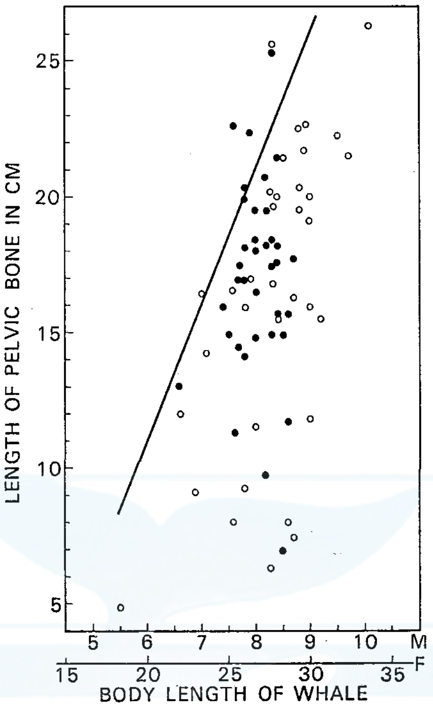

Fig. 5. Relation between length of pelvic bone and body length of minke whales from the Antarctic. The straight line in the figure is the regression line obtained by Hyerdahl jr. (1973) for minke whales from the North Atlantic. Closed circle indicates male and open circle female.

average body length of sexual maturity or 7.2 m or over in males and 8.0 m or over in females (Ohsumi and Masaki, 1975). As seen in Figs 1 and 2 there are no distinction between males and females in the length and width of pelvic bones, but some difference is present in the thickness, in males the bones are somewhat thicker than those in females in general. Width and thickness of bones are measured at their promontories.

In Fig. 3 the proportion width/length, thickness/length, and thickness/width of pelvic bones of minke whales from the Antarctic between males and females are compared. In these cases the distinction between males and females is only noted in ratio thickness/width, but in this case too ranges are overlapping in most parts, suggesting difficulty of identification of sexes individually by means of pelvic bones only.

In Fig. 4 the ratios thickness/width of the pelvic bones across the promontory are plotted against respective length of the bones. Heyerdahl jr. (1973) found that the female bones tend to maintain their proportions while the male bones diverge towards a rounder shape, with the increase of length of the bone. As seen in this figure no such tendency is obserbed in pelvic bones of minke whales from the Antarctic. There are wide range of variations.

In Fig. 5 the relation between length of pelvic bone and body length of minke whales from which respective bones were obtained. The straightline in this figure is the regression line obtained by Heyerdahl jr. (1973) for minke whales from the North Atlantic. No such regression line can be drawn for minke whales from the Antarctic. It is possible, however, in minke whales from the Antarctic the pelvic bones are smaller than those of minkes in the North Atlantic, as already noted in the preliminary report (Omura, 1978).

Presence of ossified remnant of femur in the minke whales from the Antarctic was already reported in the preliminary report (Omura, 1978), but in that report the occurrence was 25 percent against the total of 51 pairs investigated. This percent of occurrence was very higher than those from the North Atlantic. Heyerdahl jr. (1973) reports none disclosed any trace of a femur, with the exception of one of the 32 X-ray photographs. This was from a 25-ft (7.5 m) female minke whale, with remnants of femur anterior and lateral to the promontory.

TABLE 2. OCCURRENCE OF FEMUR IN PELVIC BONES OF MINKE WHALES FROM THE ANTARCTIC

Area	Male		Female		Total	
	No. examined	Femur present	No. examined	Femur present	No. examined	Femur present
III	5	1	6	4	11	5
IV	27	11	27	9	54	20
V	4	2	3	0	7	2
Total	36	14	36	13	72	27
% Occurrence		38.9		36.1		37.5

As seen in Table 2 in the pelvic bones collected in the 1978–79 season from the Antarctic the presence of ossified remnant of femur was amounted 37.5 percent of the total of 72 animals, showing much higher percent than in the 1976–77 season (Omura, 1978). This is clearly due to the fact that a special caution was paid when sampling the bone, not to miss the bone even it is very small.

The size of the ossified remnant femur bones is different individually and in most cases they present on both sides, but in some specimens it exist only on .one side. Measurements of three dimentions of these bones are given in the Appendix Table. Usually these bones are present anterior and lateral to the promontory and apart from the main bone. There present, however, clear articulating tubercles both in the main bone and femur in some specimens and in the extreme cases these bones are completely fused together, as shown in Figs 2 and 6 of Plate IV and Fig. 8 of Plate V.

Burmeister (1867) found no trace of femur in his specimen of *Balaenoptera bonaerensis* and describes "No vestige of an attachment of another bone to any part of its surface is visible; and it is the same with the European species, according to the observation of Eschricht and Reinhart". Since then most authors followed this opinion and Hosokawa (1951) classified baleen whales into the following three groups from the viewpoint of the rudimentary skeletons pertaining to the hindlimb. Group 1, to which the Greenland right whale belongs, has besides the pelvis two pairs of subsidiary bones of cartilages (femur and tibia). Group 2, in which other than the pelvis only the femur is present, comprises the humpback, the fin whale and perhaps also the blue whale. Group 3, which has neither femur nor tibia but has the pelvis only, seems to comprise the sei whale and the lesser fin whale (minke).

In his group 1 also the black right whale can be added (Omura *et al.*, 1969), and in this case femurs were all ossified. Existence of the femur in the minke whale was first noticed by Heyerdahl jr. (1973), though in his specimen the bone was a nodule of cartilage. In this study it was proved that the existence of the femur in minke whales from the Antarctic is not rare, being exceeded one third of the total minke whales examined, both in male and female. In my previous works on the skeleton of the minke whales (Omura, 1957, 1975; Omura and Kasuya, 1976) also the pelvic bones were reported, but no special statement was made on the presence of the femur. It was first noted in the collection of pelvic bones of minke whales from the Antarctic in the 1976–77 season (Omura, 1978). I have used some of them for covering photograph of the Christmas card 1978 (Fig. 6).

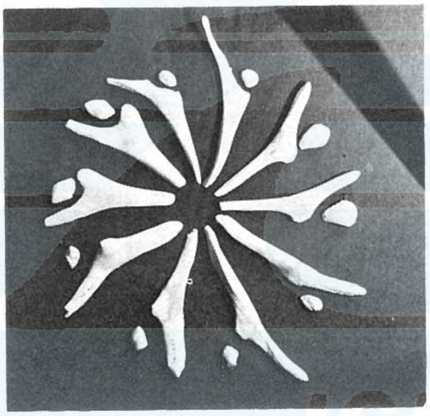

Fig. 6. Some of the pelvic bones of the minke whales from the Antarctic collected in the 1976–77 season. See text for explanation.

Hosokawa (1951) includes the sei whale also in his group 3 i.e. neither femur nor tibia present. However, this may be doubtful. A complete set of skeleton of the Bryde's whale, a very close relatives of the sei whale, was obtained in 1977 for the taxonomic study from the southern hemisphere. The study has not been completed yet, but the whale had a pair of pelvic bones with ossified femurs.

ACKNOWLEDGEMENTS

I am much indebted to Mr H. Kato of the Whales Research Institute and Dr P. B. Best of South Africa for collection of samples of the pelvic bones on board the factory ship *Nisshin Maru No.* 3. Without their help this study could not be carried out.

My sincere thanks are also due to the crew of the factory ship who helped the collection and transported them to WRI.

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APPENDIX TABLE. CATCH PARTICULARS OF THE MINKE WHALE FROM WHICH PELVIC BONES WERE SAMPLED AND MEASUREMENTS OF BONES (1978-79 SEASON)

Whale No.	Date, catch	Sex	Body length m	Position, catch		Area	Measurements in mm							
							One side				Another side			
				Lat.	Long.		Length	Width	Thickness	Femur*	Length	Width	Thickness	Femur*
78N1493	20 Jan. '79	♂	8.4	67°-20′ S	68°-39′ E	III	162	26	22	none	150	29	21	none
78N1562	24 „ „	„	7.8	67°-04′ S	62°-02′ E	„	144	28	14	„	138	27	14	„
78N1574	25 „ „	„	8.4	67°-10′ S	65°-02′ E	„	189	37	18	„	174	40	18	„
78N1603	26 „ „	„	7.6	67°-05′ S	65°-15′ E	„	222	58	14	„	230	62	14	„
78N1637	„ „ „	„	7.6	„	„	„	114	49	11	„	112	47	13	31, 25, 16
78N1414	18 „ „	♀	8.3	67°-21′ S	68°-10′ E	„	201	63	13	„	122+	Broken		none
78N1450	19 „ „	„	8.4	67°-24′ S	67°-58′ E	„	201	44	22	60, 32, 25	199	54	20	43, 21, 22
78N1529	21 „ „	„	7.6	67°-32′ S	68°-14′ E	„	80	32	10	none	80	36	11	none
78N1551	22 „ „	„	9.0	67°-34′ S	68°-04′ E	„	197	30	13	26, 24, 18	184	30	13	26, 22, 18
78N1576	25 „ „	„	9.2	67°-10′ S	65°-02′ E	„	169	34	13	22, 18, 16	141	28	16	none
78N1643	26 „ „	„	8.5	67°-05′ S	65°-15′ E	„	213	50	18	42, 25, 21	215	47	17	40, 22, 22
78N1669	27 „ „	♂	8.7	67°-09′ S	71°-48′ E	IV	172	22	18	none	181	23	18	none
78N1710	28 „ „	„	8.5	69°-58′ S	72°-11′ E	„	69	21	16	„	69	21	17	„
78N1746	29 „ „	„	8.3	67°-46′ S	73°-09′ E	„	253	28	22	28, 24, 24	252	23	19	„
78N1801	2 Feb. '79	„	8.5	67°-46′ S	74°-34′ E	„	153	29	19	26, 22, 21	145	30	22	25, 24, 20
78N1865	3 „ „	„	8.4	67°-38′ S	72°-46′ E	„	170	41	24	18, 15, 11	179	39	24	26, 19, 16
78N1885	4 „ „	„	8.2	67°-47′ S	73°-26′ E	„	177	35	25	21, 17, 13	187	32	25	none
78N1928	5 „ „	„	8.3	67°-52′ S	73°-53′ E	„	173	32	19	none	175	31	19	„
78N1966	6 „ „	„	7.8	67°-56′ S	74°-00′ E	„	202	24	19	11, 8, 7	203	28	18	„
78N1985	8 „ „	„	8.3	67°-11′ S	73°-18′ E	„	185	37	23	none	182	48	21	„
78N2016	9 „ „	„	8.6	67°-19′ S	74°-01′ E	„	89	27	24	21, 21, 11	144	24	23	24, 19, 17
78N2070	10 „ „	„	8.6	66°-14′ S	78°-25′ E	„	158	40	22	none	153	48	18	none
78N2138	12 „ „	„	8.2	65°-42′ S	89°-55′ E	„	211	40	26	34, 24, 20	203	39	23	29, 21, 17
78N2176	13 „ „	„	7.9	64°-51′ S	92°-44′ E	„	205	36	16	23, 19, 12	243	36	17	23, 17, 14
78N2201	14 „ „	„	8.2	63°-50′ S	94°-52′ E	„	191	48	24	none	199	48	26	none
78N2210	15 „ „	„	7.5	64°-02′ S	98°-53′ E	„	147	31	11	„	151	31	12	„
78N2213	16 „ „	„	8.0	64°-40′ S	104°-08′ E	„	169	20	10	„	161	21	13	„

Continned . . .

APPENDIX TABLE. Continued.

Whale No.	Date, catch			Sex	Body length m	Position, catch		Area	Measurements in mm							
									One side				Another side			
						Lat.	Long.		Length	Width	Thick-ness	Femur*	Length	Width	Thick-ness	Femur*
78N2215	16	Jan.	'79	♂	8.0	64°-40′ S	104°-08′ E	IV	194	46	23	none	196	47	18	none
78N2252	17	,,	,,	,,	8.2	65°-04′ S	106°-15′ E	,,	95	49	9	,,	98	43	9	,,
78N2258	,,	,,	,,	,,	7.8	,,	,,	,,	194	40	17	,,	203	41	17	,,
78N2300	18	,,	,,	,,	8.0	65°-17′ S	109°-33′ E	,,	177	28	20	,,	183	24	19	,,
78N2328	19	,,	,,	,,	8.3	64°-51′ S	111°-18′ E	,,	175	34	21	,,	123	32	22	,,
78N2379	20	,,	,,	,,	8.0	64°-34′ S	114°-12′ E	,,	187	34	19	,,	180	37	18	,,
78N2406	21	,,	,,	,,	8.0	64°-29′ S	117°-09′ E	,,	167	22	15	,,	129	21	14	,,
78N2422	22	,,	,,	,,	8.4	64°-39′ S	117°-45′ E	,,	217	36	23	26, 17, 14	210	31	20	26, 17, 15
78N2450	23	,,	,,	,,	6.6	65°-18′ S	123°-45′ E	,,	130	44	12	36, 23, 12	129	43	11	35, 27, 12
78N2488	24	,,	,,	,,	7.7	65°-14′ S	125°-15′ E	,,	138	21	14	none	149	23	13	none
78N2582	26	,,	,,	,,	7.7	65°-04′ S	128°-47′ E	,,	171	53	22	36, 27, 25	167	54	21	40, 28, 26
78N1648	27	Jan.	'79	♀	8.8	67°-09′ S	71°-48′ E	,,	203	48	17	33, 21, 17	202	48	18	40, 24, 19
78N1782	30	,,	,,	,,	8.8	67°-46′ S	74°-01′ E	,,	219	28	12	none	231	33	13	none
78N1799	31	,,	,,	,,	8.3	67°-43′ S	73°-42′ E	,,	252	50	17	25, 15, 12	260	52	16	,,
78N1901	4	Feb.	'79	,,	8.0	67°-47′ S	73°-20′ E	,,	168	31	13	none	164	35	14	,,
78N1915	5	,,	,,	,,	8.0	67°-52′ S	73°-53′ E	,,	112	26	16	,,	118	24	13	,,
78N1961	6	,,	,,	,,	8.4	67°-56′ S	74°-00′ E	,,	155	49	14	,,	157	48	15	,,
78N1983	8	,,	,,	,,	8.3	67°-11′ S	73°-18′ E	,,	203	19	13	,,	189	19	14	,,
78N2017	9	,,	,,	,,	9.7	67°-19′ S	74°-01′ E	,,	227	60	22	29, 21, 15	202	60	21	22, 15, 14
78N2019	,,	,,	,,	,,	9.0	,,	,,	,,	200	39	16	none	199	44	16	none
78N2109	11	,,	,,	,,	8.7	66°-07′ S	85°-51′ E	,,	75	26	17	,,	73	31	15	,,
78N2132	12	,,	,,	,,	8.9	65°-42′ S	89°-55′ E	,,	217	51	18	,,	missed			,,
78N2169	13	,,	,,	,,	8.6	64°-51′ S	92°-44′ E	,,	88	24	21	42, 30, 23	71	26	22	36, 30, 24
78N2200	,,	,,	,,	,,	9.0	,,	,,	,,	118	21	12	none	missed			none
78N2208	15	,,	,,	,,	7.9	64°-02′ S	98°-53′ E	,,	170	44	12	30, 14, 13	168	44	12	,,
78N2222	16	,,	,,	,,	8.8	64°-40′ S	104°-08′ E	,,	196	60	16	42, 28, 25	193	61	16	42, 30, 25
78N2224	,,	,,	,,	,,	10.1	,,	,,	,,	263	34	17	none	263	32	18	none
78N2294	18	,,	,,	,,	7.1	65°-17′ S	109°-33′ E	,,	141	22	12	,,	143	26	11	,,
78N2325	19	,,	,,	,,	9.5	64°-51′ S	111°-18′ E	,,	225	41	13	,,	219	40	12	,,

78N2370	20	"	"	"	7.6	64°-34′ S	114°-12′ E	"	168	51	13	31, 25, 22	161	49	13	29, 24, 20
78N2371	"	"	"	"	7.0	"	"	"	161	29	10	none	166	28	9	none
78N2403	21	"	"	"	8.3	64°-29′ S	117°-09′ E	"	165	41	9	20, 18, 16	170	47	8	27, 22, 19
78N2432	22	"	"	"	6.9	64°-39′ S	117°-45′ E	"	91	44	10	15, 14, 12	broken			18, 15, 14
78N2466	23	"	"	"	8.9	65°-18′ S	123°-45′ E	"	228	56	16	none	223	54	18	none
78N2493	24	"	"	"	5.5	65°-14′ S	125°-15′ E	"	49	28	6	"	missed			"
78N2523	25	"	"	"	7.8	65°-18′ S	127°-52′ E	"	90	26	9	"	93	23	10	"
78N2544	25	"	"	"	6.6	"	"	"	119	34	8	"	120	30	8	"
78N2574	26	"	"	"	9.0	65°-04′ S	128°-47′ E	"	156	25	10	"	161	27	10	"
78N2614	27	"	"	♂	7.8	65°-07′ S	131°-22′ E	V	180	33	23	"	181	33	23	"
78N2684	2	Mar.	'79	"	7.4	64°-55′ S	133°-45′ E	"	161	33	18	24, 15, 14	157	33	23	30, 19, 14
78N2699	"	"	"	"	7.7	"	"	"	174	46	21	none	174	45	22	none
78N2763	3	"	"	"	7.8	64°-56′ S	134°-38′ E	"	168	32	19	24, 21, 17	170	25	15	"
78N2618	27	Feb.	'79	♀	8.7	65°-07′ S	131°-22′ E	"	162	38	11	none	164	40	11	"
78N2649	28	"	"	"	8.3	65°-24′ S	131°-55′ E	"	63	21	8	"	missed			"
78N2725	3	Mar.	'79	"	7.8	64°-56′ S	134°-38′ E	"	160	49	11	"	157	44	11	"

* Three dimensions.

EXPLANATION OF PLATES

Pelvic bones of minke whales from the Antarctic collected in the 1978/79 season.

PLATE I

Fig. 1.	78N1493	Male	Fig. 6.	78N1669	Male
Fig. 2.	78N1562	„	Fig. 7.	78N1710	„
Fig. 3.	78N1574	„	Fig. 8.	78N1746	„
Fig. 4.	78N1603	„	Fig. 9.	78N1801	„
Fig. 5.	78N1637	„	Fig. 10.	78N1865	„

PLATE II

Fig. 1.	78N1885	Male	Fig. 7.	78N2138	Male
Fig. 2.	78N1928	„	Fig. 8.	78N2176	„
Fig. 3.	78N1966	„	Fig. 9.	78N2201	„
Fig. 4.	78N1985	„	Fig. 10.	78N2210	„
Fig. 5.	78N2016	„	Fig. 11.	78N2213	„
Fig. 6.	78N2070	„	Fig. 12.	78N2215	„

PLATE III

Fig. 1.	78N2252	Male	Fig. 7.	78N2422	Male
Fig. 2.	78N2258	„	Fig. 8.	78N2450	„
Fig. 3.	78N2300	„	Fig. 9.	78N2488	„
Fig. 4.	78N2328	„	Fig. 10.	78N2582	„
Fig. 5.	78N2379	„	Fig. 11.	78N2614	„
Fig. 6.	78N2406	„			

PLATE IV

Fig. 1.	78N1414	Female	Fig. 6.	78N1643	Female
Fig. 2.	78N1450	„	Fig. 7.	78N1648	„
Fig. 3.	78N1529	„	Fig. 8.	78N1782	„
Fig. 4.	78N1551	„	Fig. 9.	78N1799	„
Fig. 5.	78N1576	„	Fig. 10.	78N1901	„

PLATE V

Fig. 1.	78N1915	Female	Fig. 7.	78N2132	Female
Fig. 2.	78N1961	„	Fig. 8.	78N2169	„
Fig. 3.	78N1983	„	Fig. 9.	78N2200	„
Fig. 4.	78N2017	„	Fig. 10.	78N2208	„
Fig. 5.	78N2019	„	Fig. 11.	78N2222	„
Fig. 6.	78N2109	„			

PLATE VI

Fig. 1.	78N2224	Female	Fig. 7.	78N2432	Female
Fig. 2.	78N2294	„	Fig. 8.	78N2466	„
Fig. 3.	78N2325	„	Fig. 9.	78N2493	„
Fig. 4.	78N2370	„	Fig. 10.	78N2523	„
Fig. 5.	78N2371	„	Fig. 11.	78N2544	„
Fig. 6.	78N2403	„			

PLATE VII

Fig. 1.	78N2684	Male
Fig. 2.	78N2699	,,
Fig. 3.	78N2763	,,
Fig. 4.	78N2574	,,
Fig. 5.	78N2618	Female
Fig. 6.	78N2649	,,
Fig. 7.	78N2725	,,


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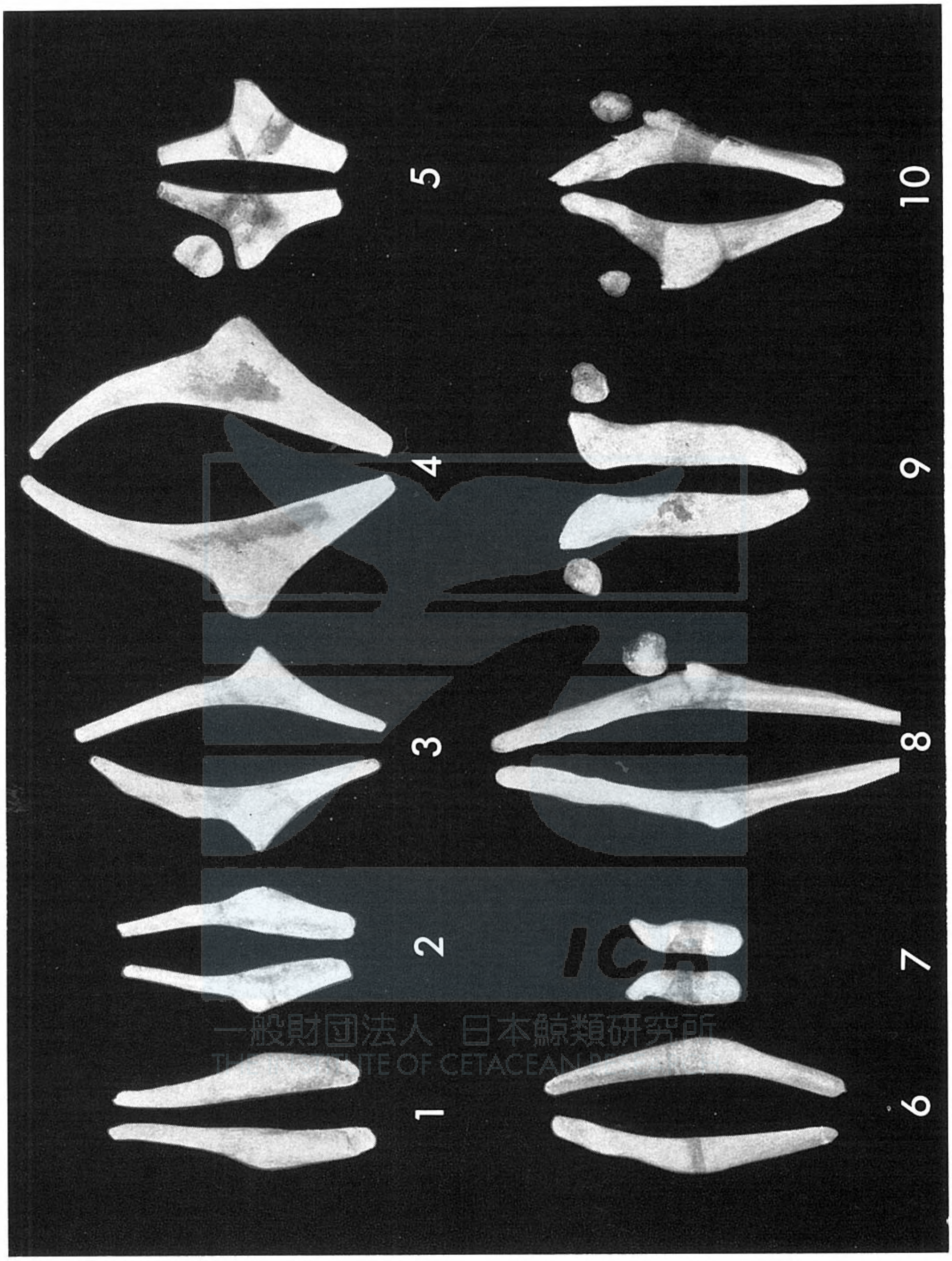
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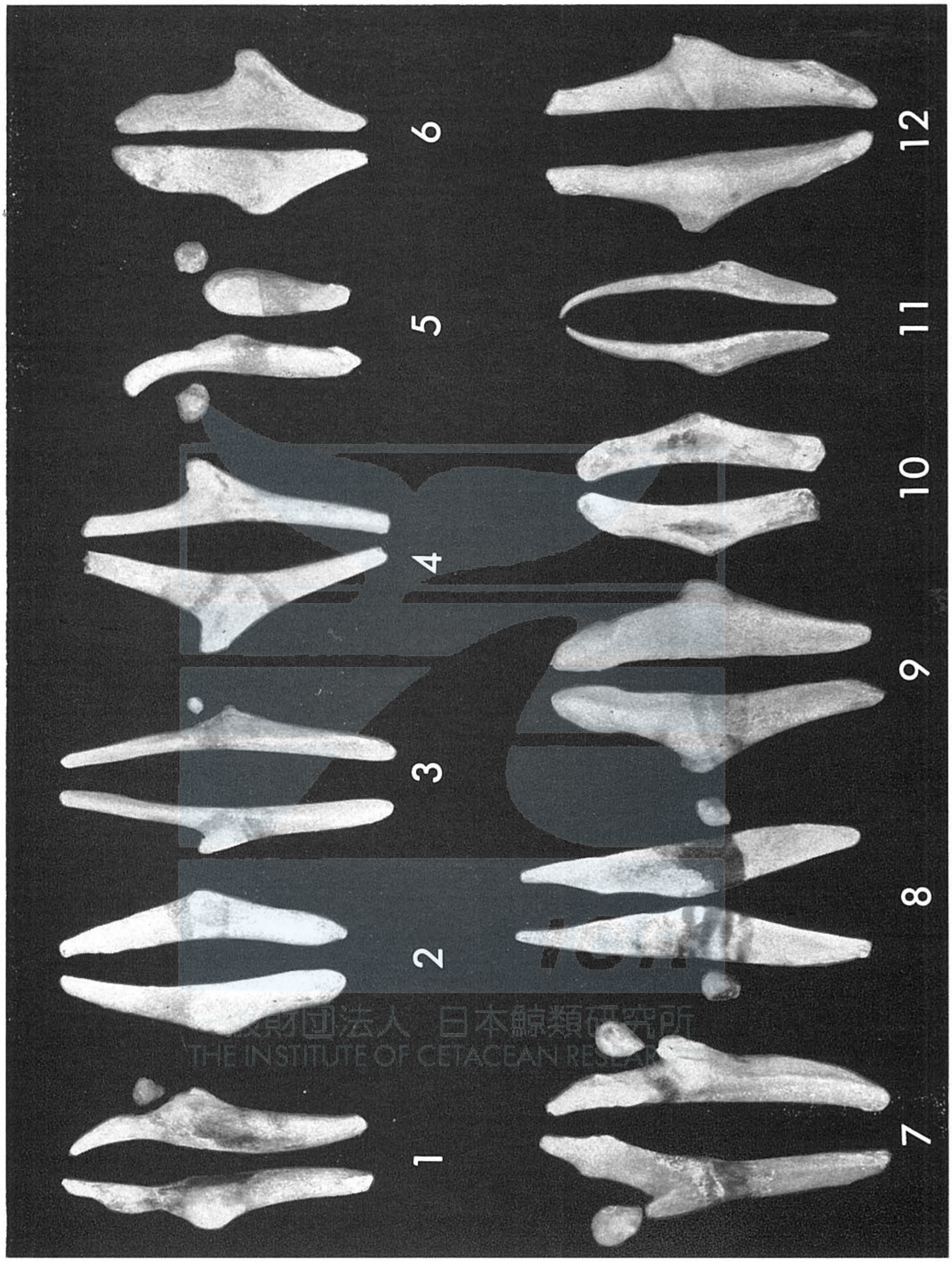
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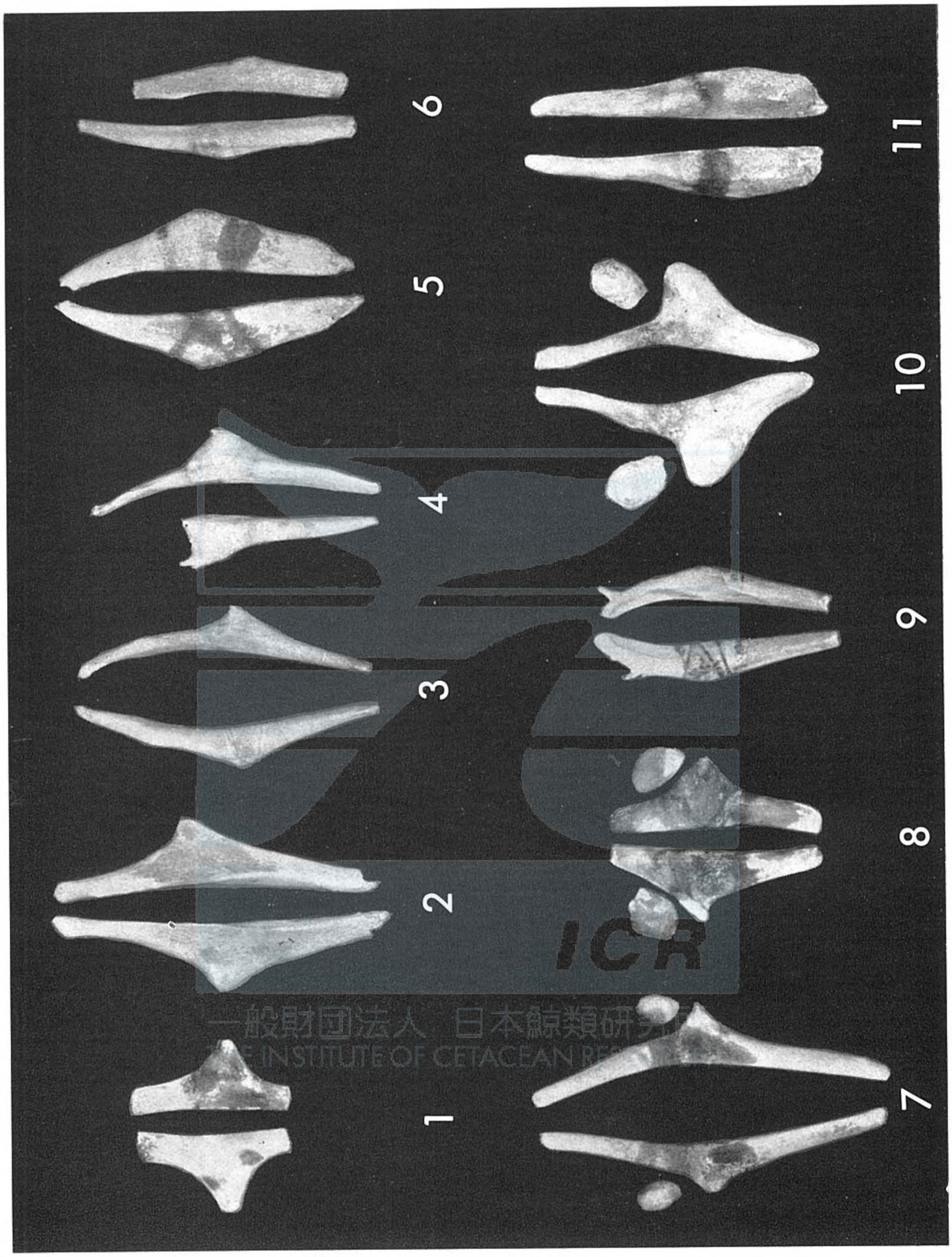
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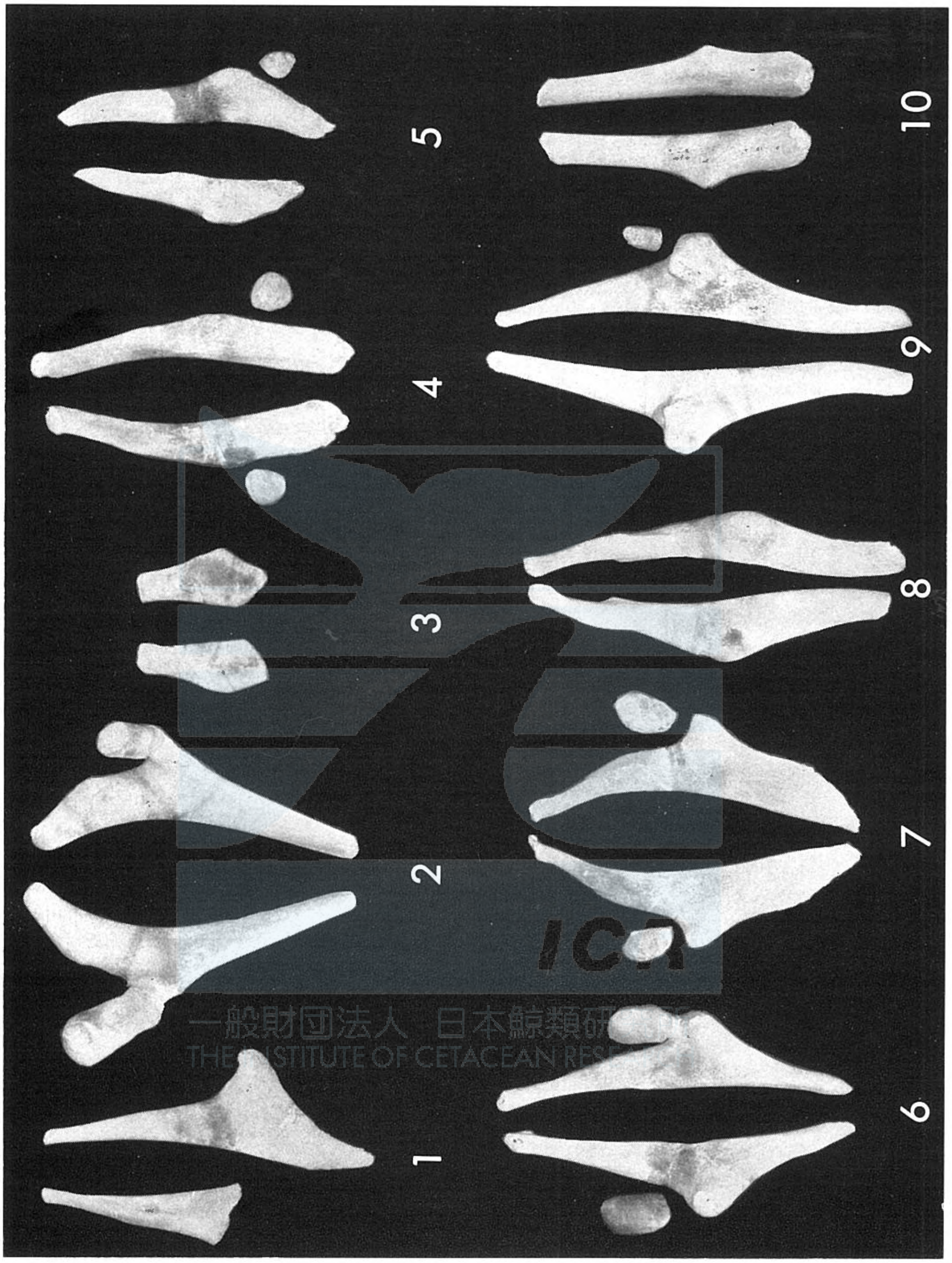
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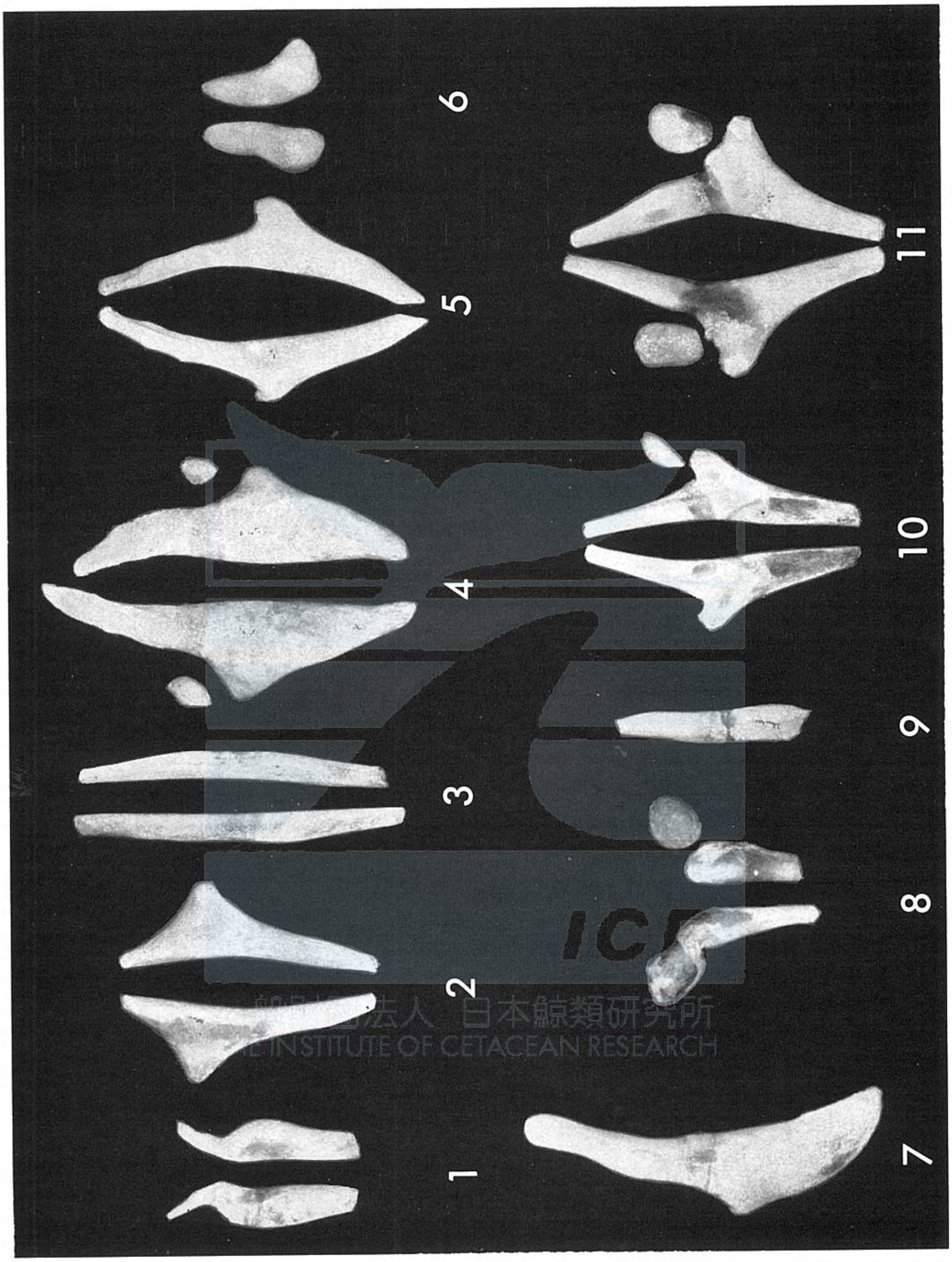
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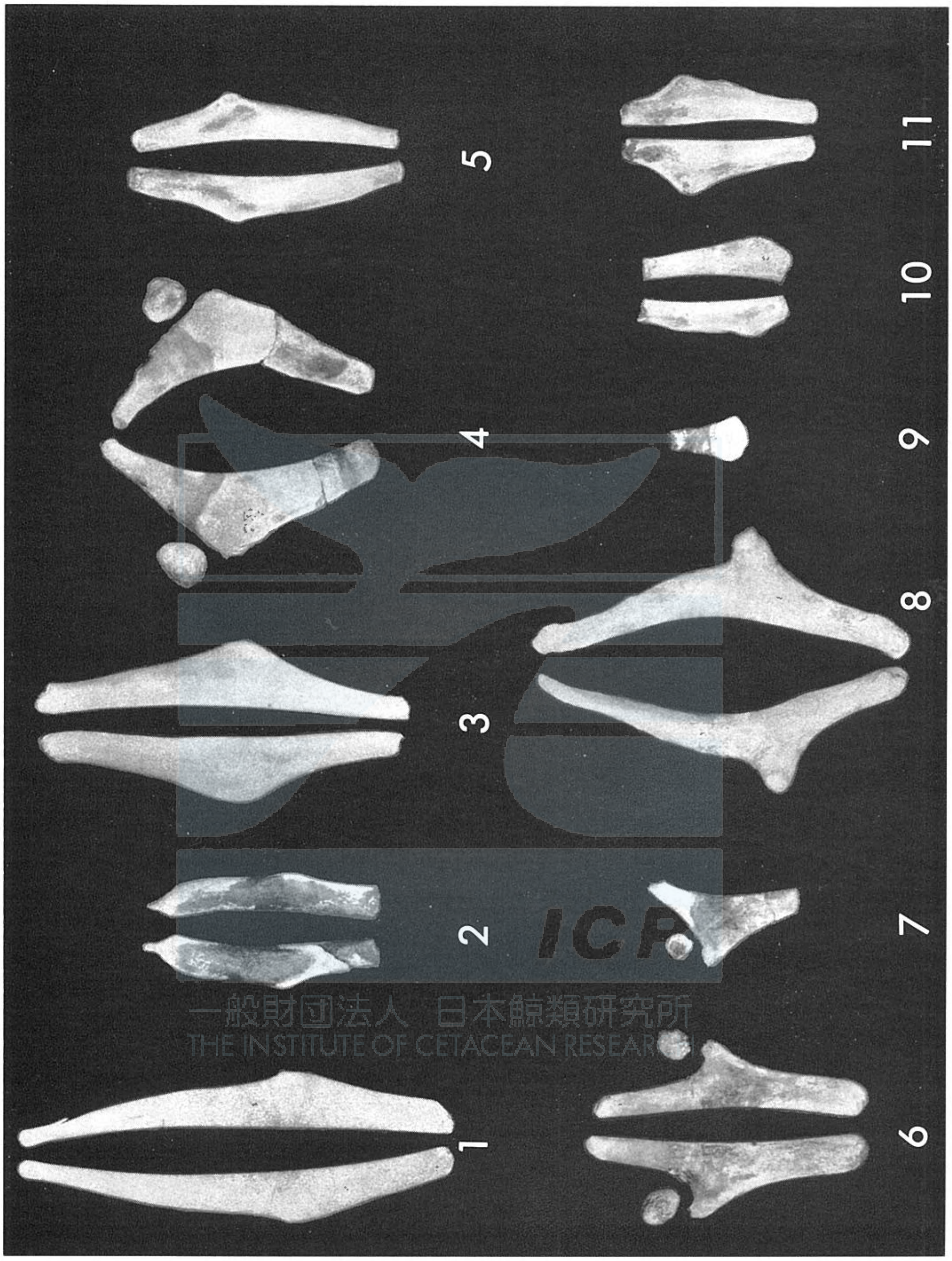
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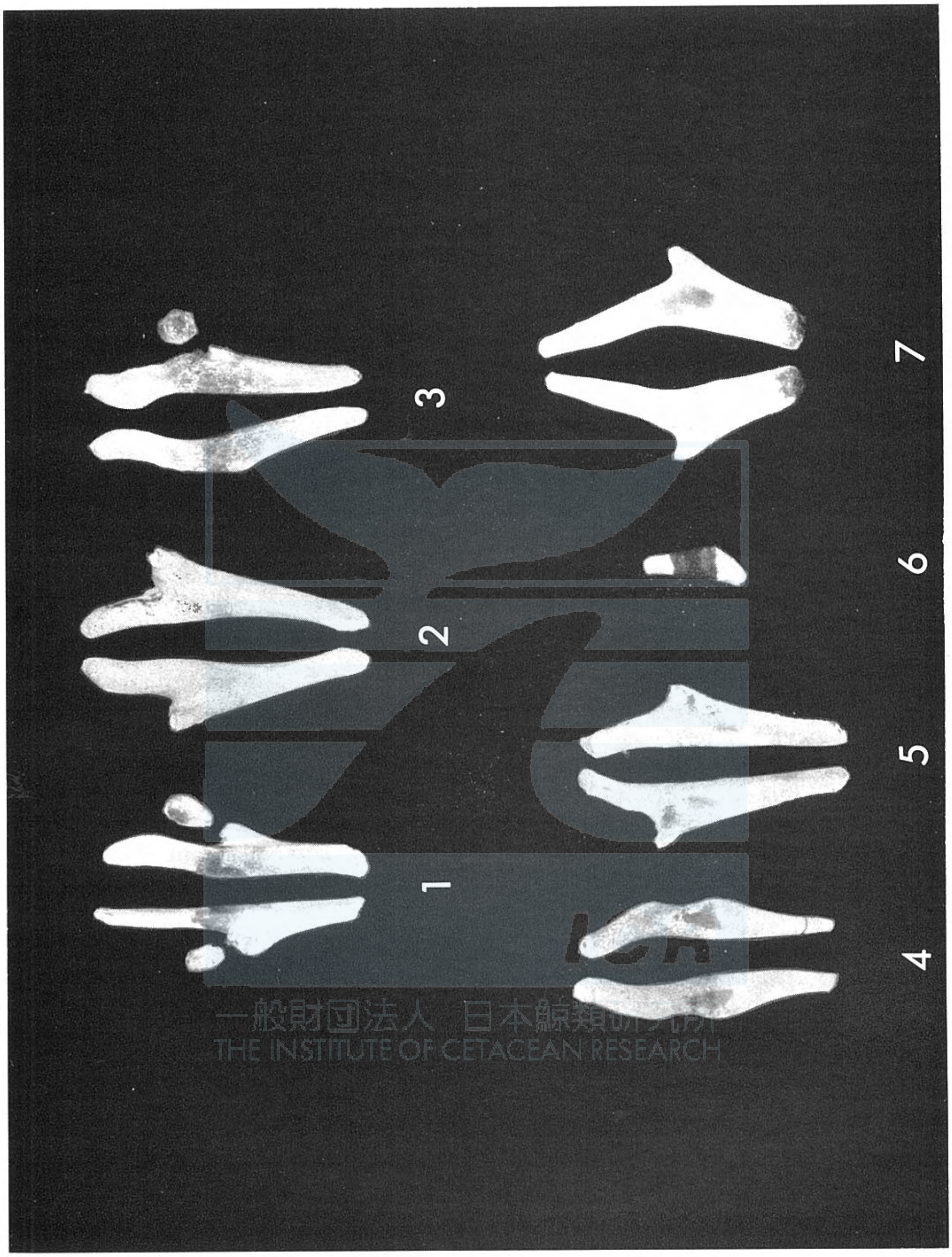
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AGE DETERMINATION AND AGE RELATED FACTORS IN THE TEETH OF WESTERN NORTH ATLANTIC BOTTLENOSE DOLPHINS

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ABSTRACT

Teeth were taken from 120 bottlenose dolphins, *Tursiops truncatus*, which had stranded on the mid-Atlantic coast of the United States. The number of annual growth layer groups (GLGs) for each animal was used to construct a growth curve. The growth rate of coastal North Atlantic Ocean *Tursiops* is similar to other cetaceans in having a high initial rate of growth, with no differences in growth between females and males. In females, the first dentinal GLG is thickest and is followed by GLGs which become progressively narrower. In males, the second GLG is thicker than the first; GLGs beyond number two become progressively smaller but at a slower rate than in females. In males and females, the translucent layer makes up proportionally larger parts of the GLG as the animal ages, but in males the percent translucent layer remains constant at about 50% while in females it continues to increase up to about 70% of the GLG. These two factors, GLGs width and translucent layer width, indicate that the sex and age of the animal influence the deposition of GLGs. Incremental layers are also present, averaging 12 per GLG, and seem similar to incremental layers described in other marine mammals. A plot of the relationship of percent growth of the last GLG to time of death suggests that the deposition of GLGs is relatively constant, at least during the first half of the year, and that North Atlantic Ocean *Tursiops* give birth in the fall as well as in the spring.

INTRODUCTION

Owen (1945) documented the existence of "concentric layers of dentine" in odontocete teeth and, similarly, the "appearance of opaque striae or conecntric layers" (pg. 512) in polished sections of pinniped teeth. Lankester (1867) also noted a layering pattern in the teeth of a beaked whale, *Ziphius sowerbiensis* (=*Mesoplodon bidens*), but did not suggest a reason or use for them. In 1950, Scheffer suggested using these layers as a method of age determination when he found layers in the dentine and cement of a fur seal, *Callorhinus ursinus*, canines that corresponded to the known age of seals branded as pups and recovered up to eight years later. Laws (1952, 1953) suggested using dentinal layers in odontocete teeth as a measure of age when he found layers in sperm whale teeth similar to those in pinniped teeth. In the following years, dentinal growth layers (growth layer groups) were discovered and used as age indicators in *Stenella coeruleoalba* (Nishiwaki and Yagi, 1953, 1954), *Berardius bairdii* (Omura *et al.*, 1955), and sperm whales (Nishiwaki *et al*, 1958).

In 1959, Sergeant described growth layer groups (GLGs) in the teeth of four bottlenose dolphins, *Tursiops truncatus*, from Marine Studios in Florida. Two of the animals were born and died in captivity; two were wild caught and died in captivity. In each case the number of GLGs in the teeth corresponded with the known or estimated age of the animals based on their time spent in captivity. The oldest animal was estimated to be 15.5 years old and had 17 GLGs. He also examined a few teeth from the pilot whale, *Globicephala melaena*, and one each from the Atlantic whitesided dolphin, *Lagenorhynchus acutus*, and the common dolphin, *Delphinus delphis*. All of the species demonstrated layering in the dentine similar to that of *Tursiops*, which was identical to that described by Nishiwaki and Yagi (1953) for *S. coeruleoalba*.

Since Sergeant's paper, dentinal GLGs have been used extensively for age determination of odontocetes. Most of the work has centered on direct application of the technique, predominantly for species involved in fisheries, for example, sperm whale (Gambell and Grzeborzewska, 1967; Best, 1970; Gambell, 1977), delphinids (Sergeant, 1962, 1973; Kasuya, 1972, 1974, 1976; Sergeant *et al.*, 1973; Kasuya *et al.*, 1974; Perrin *et al.*, 1976, 1977; Ross, 1977), the white whale (Sergeant, 1962), Baird's beaked whale (Kasuya, 1977), harbor porpoise (Nielsen, 1973; Gaskin and Blair, 1977) and Dall's porpoise (Kasuya, 1978). However, some aspects of age determination and age related factors visible in the teeth of odontocetes have been examined but not satisfactorily explained in many species. Some of these include description and clear identification of GLGs, formation rate of the layers, identification of accessory layers and the more recently discovered incremental layers, and sexual dimorphism.

Since GLGs were first suggested as a means of aging odontocetes much controversy has prevailed over the meaning of these layers, but for the most part the assumption has been that GLGs are deposited annually. However, in a few species evidence based on relative age indices indicates that GLGs are not annual. In the white whale, *Delphinapterus leucas*, Sergeant (1962) and Brodie (1969) have shown circumstantially that more than one GLG is deposited at least during the early growth of the animal, although Khuzin (1961) felt that only one GLG is formed each year. In the narwhal, *Monodon monoceros*, a species related to the white whale, Hay (in press) also feels that more than one GLG is formed. Kleinenberg and Klevezal (1962) found twice as many dentinal GLGs as maxillary bone layers in the Black Sea dolphin, *Delphinus delphis*. In sperm whales, Ohsumi *et al.* (1963) determined that one GLG is formed each year based on 11 whales captured seven to 16 years after being tagged, a rate which Best (1970) confirmed when he followed the growth of the tooth from samples which extended over six months of the year. Berzin (1961, 1964) and Gambell and Grzegorzwerska (1967), however, concluded from samples taken throughout the year that two GLGs are deposited annually. Perrin *et al.* (1977) suggest three possible hypotheses of rate of deposition of GLGs in the spinner dolphin, *Stenella longirostris*, after examining 2500 specimens, none of which is that just one layer is set down per year. They accepted the hypothesis that 1.5 GLGs are deposited in the first year, while one GLG is deposited in all other years, rather than a rate of 1.5 GLGs per year or 1.5 GLGs per year until puberty and one GLG per year thereafter.

Direct evidence on the rate of dentinal growth has supported an annual formation rate. Sergeant's (1959) finding that the number of GLGs in *Tursiops* teeth correlated with the known age or minimum known age for each animal offered the first measure. Similarly, in 1973, Sergeant *et al.* reported that in three captive *Tursiops* from Marineland of Florida the number of GLGs was approximately equal to the known age of the animal. Klevezal and Kleinenberg (1967) examined captive and wild specimens from nine orders of mammals, including cetaceans, and concluded that GLGs are an annual event. Tetracycline injected specimens have also supported an annual deposition rate of GLGs (Best, 1970; Gurevich and Stewart, in press; Perrin and Myrick, in press).

Divergencies of opinion on the periodicity of GLG formation within a species probably can be attributed to the presence of accessory layers, thin layers similar to the hypomineralized layer of the GLG. Klevezal and Kleinenberg (1967) proposed that all odontocetes form one GLG per year but in some species accessory layers are especially distinct, being almost indistinguishable from an annular layer, so that it appears as though two GLGs are deposited annually in some species. More commonly, however, accessory layers are not quite so distinct and may influence the count of GLGs to the extent that repeated counts on the same tooth by one person or several people tend to give different results (Kasuya *et al.*, 1974; Perrin, 1975; Kasuya, 1977; Kimura, in press; Perrin and Myrick, in press). The clear distinction between an accessory layer and a GLG boundary layer is still not defined in some species, for example, the killer whale (*Orcinus orca*), nor is the cause of accessory layers known.

Before the discovery of "annual" growth layers in dentine, research in dental histology had shown the existence of smaller incremental growth patterns. In 1934, Schour and Smith showed that in the continuously growing rat incisor 16 micrometers of dentine are laid down in 24 hours. In 1935, Schour and Steadman described an incremental stratification, also in the rat incisors, which appear as a succession of dark (well calcified) and light (less calcified) layers, the width of each pair totaling 16 μm. Further examination (Schour and Hoffman, 1939) showed the same 16 μm incremental mineralization pattern in 17 other species including fish, a shark, crocodile, mastodon, and several species of mammals, including man. These lines were later interpreted as incremental lines of von Ebner. Yilmaz, Newman and Poole (1977) described daily von Ebner lines in pig dentine where each band consisted of parallel light and dark portions in thin sections of teeth. These were probably equivalent to 5 μm daily von Ebner lines described by Krauss and Jordan (1965) and Newman and Poole (1974). Von Ebner lines have recently been described from the teeth of *Stenella*, where about 365 lines were counted within GLGs (Myrick, in press). Although their deposition rate has not been measured directly, the frequency of these von Ebner lines in the dolphin teeth suggests that they represent a daily growth pattern.

In 1970, Scheffer found still a different frequency incremental layer in thin sections of a *Dugong* tusk. He described a pattern consisting of "coarse layers" and "fine layers". Kasuya and Nishiwaki (1978) found the same pattern in captive dugongs where they defined coarse layers as annual growth layers or GLGs. There were 10 to 15 fine layers within each coarse layer, so the fine layers were suspected to be deposited on a monthly or lunar cycle. Kasuya (1977) found the "long cycles" (GLGs) in Baird's beaked whale teeth to contain many (11.0 to 13.4) "short cycles". Myrick (in press) noted incremental layers of the same periodicity in thin sections from teeth of several species of dolphins. In addition, scanning electron micrographs of a small sample of etched *Tursiops* teeth also showed subannual incremental layers, larger than von Ebner lines, which probably represent the same growth pattern seen by Myrick and Kasuya, appearing as a finer mineralization pattern within the mineralization pattern of the GLG (Hohn, in press). Although the deposition rate of these incremental layers has not been measured directly, this circumstantial evidence suggests a "monthly" growth or mineralization cycle which may be useful for more precise age determination, possibly back-dating the month of birth in young animals, or a better understanding of the mineralization patterns in dentine.

Sexual dimorphisms have also been described in the teeth of some odontocetes. The identification of sexual dimorphism in the growth of teeth has two advantages. First, skeletal material currently in museum collections that is missing data on sex may be more useful for systematic or other research if the sex can be determined from the material on hand, such as the teeth. Secondly, differences in the growth of teeth or other mineralized tissue probably reflects differences in habits or intrinsic factors between the sexes. These differences may help explain the cause of formation of growth layers.

Van Utrecht (1969) found a sexual dimorphism in the extent that the neonatal line overlaps the cementum in teeth of the harbor porpoise, *Phocoena phocoena*, and a small sample of the white-beaked dolphin, *Lagenorhynchus albirostris*. Although Nielsen (1972) confirmed this finding in the harbor porpoise, it has not been described in other odontocetes. Another sexual dimorphism in the teeth of *Phocoena* is found in the ratio of the width of the opaque layer to the width of the translucent layer (Gaskin and Blair, 1977). In males, this ratio remains constant while in females it decreases steadily with age. Gaskin and Blair (1977) also found differences in the amount of dentine deposited annually, which they attributed to size differences of the sexes at any given age. Similar or additional sexual dimorphisms in the teeth have not been described in other odontocetes.

The purpose of this study is to describe dentinal GLGs and accessory layers, including their appearance and position, in western North Atlantic Ocean bottlenose dolphins; to examine age-related changes in GLG deposition and any sexual dimorphisms in dentinal characteristics; and to construct a growth curve for coastal North Atlantic Ocean bottlenose dolphins.

MATERIALS AND METHODS

The Sample

Teeth were collected by the Smithsonian Institution's Marine Mammal Salvage Program (MMSP) from *Tursiops* stranded along the Atlantic coast of the United States between South Carolina and New Jersey. 118 of these animals have complete data, including sex and total length. Two specimens were missing at least one piece of data and were included for GLG counts but not in other analyses.

Preparation of Sections

At least one tooth was taken from each specimen. A medial longitudinal cut was made on each of the teeth on a Buehler Isomet 11–1180 low speed saw using a rotating diamond blade with a saw speed of 5 to 6 on a relative scale of 1 to 10 (up to 300 rpm), following the method of Hohn (in press). One of the half-sections from each tooth was prepared for scanning electron microscopy. These were soaked in 5% formic acid for 3 hours, rinsed in water for at least one-half hour to remove the acid, cleaned in an ultrasonic cleaner with acetone for 15 to 60 seconds to remove extraneous surface particles, dipped in 70% ethanol to dehydrate and air dried. These etched sections were examined by scanning electron microscopy (SEM) (Hohn, in press). During an SEM session, a standard set of micrographs was taken which included serial micrographs of the entire tooth at low magnification (15 to 20×), requiring up to five micrographs, and higher magnifications (greater than 25×) for difficult to count, narrow GLGs, GLGs bordering the pulp cavity, and possible incremental layers. Specimens were prepared for SEM not more than two or three days before each session to help reduce their absorbing moisture.

For each tooth, a 150 μm thin section was also prepared. In most cases, the cut surface of the remaining half section was glued to a microscope slide and all but 150 μm cut off leaving the thin section adhering to the slide. The thin sections were removed by dissolving the adhesive in acetone, then mounted for examination on a clean slide.

Data Collection and Analysis

GLG counts were made for all of the specimens from the SEM micrographs and from the thin sections using a dissecting microscope with transmitted light (at 25×). The number of GLGs was plotted against total length for each animal. The total length of animals in each of the first 3 age classes (GLGs) was compared for males and females to examine differences in growth rates. The sample sizes were too small for statistical analyses for animals with more than four GLGs.

Measurements for GLG and translucent layer widths were taken for 19 females and 19 males from the thin sections using a dissecting microscope (at 50×) equipped with an ocular micrometer and a polarizing filter. Measurements of the first few GLGs were made near the base of the neonatal line on the concave side of the tooth. In sections in which it was difficult to measure at this point because of unclear boundaries, the GLG width was determined closer to the crown or tip of the tooth. The width of the first GLG is approximately the same from the base of the neonatal line to below the crown so a slight change in position did not affect the measurements. Later layers were measured where they were most clearly defined but in the upper half of the length of the GLG before it becomes compressed in the root, and below the apical end where the layers are especially wide. Sections that did not allow determination of boundaries of adjacent GLGs were not included.

Preliminary examination suggested the growth of the tooth by width of GLGs to be different in males and females. To test this, the width of each GLG was determined for each sex and compared using a Mann-Whitney Rank Sum test. In addition, the ratio of width of the translucent layer to entire GLG was plotted against GLG number, again considering males and females separately.

The optical density and extent of growth of the last GLG were determined and plotted against time of death for 16 males and 12 females whose teeth had fewer than four GLGs. Older animals were excluded because the GLGs become too narrow, and sometimes the boundaries too irregular, to get accurate measurements of a partial layer.

Incremental layers and accessory layers were treated separately. The number of incremental layers per GLG was determined where all of the increments of a GLG could be distinguished. The widths of individual increments were measured by position within different GLGs, i. e., on a ridge or in a groove for GLG 1, 2, or 3, or beyond GLG 3, using the SEM micrographs. The distribution and appearance of irregular accessory layers was noted. For accessory layers that appeared more regularly, their position within the GLG was measured.

Five variables were tested specifically for possible sexual dimorphism related to the neonatal line. First, the extent of the neonatal line beyond the bottom of the enamel was measured in thin sections on the concave and convex side of 42 teeth from mixed males and females. This is similar to the study by van Utrecht (1969). In addition, the width of the prenatal zone at the base of the enamel was determined, also from thin sections on both sides of the tooth. Finally, the width of the translucent neonatal line was compared in females and males. Means for each measurement were compared for males and females using a Student's t-test.

RESULTS

Age and Growth

A scatterplot of 64 females, 54 males and two specimens of unknown sex shows the general growth curve for *Tursiops* from the western North Atlantic Ocean (Fig. 1). For each of the first few age classes, including neonates, and for a cumulative average for animals with more than four GLGs, the mean total length is not significantly different for males and females using a Mann-Whitney test (Table 1). The minimum and maximum total lengths within each age class indicates the large overlap in total length of individuals in different age classes. The decrease in growth,

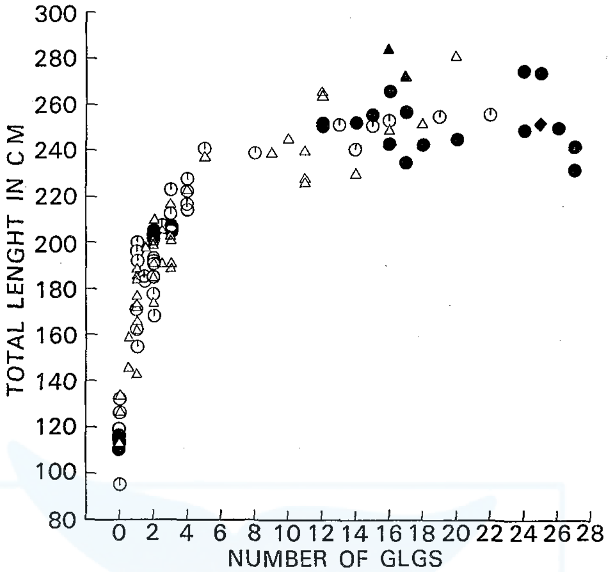

Fig. 1. Scatterplot of the number of growth layer groups (GLGs) to the nearest half-GLG and total length for 120 western North Atlantic Ocean *Tursiops*. Circles are females, triangles are males, diamonds are animals whose sex is unknown. Solid symbols represent a closed pulp cavity.

TABLE 1. SOME DESCRIPTIVE STATISTICS FOR TOTAL LENGTHS OF *TURSIOPS* BY NUMBER OF GLGS AND SEX

No. of GLGs	Sex	N	Total Length (cm)		
			Mean	Min.	Max.
0	F	9	116	95	132
(Neonates)	M	9	118	110	134
0.5	F	0			
	M	2	153	146	159
1	F	6	180	155	200
	M	9	172	143	189
1.5	F	2	184	183	185
	M	1	198		
2	F	11	183	168	205
	M	8	196	174	210
2.5	F	2	207	206	207
	M	1	191		
3	F	6	210	205	223
	M	8	203	189	217
4	F	4	220	214	227
	M	2	220	216	223
More than 4 GLGs	F	24	249	232	275
	M	14	250	226	284
	F & M	38	250	226	284

large ranges in total length, and small sample size for animals with more than four GLGs allows for the determination of average "adult" total length of approximately 250 cm.

Description of GLGs

For the most part, GLGs in thin sections of teeth of these *Tursiops* appear as described in other odontocetes, particularly delphinids and *Tursiops* (Sergeant, 1959), as alternating translucent and opaque layers (see Perrin and Myrick, in press). The prenatal zone is a relatively uniform area easily distinguished by its lack of substructure, e. g., incremental and accessory layers, seen in post-natal dentine.

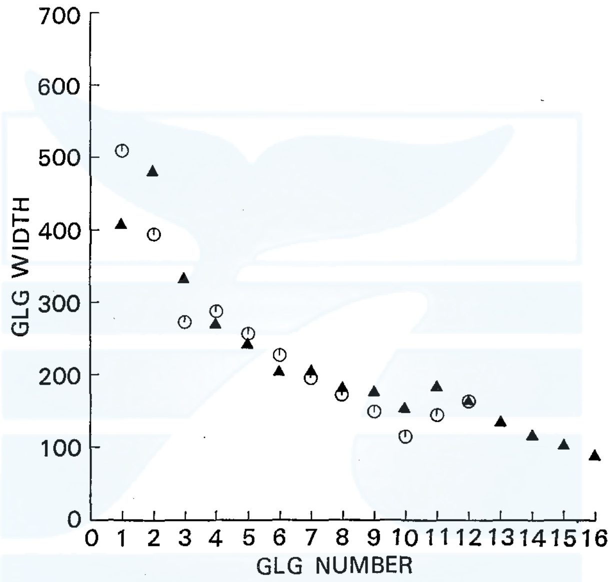

Fig. 2. Average width of GLGs for females (circles) and males (triangles), in micrometers. Measurements based on thin sections of teeth from *Tursiops*.

The neonatal line is a narrow translucent layer usually followed by a narrow, intense opaque layer. The first GLG begins after the neonatal line with a wide, variably opaque layer riddled with accessory layers, and ends with a narrow translucent layer often less apparent than some of the accessory layers. The second GLG is similar to the first in having the wide, variably opaque layer followed by a narrow, relatively, but indistinctly, translucent layer. The third and sometimes fourth GLGs have more distinct opaque and translucent layers and, although accessory layers can still be seen, they are not as overwhelming as in the first two GLGs. Subsequent GLGs have better demarcated opaque and translucent layers, less variability in mineral densities within a layer, and fewer accessory layers.

The same basic description is applicable to etched half-sections where opaque layers are equivalent to grooves and translucent layers are equivalent to ridges.

However, the numerous accessory layers in the first few GLGs are usually not as prominent in the etched sections. The exception is when the mineral density differences, normally accentuated by etching, are small across a GLG (usually in the first two GLGs), then incremental layers and accessory layers in the opaque zone of the GLG are almost indistinguishable from the translucent (boundary) layer of the GLG. This also occurs in thin sections. Furthermore, in etched sections, there are not clear boundaries between GLGs, i.e., there is not an abrupt end to the translucent layer or ridge. Rather, the topography of the surface might be likened to rolling hills with a rounded crest and slopes, and valleys inbetween. This does not allow for clear points or ends of layers from which to make measurements.

In general, the widths of GLGs decrease as the animals get older (Fig. 2). The first few GLGs are the largest and the last few are the smallest (Table 2). More specifically, in females, the first GLG is the widest averaging 509 μm, the

TABLE 2. SUMMARY OF DESCRIPTIVE STATISTICS FOR TOTAL GLG WIDTHS MEASURED FROM THIN SECTIONS OF TEETH FROM *TURSIOPS*. SIGNIFICANT DIFFERENCES DETERMINED USING A MANN-WHITNEY RANK SUM TEST. MEASUREMENTS IN MICROMETERS

GLG No.	Sex	N	Mean Width	Min.	Max.	Significant Differences
1	F	19	509	418	570	$p < .005$
	M	19	407	342	475	
2	F	12	393	285	475	$p < .05$
	M	11	480	380	608	
3	F	6	272	190	342	$p < .05$
	M	10	331	190	418	
4	F	6	285	228	380	
	M	7	269	209	342	
5	F	6	253	171	342	
	M	6	241	152	380	
6	F	6	225	152	285	
	M	6	203	152	266	
7	F	5	194	152	266	
	M	6	203	152	247	
8	F	5	171	95	247	
	M	6	181	133	228	
9	F	5	148	95	228	
	M	6	174	114	228	
10	F	4	114	76	190	
	M	5	152	114	209	
11	F	2	143	114	171	
	M	4	181	133	209	
12	F	2	162	133	190	
	M	4	162	152	190	
13	M	3	133	95	171	
14	M	2	114	95	133	
15	M	4	100	76	135	

TABLE 3. SUMMARY OF DESCRIPTIVE STATISTICS FOR TRANSLUCENT LAYER WIDTH DIVIDED BY GLG WIDTH (=PERCENT TRANSLUCENT LAYER) FOR EACH GLG MEASURED FROM THIN SECTIONS OF TEETH FROM *TURSIOPS*. SIGNIFICANT DIFFERENCES DETERMINED USING A MANN-WHITNEY RANK SUM TEST. RESULTS EXPRESSED AS PERCENTS

GLG No.	Sex	N	Mean Width-%	Min.	Max.	Significant Differences
1	F	19	9	1	17	
	M	19	10	4	14	
2	F	10	15	4	33	
	M	11	14	4	32	
3	F	6	39	18	67	$p<.10$
	M	9	23	5	50	
4	F	6	40	17	60	
	M	6	33	13	50	
5	F	6	41	22	56	
	M	6	41	10	75	
6	F	6	48	33	36	
	M	6	41	14	56	
7	F	5	48	38	58	
	M	6	45	36	50	
8	F	5	50	33	60	
	M	6	49	23	57	
9	F	5	57	40	71	
	M	6	48	33	67	
10	F	4	57	50	67	$p<.10$
	M	6	45	27	56	
11	F	2	73	67	78	$p<.05$
	M	4	44	27	57	
12	F	2	71	70	71	$p<.05$
	M	4	52	38	63	
13	M	3	51	50	52	
14	M	2	47	43	51	
15	M	4	50	50	51	

second is smaller at 393 μm, with subsequent GLGs decreasing in width. An exception is a slight increase in size at GLGs 11 and 12 which might be an artifact of small sample sizes (N=2). In males, the trend is similar except that the second GLG, which is 480 μm, is larger than the first, which is 407 μm. The third GLG is smaller than the first and subsequent GLGs follow the same pattern as in the teeth of females. Again, there is a slight increase in size at GLG 11. Measurements of the widths of GLGs 1, 2 and 3 are statistically significantly different between males and females (Table 2).

The width of the translucent layer follows the opposite pattern. GLGs set down in older animals have wider translucent layers or the width of the translucent layer to the entire GLG (percent translucent layer) increases (Table 3). In females there is a leveling off of percent translucent layer at GLGs 6 through 8, then an increase for subsequent GLGs. In males, the percent translucent layer increases initially, then remains fairly constant after GLG 4. This gives GLGs in the teeth of male *Tursiops* a more even appearance in size and spacing, which is especially apparent in SEM micrographs (Plate I, Fig. 1).

The translucent layer widths between females and males are statistically significantly different at GLGs 1, 3, 6, and 12. The percent translucent layer is significantly different between females and males at GLGs 3, 10, 11, and 12 (Table 3). There are no measurements for females beyond GLG 12.

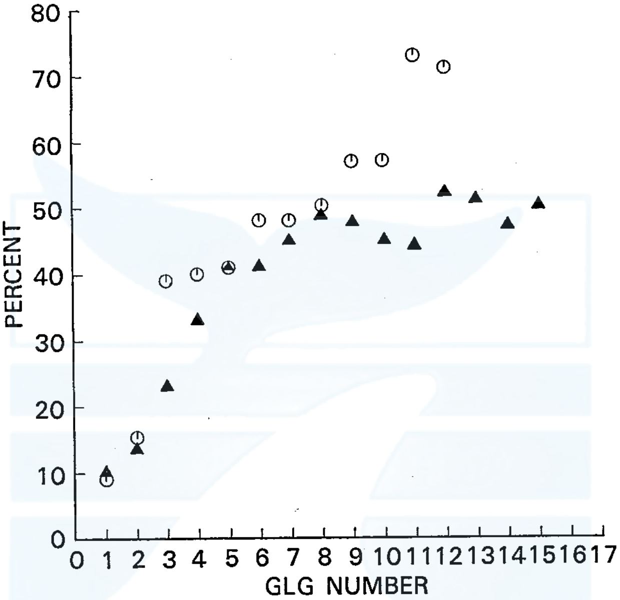

Fig. 3. Average percent translucent layer for each GLG. Circles are females, triangles are males.

Last GLG

A plot of percent growth of the last layer against time of death for 28 female and male *Tursiops* shows most of the points to set roughly on a line representing the expected growth of the current GLG if the deposition of dentine is constant and the new GLG begins in late January or early February (Fig. 4, Table 4). For the cluster of 14 points which occurs during February and March, with four additional points in May, the extent of growth of the GLGs increases proportionally with time along this line. Some of the points which do not fit this line fall on or close to another line representing the expected tooth growth of animals whose new GLG begins in September. However, there are only six specimens representing this group.

In most cases the last layer is opaque (Table 5). The translucent layer borders the pulp cavity in four of the specimens, and one of these is a translucent accessory layer and not a GLG boundary layer. Two of the GLG translucent layers

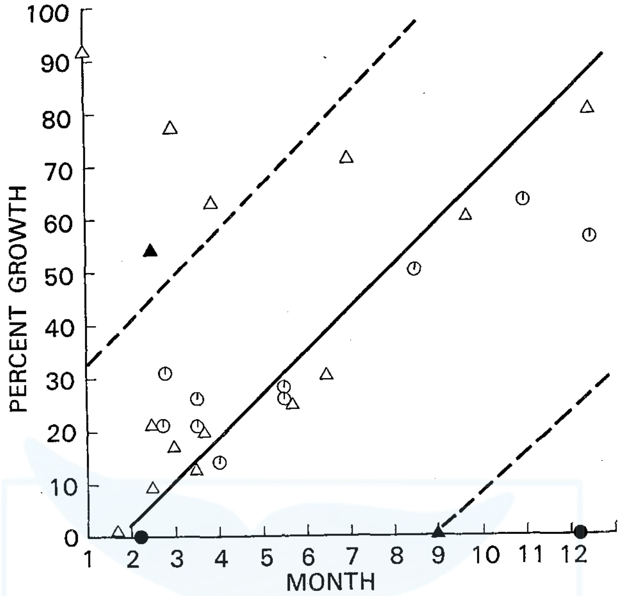

Fig. 4. Scatterplot of the percent growth of the last GLG in teeth of young *Tursiops* on approximate date of death. Percent growth calculated for each animal from actual width of the last layer divided by the average total width of the GLG. Solid line presents expected growth of the GLG throughout the year if the GLG begins in late Jan.-early Feb. and grows at a constant rate. Hatched line represents the same for GLGs which begin in September. Circles are females, triangles are males. Hollow symbols indicate an opaque last layer, solid symbols represent a translucent last layer.

occur in late January to early February and one occurs in September. The accessory layer that falls in mid-March is an animal whose dentinal growth pattern falls on the line for GLGs which begin in the fall.

Non-GLG Layered Structures

In addition to GLGs three layered structures can be differentiated in the teeth of *Tursiops*. Incremental layers are relatively evenly spaced layers which are found throughout the GLGs and are most easily seen in SEM micrographs of etched sections. Accessory layers are layers of opposite mineral density that would be expected within a GLG with an even mineral density. The third structure is similar to an accessory layer because it appears in a layer of opposite mineral density of the dentine adjacent to it.

Incremental layers could be counted and measured from some of the SEM micrographs (Plate I, Fig. 2). The average number of incremental layers per GLG is 11.8 for three GLGs from 39 specimens (Table 5). Of the three GLGs in which incremental layers could fairly consistently be counted, GLG 2 was the easiest for counting. Incremental layers are rarely visible in the compressed GLGs set down

TABLE 4. PERCENT GROWTH OF THE LAST FORMED GLG. GROWTH OF THE LAST GLG AND TIME OF YEAR OF DEATH FOR SOME *TURSIOPS* MALES AND FEMALES. PERCENT LAST LAYER CALCULATED FROM EXPECTED AVERAGE SIZE OF THE FULLY FORMED GLG. OPTICAL DENSITY OF THE DENTINE BORDERING THE PULP CAVITY IS BASED ON THIN SECTIONS USING TRANSMITTED LIGHT

Catalogue No.	No. of Complete GLGs	% Growth Last GLG	Approx. Date of Death	Optical Density
Females				
504565	1	31	late Feb	opaque
504590	1	26	mid-March	opaque
504403	1	26	15 May	opaque
CWP094	1	37	22 May	opaque
SEAN3331	1	50	mid-Aug	opaque
504539	1	56	late Dec	opaque
504550	2	0	early Feb	translucent
504592	2	14	30 March	opaque
504399	2	28	15 May	opaque
504583	2	21	early Mar	opaque
395179	2	63	4 Nov	opaque
504528	2	0	early Dec	translucent
504549	2	21	mid-Feb	opaque
Males				
504578	0	54	late Feb	translucent*
JGM401	0	80	14 Dec	opaque
504536	1	1	21 Jan	opaque
504553	1	9	mid-Feb	opaque
504567	1	21	late Feb	opaque
504218	1	17	1 March	opaque
395790	1	25	22 May	opaque
504535	1	92	early Jan	opaque
504561	2	77	early Mar	opaque
504591	2	25	early Mar	opaque
504290	2	35	mid-June	opaque
504122	2	60	21 Sept	opaque
504551	3	13	11 Feb	opaque
504765	3	13	14 Mar	opaque
CWP084	3	44	late Mar	opaque
504291	3	71	27 June	opaque
504313	3	0	3 Sept	translucent

* translucent accessory layer.

in the teeth of "old" animals, e.g., beyond GLG 10, in etched sections. Even in the first few GLGs incremental layers were not always clear enough to count. On the etched surface of the tooth, they were most clear on the "slopes" rather than on the top of a ridge, where one prominent very wide increment often turned out to be two, or in the grooves, where it is was "dark". The incremental layers have the same three-dimensional pattern as GLGs and are only visible when there is a contrast between the ridges and grooves of adjacent increments.

TABLE 5. NUMBER OF INCREMENTAL LAYERS PER GLG IN *TURSIOPS* DENTINE

Catalogue No.	GLG 1	GLG 2	GLG 3	>3 GLGs
291472	12–13	12	12	10–11
504122	9	13	—	—
291431	12	11	13	8–9
291403	—	12	10	11–12
291402	—	13	—	9
12277	—	11	—	—
291462	12	11	—	—
CWP088	—	—	—	11
				11
191456	14	—	—	9
504534	14	12	12	—
504864	12–13	—	11–12	—
504726	—	11	10	—
291498	—	11	10	10–12
291466	—	—	11–12	—
395430	—	—	—	10
395179	12	—	—	—
504561	—	11	—	—
JGM399	11	—	—	—
291426	—	15	11	—
		Summary		
Means	12.2	11.8	11.3	10.8
Std. dev.	1.6	1.2	1.1	1.2

The widths of the incremental layers varied slightly (Table 6). Their mean width in GLG 1 was 26 μm and 23 μm, for ridges and grooves, respectively, 28 μm and 26 μm in GLG 2, 27 μm and 24 μm in GLG 3, and 23 μm and 20 μm for measurements made from GLGs later than three. It appears, in general, that increments in the grooves are smaller than those on the ridges in the same GLG and that the increments become smaller with successive GLGs.

Conversely, accessory layers tend to be variable in position and intensity, but are usually thin translucent layers or lines within the opaque layer of the GLG. In addition, in each of the first two GLGs there is an especially wide, prominent layer about halfway through the GLG (Plate II, Fig. 1). In the first GLG, this accessory layer occurs an average of 50% through the GLG in females and 64% of the width of the GLG in males. It occurs approximately in the middle of the second GLG in females and males. In some teeth these accessory layers are more conspicuous than the GLG boundary layer. This is particularly true since in the first two GLGs the translucent boundary layer is very narrow. In GLGs beyond number three, accessory layers become less frequent and the center, wide accessory layer is not as pronounced. Accessory layers are not found in the compressed GLGs set down in old animals.

A third non-GLG layered structure might also be called an accessory layer. These layers occur adjacent to any accessory or GLG boundary layer as very in-

TABLE 6. WIDTHS OF INCREMENTAL LAYERS IN *TURSIOPS* DENTINE MEASURED FROM SEM MICROGRAPHS OF ETCHED SECTIONS. MEASUREMENTS ARE SEPARATED BY THEIR LOCATION WITHIN A GLG AND BY GLG NUMBER. MEASUREMENTS IN MICROMETERS

Catal. No.	GLG 1		GLG 2		GLG 3		>3 GLGs	
	Ridge	Groove	Ridge	Groove	Ridge	Groove	Ridge	Groove
291472	38.8	35.4	34.6	28.9	25.4	26.6	20.3	—
504122	29.8	20.0	26.0	24.0	—	—	—	—
291431	34.5	25.0	—	31.8	—	36.3	23.9	—
291403	—	—	27.5	25.0	—	—	—	17.5
291402	—	—	25.8	20.0	—	—	25.0	22.8
12277	—	—	32.0	30.0	32.5	22.5	—	—
291462	29.3	32.5	31.5	—	—	—	—	—
CWP088	—	—	—	—	—	—	30.8	—
							16.8	—
291456	—	—	—	—	—	—	20.3	—
504534	22.1	18.9	19.8	—	—	17.1	—	—
504864	22.5	15.0	20.3	20.2	—	16.7	—	—
504726	—	—	—	35.7	28.6	—	16.3	—
291498	—	—	18.4	15.2	18.0	—	—	—
291475	—	—	31.0	22.8	—	—	—	—
291466	—	—	—	—	40.0	20.0	26.6	—
395179	14.3	11.9	—	—	15.1	—	—	—
504561	—	20.0	14.4	—	—	—	—	—
JGM399	—	28.6	47.7	28.6	—	—	—	—
504532	—	—	29.9	29.2	—	—	27.8	—
291426	31.3	—	—	29.8	—	28.0	22.5	—
395430	—	—	20.0	—	—	—	—	—
				Summary				
Means	26.2	23.4	27.6	26.2	26.6	23.9	23.0	20.2
Std. Dev.	7.5	8.4	8.7	5.7	9.2	7.0	4.7	—
Overall mean		26.1						
Std. Dev.		7.0						

tense narrow bands of the opposite mineral density as the structure they abutt. Most often, this layer is opaque and follows a translucent layer. It is very noticeable following the neonatal line, the wide central accessory layer, and some of the irregular accessory layers throughout the GLGs. When this structure occurs by thin translucent boundary layers, it is sometimes more prominent than the translucent layer so more easily used as the boundary layer (Plate II, Fig. 2).

Sexual Dimorphism

Measurements of four of the five variables specifically tested for possible sexual dimorphism similar to that found by van Utrecht (1969) proved not to be significantly different (Table 7). The difference in the fifth variable, neonatal line width, was highly significant ($p<.005$) using a t-test with males having a wider neonatal line than females.

TABLE 7. SUMMARY OF MEASUREMENTS FOR POSSIBLE SEXUAL DIMORPHISMS IN THE TEETH OF *TURSIOPS*. MEASUREMENTS IN MICROMETERS

Variable	Sex	N	Mean	S. E.
Extent neonatal line extends beyond enamel, convex side*	F	13	418.0	64.2
	M	18	471.8	52.5
Extent neonatal line extends beyond enamel, concave side*	F	17	429.2	54.4
	M	18	405.3	53.3
Width of prenatal zone, convex side*	F	13	58.5	4.4
	M	18	54.4	4.3
Width of prenatal zone, concave side*	F	16	54.6	5.2
	M	18	48.1	4.6
Neonatal line width convex side**	F	21	27.0	0.8
	M	22	37.3	1.3

* Not significantly different using Student's t-test.

** Significant at $p < .005$.

DISCUSSION

Age and Growth

The growth rate of *Tursiops* is similar to that of many other odontocetes. During its first year, an average western North Atlantic *Tursiops* increases its length by 53%, approximately the same increase found for the same age animals of *Stenella attenuata* (Perrin *et al.*, 1976), *S. coeruleoalba* (Kasuya, 1972, 1976), *Globicephala melaena* (Sergeant, 1962), *Tursiops* from Florida (Sergeant *et al.*, 1973), and *Tursiops* from South Africa (Ross, 1977). The rate of growth decreased during the second year of life, averaging only a 10% increase in total length in these *Tursiops* and an average of 10 to 15% in the other species mentioned above. After three GLGs the growth rate slows considerably.

Cetaceans have been described as having high rates of growth while they are young (Bryden, 1972). However, there is a great deal of variability in total lengths of individuals in any age class. In *S. longirostris*, animals with one GLG range from about 100 cm to 135 cm in total length, those with two GLGs range from 110 to 145 cm, with equivalently large variation in older animals (Perrin *et al.*, 1977). In pilot whales, *G. melaena*, neonates range from 165 to 195 cm in total length (Sergeant, 1962). A sample of harbor porpoises from the Bay of Fundy ranged from 75 to 105 cm at birth, 105 to 130 cm at one year, 118 to 135 cm at two years, 125 to 145 cm at three years, again continuing this variation in length within each age category for older animals (Gaskin and Blair, 1977). The large variability and overlap of different aged animals illustrates that, although it is useful to construct growth curves and use mean total lengths for examining growth rates, it is not reliable to use total length to determine the age of an individual.

In the western North Atlantic *Tursiops* an especially large range in total length exists in each age class. This may be due to strandings of individuals from two different population of *Tursiops*, coastal and offshore, where the offshore animals seem to be larger than those found along the coast (J. G. Mead, unpub. data). At this time, however, it is not possible to differentiate to which population a young stranded animal belonged, so all specimens less than 280 cm have been included.

Differences in adult total length or rate of growth between males and females have been found in some cetaceans. When it occurs, generally males are larger than females as adults in odontocetes (e.g. pilot whales and sperm whales), while in mysticetes males are smaller than females as adults (e.g. humpbacks and fin whales) (Bryden, 1972). But delphinids generally have not been found to be dimorphic in adult total length (True, 1889; Sergeant *et al.*, 1973). The results from this study seem to support this.

Two studies have been published on the growth rate of wild *Tursiops*. Sergeant *et al.* (1973) looked at *Tursiops* from Florida waters. Although they reported birth to occur at 100 cm, they present no data for neonates. The growth curve, based on 22 males and 24 females, is similar to that of western North Atlantic *Tursiops* but with younger animals (less than five GLGs) apparently smaller in Florida. The apparent difference between the two groups may be due to differences in our definition of GLGs. The asymtotic length of males from Florida was found to be 270 cm and that of females to be 250 cm. The coastal *Tursiops* in this study appear to have the same asymptotic length for males and females at 250 to 260 cm. Ross (1977) gives some biology of *T. aduncas* from South African waters. The age of birth ranged from about 84 cm to 112 cm. Females reached sexual maturity at a smaller length than males. The largest female was 252 cm and the largest male 254 cm which makes them smaller than the western North Atlantic *Tursiops*. Although the *Tursiops* from Florida waters might be the same type as those from further north along the coast, those from Africa are probably not.

GLG Widths

As a dolphin tooth grows and deposits more dentine, the pulp cavity becomes increasingly smaller until it finally occludes and no more dentine deposition can occur. Correspondingly, as the pulp cavity becomes smaller, the GLGs become narrower. This decrease in GLG width could be solely the result of the new forming GLG being compressed into a smaller pulp area. If this is the case then each GLG would be a little smaller than its preceding GLG and a plot of the relationship between GLG width and number would be approximately a straight line with a negative slope. If this relationship follows a different pattern then it would suggest that there are other factors influencing the deposition or mineralization of dentine.

There are some general patterns that can be found in a plot of average GLG width against GLG number that suggest that physiological factors affected by the age or sex of the animals are important in GLG growth. These patterns can be visualized in Fig. 2. First, there are significant differences between males and females in the widths of the first two or three GLGs. It is particularly interesting that the second GLG is, on the average, wider than the first GLG in teeth from males, and that the third GLG decreases so that it is narrower than the first. Secondly, the changes in width of the first three GLGs is large, but subsequent GLGs show a marked decrease in this rate, i.e., GLGs following number three are not much narrower than their adjacent preceding GLG. This appears to be an affect of age of the animals since it occurs in females and males. Again it is interesting that this abrupt decrease in GLG deposition rate occurs at the same time that the growth curve of *Tursiops* (Fig. 1) shows a noticeable decrease in rate of growth. Thirdly, the average width of each GLG is larger in females than in males from GLGs four to six and smaller in GLGs which follow. The effect is an almost constant decrease in width of GLGs four through ten in females. In males, the rate of change in width of GLGs appears smaller than in females for GLGs six through ten. In an etched section of tooth, these GLGs appear evenly spaced and sized across the surface and almost can be considered diagnostic to determine teeth from males. Similarly, the characteristic constant decrease in size of GLGs in teeth from females is apparent in etched sections. Perrin *et al.* (1977) plotted the percent decrease in width from one GLG to its adjacent GLG in the spinner dolphin beginning at GLG 3 and continuing to GLG 16. They found that each GLG average more than 95% of the width of the preceding GLG. They did not consider females and males separately, which in *Tursiops* teeth gives different results, as discussed above. A progressive decrease in width of GLGs has also been described from the harbor porpoise (Nielsen, 1972; Gaskin and Blair, 1977), striped dolphin (Kasuya, 1972), and the pilot whale (Sergeant, 1962). Christensen (1973) found an initial decrease in bottlenose whales followed by constant thickness after the fourth GLG. Except for Gaskin and Blair (1977), measurements of widths were not given, nor were specific differences by sex or age noted. The mean widths of GLGs given by Gaskin and Blair (1977) show that GLGs are wider in teeth from female harbor porpoises than those from males.

The translucent layer can also be used as an indicator of physiological changes affecting GLGs. The absolute value of the width of the translucent layer is probably not an important parameter by itself, except to help determine the time span over which it is deposited, because it is dependent on the GLG number and width. The percent translucent layer is a more useful quantity. As with GLG width, the trend in percent translucent layer is different in females and males although significant differences occur only in GLGs 3 and 10 through 12. In females, the percent translucent layer increases almost continuously with age. Beyond GLG 10 more than half of the GLG consists of the translucent layer, reaching about 70%. This trend appears as an initial rapid increase in percent translucent layer which levels almost as a plateau (between GLGs 3 through 8) then increases rapidly again after GLG 8. This is noticeably different than males where an initial rapid increase in percent translucent layer leads to a nearly constant level, with some fluctuation. The translucent layer comprises only about 50% of the GLG after GLG 8. The change in percent translucent layer around GLG 8 through 10 in females and males may be related to physiological changes associated with the onset of sexual maturity, since this seems to be approximately the age at which the animals become sexually mature (Harrison, 1969; Ridgway, 1972).

The changes at GLGs 3 to 4 may be influenced by the decreasing growth rate at that age. The large percent translucent layer in females beyond age ten can be speculated about with even less certainty. The most obvious explanation since there are such large differences between males and females would be that the wide translucent layer, which is hypomineralized (Hohn, in press), is the result of a calcium drain caused by reproduction. At this time, there is no direct evidence for this. Gaskin and Blair (1977) noticed a progressive increase in proportional thickness of the translucent layer with age in harbor porpoises but only in females, so they attributed it to calcium mobilization. They constructed a regression line through a scatterplot of the proportion of opaque layer to translucent layer but did not mention specific differences at any age. However, their results, along with mine, indicate that percent translucent layer is worth examining in other species for possible dimorphism and explanation for the formation of the layers.

Last GLG

Most of the strandings of *Tursiops* occurs during February and March. Since calving also occurs during this season, it should be about this time when the neonatal line appears in the teeth. If the deposition of dentine is fairly constant, animals born in the late winter to early spring would have completed each GLG during that season in successive years and then started another GLG. Each month more of the new GLG would have accumulated following a hypothetical line representing constant growth by percent GLG formed throughout the year, one twelfth or 8% monthly, as in Fig. 4. Most of the 28 animals examined for percent growth of the last GLG follow this hypothetical line, at least during the spring of the year when most of the animals strand. However, this line begins in January or early February, earlier than when neonates are generally found. By late February or March, 10 to 20% of the new GLG has already formed, the amount that would be expected at a constant deposition rate of dentine with the new GLG beginning in January. This would suggest that the end of the previous GLG, which is the translucent layer, occurs in December or January. Scatter around this line is probably due to individual variation in time of birth and actual widths of GLGs, and possibly to abnormal physiological states of the animals before they strand.

Tursiops may have two seasons of parity: one in the spring and another in the fall (Townsend, 1914; Harrison, 1969; Ridgway, 1972; Ross, 1977). In particular, Townsend (1914) believed that North Atlantic Ocean *Tursiops* give birth during both seasons. Ross (1977) has found stranded neonates in the fall and spring which suggests more than one or an extended breeding season. But neonates have not been found through the MMSP during the fall, even though many are picked up during the spring. However, if the growth of the tooth can be used as an indicator of season of birth, i.e., animals born in the spring have formed one GLG the following spring as previously discussed, then *Tursiops* which have formed 50% of a GLG in the spring must have started that GLG during the fall. Similarly, an animal whose last GLG ends in the fall, probably also began deposition of GLGs during the fall. A hypothetical line drawn to represent the expected growth of teeth which begin GLGs in the fall should parallel the equivalent line for animals whose GLGs begin in the spring, but off-set by approximately six months. This hypothetical line, represented in Fig. 2, has several points which fall on or close to it. This would suggest that these animals were also born in the fall rather than in the spring as we would have anticipated based on stranding records. This may provide evidence to support Townsend's (1914) idea of two seasons of calving for *Tursiops* in the North Atlantic Ocean.

Although growth layers in teeth and bone have been used for about 30 years for age determination, there have been only speculative suggestions as to the cause of the rhythmic deposition of the layers. The environmental or endocrinological mechanisms influencing or regulating the mineralization pattern in hard tissue is unknown. In several species of odontocetes, the optical or mineral density of the GLG layer bordering the pulp cavity when an animal dies has been used as an indicator of the physiological or nutritional state of the animal. Sergeant (1959) found the "clear zone" (translucent layer) to begin in February and occur through April in captive *Tursiops* from Florida. Sergeant *et al.* (1973) said they could not determine the density of the last layer in mostly wild *Tursiops* from Florida based on their sample size (N=62). Sergeant (1962) found the opaque zone to occur adjacent to the pulp cavity in pilot whales, *Globicephala melaena*, from Canadian waters caught in the summer. In a mass stranding of pilot whales, *G. macrorhynchus*, in South Carolina during mid-October, the opaque layer bordered the pulp cavity (unpub. data). Nishiwaki and Yagi (1954) found that the well stained (=opaque) layers occur in December and May through June in *S. coeruleoalba*. Similarly, the opaque layer borders the pulp cavity in June through February in harbor porpoises from the Bay of Fundy (Gaskin and Blair, 1977), in the summer in Baird's beaked whales from the North Pacific (Kasuya, 1977), in May and June in bottlenose whales from the North Atlantic (Christensen, 1973), and in June through November in dugongs from the equatorial and North Pacific (Kasuya and Nishiwaki, 1978). In summary, the opaque layer appears to border the pulp cavity at least during the summer months, and usually longer, in most species. Conversely, the translucent layer is more often at that point during the winter or early spring. In *Tursiops*, the translucent layers, as accessory layers or GLG boundary layers, are deposited in the fall (September, N=1), and in late January, early February, or March (N=3). However, all the animals examined were young which is when the translucent layer is very narrow. As males and females age, a higher proportion of each layer becomes translucent, so the time of deposition of each layer of a GLG would depend on the age of the animal, at least in *Tursiops*. This, again, assumes that the dentine continues to be deposited at a constant rate and only the mineralization pattern changes. The GLG number at which previous researchers determined the optical or mineral density of the layer bordering the pulp cavity, or changes in the relative amount of translucent dentine, has not been mentioned. The collection of enough data of this kind may help us to understand the cause of layering.

Non-GLG Layered Structures

Incremental layers. It is difficult to count incremental layers from SEM micrographs because the small mineral changes throughout an increment and between increments does not always produce enough contrast in etched sections to make individual increments clear (Plate III). In addition, increments are difficult to see on the "back side" of a ridge or in a groove where it is "dark" because fewer electrons reach the collecting plate. The effect is probably that counts are slight underestimates of actual numbers of incremental layers.

Partially for the same reasons, it may not be accurate to measure widths of incremental layers from etched sections. The etching process produces the ridge and groove pattern in GLGs and in incremental layers, so there is no longer a flat surface. This is compounded by the tilting of the sections in the SEM chamber. Although the quantitative effect of these factors is unknown, the average number of increments per GLG (12) multiplied by the average width of the increments (26 μm) is not equivalent to the average width of the first three GLGs measured from thin sections (approximately 420 μm). Measurements are probably an underestimate of actual sizes of increments. SEM of etched sections, however, seems to provide the best way to visualize incremental layers.

The appearance of incremental layers in *Tursiops* dentine supports the idea of Schour and others that dentine grows or is mineralized in spurts or increments. The frequency of approximately 12 increments in one annular layer or GLG suggests that this sub-annual growth is similar to that described in dugongs (Kasuya and Nishiwaki, 1978), Baird's beaked whale (Kasuya, 1977), and dolphins of the genus *Stenella* (Myrick, in press). However, the width of the increments has not been determined for those species. The average size (26 μm) of incremental layers in *Tursiops* dentine seems much too large to represent daily von Ebner's lines of 5 μm width described by Krauss and Jordan (1965) and Newman and Poole (1974) in human teeth, or von Ebner's lines in pig dentine (Yilmaz, Newman, and Poole, 1977). If incremental lines in *Tursiops* are approximately monthly, daily increments would have to average 0.87 μm, measured from SEM micrographs. Myrick (in press) has found daily increments in dolphin dentine, but has not determined the width of either these von Ebner's lines or the "monthly" growth increments. Schour and Hoffman (1939) measured the "calcification" rhythm in 17 species of vertebrates and found it to recur at intervals of 16 μm (no time interval was mentioned). They were counting accentuations (light or more calcified areas) which alternated with dark areas. It is possible that "monthly" increments in *Tursiops*, which are the result of mineral differences, are similar to the pattern found in other vertebrates by Schour and Hoffman (1939).

One of two basic assumptions seems to be made when considering the deposition or mineralization of dentine. The first presumes the increments are time-regulated by some extrinsic or intrinsic factor so that the common denominator is the number of increments set down during a given period of time. The second assumption is that these processes continue at a constant rate regardless of the age or the species of the animals. The latter would seems to be supported by Schour and Hoffman's (1939) observations of the 16 μm calcification rhythm and researchers looking at constant sizes of von Ebner's lines (Krauss and Jordon, 1965; Newman and Poole, 1974). However, the authors do not specify the age of the dentine where the measurements were made, e.g., immediately subjacent to the enamel or several years growth away from the enamel. Nor do they mention making a series of measurements throughout each tooth, except over short periods of time such as days or weeks. Although my measurements of incremental layers are subject to error, as discussed previously, the trends suggest that the increments decrease in size in GLGs set down later in an animal's life. Increments in GLGs beyond number three are smaller than those in the first three GLGs. This may be an artifact of etched sections. However, in order for the number of increments to remain the same in all of the GLGs, the increments must become narrower as the GLGs become narrower; again with the assumption that the number of incremental layers is relatively constant, which seems to be more supported by the data from *Tursiops* teeth.

The assumption of constant size of increments also seems to be disputed by the differences in width of incremental layers on the ridges and grooves in etched sections. Increments in the grooves measure, on average, smaller than increments on the ridges and slopes of the GLGs. This size difference may be a result of the collapse of the tissue when the mineral is removed or it may be a real difference in widths of increments in the hypomineralized and hypermineralized parts of the GLG. This should be checked in untreated dentine, possibly in thin sections using a petrographic microscope (Myrick, in press).

It is tenable that the mineralization or deposition of dentine could be regulated by monthly or lunar factors, that this produces the relatively constant number of increments per GLG in *Tursiops* teeth and possibly all species, that the size of the increments changes progressively with the age of the animal and possibly between the hypo- and hypermineralized layers of the GLGs, and that the incremental layers can be used to gain more information about the biology of species and the growth of mineralized tissue. However, this must be measured by direct marking of individuals, e.g., tetracycline, or by the examination of many more species before any conclusions are drawn.

Accessory layers. There appears to be two kinds of accessory layers as they have been described formally or referred to in the literature. The first are the narrow accessory layers which appear irregularly in GLGs. These are approximately the same size as incremental layers and can be distinguished from incremental layers only because their mineral density, seen as optical density, differs appreciably from that of the GLG layer in which they occur. The second kind are the very prominent, wider than incremental layer accessory layers which occur regularly, approximately in the center of the GLG. It is undoubtedly these prominent accessory layers which are responsible for the debate about number of GLGs set down annually in odontocete teeth. An unexperienced person would almost assuredly count these regular accessory layers as GLGs. For example, Leatherwood *et al.* (1978) counted five GLGs in thin sections of teeth from a young *Tursiops* (USNM 504122). In the same animal I counted a little more than two GLGs (Plate 5). The SEM micrograph shows only two GLGs (although the first prominent ridge is an accessory layer - the first translucent layer is hardly visible). Similarly all of their counts of GLGs from seven *Tursiops* used in both studies are in disagreement with mine, with their counts from the teeth of young animals doubling mine. Kleinenberg and Klevezal (from Klevezal and Kleinenberg, 1967) described an annual deposition of two GLGs in the teeth of the Black Sea dolphin, *Delphinus delphis*, which they later (1967) attributed to the presence of this accessory layer. In general, they agreed that GLGs are annual but this prominent center accessory layer often gives the impression that two GLGs are deposited.

Myrick (in press) refers to incremental layers in *Stenella* teeth as accessory layers. It seems that incremental layers are visible due to their mineralization cycle within GLGs. If this cycle is subject to extrinsic or intrinsic influences then incremental layers will be more obvious within a GLG when the expected mineral density is disrupted. This disruption would make the incremental layer appear as one of the narrow, irregular accessory layers. In the first two GLGs where the translucent layer is very narrow, these accessory layers would and do make it difficult to determine where the GLG ends. However, incremental layers by themselves do not usually interfere in the process of counting GLGs in *Tursiops* teeth, especially using SEM.

Regardless of the kind of accessory layer, accessory layers make counting GLGs very confusing in the first few GLGs. A person experienced in "reading" odontocete teeth can probably estimate very close to the actual number of GLGs in a tooth section, but identifying the exact end of a GLG becomes very difficult in some teeth. There is also a great deal of variability between animals. Accurate age determination of some species of odontocetes, e.g. *Tursiops*, depends on experience, from looking at many teeth from all ages of the animals to accurately identify accessory layers before trying to count GLGs.

Small scale mineral changes. The narrow opaque accessory-type layers which follow translucent layers appear to be the result of abrupt small-scale changes in the dentine. Irving and Weinmann (1948) described a similar occurrence in rat incisors. They injected rats with strontium to observe the effects on calcification in the teeth and found that the strontium caused a hypocalcified layer (16 μm wide) to occur. Immediately following this layer, a very evident narrow "calciotraumatic" line was found which sharply demarcated the hypocalcified dentine from the normal, calcified dentine. They attributed this line to be caused by a shock to calcium metabolism in the rat by the strontium. The same effect was found in rats after administration of calciferol or parathyroid hormone (Schour and Ham, 1934; Schour *et al.*, 1934), or immediately following parathyroidectomy (Schour *et al.*, 1937), where the parathyroid helps regulate mineralization processes. In addition, Kronfeld and Schour (1939) found the calciotraumatic line to occur following the neonatal line. It may be this same calciotraumatic line that is present in thin sections of *Tursiops* teeth following the neonatal line and other translucent zones.

There has been some question about the mineral density of the narrow layers in odontocete teeth, for example, the neonatal line. The consensus is that they are translucent and hypomineralized. But Nielsen (1972), Klevezal and Kleinenberg (1967), and Kasuya (1976) have suggested that the narrow layers are translucent but hypermineralized for some species. The wide layers are then relatively hypomineralized, so the relationship between mineral and optical densities is different from that of other odontocetes. Because of this, Nielsen (1972) has suggested that optical density cannot be used as an indicator of mineral density. However, it may be that where the translucent layer is very narrow, the opaque "calciotraumatic" line is more apparent and is considered the layer. In some tooth sections of *Tursiops* it is easier to use this opaque line than the preceding translucent layer to follow a GLG down the extent of the tooth. However, the neonatal is still considered to be translucent and hypomineralized and subsequent boundary layers are translucent and hypomineralized. The calciotraumatic line needs more examination for its occurrence and effect in odontocete teeth.

Sexual Dimorphisms

The sexually dimorphic trait found by van Utrecht (1969), i.e. the greater extent of the neonatal line in males, in teeth from 20 harbor porpoises, *Phocoena phocoena*, is not significantly different in the teeth of male and female *Tursiops*. Van Utrecht also mentioned that the same trait was applicable to *Lagenorhynchus albirostris*, a delphinid, but this was based on only three females and three males. Teeth of species from the family Phocoenidae are considerably different from those of the family Delphinidae. Instead of the nested "cone" appearance of GLGs in *Tursiops* teeth, the GLGs in *Phocoena* are bulbous in the crown or spatulate end, then continue in the narrower root parallel to the long axis, as in the handle of a spatula. The difference in growth between phocoenid teeth and delphinid teeth presumably allows for any dimorphic growth of the neonatal line relative to the top of the cement in *Phocoena* but not in *Tursiops*.

The second trait examined for possible differences between sexes of *Tursiops* seems related to the first. If the neonatal line was to extend further down the root of the tooth in male *Tursiops* as it does in male *Phocoena*, it might be because there was a greater amount of prenatal dentine in males. Having more prenatal dentine could have suggested that the neonatal line was deposited at a later time in males or that the tooth began development earlier. But neither trait was significant so should not be used to identify an animal of unknown sex in *Tursiops*.

The greater extent of the neonatal line could also be related to the width of the neonatal line. If the measurements were made from the outer edge of the neonatal line, a wider neonatal line would extend its length if the deposition of the neonatal line was initiated at the same time in males and females. In the case of *Tursiops*, the width of the neonatal line is significantly different in males and females. However, the greater neonatal line width in males is coupled with insignificant differences in either the extent of the neonatal line or width of the prenatal zone. This is probably because the neonatal line is very narrow, especially relative to its length, and the 10 μm mean difference in this width between males and females does not significantly alter the overall measurement of the extent of the neonatal line. In addition, it is very difficult to accurately measure the neonatal line width because it is so small and, although not difficult to identify, its boundaries are not always clear. Even though the width of the neonatal line proved to be a significantly different sexually dimorphic trait, I would not recommend that it be used as the sole identifier of the sex of an unknown specimen of *Tursiops*.

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EXPLANATION OF PLATES

PLATE I

Fig. 1. SEM micrograph of etched longitudinal section of tooth from an old male *Tursiops* showing relative evenness in GLG width, translucent layer width, and spacing of GLGs. Magnification: ×17.

Fig. 2. Etched longitudinal section of tooth from a 2.5 year old male *Tursiops*. The small layers running parallel to the GLGs are incremental layers. Although more than two GLGs are present, the first is deceptively masked so that the actual boundary layer, marked by the arrow, is not the first prominent ridge. The beginning of the second prominent ridge serves as the boundary for GLG 2. nl—neonatal line, al—accessory layer, PC—pulp cavity
Original magnification: ×18.

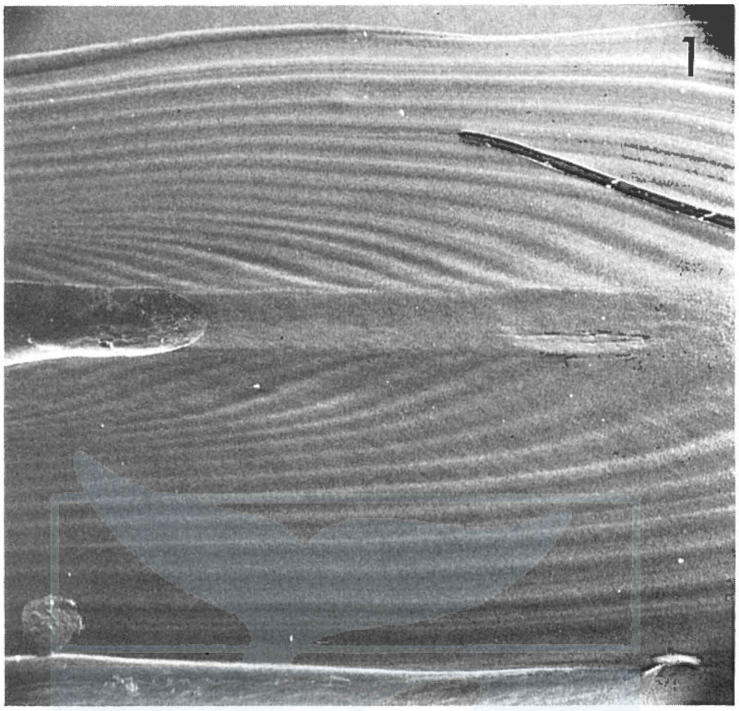
PLATE II

Fig. 1. Longitudinal thin section (transmitted light) of a young *Tursiops* tooth. The dark evident line following the neonatal line (nl) may be a " calciotraumatic line ". One GLG is complete, the second is beginning. The center accessory layer (al) is very evident and could easily be mistaken for an additional GLG.
Magnification: ×18.

Fig. 2. Longitudinal thin section of a tooth from a male which could have from 1.5 to 6 GLGs. This animal is probably just over 3 three years old. The GLGs are marked by arrows. Notice the accessory layers which occur centrally in the first two GLGs.
nl—neonatal line
Magnification: ×12.

PLATE III

Fig. 1. Etched section of same 2.5 year old male in Plate II, Fig. 2 at a higher magnification. Notice especially that it is difficult to separate individual incremental layers (il) because two adjacent layers with small mineral density differences appear as one.
nl—neonatal line, al—accessory layer
Magnification: ×50.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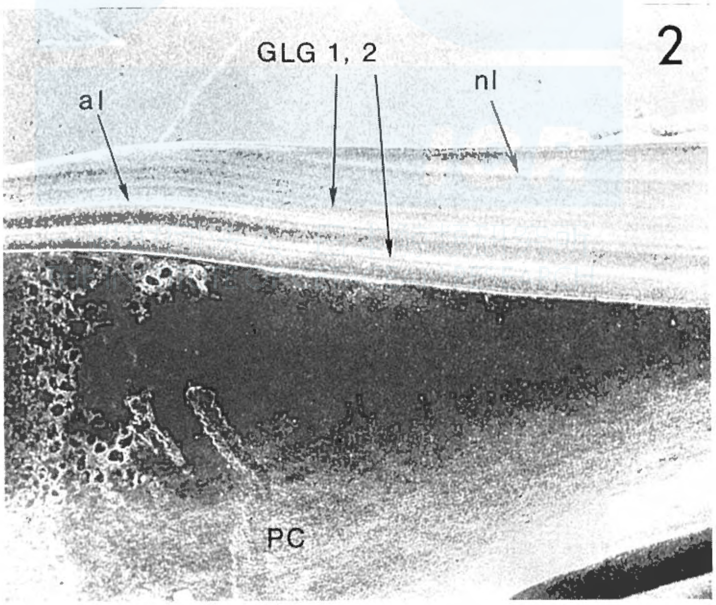
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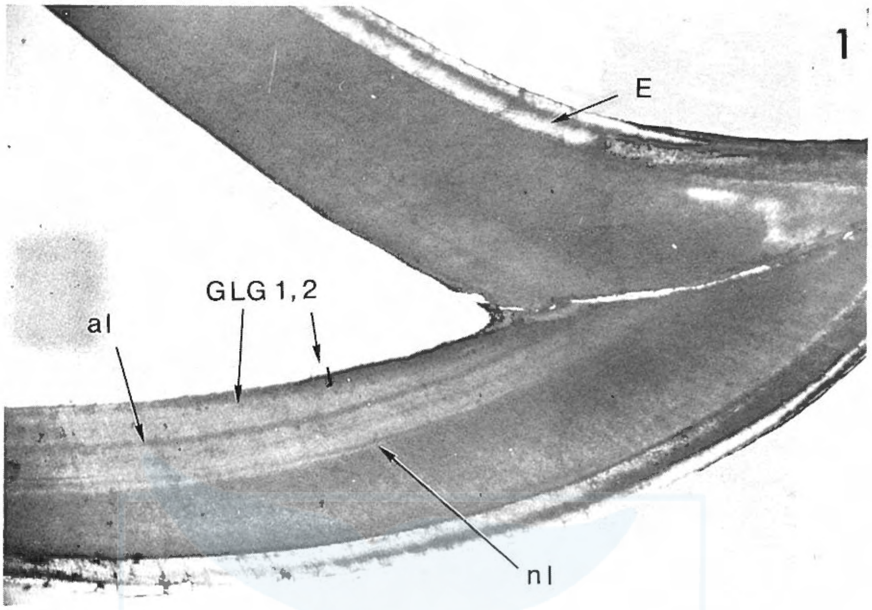
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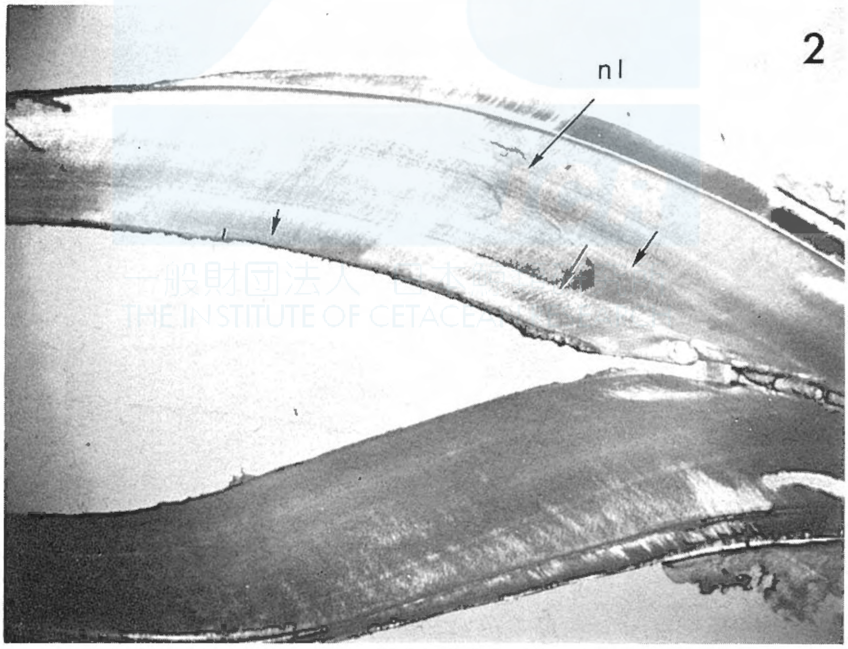
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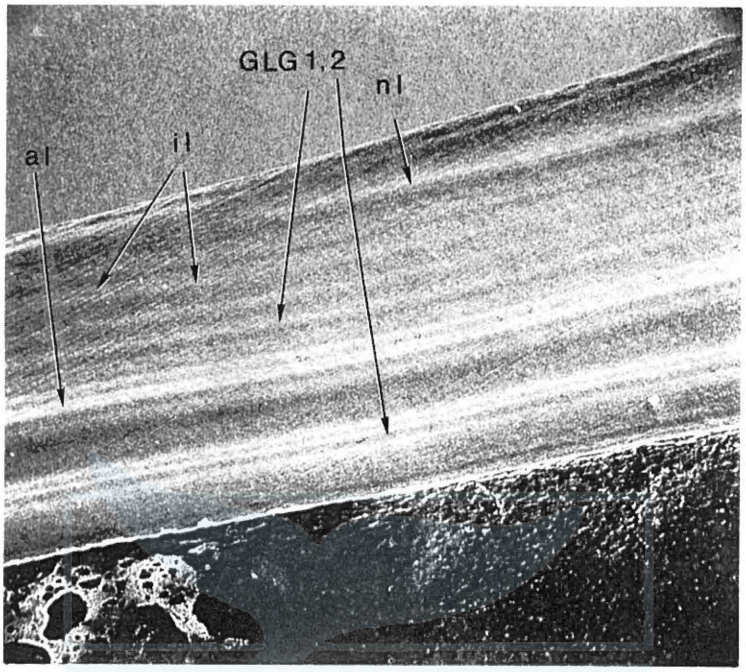
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ON THE EXTERNAL CHARACTERS OF *GLOBICEPHALA MACRORHYNCHUS* OFF TAIJI, PACIFIC COAST OF JAPAN

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ABSTRACT

The external measurements of 211 short-finned pilot whales off the Pacific coast of Japan and the observation of the pigmentation of some of those individuals are analyzed. They have pigmentation pattern fundamentally common to the genus *Globicephala.* The growth of the trunk is characterized by the highest growth rate of rostrum portion in fetal stage, and that of the region between umbilicus and anus in postnatal stage. On some appendages, the change of growth pattern occurs at parturition and/or after the attainment of sexual maturity of male. *G. macrorhynchus* is morphologically different from *G. melaena* in smaller size of body, and shorter flipper and tail region.

INTRODUCTION

Although the recent existence of the long-finned pilot whale, *Globicephala melaena* (Traill, 1809), is not confirmed, that of the short-finned pilot whale, *G. macrorhynchus* Gray 1846, is known from the coastal waters of Japan (Kasuya, 1975). The species is less common in the Sea of Japan than off the Pacific coast. They are believed to migrate seasonally along the Pacific coast between southwestern Japan and Hokkaido, though the summer resident are present in the southwestern waters. The seasonal movement of the northern range of the species between 34°N and 42°N seems to be related to the movement of the subarctic convergence. In recent years, the driving fishery at Taiji on the Pacific coast of central Japan is the only fishery taking the species constantly in the above range. It is operated usually within a radius of 15 km from Taiji.

The purpose of this study is, based on the sample obtained from the catch of this fishery, to make a brief description of the external morphology of the species and provide some basic data for future analyses of between populations difference of the external characters.

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The present study was started as a graduation thesis of Yonekura under the supervision of Matsui. Later Kasuya joined the study, collected some additional data, reanalysed data, and added a section of external pigmentation.

MATERIALS AND METHOD

All the observations of the colour pattern and the external measurements were obtained from the catch by driving fishery off Taiji (33°35′N, 135°58′E).

The measurements of the body proportions used in this study are as follows. With exceptions of nos. 12 through 19, all the measurements were made parallel to the long axis of the body. Though some of the measurements may differ from those customarily used for whales, it does not mean the recommendation of the present method.

1. Standard length, from the tip of snout to bottom of the notch of tail flukes.
2. Tip of snout to center of eye.
3. Tip of snout to blowhole.
4. Tip of snout to angle of gape.
5. Tip of snout to anterior insertion of flipper.
6. Tip of snout to tip of flipper.
7. Center of eye to center of ear.
8. Bottom of notch of flukes to the apex of dorsal fin.
9. Bottom of notch of flukes to center of anus.
10. Bottom of notch of flukes to center of genital aperture.
11. Bottom of notch of flukes to center of umbilicus.
12. Flipper, straight length from anterior insertion to tip.
13. Flipper, straight length from axilla to tip.
14. Flipper, curvilinear length along anterior edge.
15. Flipper, maximum width.
16. Dorsal fin, length of base.
17. Dorsal fin, height from base to apex.
18. Width of tail fluke at base, from anterior insertion to bottom of fluke notch.
19. Distance between apices of tail flukes.
20. Projection of melon beyond the tip of snout, measuered when anterior end of melon projects over the tip of snout.

The measurements nos. 1 to 19 were made by Yonekura on 143 postnatals and 17 fetuses in eight schools caught from May to November of 1976. The length frequency of these specimens is shown in Fig. 1. The provisional analysis of the growth of *G. macrorhynchus* off the Pacific coast of Japan suggests that the calves are born between 135 and 146 cm, and that the growth stops with large individual variation at a length between 340 and 395 cm in females and between 430 and 525 cm in males (Kasuya, unpublished). The lower boundary of these ranges situates about 10 cm above the mean length at the onset of sexual maturity. However,

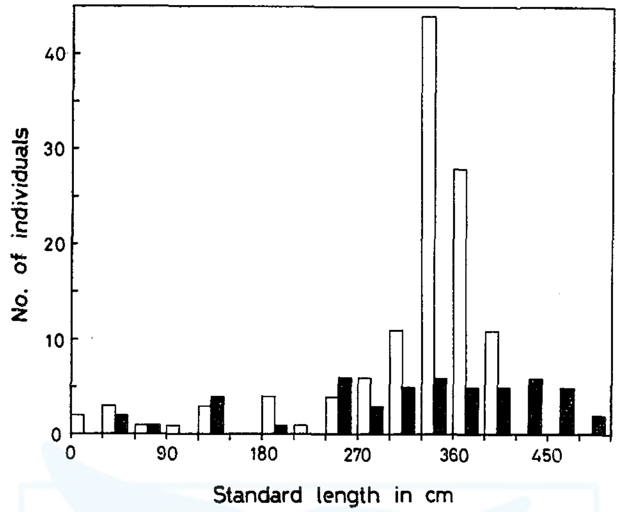

Fig. 1. Length frequency of 160 samples (52 males and 108 females) used for the external measurement nos. 1 through 19. Shaded square indicates male and the white female. Samples smaller than 150 cm in standard length are fetuses.

these figures are based on the body length measured including the projection of melon beyond the tip of snout. The standard lengths corresponding to these ranges are calculated at 337 to 390 cm and 423 to 512 cm respectively. The mode in female frequency in Fig. 1 may indicate the mean asymptotic length.

The observation of colouration was done by Kasuya, and the measurement no. 20 was taken by Kasuya and Matsui on the individuals in four schools caught in February 1980. The purpose of the measurement no. 20 is to analyze the possible sexual dimorphism and to get some clue to convert the "standard length" generally used in this study into the "body length" measured from the anteriormost point of head to fluke notch, which might be commonly used for the short-finned pilot whale. Though the use of the standard length might be adequate for the morphological comparizon between the two species of pilot whales, the accurate measurement is difficult on adult *G. macrorhynchus* because, different from *G. melaena* (Sergeant, 1962a), the anterio-ventral surface of melon directly merges into the tip of snout.

The statistical analyses of the significance of sexual difference of the external measurements are made for each 30 cm length groups, and on the proportion expressed as the percentage of standard length.

PIGMENTATION PATTERN

Except for a few pale areas mentioned below, most of the part of the body of *G. macrorhynchus* is pigmented dark brown on living or freshly dead individuals. This brown colour changes black soon after the death.

The most faint lightly pigmented part is the blaze behind the eye, which is an

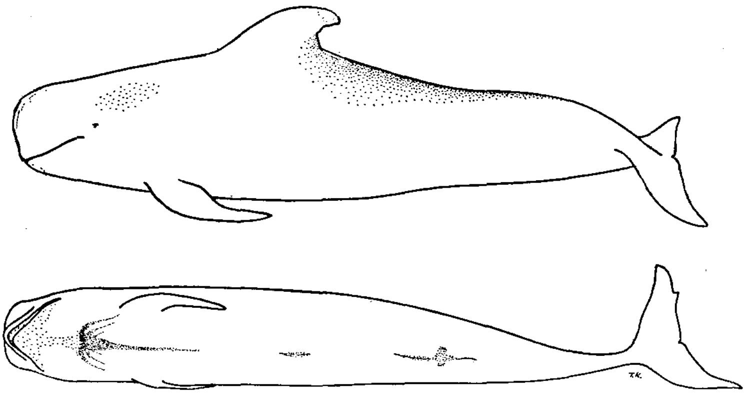

Fig. 2. Body contour and pigmentation of *G. macrorhynchus* off the Pacific coast of Japan. Dotted area indicates paler part of body. Drawings are based on photographs and measurements of an adult female.

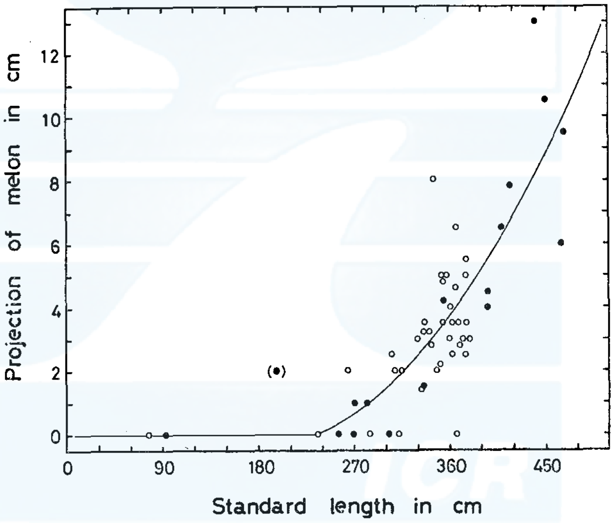

Fig. 3. Relationship between standard length and projection of melon beyond the tip of snout. Open circle indicates female and the closed male. A male in parentheses is not used for the calculation of regression.

oblong patch extending from the posterio-dorsal region of the eye to anterior insertion of dorsal fin. Though this patch was found on all the individuals examined, size and clearness were variable between individuals. This is usually discernible only through very careful observation of wet skin of the freshly killed individuals. It is not frequent to recognize it from a distance even on a live specimen. Though this postorbital patch is not described by Norris and Prescott(1961), it might be universal in the genus of *Globicephala*.

The second is the postdorsal saddle-mark, which has been described on *Globice-*

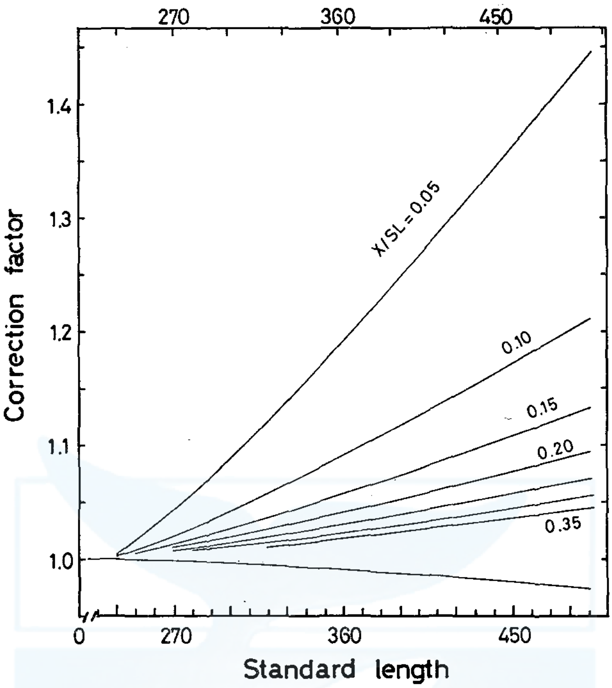

Fig. 4. Correction factors to convert the external proportions expressed as the ratio of standard length into those of body length measured from the protruded tip of melon to fluke notch. The downward line at the bottom is for the measurement not including the protruded melon, and other lines for the measurement including it. X indicates length from tip of snout, SL the standard length, and the scale at the top the body length converted from standard length.

phala (Norris and Prescott, 1961; Sergeant, 1962a). This has large individual variation and generally conspicuous on adult individuals. Though this mark becomes indiscernible on specimens dead long, it is more conspicuous than the blaze behind eye. This is most clear when observed on live animals and through the water (Plate I, Figs 1 and 2).

The third is the ventral mark. The pattern is principally common to *G. melaena* and *G. macrorhynchus*. The colour, however, seems to be much darker in the later species as mentioned by Sergeant (1962a), and no individual of *G. macrorhynchus* observed in the present study showed such a brightly pale colour of the inguinal region as *G. melaena*.

GROWTH OF TRUNK

Projection of melon

The melon of full term fetus is small and shaped of the ordinary delphinids' melon (Plate II, Fig. 1.), however it seems to start the rapid growth after birth and soon attains the bulbous form. The projection of the front end of the melon

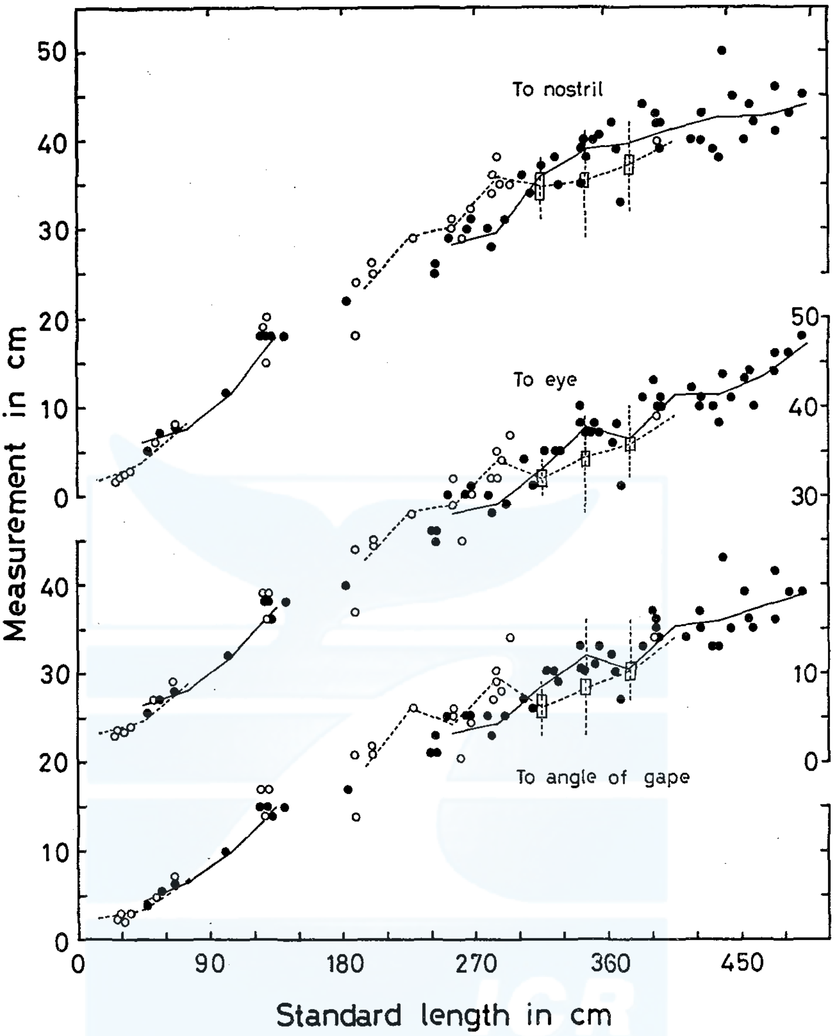

Fig. 5. Measurement nos. 2, 3, and 4, measured from tip of snout and expressed by actual length. Open circle and dotted line indicate female and the closed circle and solid line male. The square and vertical line indicate the range of data and 95% confidence range of the mean based on 10 or more female samples. The scale at the top indicates calculated body length between fluke notch and projected melon.

over the snout occurs at the length of about 240 cm, which correspond to the age of about 2 years (Kasuya, unpublished). The relationship between standard length and the degree of the melon projection is shown in Fig. 3. Both sexes are expressed by the following least squares equations.

$$y = 0 \quad , \quad SL \leqq 236$$
$$y = 1.257 \times 10^{-4} SL^2 - 4.517 \times 10^{-2} SL + 3.649 \, , \quad SL \geqq 237$$

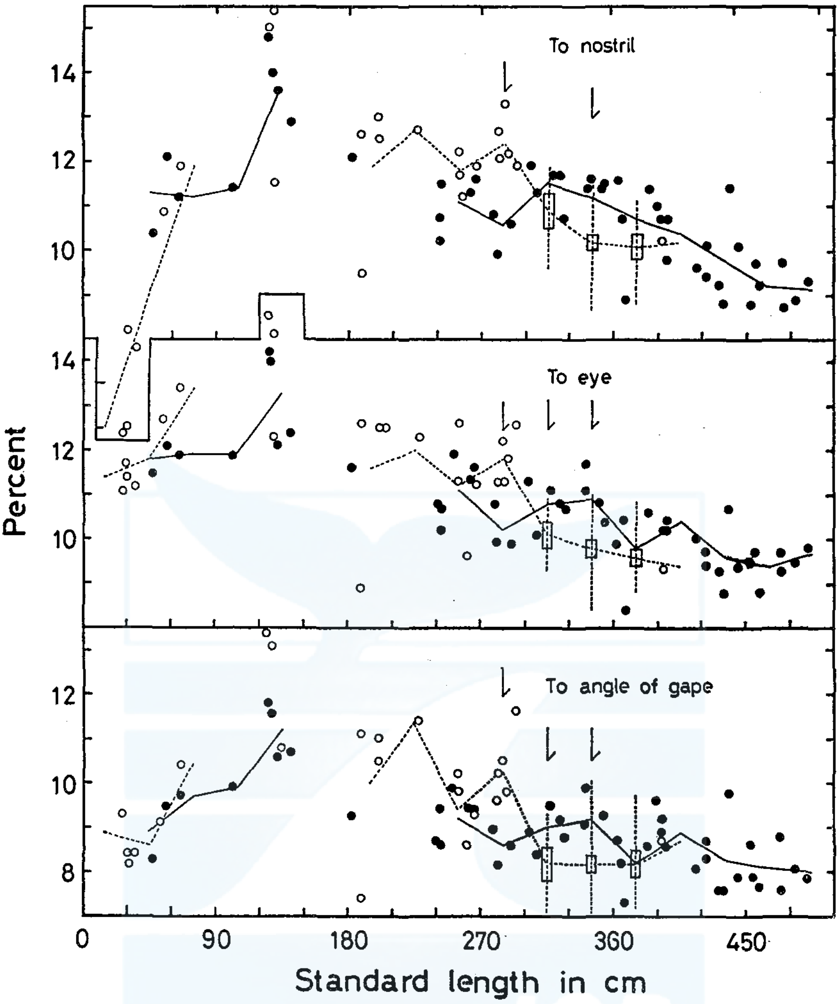

Fig. 6. Measurement nos. 2, 3, and 4, expressed as the percentage of standard length. Arrow indicates the presence of significant sexual difference of mean values ($p<0.05$). For further explanations see Fig. 5.

where SL indicates the standard length in cm, and y the projection of melon beyond the tip of snout. Though it is generally believed in *G. melaena* that the development of a huge melon is one of the secondary sexual characteristics, it is shown on *G. macrorhynchus* that the size of the melon may not be different when compared between sexes of same body length. And even on the adult males exceeding the maximum standard length of the female, the development of melon is on the same line. This suggests that the large size of the melon in the adult male is the simple result of the augmentation of body.

From the above equations the correction factor (r) is calculated in order to convert the measurement expressed as the percentage of "standard length (SL)"

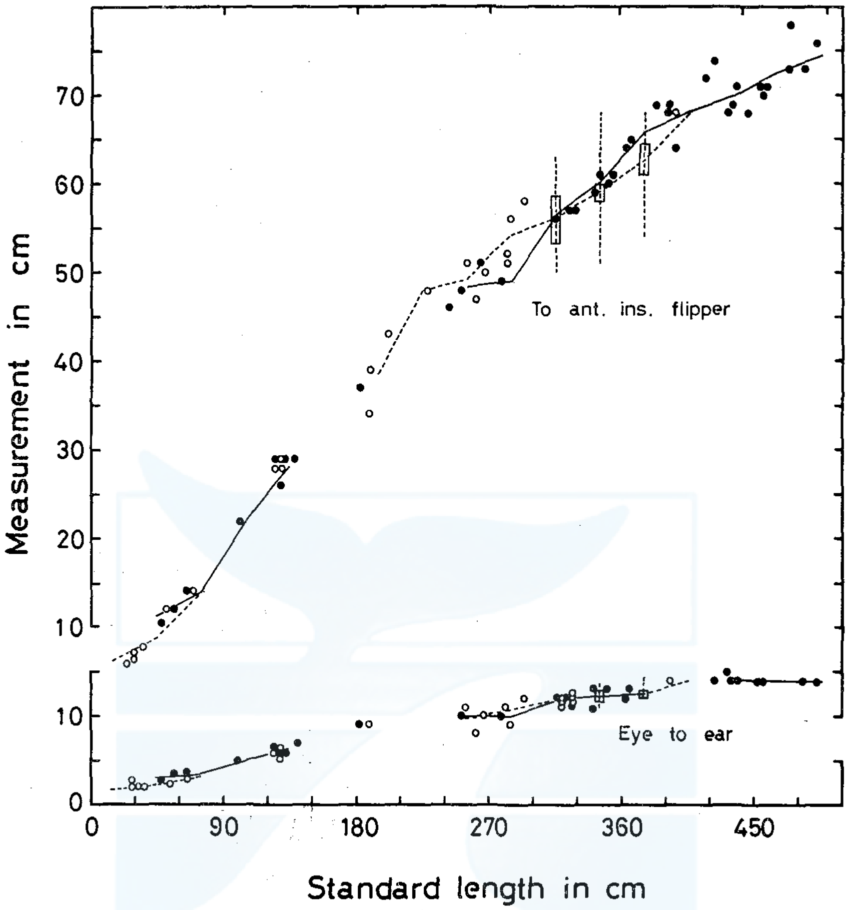

Fig. 7. Measurement nos. 5 and 7, expressed by actual length. For further explanations see Fig. 5.

to that expressed as the ratio of "body length (BL)" measured from the end of projected melon to fluke notch. When the measurement does not include the projection of melon, there is a following equation.

$$r=\left(\frac{1}{BL}\right)\Big/\left(\frac{1}{SL}\right)=\frac{SL}{y+SL}$$

If the corrected measurement includes the projection of melon, the correction factor r is obtained by the following equation,

$$r=\left(\frac{X+y}{SL+y}\right)\Big/\left(\frac{X}{SL}\right)$$

where X indicates an actual length measured from the tip of snout excluding the projection of melon. The value of r is shown in Fig. 4 for the selected values of X/SL.

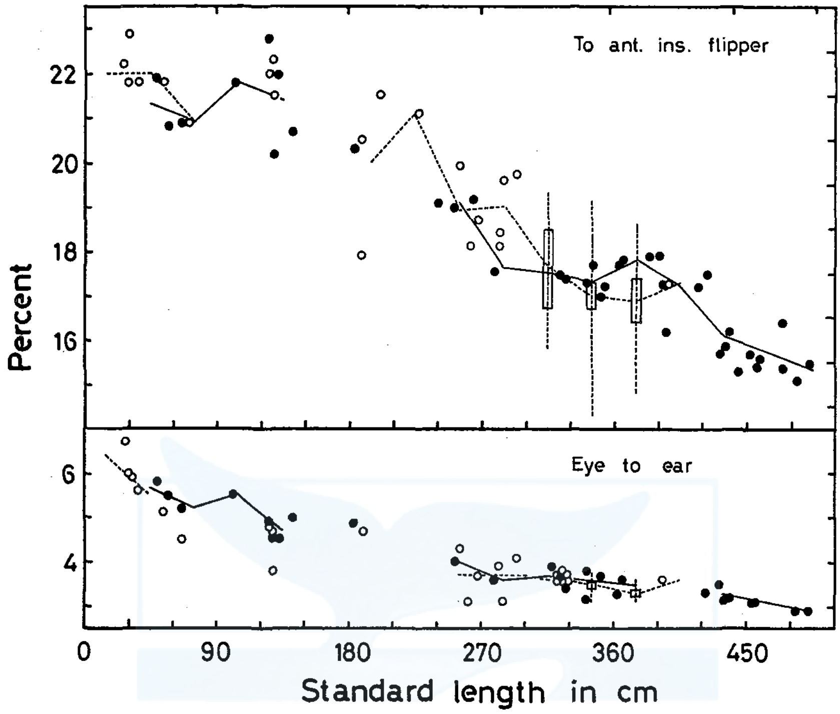

Fig. 8. Measurement nos. 5 and 7, expressed as the percentage of standard length. For further explanations see Fig. 5.

TABLE 1. COMPARISON OF BODY PROPORTION OF *G. MACRORHYNCHUS* BETWEEN FETUS, FULL TERM EETUS, AND FULL GROWN MALE AND FEMALE[1]

Standard lenth, cm	30 (♂ ♀)		135 (♂ ♀)			360 (♀)			465 (♂)		
	cm	%	R	cm	%	R	cm	%	R	cm	%
Projection of melon	0	0		0	0		3.7	1.0		9.8	2.1
Rostrum tip to eye	3.4	11.4	4.4	18.4	13.7	0.89	35.0	9.7	1.4	43.4	9.3
Eye to ear	1.8	6.0	2.4	6.2	4.6	0.98	12.3	3.4	1.3	14.0	3.0
Ear to ant. ins. flipper	1.4	4.8	2.4	4.8	3.6	1.8	13.4	3.7	2.2	15.2	3.3
Flipper to umbilicus	8.7	29.1	3.4	38.7	28.7	1.5	98.3	27.3	2.1	118.4	25.5
Umbilicus to anus	5.5	18.0	3.6	25.5	18.9	2.2	82.1	22.8	3.4	112.0	24.1
Anus to genitals ♂	—	—	—	11.1	8.2	—	—	—	3.5	49.8	10.7
♀	0.54	1.8	6.0	3.8	2.8	2.6	13.7	3.8	—	—	—
Anus to fluke notch	9.2	30.7	3.5	41.4	30.7	1.9	118.9	33.0	2.9	162.0	34.8

[1] Ratio is shown as the percentage of standard length. R indicates the relative growth rate.

Growth of anterior portion

The characteristic feature of the growth of anterior portion of *Globicephala* is in the rapid growth in the fetal stage, and in the gradual decrease of the rate after the parturition (Sergeant, 1962a). The details of the growth pattern, however,

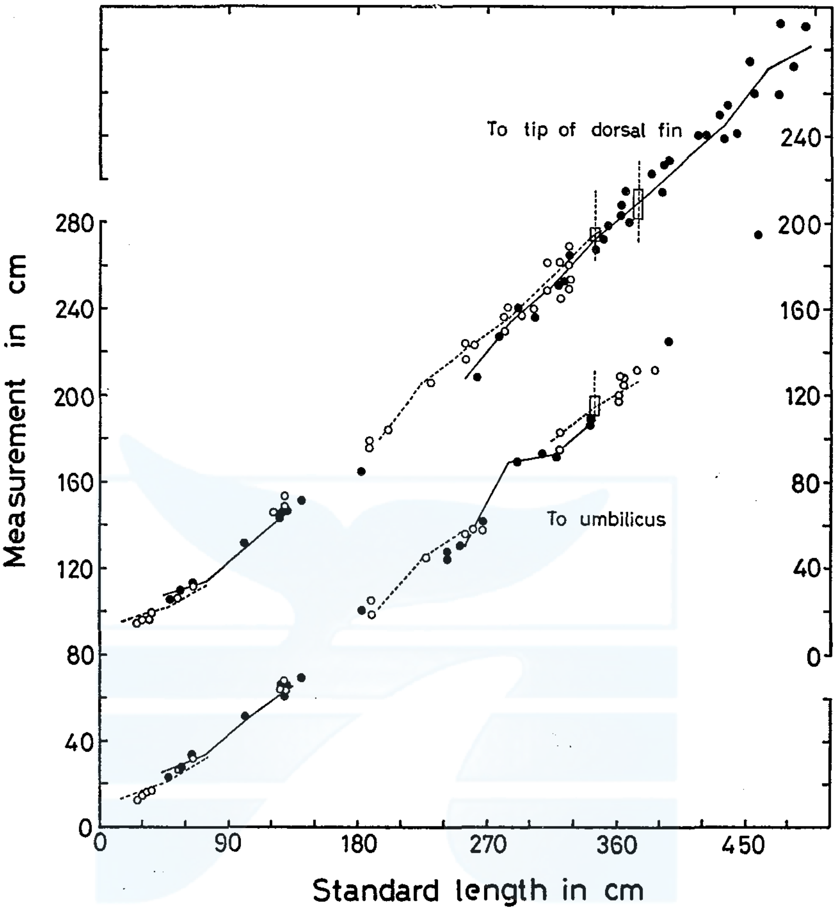

Fig. 9. Measurement nos. 8 and 11, measured from fluke notch and expressed by actual length. For further explanations see Fig. 5.

differ between the portion at the front of eye and that posterior of it.

The position of the nostril changes drastically. In the early fetal stage it situates at about 6% of the standard length from the tip of rostrum namely at the front of eye and of angle of gape, and continues to move posteriory during entire fetal stage. As this movement is much faster than the growth of the rostrum, the nostril finally comes on a level same with that of eye and angle of gape by the stage of 120 to 150 cm in standard length, or the length at birth. At this stage, if calculated combining both sexes, the relative positions of nostril, eye, and angle of gape measured from the tip of rostrum are 13.8%, 13.7%, and 11.7% of standard length respectively. Though the ratio of head region in the standard length continues to decrease after birth, the relative position of these organs remains almost unchanged. Another peculiarity of the growth pattern of the rostrum region is the possible presence of sexual difference in the postnatal growth stage. As shown in Fig. 5, nos-

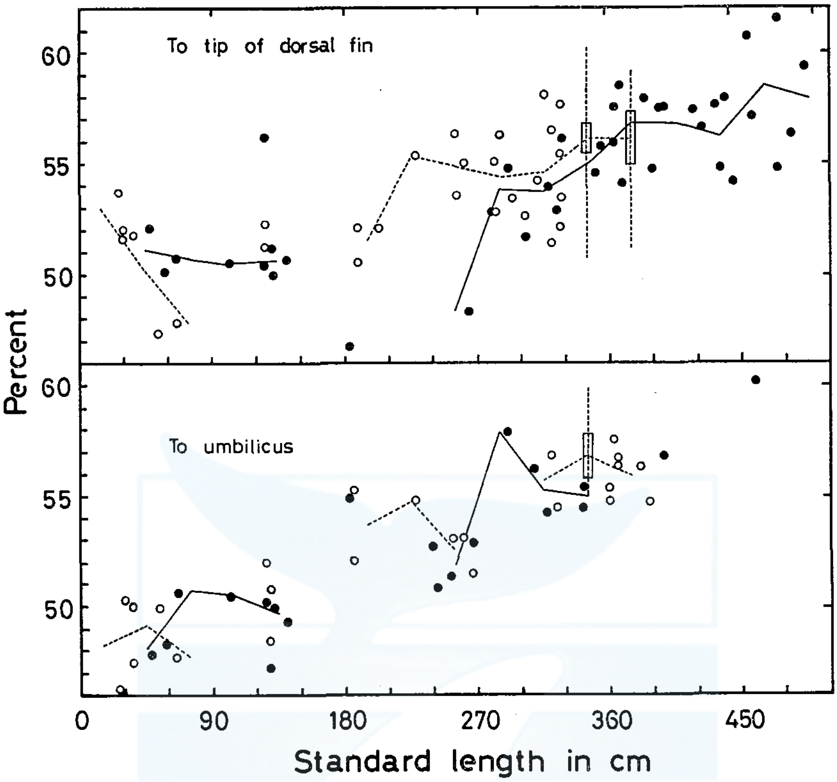

Fig. 10. Measurment nos. 8 and 11, expressed as the percentage of standard length. For further explanations see Fig. 5.

tril, eye, and angle of gape of juvenile females situate posterior to the corresponding positions of the male of the same body length. However their relative position is reversed in the later growth stage. This change occurs at the standard length of 300 to 330 cm. Though the samples are not sufficient for the statistical analysis of all the length groups, the sexual difference is significant in some of the groups (Fig. 6). The growth rate of the rostrum region, which decreases after birth, becomes slightly higher at the standard length of 285 to 375 cm in males. This growth spurt of the rostrum is again followed, after 375 cm, by a stage of relatively slow growth. On the other hand, the spurt occurs in females at smaller body length or from 195 to 285 cm. This will explain the presence of sexual difference in the proportion of rostrum portion at restricted growth stages.

The proportional length between eye and ear also shows a higher relative growth in fetal stage than in the postnatal. No secondary growth spurt nor sexual dimorphism is expected for this part. The increase of the actual length of that section ceases at 330 cm in females and at 420 cm in males. The occipital portion represented by this measurement is, as in the case of neck region, the place where the growth is the smallest in both fetal and postnatal stages (Table 1).

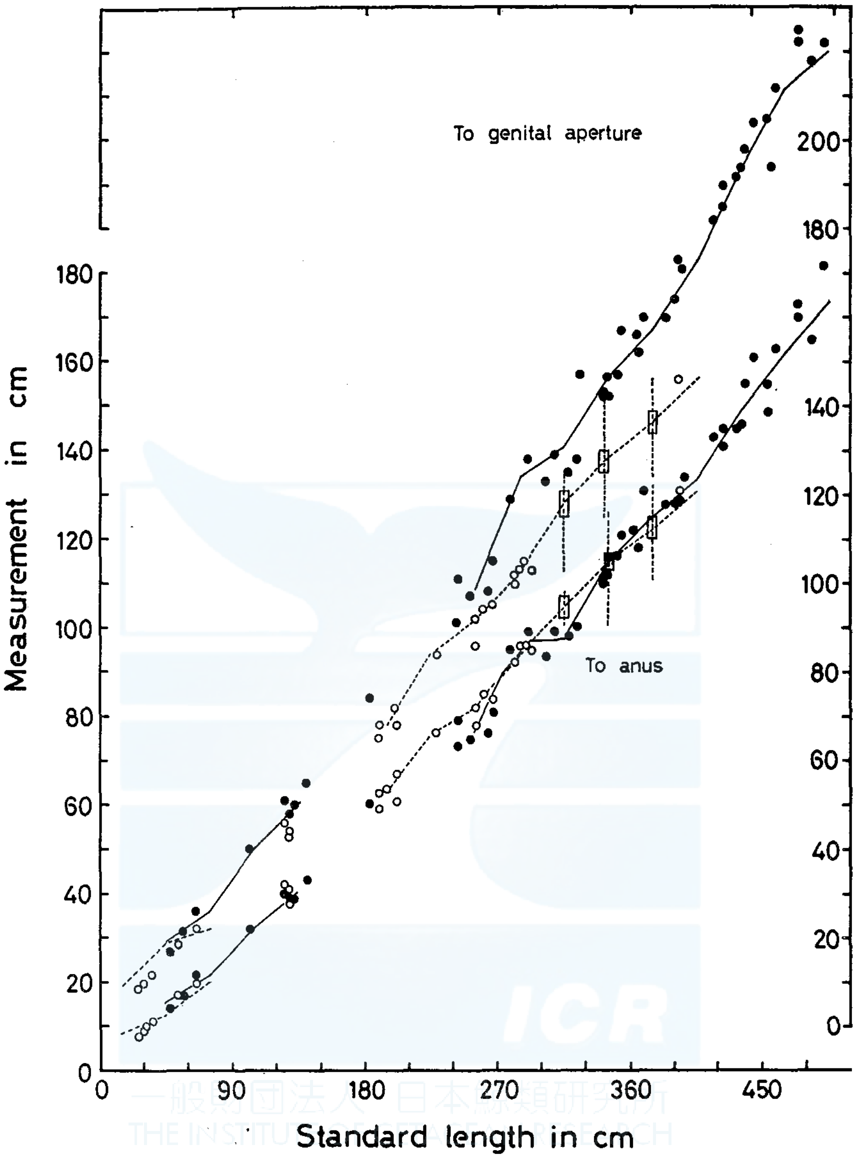

Fig. 11. Measurment nos. 9 and 10, measured from fluke notch and expressed by actual length. For further explanations see Fig. 5.

The growth of the portion between tip of snout and anterior insertion of flipper shows a pattern similar to that of rostrum region. However, the ratio to standard length does not increase even in the fetal stage as observed in the growth of other part of head region, but decreases rather slowly, which is followed by a rapid decrease after parturition. The speed of decrease of the ratio in postnatal stage is higher than that observed on the rostrum portion. This is also an indication that

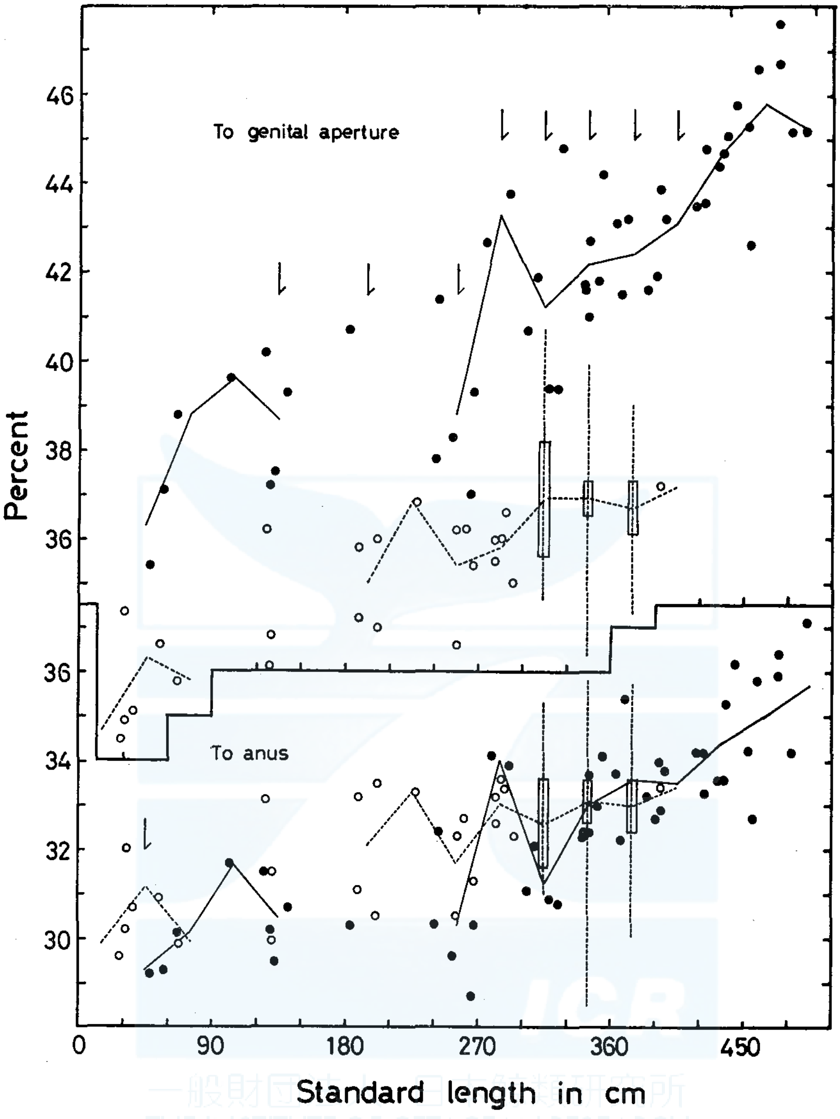

Fig. 12. Measurement nos. 9 and 10, expressed as the percentage of standard length. For further explanations see Fig. 6.

the growth of the portion between eye and anterior insertion of flipper is smaller than its anterior section.

Growth of rear portion

The four measurements on the posterior region of the body, the lengths measured from fluke notch to anus, to genital aperture, to umbilicus, and to apex of dorsal fin show a similar feature in the growth pattern, namely the ratio is constant

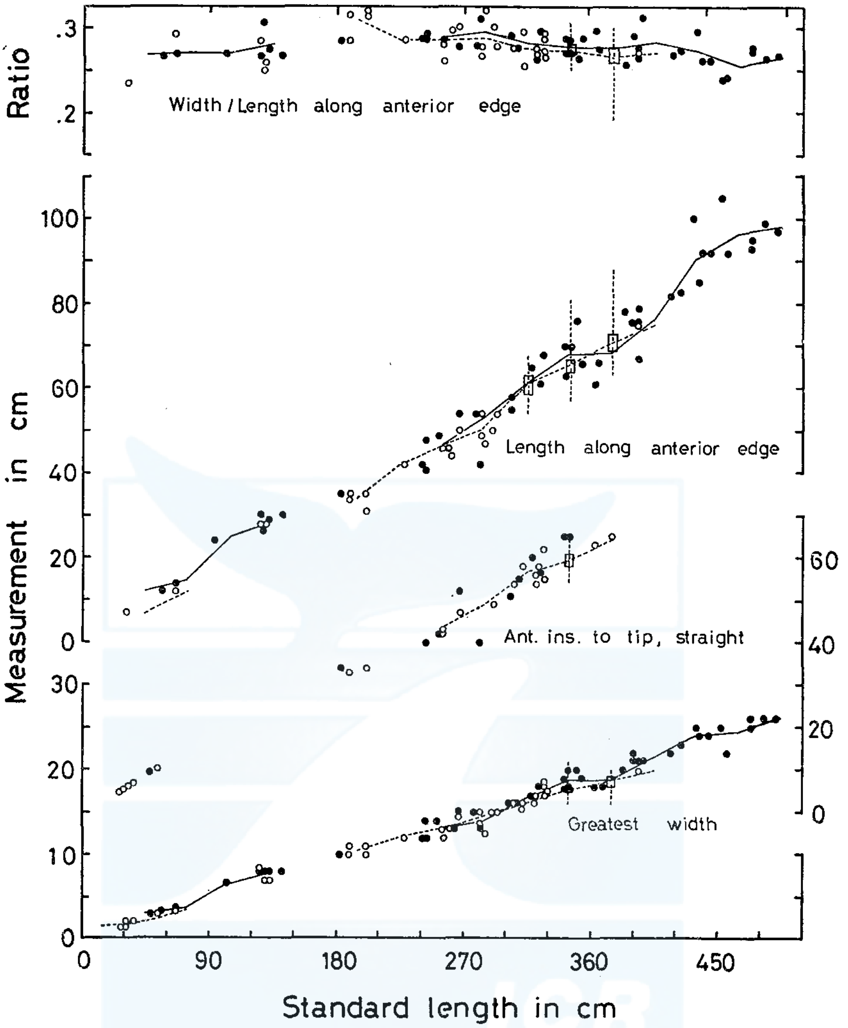

Fig. 13. Dimensions of flipper, measurement nos. 12, 14, and 15. For further explanations see Fig. 5.

or slightly increasing accompanied by the growth of body. This is the reflection of the fact that this portion retains high growth rate until the cessation of growth in body length.

No sexual dimorphim is indicated except for the position of the genital aperture. Though, obstacled by the scarcity of the samples, the between sexes difference of the position is not statistically significant in all the length groups examined (Fig. 12), the difference must appear significant in more length groups when larger samples are accumulated.

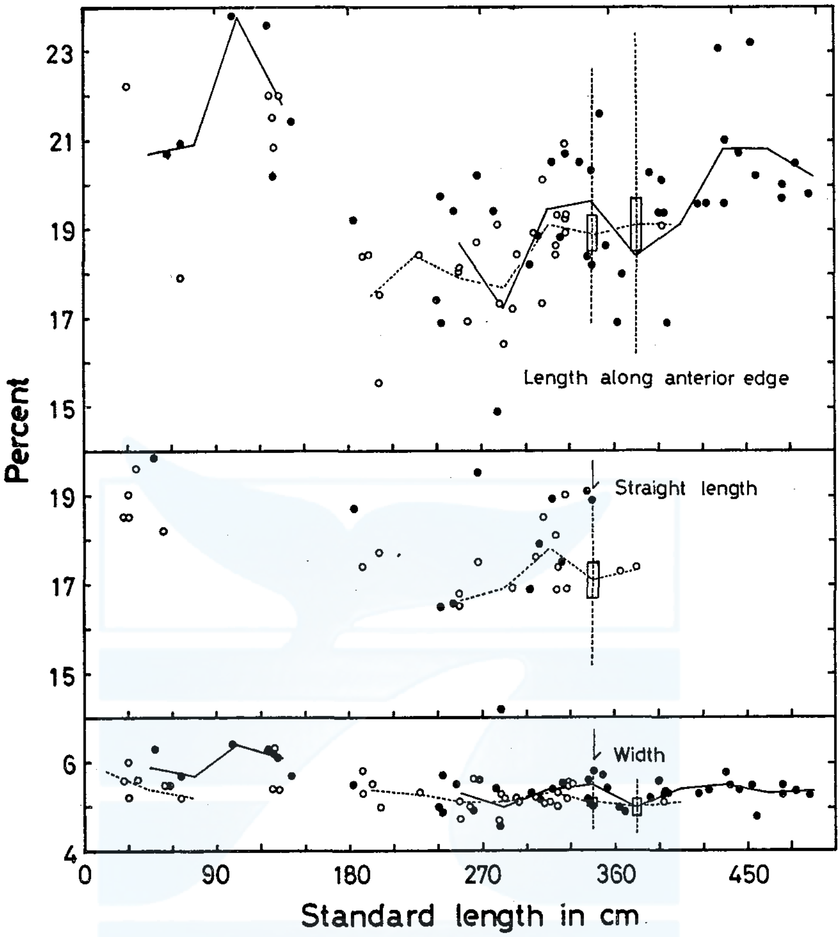

Fig. 14. Dimensions of flipper (measurement nos. 12, 14, and 15) expressed as the percentage of standard length. For further explanations see Fig. 6.

Growth of each segment

The lengthwise dimensions expressed as the percentage of standard length become almost constant, in females, after the length of 330 cm. This lower limit coincides, as mentioned above, with the lower range of the asymptotic length or with the mean length at sexual maturity. Though the corresponding length of the male will be about 420 cm, the body propotion in the male seems to change even after the length. Table 1 shows the mean body proportions calculated from the present data of nearby size (±15 cm). They are mean values at the standard lengths of 30 cm (early fetus), 135 cm (near term fetus), 360 cm (female, approximately at the mean asymptotic length), and 465 cm (male, same as female). This is considered to give a rough idea on the body shape of the species. The position of apex of dorsal fin is not listed, because it situates in any stage of the growth

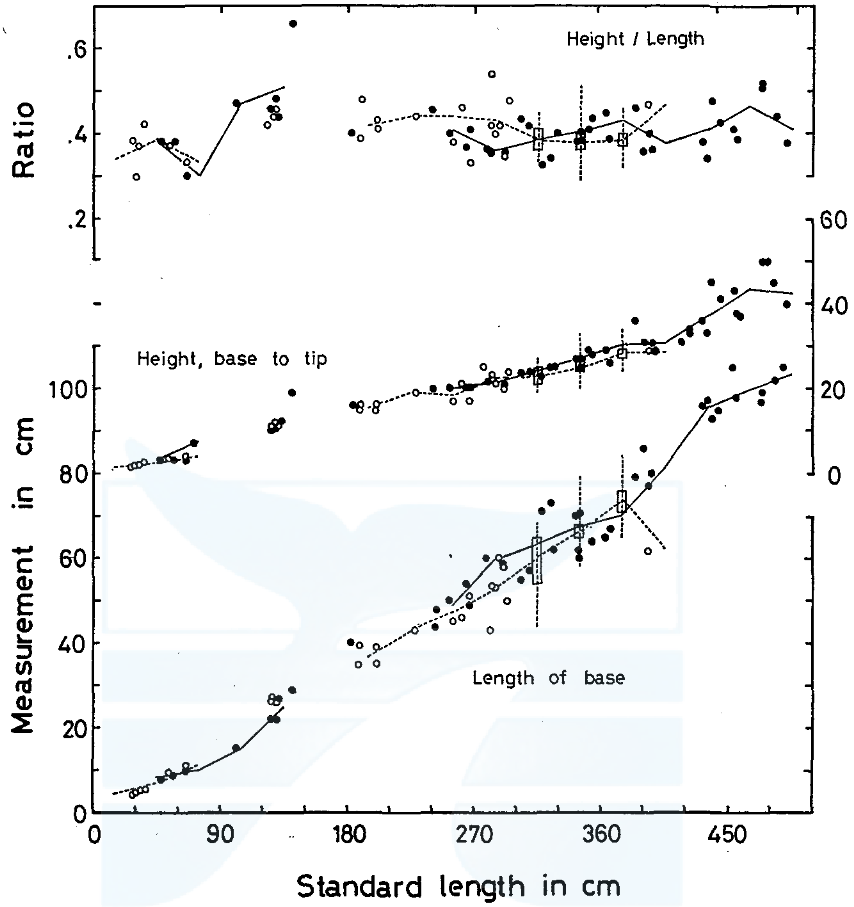

Fig. 15. Dimensions of dorsal fin, measurement nos. 16 and 17. For further explanations see Fig. 5.

nearly at the same level with that of umbilicus. The growth rate of each segment is calculated using the following equation and the data in Table 1,

$$R_X = \frac{X_2 - X_1}{X_1}$$

where R_X indicates the growth rate of segment X, X_1 the length of X segment at the start, and X_2 that at the end. When fetus grows from 30 cm to 135 cm, the highest growth rate is found at the segment between tip of rostrum and eye, and the next highest at the segment from umbilicus to anus which is followed by the segments of tail and of flipper to umbilicus. The growth rate of the segment between anus and genital aperture is not included in this comparison, because it is special and included in the segment between umbilicus and anus. In the postnatal growth stage the feature is same in both sexes and the highest growth rate is observed in the segment between umbilicus and anus, the second highest in the tail seg-

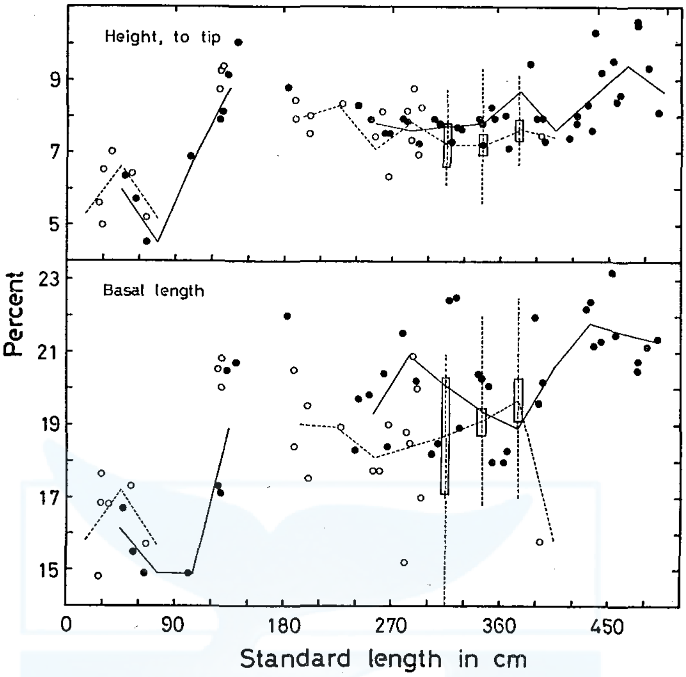

Fig. 16. Dimensions of dorsal fin (measurement nos. 16 and 17) expressed as the percentage of standard length. For further explanations see Fig. 5.

ment, and followed by the segments of ear to flipper and of flipper to umbilicus.

GROWTH OF APPENDAGES

Flipper

Since the straight length of flipper was measured on limited number of samples and the data is entirely lacking in adult males, following analyses are done on the length along anterior edge and on the maximum width. During the fetal stage the length of flipper increases both in actual length and in the ratio of standard length. However the growth in the actual length decreases between the full term fetuses of about 135 cm and newborn calves of 180 cm, and the ratio of the length expressed as percentage of standard length drastically decreases. This is already observed on *G. melaena* in the North Atlantic (Sergeant, 1962a). After this period the ratio again continues a slow increase, until the animal attains the asymptotic length over 330 cm in females and over 420 cm in males.

The width of flipper expressed as the percentage of standard length shows a slight increase during fetal stage. After the birth the ratio decreases until 270 cm in standard length, and then stays almost constant.

The width/length ratio increases in fetal stage and continues to decrease in all the postnatal period.

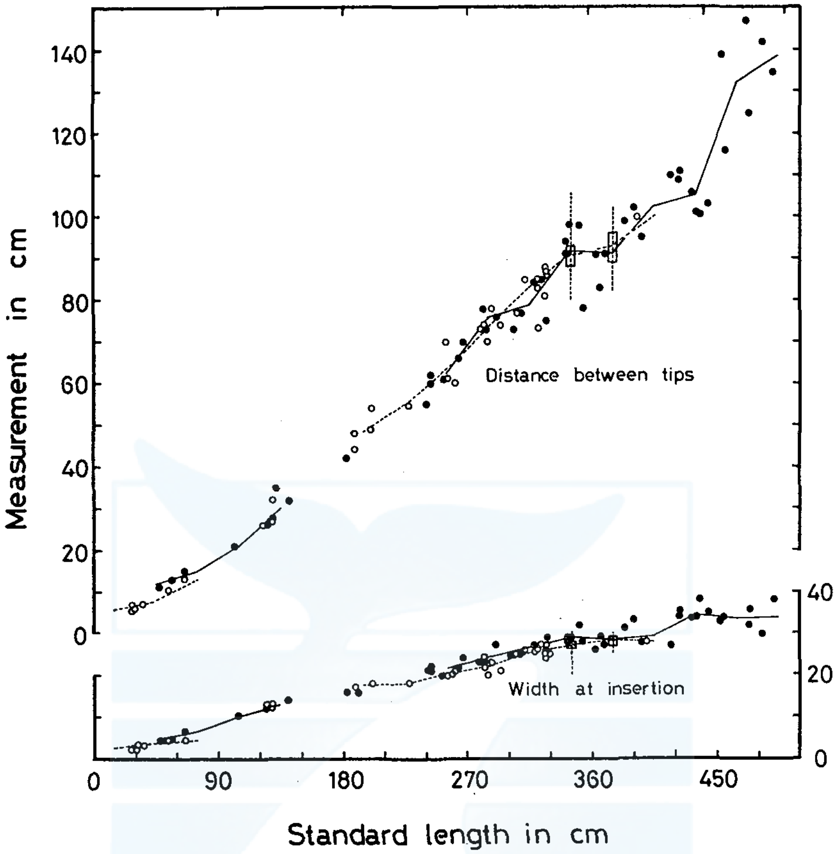

Fig. 17. Dimensions of tail flukes, measurement nos. 18 and 19. For further explanations see Fig. 5.

Sexual dimorphism may not exist even where the difference of the means are statistically significant in the present data.

Dorsal fin

Length of the base of dorsal fin expressed as the percentage of standard length increases rapidly in fetal stage and then stays nearly constant in all the postnatal females and in males below 390 cm. In males the basal length, as in the case of the height mentioned below, shows a rapid increase at about 420 cm, which may correspond to the age of sexual maturity. The decrease of the relative basal length near the parturition indicated by Sergeant (1962a) on *G. melaena* is not detected on the present species.

The relative height of the dorsal fin increases in fetal stage and then continues, in females, to decrease until the maximum body length. In males, on the other hand, the height too shows a rapid growth at 420 cm in standard length. In *G. melaena* the growth of height of dorsal fin is reported to follow the pattern of flipper (Sergeant, 1962a), but it is different in female *G. macrorhynchus*.

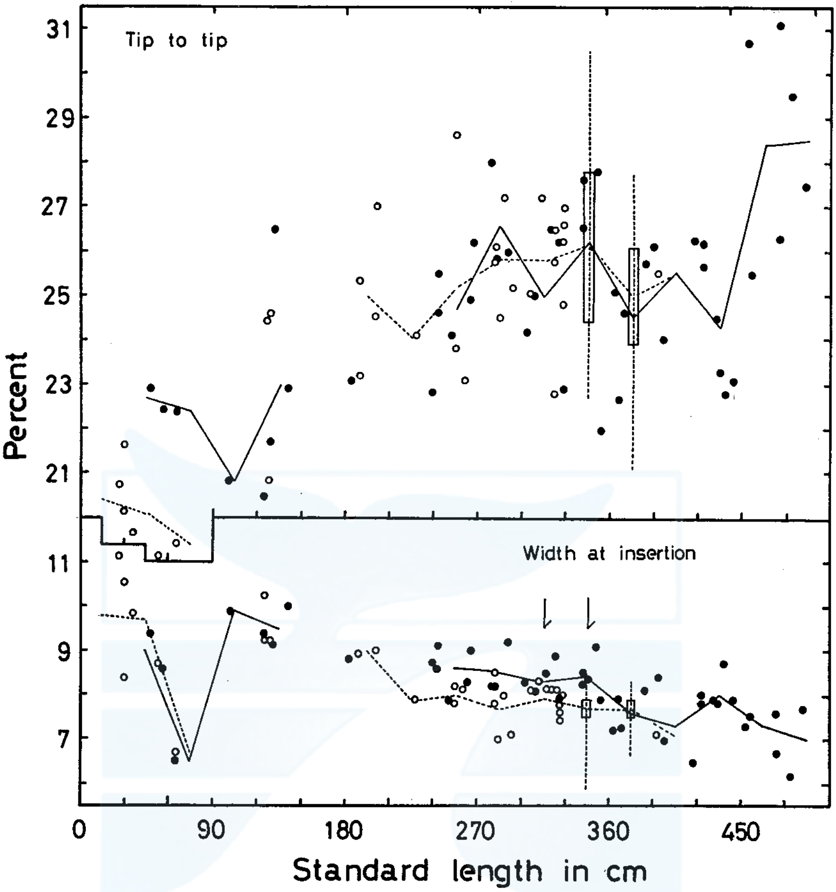

Fig. 18. Dimensions of tail flukes, measurement nos. 18 and 19, expressed as the percentage of standard length. For further explanations see Fig. 6.

The height/length ratio increases in fetal stage, and after birth it stays almost constant.

No sexual dimorphism is detected, when compared between the sexes of the same body length. However, both the height and length of dorsal fin are larger in relation to the standard length in full grown males than the females of corresponding stage.

Tail fluke

Becuase the tail flukes of the fetus are coiled ventrally, the correct measurement of the distance between the apices is difficult to be done. The distance between apices expressed as the ratio of standard length increases rapidly in fetal stage. After birth the ratio stays almost constant in all the females and in males below 450 cm in standard length. In the larger full grown males, the distance between apices expressed as percentage of standard length tends to be larger.

The ratio of the width of tail fluke at insertion shows a constant decrease from early fetal stage to full grown individuals of both sexes. In some of the length groups, the mean of the relative width is significantly smaller in females than in the males of the same body length (Fig. 18). Though such a length range is limited between 300 and 360 cm, the presence of similar trend in smaller length groups suggests that the difference might be proved as significant in other body length groups if more samples are accumulated.

DISCUSSION

A comparison of some important external proportions is made between *G. macrorhynchus* of the present study and *G. melaena* in the western North Atlantic. Only the individuals of adult size were selected from the former species. They are 73 females above 330 cm and 13 males above 420 cm in standard length. The data of *G. melaena* selected are females above 400 cm and males over 500 cm, which are expected to be composed mainly of adult individuals (Sergeant, 1962b).

TABLE 2. COMPARISON OF EXTERNAL PROPORTIONS BETWEEN TWO SPECIES OF *GLOBICEPHALA*

		G. macrorhynchus			*G. melaena*		
		n	range	mean1)	n	range	mean1)
1. Standard length (cm)	♂	13	424-491	452.6	10	500-610	551.8
	♀	73	334-392	357.5	10	405-472	440.7
2. Tip of snout to eye (%)	♂	13	8.8-10.7	9.5±0.3	9	7.2-9.3	8.3±0.5
	♀	63	8.4-11.0	9.7±0.2	10	9.0-10.6	9.8±0.4
5. Tip of snout to ant. ins. of flipper (%)	♂	12	15.1-17.5	15.8±0.4	9	12.6-14.9	13.7±0.6
	♀	53	14.3-19.0	17.0±0.3	10	14.4-16.3	15.5±0.5
8. Notch of flukes to apex of dorsal fin (%)	♂	11	54.2-61.5	57.4±1.5	8	52.1-57.8	54.6±1.5
	♀	47	51.3-60.1	56.1±0.3	9	48.2-53.1	51.2±1.5
11. Notch of flukes to umbilicus (%)	♂	1	60.2	60.2	8	58.2-68.0	61.2±2.4
	♀	16	54.8-59.9	56.3±0.2	9	57.7-63.2	60.3±1.3
9. Notch of flukes to anus (%)	♂	13	32.7-36.4	34.8±0.3	10	33.9-41.4	38.2±1.3
	♀	65	28.5-35.8	33.0±0.3	10	33.8-37.0	36.1±0.8
12. Flipper, ant. insertion to tip (%)	♂	0			9	24.1-27.4	26.2±0.8
	♀	18	15.8-18.9	16.3±1.8	10	21.9-26.2	23.7±1.0

1) Mean and its 95% confidence range are indicated.

The comparison in Table 2 shows no significant difference between the two species in the length from tip of snout to eye, but certainly significant difference in the length of the tail portion. The length of tail is 3.1% (female) to 3.4% (male) shorter in *G. macrorhynchus*. If the proportion of other segment is calculated from Table 2, the length between anus and umbilicus is 23.3% in the female of this species and 0.9% shorter than the same sex of *G. melaena*. The segment between eye and anterior insertion of flipper and that between anterior insertion of flipper and umbilicus are 7.3% and 26.7% in female *G. macrorhynchus* respectively. These figures are 1.7% and 2.5% larger than correspoding figures of female *G. melaena*. The eye to flipper segment of male *G. macrorhynchus* is 6.3% and also 0.9% larger than the value of *G. melaena*. Though in male *G. macrorhynchus* the position of umbilicus is not accurately calculated, the length between anterior insertion of flipper and anus is 49.4%. This is almost same with the corresponding value of the female 50.0%. Accordingly we conclude that *G. macrorhynchus* has shorter tail and umbilicus to anus egments, and larger eye to umbilicus segment.

In Sergeant (1962a), the measurement no. 8 "Notch of flukes to back of dorsal fin" is specified as "Measured to point vertically below apex of fin". This measurement is considered to be same with our measurement no. 8 "Notch of flukes to apex of dorsal fin meaured parallel to the long axis of body". Then, Table 2 suggests that the tip of dorsal fin of *G. macrorhynchus* is situated 2.8% (male) to 4.9% (female) anterior to the corresponding position of *G. melaena*. This is different from the conclusion obtained by Sergeant (1962a) on the position of the anterior end of the dorsal fin, where no significant difference between the species was detected.

About the appendages, the height of dorsal fin is measured in the present study from the base to the apex. This is not same with the ordinary measurement of vertical height of dorsal fin. Though present method may give a smaller value, the height in the adult *G. macrorhynchus* is from 33 to 50 cm in males and 20 to 34 cm in females. And the similar but different measurements of *G. melaena* in Sergeant (1962a) are slightly smaller than these range giving the value from 34 to 46 cm in males and from 25 to 32 cm in females. This is a suggestion that *G. macrorhynchus* may have the higher dorsal fin. Based on the same principle, we measured the width between the apices of tail flukes which certainly give a smaller figure than the measurement of "Total spread of flukes". Though the difference can be significant in fetuses, it may not be large in the adult. The comparison between Fig. 7 of Sergeant (1962a) and our Fig. 18 shows that the mean values of the distance between apices in *G. macrorhynchus* situate above the range of the total spread of tail flukes of *G. melaena*. This is an indication that the latter species may have smaller tail flukes. No discussion will be necessary on the shortness of the flipper of *G. macrorhynchus* compared to that of *G. melaena* (Table 2).

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APPENDIX EXTERNAL MEASUREMENTS OF *G. MACRORHYNCHUS* OFF TAIJI**

No.	1*	2*	3*	4*	5*	6*	7*	8*	9	10	11	12
Sex	♂	♂	♂	♂	♂	♂	♂	♂	♂	♂	♂	♂
1	48	58	67	101	127	129	132	140	182	241	234	244
2	5.5	7	8	12	18	18	16	18	20	26	26	25
3	5	7	7.5	11.5	18	18	18	18	22	—	26	25
4	4	5.5	6.5	10	15	15	14	15	17	21	21	23
5	10.5	12	14	22	29	26	29	29	37	46	—	—
6	19	20.5	26	44	57	50	58	55	64	83	—	—
7	2.8	3.2	3.5	5	6.2	5.8	6	7	9	—	—	—
8	25	29.5	34	51	64	66	66	71	85	—	—	—
9	14	17	21.5	32	40	39	39	43	60	73	—	79
10	17	21.5	26	40	51	48	50	55	74	91	—	101
11	23	28	34	51	66	61	66	69	100	127	—	124
12	9.5	—	—	—	—	—	—	—	34	—	40	—
13	7	—	—	—	—	—	—	—	26	—	31	—
14	—	12	14	24	30	26	29	30	35	42	41	48
15	3	3.2	3.8	6.5	8	8	8	8	10	12	12	14
16	8	9	10	15	22	22	27	29	40	44	—	48
17	3	3.4	3	7	10	10.5	12	19	16	20	—	—
18	4.5	5	6.5	10	12	—	12	14	16	21	22	21
19	11	13	15	21	26	28	35	32	42	55	62	20

* Fetus. ** For position of measurement see text.

APPENDIX Continued.

No.	13	14	15	16	17	18	19	20	21	22	23	24	25
Sex	♂	♂	♂	♂	♂	♂	♂	♂	♂	♂	♂	♂	♂
1	253	265	267	279	282	292	302	308	317	325	328	341	343
2	30	30	31	30	28	29	34	31	35	35	35	38	40
3	29	30	31	30	28	31	36	34	37	38	35	39	35
4	25	25	25	25	23	25	27	26	30	30	29	31	34
5	48	51	—	49	—	—	—	—	56	57	57	59	—
6	90	92	—	102	—	—	—	—	118	115	107	126	—
7	10	—	—	10	—	—	—	—	12	12	11	13	11
8	—	128	—	147	—	160	156	—	171	172	184	—	—
9	75	76	81	95	—	99	94	99	98	100	—	110	111
10	97	98	105	119	—	128	123	129	125	128	147	142	143
11	130	—	141	—	—	169	—	173	172	—	—	189	187
12	42	—	52	—	40	—	51	55	60	57	—	65	—
13	31	—	40	—	31	—	39	41	46	43	—	50	—
14	49	—	54	54	42	—	55	58	65	61	68	70	18
15	14	13	15	15	13	—	16	16	17	18	—	19	18
16	50	54	49	60	—	59	55	57	71	73	62	70	—
17	20	20	20	22	—	21	24	24	23	25	25	27	—
18	20	22	24	23	23	27	25	25	27	29	26	28	29
19	61	66	70	78	73	76	73	77	84	85	75	94	91

APPENDIX Continued.

No.	26	27	28	29	30	31	32	33	34	35	36	37	38	39
Sex	♂	♂	♂	♂	♂	♂	♂	♂	♂	♂	♂	♂	♂	♂
1	344	346	352	355	362	363	366	370	385	391	392	394	396	418
2	37	37	38	37	36	—	38	31	41	43	40	40	41	42
3	40	38	40	41	42	—	39	33	44	43	42	42	39	40
4	33	30	31	33	32	—	30	27	33	37	36	35	34	34
5	61	—	60	61	64	—	65	—	69	69	—	68	64	72
6	127	—	124	116	117	—	119	—	136	137	—	128	116	142
7	12	—	13	—	12	—	13	—	—	—	—	—	—	—
8	187	—	192	198	208	203	214	200	223	214	—	227	228	240
9	116	112	116	121	122	—	118	131	128	128	128	134	134	143
10	147	142	147	157	156	—	152	160	160	164	—	173	171	182
11	—	—	—	—	—	—	—	—	—	—	—	—	225	—
12	65	—	—	—	—	—	—	—	—	—	—	—	—	—
13	52	—	—	—	—	—	—	—	—	—	—	—	—	—
14	70	63	76	66	61	—	66	—	78	76	76	79	67	82
15	20	17	20	19	18	—	18	—	20	22	21	21	21	22
16	70	62	71	64	65	—	67	—	79	86	77	—	80	—
17	27	25	29	28	29	—	26	—	36	31	31	—	29	31
18	29	—	32	28	26	—	29	27	31	33	—	—	28	27
19	98	—	98	78	91	—	83	91	99	102	—	—	95	110

APPENDIX Continued.

No.	40	41	42	43	44	45	46	47	48	49	50	51	52
Sex	♂	♂	♂	♂	♂	♂	♂	♂	♂	♂	♂	♂	♂
1	424	424	432	434	439	445	453	455	459	473	475	482	491
2	40	41	40	38	47	42	43	44	40	44	46	46	48
3	40	43	39	38	50	45	40	44	42	41	46	43	45
4	35	37	33	33	43	35	39	36	35	36	42	39	39
5	74	—	68	69	71	68	71	70	71	73	78	73	76
6	136	—	156	131	151	151	162	148	153	142	159	155	161
7	14	—	15	14	14	—	14	14	—	—	—	14	14
8	240	—	249	238	254	241	275	260	—	259	292	272	291
9	145	141	145	146	155	161	155	149	163	170	173	165	182
10	190	185	192	194	198	204	205	194	212	225	222	218	222
11	—	—	—	—	—	—	—	—	274	—	—	—	—
12	—	—	—	—	—	—	—	—	—	—	—	—	—
13	—	—	—	—	—	—	—	—	—	—	—	—	—
14	83	—	100	85	92	92	105	92	—	93	95	99	97
15	23	—	—	25	24	24	25	22	—	25	26	26	26
16	—	—	96	97	93	95	105	98	—	97	99	102	105
17	34	33	36	33	45	41	43	38	37	50	50	45	40
18	33	34	34	34	38	35	33	34	—	36	32	30	38
19	109	111	106	101	100	103	139	116	—	147	125	142	135

APPENDIX Continued.

No.	53*	54*	55*	56*	57*	58*	59*	60*	61*	62	63	64	65
Sex	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀
1	27	29.8	30.6	35.8	55	67	127	130	130	190	190	200	200
2	3	3.5	3.5	4	7	9	19	19	16	24	17	25	25
3	1.6	1.8	2.5	2.8	6	8	19	20	15	24	18	26	25
4	2.5	2.5	2.5	3	5	7	17	17	14	21	14	22	21
5	6	6.5	7	7.8	12	14	28	29	28	39	34	43	—
6	10.5	11.5	12	14	21	24	54	55	—	69	62	72	—
7	1.8	1.8	1.8	2	2.8	3	6	6	5	—	9	—	—
8	14.5	15.5	15.8	18.5	26	32	65	68	73	99	96	104	—
9	8	9	9.8	11	17	20	42	41	39	59	63	61	67
10	8.5	9.5	10.5	11.5	18.5	22	46	44	43	65	68	68	72
11	12.5	15	15.5	17	27.5	32	66	63	66	99	105	—	—
12	5	5.5	5.8	7	10	—	—	—	—	—	33	—	34
13	4	4	4.4	5.5	7	—	—	—	—	—	25	—	26
14	—	—	6.8	—	—	12	18	28	27	35	35	31	35
15	1.5	1.8	1.6	2	3	3.5	8	7	7	11	10	10	11
16	4	5	5.4	6	9.5	10.5	26	27	26	85	39	39	35
17	1.5	1.5	2.0	2.5	3.5	3.5	11	12	12	16	15	16	15
18	3	2.5	3.2	3.5	4.8	4.5	13	12	12	—	17	—	18
19	5.6	6	6.6	7	10.5	13	31	32	27	48	44	49	54

APPENDIX Continued.

No.	66	67	68	69	70	71	72	73	74	75	76	77	78
Sex	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀
1	228	254	256	260	268	282	283	286	287	290	294	304	307
2	28	32	29	25	30	32	32	35	34	—	37	30	30
3	29	31	30	29	32	34	36	38	35	—	35	34	31
4	26	26	25	21	25	27	29	30	28	—	34	26	24
5	48	—	51	47	50	51	52	56	—	—	58	56	50
6	84	—	90	—	100	99	96	92	—	—	101	—	—
7	—	—	11	8	10	—	11	9	—	—	12	—	—
8	126	136	144	143	—	149	156	161	—	—	157	160	—
9	76	82	78	85	84	92	94	96	96	—	95	—	98
10	84	92	86	94	95	100	102	103	105	—	103	—	125
11	125	—	136	138	138	—	—	—	—	—	—	—	—
12	—	42	43	—	47	—	—	—	—	49	—	—	54
13	—	30	33	—	35	—	—	—	—	35	—	—	41
14	42	46	46	44	50	54	49	47	—	50	54	—	58
15	12	13	12	13	15	15	13	15	—	15	15	—	16
16	43	45	—	46	51	53	43	53	60	58	50	—	64
17	19	17	—	21	17	22	23	21	25	20	24	—	23
18	18	20	21	21	—	24	22	20	23	—	21	—	25
19	55	70	60	60	—	73	74	70	78	—	74	—	77

APPENDIX Continued.

No.	79	80	81	82	83	84	85	86	87	88	89	90	91
Sex	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀
1	312	313	320	321	322	326	326	327	328	334	334	335	338
2	32	34	33	31	30	33	33	33	32	35	31	38	31
3	37	36	35	33	31	35	35	38	37	37	36	29	34
4	26	29	28	25	23	26	27	28	26	28	26	24	27
5	61	—	57	54	51	56	54	63	58	58	59	—	56
6	107	—	—	103	104	113	108	114	112	107	111	—	115
7	—	—	—	12	12	12	12	11	12	12	12	—	13
8	169	182	—	165	182	174	170	181	189	183	190	190	—
9	110	108	108	101	103	104	101	105	106	110	112	114	113
10	120	118	121	113	116	113	115	117	122	124	125	124	126
11	—	—	—	175	183	—	—	—	—	191	—	192	—
12	—	58	54	58	56	55	62	—	—	59	59	—	64
13	—	43	42	41	42	41	49	—	—	45	44	—	48
14	54	63	59	62	60	63	68	63	62	67	65	62	70
15	16	16	—	17	16	17	18	18	18	18	17	—	18
16	49	44	61	60	56	68	65	66	67	64	71	59	73
17	22	19	20	22	20	27	23	29	24	25	22	21	25
18	—	26	26	26	26	24	25	26	25	28	27	27	25
19	—	85	73	85	83	88	81	87	86	92	91	85	90

APPENDIX Continued.

No.	92	93	94	95	96	97	98	99	100	101	102	103	104	105
Sex	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀
1	338	340	340	341	341	342	342	343	343	344	344	345	345	345
2	30	34	35	35	34	34	32	37	—	—	—	33	33	31
3	30	35	35	37	36	35	35	38	—	—	—	35	37	32
4	23	28	30	29	27	28	25	34	—	—	—	27	26	24
5	—	58	65	63	55	61	56	60	—	—	—	60	59	58
6	—	115	116	115	110	116	110	112	—	—	—	112	111	111
7	—	13	—	12	12	—	12	—	—	—	—	12	—	12
8	197	192	176	188	201	195	—	193	—	192	—	190	198	196
9	110	111	120	110	109	120	111	117	120	—	102	113	112	112
10	120	129	130	126	119	134	123	127	131	—	115	127	129	126
11	—	—	—	—	188	—	—	—	198	—	193	—	—	—
12	—	58	—	—	56	—	54	—	—	—	—	—	—	55
13	—	43	—	—	42	—	42	—	—	—	—	—	—	42
14	—	67	68	67	66	61	57	66	—	—	—	61	71	59
15	—	18	18	19	18	18	17	18	—	—	—	17	18	18
16	60	60	60	66	61	68	65	60	—	—	—	60	58	71
17	22	24	30	25	20	28	25	28	—	—	—	21	26	26
18	—	26	20	28	28	28	25	23	—	—	—	27	26	28
19	—	87	88	92	85	95	81	95	—	—	—	85	93	81

APPENDIX Continued.

No.	106	107	108	109	110	111	112	113	114	115	116	117	118	119
Sex	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀
1	346	347	347	347	347	348	348	352	352	353	353	354	354	354
2	32	35	34	32	—	38	33	38	31	35	33	37	36	32
3	32	40	35	32	—	40	35	39	34	35	35	38	36	35
4	26	29	28	26	—	35	27	32	27	29	28	28	30	26
5	57	60	58	55	—	57	57	66	—	59	60	60	59	58
6	122	125	122	110	—	114	112	123	—	121	112	119	118	113
7	13	12	13	11	—	11	12	11	—	12	13	—	12	13
8	203	188	—	—	192	206	—	—	196	196	191	201	206	190
9	111	119	110	120	—	118	111	115	126	122	119	115	118	122
10	124	129	123	132	—	128	123	130	137	141	132	128	128	138
11	195	—	191	—	—	—	197	—	211	—	—	—	—	—
12	60	—	60	—	—	—	59	—	—	—	61	—	—	64
13	45	—	45	—	—	—	45	—	—	—	43	—	—	47
14	65	74	68	65	—	62	68	—	60	63	67	63	61	70
15	18	19	17	17	—	19	18	—	—	18	18	17	16	18
16	64	70	67	67	—	63	73	70	63	77	69	62	66	72
17	24	24	25	23	—	32	25	27	24	26	22	23	27	21
18	27	28	27	27	—	24	26	—	30	30	28	—	24	25
19	90	106	93	86	—	90	93	—	80	—	101	78	91	104

APPENDIX Continued.

No.	120	121	122	123	124	125	126	127	128	129	130	131	132
Sex	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀
1	354	355	355	353	356	357	357	357	358	358	358	358	360
2	—	35	34	39	34	37	32	—	39	36	34	34	36
3	—	37	35	34	37	33	34	—	41	37	39	37	39
4	—	30	29	33	28	32	27	—	36	29	31	27	31
5	—	64	60	—	51	65	56	—	68	59	62	54	62
6	—	116	115	—	105	120	112	—	—	119	116	110	129
7	—	13	13	—	11	11	13	—	13	13	12	—	13
8	—	198	201	—	189	206	—	189	205	—	215	193	—
9	101	122	122	112	110	120	115	—	123	122	114	112	122
10	125	132	137	125	124	132	130	—	136	137	126	129	135
11	—	—	—	200	—	—	—	—	—	—	—	—	—
12	—	—	—	—	60	—	60	—	—	63	—	58	—
13	—	—	—	—	48	—	45	—	—	47	—	43	—
14	—	67	65	60	67	65	66	—	81	71	64	67	76
15	—	19	17	17	18	18	17	—	21	18	18	18	20
16	—	71	67	65	73	70	65	—	79	—	66	70	69
17	—	33	20	25	25	23	24	—	33	24	32	22	25
18	—	28	29	28	29	—	27	—	29	29	25	28	30
19	—	99	82	91	90	83	89	—	102	94	90	90	96

APPENDIX Continued.

No.	133	134	135	136	137	138	139	140	141	142	143	144	145	146
Sex	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀
1	361	361	361	361	363	364	365	365	365	367	369	369	371	372
2	39	37	—	—	34	35	33	32	32	—	37	37	38	33
3	40	32	—	—	35	35	36	36	32	—	38	41	35	36
4	35	32	—	—	27	28	27	28	29	—	33	29	31	27
5	67	—	—	—	62	60	58	54	—	—	66	63	67	60
6	113	—	—	—	118	121	114	113	—	—	128	122	119	106
7	—	12	—	—	12	12	12	12	—	—	—	13	12	12
8	199	—	198	202	195	202	—	—	—	—	205	218	213	—
9	118	116	111	—	121	125	—	117	—	131	127	127	127	120
10	131	127	124	—	133	140	—	126	—	143	143	138	—	136
11	—	200	198	—	209	—	—	205	—	208	—	—	—	—
12	—	—	—	—	—	63	—	—	—	—	—	—	—	—
13	—	—	—	—	—	47	—	—	—	—	—	—	—	—
14	68	65	—	—	72	68	—	69	—	—	74	67	70	66
15	20	16	—	—	20	18	—	18	—	—	20	18	19	18
16	70	—	—	—	75	73	70	—	—	—	76	—	72	71
17	30	—	—	—	28	24	24	—	—	—	29	31	27	27
18	26	28	—	—	30	28	—	—	28	—	29	29	30	28
19	100	85	—	—	98	95	—	—	86	—	102	100	88	84

APPENDIX Continued.

No.	147	148	149	150	151	152	153	154	155	156	157	158	159	160
Sex	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀
1	373	373	374	374	374	376	377	378	378	381	387	388	388	392
2	39	36	38	36	33	35	37	40	36	34	35	36	36	39
3	37	37	41	36	37	38	41	37	42	39	38	38	—	40
4	35	31	33	30	27	29	30	36	31	28	32	30	31	34
5	65	—	—	60	66	65	—	67	—	59	—	62	68	68
6	122	—	—	116	112	121	—	126	—	123	—	124	123	134
7	—	—	—	13	12	—	—	—	—	12	—	—	14	14
8	215	—	—	214	192	—	—	220	—	204	—	229	223	—
9	121	—	123	126	117	118	—	122	126	132	117	126	130	131
10	136	—	142	140	132	133	—	135	141	146	135	140	144	146
11	—	—	—	—	—	212	—	—	—	—	212	—	—	—
12	—	—	—	—	65	—	—	—	—	—	—	—	—	—
13	—	—	—	—	47	—	—	—	—	—	—	—	—	—
14	67	—	88	66	72	73	—	71	72	73	71	63	78	75
15	20	—	17	18	18	20	—	20	19	20	20	17	19	20
16	65	—	84	73	77	—	—	80	75	74	70	82	66	62
17	30	—	34	28	28	—	78	33	30	—	28	26	20	29
18	30	—	—	30	28	—	30	28	—	25	—	28	28	28
19	95	—	—	83	100	—	—	100	—	91	—	82	91	100

EXPLANATION OF PLATES

PLATE I

Figs 1 and 2. Probable *G. macrorhynchus* showing the saddle mark behind the dorsal fin. 11 June 1975. 40°38′N, 142°15′E. Surface water temperature 15.9°C. (Photo by T. Kasuya)

Fig. 3. Full term fetus, 144 cm, female. 3 June 1980. Taiji. (Photo by T. Kasuya)

Fig. 4. Adult female, 345 cm in body length. The dorsal fin and keel on the dorsal edge of tail peduncle are bent on the right side. 16 January 1976. Taiji. (Photo by T. Kasuya)

Figs 5 and 6. Adult male, 479 cm in body length. 9 October 1976. Taiji. (Photo by T. Kasuya)

PLATE II

Fig. 1. Same individual as in Plate I, Fig. 1.

Fig. 2. Adult female, 237 cm in body length. 2 June 1980. Taiji. (Photo by T. Kasuya)

Figs 3 and 4. Adult male, 498 cm in body length. 3 June 1980. Taiji. (Photo by T. Kasuya)

Fig. 5. Full grown male, 518 cm in body length. 14 January 1976. Taiji. (Photo by T. Kasuya)

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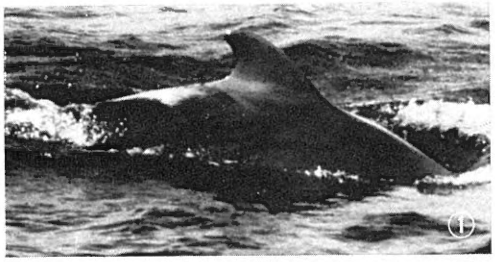
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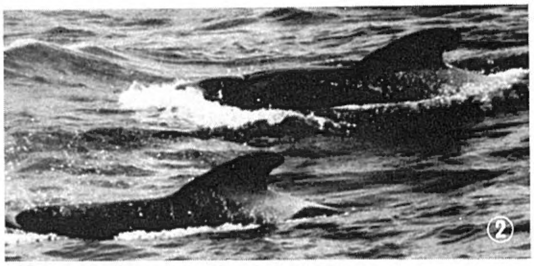
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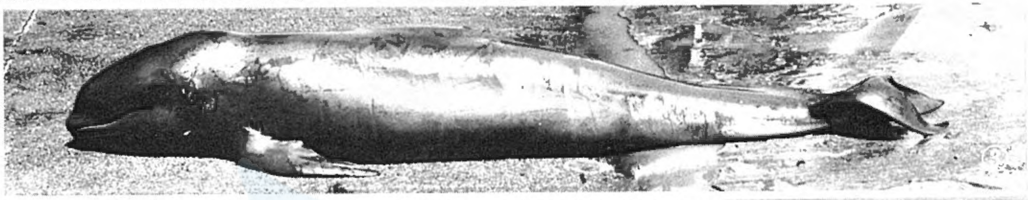
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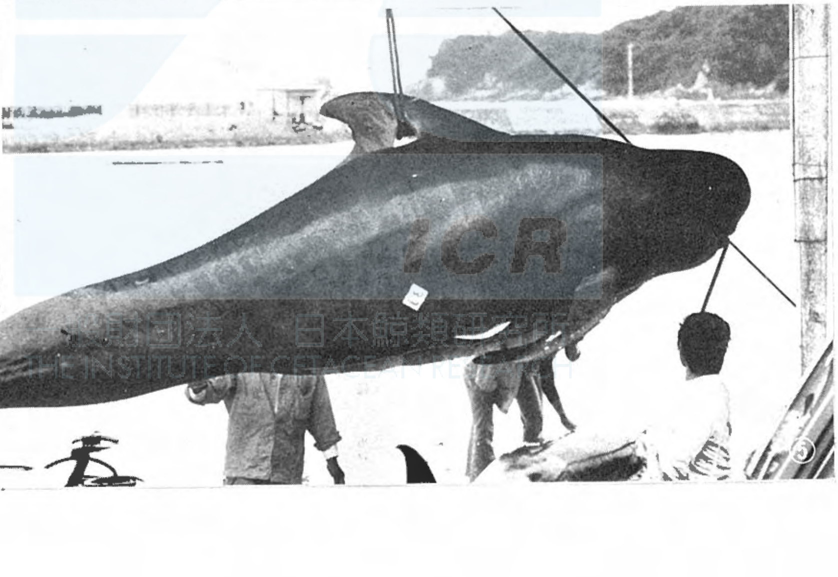
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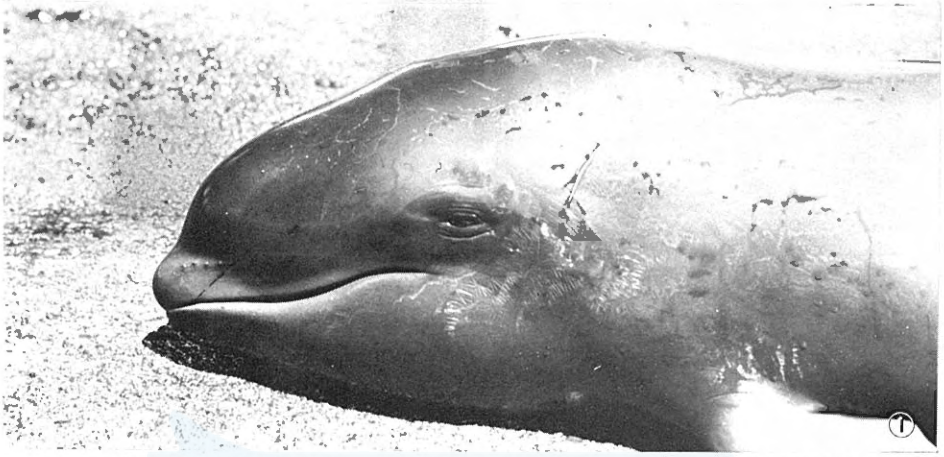
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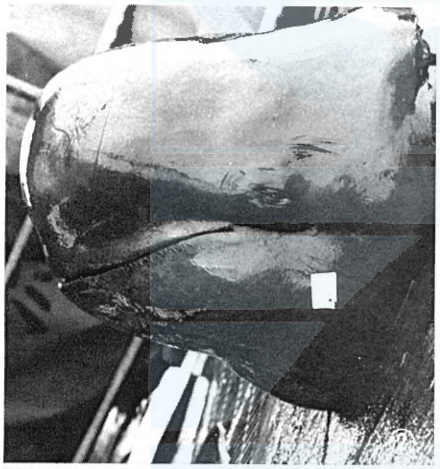
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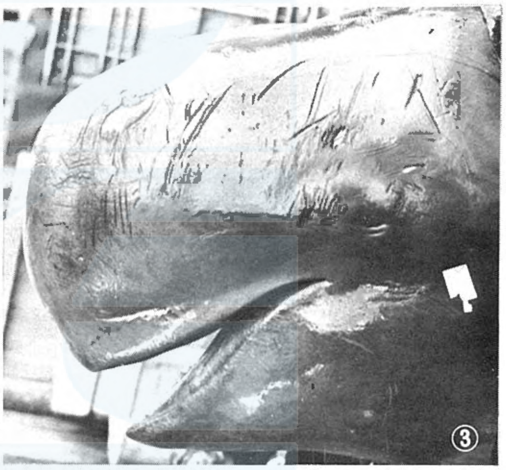
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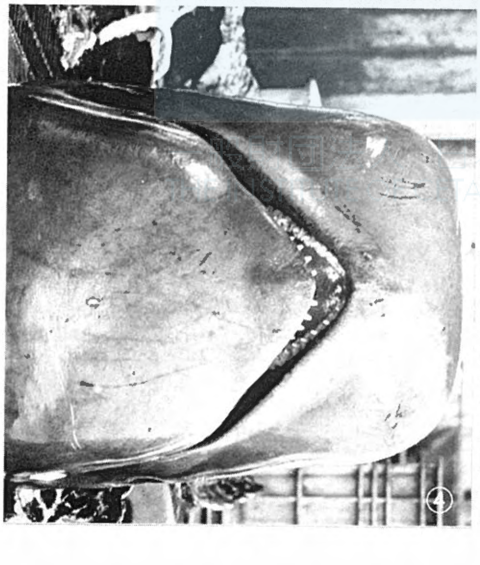
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DIATOM FILMS ON WHALES IN SOUTH AFRICAN WATERS

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ABSTRACT

Diatoms found on the skin of minke whales and 4 species of toothed whales in the waters off South Africa were examined. Typical *Cocconeis ceticola* was common on minke whales and was also found on a southern bottlenose whale. *C. ceticola* f. *constricta* was, on the other hand, found only on a southern bottlenose whale and *C. ceticola* f. *berardiusii* was found on a Cuvier's beaked whale. *Stauroneis olympica* was found on a Cuvier's beaked whale, a killer whale and a strap-toothed whale. *Gomphonema aestuarii* and *Synedra* sp. were also found on a strap-toothed whale, while an unidentified *Navicula* sp. was also found on a minke whale and a strap-toothed whale.

On the assumption that typical *C. ceticola* is only contracted in high latitudes, its occurrence on whales in the waters off South Africa shows that these animals may recently have migrated from colder waters.

INTRODUCTION

Many diatom species on whales have been described in the North Pacific and in the Antarctic (Hart, 1935; Hustedt, 1952; Nemoto, 1956, 1958). Diatom films on the skin of whales have been mostly found in the waters of high latitudes, and they have generally been considered common in the colder waters of both hemispheres. There are few observations of diatoms on whales caught in the waters off South Africa (Mackintosh and Wheeler, 1929; Best, 1969). It is generally accepted that diatoms (mainly *Cocconeis ceticola* and its related forms) propagate and form films on the skin of cetaceans in colder waters and are not so common in temperate waters, although Gambell (1972) has speculated that the lack of ectoparasites on whales at Durban may have been due to the greater rate of epidermal decomposition in the higher sea temperatures prevailing there.

In recent studies of whales caught or stranded on the coast of South Africa, 22 specimens of diatom films from skin or teeth have been collected. These specimens are examined taxonomically and the occurrence of diatoms as skin films of whales is discussed in relation to hydrographic conditions.

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No. 32, 1980, 97–103

MATERIALS AND METHODS

Diatom samples were collected between 1969 and 1973 by one of us (Best) from whales caught or stranded around South Africa. Host species included both baleen and toothed whales (Table 1).

Diatom specimens were mostly collected from the skin but one diatom film was collected from the teeth of a strap-toothed whale. The samples from minke and bottlenose whales were collected immediately after death while they were alongside or on the deck of the catcher. Those from the other species were collected from stranded animals some unknown time after death. All samples were preserved in 10% formalin/sea water with the skin of the whales. The diatom samples were then scratched from the skin and washed with distilled water and rinsed three or four times. After preservation in potassium permanganate for 24 hours, hydrochloric acid was added and the samples kept for a further 24 hours. After boiling for 5 minutes, the samples were washed and rinsed several times, and frustules of diatoms were kept on plates. Double coating of carbon and gold was used for electron

TABLE 1. DIATOM SAMPLES* FROM WHALES FROM SOUTH AFRICA

Specimen no.	Date collected	Species	Length (m)	Sex	Locality†
69/10	July 5 '69	Killer whale (*O. orca*)	6.10	M	Bordjies Drif Cape Point
73/10	Oct. 25 '73	Cuvier's beaked whale (*Z. cavirostris*)	5.77	F	Still Bay
75/1	Jan. 19 '75	Southern bottlenose whale (*H. planifrons*)	6.43	M	33°36′ S 28°04′ E
78/15	Apr. 6 '78	Strap-toothed whale (*M. layardii*)	5.46	M	Milnerton
U71/2200	Aug. 28 '71	Minke whale (*B. acutorostrata*)	8.53	M	29°30′ S 32°51′ E
U71/2201	Aug. 28 '71	„	7.62	M	„ „
U71/2202	Aug. 29 '71	„	9.14	F	29°57′ S 31°19′ E
U71/2203	Aug. 29 '71	„	7.62	F	30°46′ S 31°19′ E
U71/2211	Aug. 30 '71	„	7.92	F	30°48′ S 31°58′ E
U71/2232	Aug. 31 '71	„	8.23	M	31°10′ S 30°55′ E
U71/2243	Sept. 5 '71	„	8.23	M	31°06′ S 31°01′ E
U71/2245	Sept. 5 '71	„	8.23	F	31°11′ S 30°46′ E
U71/2313	Sept. 16 '71	„	8.23	F	31°05′ S 31°47′ E
U71/2315	Sept. 18 '71	„	8.84	M	30°04′ S 31°35′ E
U73/1255	June 24 '73	„	9.14	M	30°42′ S 33°25′ E
U73/1256	June 24 '73	„	8.64	F	„ „
U73/1299	June 26 '73	„	8.28	M	31°10′ S 31°01′ E
U73/1304	June 27 '73	„	8.15	M	30°32′ S 31°49′ E
U73/1306	June 27 '73	„	8.28	M	30°22′ S 32°04′ E
U73/1446	July 17 '73	„	8.86	M	31°15′ S 31°25′ E
U73/1559	July 29 '73	„	8.43	M	30°27′ S 31°17′ E
U73/1839	Sept. 28 '73	„	8.61	F	29°45′ S 32°12′ E

* All samples taken from skin except 78/15 where sample taken from teeth.

† All animals collected at sea apart from 69/10, 73/10 and 78/15, which were all stranded animals.

microscopy. The specimens were examined with both scanning and ordinary electron microscopes.

The scanning electron microscope JSM-35 was mainly used for the identification of species. Some species are still under examination, but their preliminary identification is described in this paper.

DESCRIPTION OF SPECIES

The species of diatoms identified and the host species of whales involved are shown in Table 2.

TABLE 2. DIATOMS OCCURRING ON THE SKIN AND TEETH OF WHALES IN THE WATERS OFF SOUTH AFRICA

	Minke whale	Southern bottlenose whale	Cuvier's beaked whale	Killer whale	Strap-toothed whale
Cocconeis ceticola (typical form)	18	1	—	—	—
C. ceticola f. *constricta*	—	1	—	—	—
C. ceticola f. *berardiusii*	—	—	1	—	—
Stauroneis olympica	—	—	1	1	1
Navicula sp.	1	—	—	—	1
Gomphonema aestuarii	—	—	—	—	1
Synedra sp.	—	—	—	—	1

Only pennate diatoms were found in the diatom films examined. There were clear differences between the diatom species on different host whales. The typical form of *Cocconeis ceticola* Nelson was found on every minke whale but only a very few individuals on one of the toothed whales examined (southern bottlenose whale). On the skin of the southern bottlenose whale, some specimens of *C. ceticola* were somewhat deformed and a clear constriction was observed. The edge of the valves was sometimes absent as shown in Fig. F in Plate I. Small numbers of a slender form of *C. ceticola* were also found on this whale. On the Cuvier's beaked whale the more slender form of *C. ceticola* was found, but with no constriction at the edge where the stauros of the lower raphe reaches the edge. This type of *C. ceticola* has been found previously on the skin of Baird's beaked whale *Berardius bairdii* (Kriashtorin, 1962), and is named as the form *berardiusii*.

The constricted form of *Cocconeis ceticola* has often been observed in toothed whales. As indicated in Plate I F, the constricted parts sometimes lack the outer edge of the valve, and the hole on the inside is deformed as indicated in Plate I H. The hole in the edge of typical *Cocconeis ceticola* is rather similar to other holes along the edge (shown in Plate I B, C) or a little deformation is observed as shown in Plate I E.

Four other species of pennate diatoms were found on toothed whales. *Stauroneis olympica* Hustedt was found on the Cuvier's beaked whale, killer whale and strap-toothed whale. This species has clear pseudosepten from the tips of the cell, which is different from the pseudosepten and the shape of the tip of *S. omurai* Nemoto (Nemoto, 1956) found on sperm whales in the North Pacific. The shape of *S. olympica* as originally described (Hustedt, 1952) is more slender than these specimens and the structure of the stauros may be somewhat different. However, considering the varieties within one diatom species on different species of whales, these specimens may be attributed to the *Stauroneis olympica* complex. The closely related species *S. aleutica* reported by Nemoto (1956) can also be put in this group. *Stauroneis* diatoms were also present on sperm whales off South Africa, Chile and Australia (Best, 1969). The presence of *Navicula* species (possibly *Stauroneis olympica*, as described from the epiphytes on barnacles on a humpback whale from the Antarctic) was described on a sperm whale landed in the Outer Hebrides (Hart, in Clarke, 1956). This species is possibly cosmopolitan or bipolar on sperm whales and toothed whales (Hart, in Best, 1969).

Small naviculoid diatoms were found on the strap-toothed whale, and were also found in the film of *Cocconeis ceticola* on the skin of one minke whale. *Gomphonema aestuarii* Cleve which is also described by Giffen (1966) in South African waters, and *Synedra* sp., which is very close to *S. tabulata* (Ag.) Kupzing (Harrison and Thurley, 1974), were also found on the teeth of this strap toothed whale.

DISCUSSION

Studies of skin films of *Cocconeis ceticola* have suggested that these diatoms are most common on cetaceans in the colder water of high latitudes.

Mackintosh and Wheeler (1929) concluded that such diatom films on whales are undoubtedly contracted in the austral summer in Antarctic or sub-Antarctic waters. Hart (1935) described the general tendency for the rate of diatom film infestation of blue and fin whales to increase as the season progressed at South Georgia. Gambell (1968) also noted the diatom infestations on sei whales caught at South Georgia, and that sei whales newly arrived from the breeding grounds in the middle of the summer season do not bear diatoms. However, Mackintosh and Wheeler (1929) also noted that small spots of *C. ceticola* were seen on a few immature (fin and blue) whales at Saldanha Bay, South Africa. Best (1969) and Bannister (1969) recorded the presence of *C. ceticola* on sperm whales (mostly large or medium-sized males) off Donkergat (South Africa) and Albany (Western Australia) respectively, during the autumn and winter. *Cocconeis* diatoms have also been recorded from whales in the Eastern Pacific off South America (A. Aguayo L., pers. comm.). Clarke (1956) found no clear infestation with diatoms of *Cocconeis* type on the sperm whales caught in the Azores.

Diatoms in the northern part of the North Pacific, where many diatoms are found on the baleen and sperm whales, have been described by Nemoto (1956). Diatom infestation is common in the Bering Sea and its adjacent waters, while in the coastal waters, *Cocconeis* diatoms are often observed on both sides of the Pacific; off British Columbia (Pike, 1953) on the eastern side, and in the Okhotsk Sea and off Hokkaido waters in Japan on the western side (Omura, 1950). *Cocconeis ceti-*

cola Nelson is the most common diatom on baleen whales. The varieties and forms of *C. ceticola* in the North Pacific have been described and discussed by Usachev (1940), Nemoto (1956, 1958), Nemoto *et al.* (1977) and Kriashtorin (1962). According to these authors, the typical *Cocconeis ceticola* form is only described from baleen whales. Kriashtorin (1962) reported some large-sized *C. ceticola* as a new variety, *C. ceticola* var. *arctica*, but this is clearly the same type of *C. ceticola* from its shape and size. The fact that the typical form of *C. ceticola* has now been found on the skin of minke whales caught off South Africa suggests that minke whales are similar to other rorquals as host-types. *C. ceticola* has also been recorded from minke whales in the Antarctic (Ohsumi *et al.*, 1970), but no remark was made concerning the type of *C. ceticola* involved.

Cocconeis ceticola f. *constricta* Nemoto is found on the skin of sperm whales in the North Pacific (Nemoto, 1956). *C. ceticola* has also been recorded from sperm whales off Donkergat, South Africa (Best, 1969) and off Albany, Western Australia (Bannister, 1969): no distinction was made, however, between form *constricta* and typical *ceticola*. *Cocconeis* diatoms found on the *Hyperoodon planifrons* in the waters off East London, South Africa, were of two types. A very few specimens of typical *C. ceticola* forms were found, but the rest were all constricted forms. Constricted forms found in this study show some variation although there was no clear boundary to separate them. One was typical *C. ceticola* f. *constricta* which was previously found on sperm whales (Nemoto, 1956). Kriashtorin (1962) also described the same type from sperm whales in the Far Eastern seas. It was clearly shown that the edge of the raphe-valve where the stauros reaches was absent or deformed. The second type of *constricted* form was similar to *C. ceticola* f. *berardiusii* which was first described by Kriashtorin (1962) from *Berardius bairdii*. This type (Kriashtorin, 1962 in Fig. 1e) is the same as the type M in Fig. 3 in Nemoto (1958), and was common among the diatoms on the *Z. cavirostris* examined in this paper. As no *Cocconeis* specimen was found on the killer whale in this study, it is difficult to assess the position of *Cocconeis orcii* Kriashtorin described by Kriashtorin (1962). From the surface structure shown by him, *C. orcii* is one variety of *C. ceticola* and is not a valid species.

The global distribution and occurrence of parasitic diatoms on whales are interesting. As stated previously, *Cocconeis* diatoms are mainly described from the high latitudes of the North Pacific and Southern Hemisphere, where they can form films over a large part of the body (Bennett, 1920). *Cocconeis* diatom infestation on whales in lower latitudes is usually rarer and much smaller in extent ("small spots"-Mackintosh and Wheeler, 1929), so it might be concluded that such animals are recent migrants from higher latitudes. The only resident cetacean population outside the Antarctic known to carry *Cocconeis* films is the Franciscana dolphin, which lives in water from 13–23°C (Nemoto *et al.*, 1977). Presumably therefore it is possible to contract *Cocconeis* films in water as warm as 13°C, but as little is known about the seasonal incidence of diatoms on or movements of the Franciscana dolphin it is impossible to give an upper limit to the temperature range in which *C. ceticola* can survive. On the assumption that the films of *Cocconeis* on the larger cetacea are contracted only in high latitudinal waters, the presence of *C. ceticola* on minke whales off Durban from June to September indicates that the animals have recently arrived from colder waters, and that the migration may be more protracted over time than for other baleen whale species. The presence of *Cocconeis* films on *H. planifrons* and *Z. cavirostris* off South Africa is the first indication that these species may also migrate from Antarctic or sub-Antarctic to warmer waters.

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EXPLANATION OF PLATE

PLATE I

Figures A.D.F.G. are taken by light microscope, B.C.E.H.K.L. are taken by scanning electron microscope and I.J. are taken by Electron microscope.

A.*—raphevalve of *Cocconeis ceticola* Nelson typical form found on minke whale (*B. acutorostrata*) U73/1299. B.—raphevalve of *C. ceticola* typical form on minke whale U73/1304. C.—raphevalve of *C. ceticola* typical form on minke whale U71/2200. D.*—raphevalve of *C. ceticola* typical form on minke whale U71/2203. E.—raphevalve of *C. ceticola* typical form on minke whale U71/2245. F.*—raphevalve of *C. ceticola* f. *constricta* Nemoto on southern bottlenose whale 75/1. G.—rapheless valve of *C. ceticola* f. *constricta* on southern bottlenose whale 75/1. H.—raphevalve of *C. ceticola* f. *constricta* on southern bottlenose whale 75/1. I.*—*Gomphonema aestuarii* on strap-toothed whale, 78/15. J.*—*G. aestuarii* on strap-toothed whale. K.—*Stauroneis olympica* Hustedt found on killer whale 69/10. L.—*S. olympica* found on killer whale 69/10.

* External views of valves, others are internal views.

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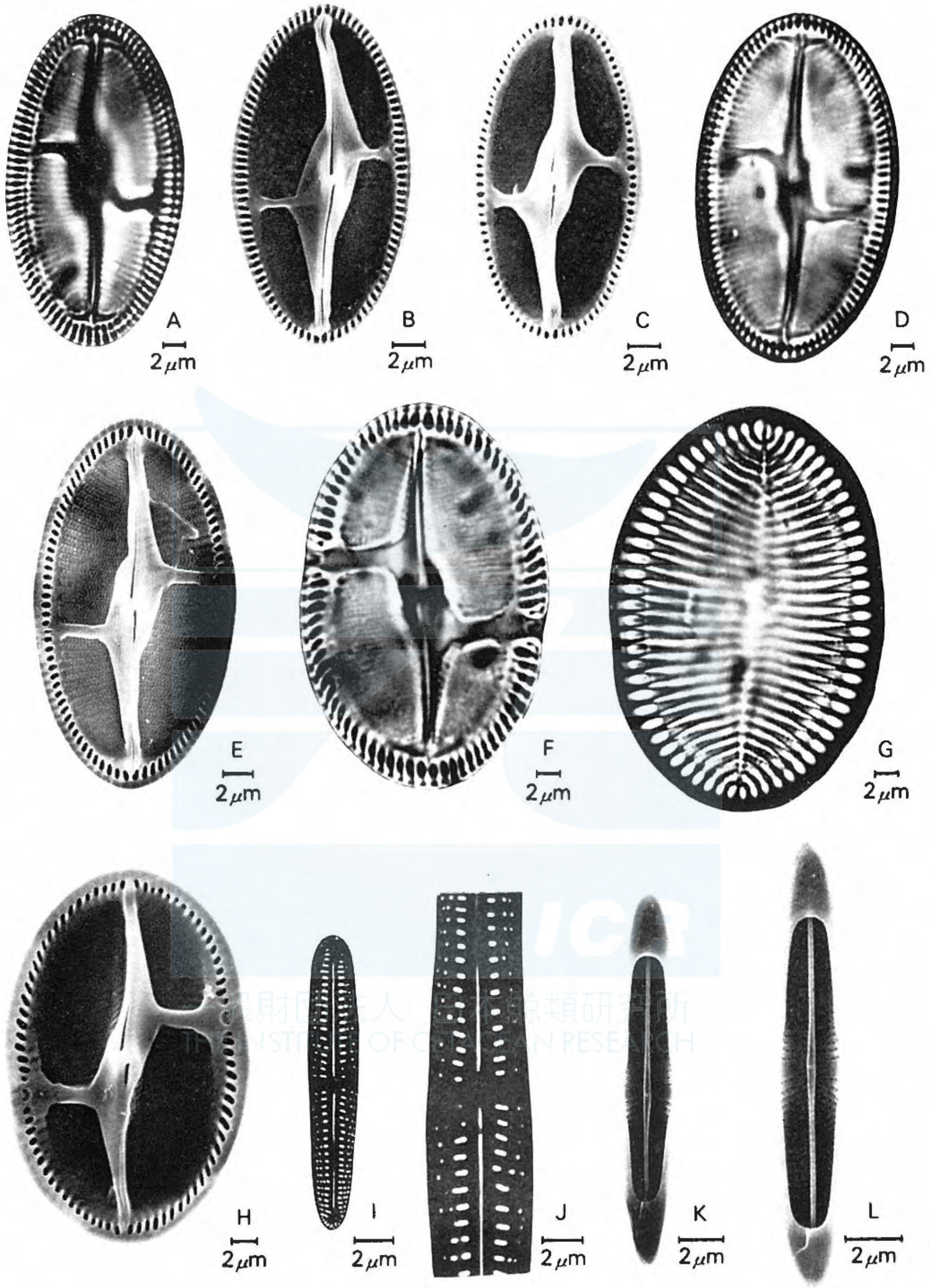
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BRAIN ORGANIZATION IN *PLATANISTA GANGETICA*

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ABSTRACT

The quantitative composition of the brain of a young individual of *P. gangetica* is presented both in simple percentages and with progression indices refering to a basal mammalian type. The neocortical development is emphasized as well as the hippocampal reduction. This species ranks low among Odontoceti and even among Platanistids, which may be considered in agreement with its life-habits. Qualitative features of transverse sections are also presented.

INTRODUCTION

A detailed study of dolphin brains is not easy because the size of that organ in most species makes it difficult to prepare histological sections. We have, however, been able to carry out a gross and microscopical examination of one such brain belonging to a young individual of the Ganges dolphin (*Platanista gangetica indii*), collected by the first author in the Indus River in Pakistan. We present here our observations of the most important quantitative characteristics of the composition of that brain with an appendix on some of its external and internal features. We hope that, although the animal was not an adult, a basic description of its brain will be useful as a reference type for those having to identify the main characteristics of bigger, more unwieldy specimens.

MATERIAL AND TECHNIQUES

An individual of *Platanista gangetica* mesuring 106.5 cm and weighing 17.5 kg was collected from the Indus River in Pakistan. It is assumed to have been about one year old at the time of death. The weight of its brain was 170 g. That brain was fixed in 1/6 formalin solution. One sagitally cut half of it was embedded in paraffin, sectioned at 10 μm and Nissl stained. Photographs of 108 sections from front-end to back-end were prepared. The above laboratory operations took place in Montreal (collection number P285) while the final study was carried out in Tokyo. The photographs were used to estimate the volumes of nine main components of

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the brain according to the technique explained elsewhere (e. g. Stephan, Bauchot and Andy, 1970).

ABBREVIATIONS

Here are the abbreviations used throughout this paper for the brain components. N=neocortex; Rh=rhinencephalon or paleocortex (P); S=septum; D=diencephalon; St=striatum including the area of the capusula interna that is spread out considerably; H=hippocampus; M=mesencephalon; C=cerebellum including pontine fibers; O=medulla oblongata.

RESULTS AND COMMENTS

We shall report here on the quantitative aspects of the brain of *P. gangetica*, leaving for the appendix a few remarks on its qualitative morphology. In fact, quantitative comparisons are not easy in this case because few biometrical data have been published on dolphin brains. We do not know of any analysis of such material carried out with a method similar to the one applied in the present paper. Therefore, we shall have to refer to studies of other animals. We will consider especially some Primates since it is classical to insist on the high degree of both encephalization and corticalization in the two orders Cetacea and Primata. For comparison purposes, we have selected a small number of data from Stephan, Bauchot and Andy (1970—see their Tables 1 to 6 for more details).

A. *Percentage composition*

Table 1 presents the absolute and percentage composition of the brain of *P. gangetica* while Table 2 shows the percentages of its telencephalic parts only. An approximate idea of brain structure can be gained by looking at those simple ratios; however, these do not indicate the comparative evolutionary trends since they do not take into account the allometrical correlation between brain and body. They only provide a general picture of the subdivision of the brain, the functional significance of which must be interpreted if comparisons are made. We picked up about a dozen Prosimians and as many Simians from the Tables in Stephan, Bauchot and Andy (1970) and made approximate estimates of some proportions of brain-parts in those Primates.

We can offer the following brief comments.

a) The absence of an olfactory bulb is well known in Odontoceti, as is the case for *P. gangetica.*

b) The most important component of *P. gangetica*'s brain is the neocortex. The abundance of sulci and gyri in many cetaceans has been observed since long, just like the increasing complexity of cortical folding in an ascending series of Primates.

c) The second largest component is the cerebellum. One could possibly expect this on the assumption that agile swimmers need a well developed cerebellum in order to steer their complicated movements through their environment. Breatnach (1960) mentions that Mysticeti have a slightly larger cerebellum (20%) than Odontoceti (15%) and our specimen stands even a little lower (12.77%). That author also questions the direct relationship often established between aquatic manoeuvering and cerebellar size (o.c. p.221). Other ecological situations and types of locomotion, especially flying and climbing, are also expected to require an important cerebellum, as the common belief goes. We may note that the cerebellum may range quantitatively from 11 to 16% of total brain in Prosimians of all sizes and from 8 to 15% in Simians and man. In Megachiroptera, it varies from 12 to 16% approximately and in Microchiroptera from 15 to 22% (Pirlot and Pottier, 1977).

d) Among cortical structures, the rhinencephalon (paleocortex with amygdaloid area) is notably small in *P. gangetica*. This agrees, of course, with the loss of olfactory bulb and nerve. However, the amygdala complex is still present and constitutes most of the volume and probably almost all of the functions of that component (strictly speaking, the name *rhinencephalon* for that region in a dophin is hardly appropriate if it is true that most or all of the olfactory function has disappeared). Note that the relative size of that component remains fairly large in some Primates although, in the course of evolution, it has regressed in many of them more than in our dolphin.

TABLE 1. VOLUMES AND PROGRESSION IN THE BRAIN OF *P. GANGETICA*

Components	Volumes (mm^3)	Percentages of total brain	Progression indices
N	107,504.73	67.98	3,903
Rh	3,599.59	2.27	123
S	332.90	0.21	132
D	9,893.12	6.25	719
St	5,743.82	3.64	739
H	1,161.10	0.73	99
M	3,564.35	2.25	432
C	20,193.24	12.77	671
O	6,171.96	3.90	325
	158,164.90	100.00	—
Total brain	170 g with body-weight 17.5 kg		842

TABLE 2. TELENCEPHALIC COMPOSITION (%)

	P. gangetica	Prosimians	Simians
N	90.85	Max. 80	Up to 88∼95
Rh	3.04	4∼10	<4, even <1
S	0.28	—	—
St	4.85	5∼8	2∼3
H	0.98	5∼10	<5, even <1
	100.00	—	—

e) The relative smallness of the hippocampus is amazing. This fact is also mentioned for cetaceans in general and in particular for *Tursiops turncatus* but without any figure by Kruger (1966). We would also agree up to a point with Breatnach and Goldby (1954, p.280) who point to the "indefinitedness of the boundary" of the hippocampus, resulting in the introduction of "quite a large uncertainty into the estimate of the sectional area" of that component. We did experience difficulties in drawing some hippocampal demarcations from Nissl stained sections but we believe that our method was not grossly inaccurate.

f) The septum as demarcated in our dolphin brain cannot probably be compared with other published data because we have restricted our demarcation to a minimal area including the nuclei in strictly paraseptal location, which probably is not the case in other works. We follow Jacobs, Morgane and McFarland's (1971) practice of including the diagonal band within the olfactory area (o.c. p. 206) whereas other authors prefer to pool it with the septal nuclei (Stephan, Bauchot and Andy, 1970, p. 295).

In conclusion, the quantitative composition of the brain in the young *P. gangetica* is characterized by an overwhelming predominence of the neocortex that approaches that found in higher Primates. Most components are relatively small mainly because the neocortex and, to a lesser but also significant degree, the cerebellum are enormously developed. The oversizing of the neocortex can be demonstrated to take place in early prenatal life already while the fast growth of the cerebellum seems to occur mainly in late prenatal life (Pirlot and Kamiya, in preparation).

B. *Evolutionary progression*

The method of progression indices proposed firstly be Stephan to describe the evolutionary level attained by mammals, then applied by him and other authors (e. g. Stephan, 1967; Pirlot and Stephan, 1970; Stephan and Pirlot, 1970; Pirlot and Pottier, 1977) to various species, has also been used here. A summary of its principles can be found in Pirlot and Stephan (1970) and the relevant technique is described in Stephan, Bauchot and Andy (1970). In brief, comparisons are made between the volumes of the brain (or brain-component) in the species under investigation and the volumes of the brain (or brain-components) in an idealized primitive type ("basal Insectivore") that would have *the same body-weight* as the animal being studied. So, the allometrical relationship between brain and body is taken into account, which allows to describe and compare *evolutionary stages* in animals with various overall sizes. The basal value is 100 so that any figure above 100 indicates evolutionary progression while any figure below 100 betrays evolutionary regression.

From that viewpoint, it can be seen that *P. gangetica* stands rather low among dolphins. Its encephalization index (brain-to-body progression) is 842 and this is not high for its order. Still it is probably a little higher than it would be if the individual investigated were not a young but a fully adult individual. An average index found from a sample of 8 individuals was 675 (Pirlot and Kamiya, 1975).

From the latter publication, it can also be seen that several other dolphins have much higher encephalization indices, up to 2,308. It may noted that, from Stephan, Bauchot and Andy's tables (1970), a progression index of about 2,900 can be obtained for *Homo sapiens.*

As could be expected from the simple percentages, whatever progression there is in the total brain of *P. gangetica* is due mainly to its neocortex being so large (3,903). That figure stands higher than those for a number of Primates but remains much lower than those for several monkeys and, of course, for apes and man (see a selection in Table 3).

TABLE 3. COMPARATIVE PROGRESSION INDICES

	Br	N	Rh	C
Homo sapiens	2,881	15,576	142	1,872
Pan troglodytes	1,132	5,858	54	780
Cercopithecus ascanius	872	4,448	100	551
Colobus badius	688	3,353	59	536
Cobus albifrons	1,205	6,065	87	921
Tarsius syrichta	507	2,148	78	514
Galago senegalensis	417	1,485	85	490
Platanista gangetica	842	3,903	123	671

Br=total brain; other abbreviations as above. Figures rounded.

The rhinencephalic cortex *sensu lato* (paleocortex) is low but progressive whereas it may be very regressive in Primates. As already suggested above, if olfaction has been lost altogether in this dolphin, some other not unimportant activity may have been taken up by that brain region (amygdaloid area in particular).

Septum development probably follows Rh to some extent. However, one must keep in mind the remark made before that we have pooled the diagonal bands together with Rh, not with S.

The striatum and diencephalon are less progressive than in *Homo* but they probably yield "average" values for higher mammals.

The hippocampus' lack of progression is puzzling (its value lies practically at the neutral level 100). In percentage of the telencephalon, its value is close to man's own (about 0.95), but in the latter the evolutionary progress is around 400 (rough estimate from figures in Stephan, Bauchot and Andy, 1970). We have refered earlier to other authors who seem to be as unable as we are to propose an explanation for the hippocampus of the delphinids being very small. True enough, we are surprised to find it *so small.* That fact suggests both an evolutionary functional regression as well as a relative undersizing (influenced by the relative enlargement of the cortex). Contrary to our observations and those of Kruger (1966) and other authors apparently (through Kruger), Pilleri (1972) finds the amygdala and hippocampal gyrus ". . comparatively" large (o.c. p. 51). Pilleri does not give any measurement and thus we wonder what his words "comparatively large" may mean. The gyrus hippocampi is present on but a few sections from our animal.

The mesencephalon can probably be considered fairly progressive (cf. Primates, Chiroptera, etc.) and so can the oblongata.

The cerebellum, often expected to be very progressive in skilled swimmers such as dolphins, is not remarkably high by Primate standards, however. It is much more progressive than in bats (range 200~400), on the other hand, and the bats that are highest in that respect are those performing complex and accurate slow movements such as vampire, rather than the fast straight-line flyers that catch insects on the wing.

CONCLUSION

Although showing a great development of its brain and some of its brain components, *P. gangetica* appears as a rather modest dolphin from that viewpoint. The relative size of its neocortex, by comparison with other mammals including other dolphins, may look impressive but, when refered to body-size, probably remains among the most lowly of the family. We do not, unfortunately, possess accurate data for such apparently "smarter" genera as *Tursiops*, *Delphinapterus*, *Phocoena* and even *Inia* among the Platanistidae. But knowing the general size parallelism between total brain and neocortex in advanced mammals (Primates, Cetaceans), we may expect those other genera to possess more progressive cortices than *Platanista*. The idea almost immediately arises that, in a general way, a river dwelling and only modestly sociable dolphin like *P. gangetica* (Pilleri, 1970) has remained "in-

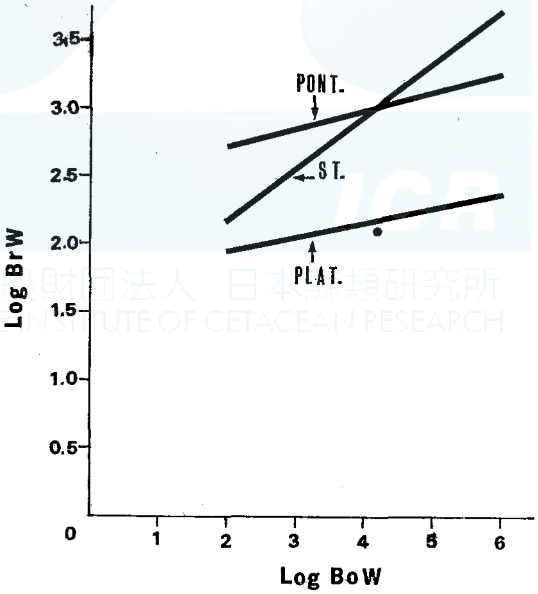

Fig. 1. Log regression for brain-to-body growth in *Stenella*, *Pontoporia* and *Platanista*. The black dot represents the specimen used for brain analysis in this study.

ferior" in neocortical performances to species that are open-sea dwellers, live in large schools and are said to maintain refined social communications between individuals (*Stenella*, *Tursiops* etc.) In order to illustrate the relative encephalization of *P. gangetica* by comparing it with *Pontoporia* (coastal dolphin) and *Stenella* (high sea dolphin), we have reported the position of our specimen of *P. gangetica* on a graph showing average regression BrW/BoW straight lines for those three genera (Fig. 1). In all likelihood the stronger increase in relative brain-size observed in *Stenella* is to be related with the postnatal "training" that seems to occur in that social species (Pirlot and Kamiya, 1975).

On the other hand, structures directly concerned with accousti functions, such as the subcortical components O and especially M, do show a strong progression in *Platanista*. This fact appears quite remarkable if one compares dolphins with bats which yield indices in the 200～250 range for M and in the 100～200 range for O (Stephan and Pirlot, 1970; Pirlot and Pottier, 1977). Considering that dolphins, like bats have simplified optic but highly sophisticated acoustic functions, those figures are particularly significant in *Platanista* (432 and 325).

The basic quantitative findings reported in this paper clearly suggest that further and more detailed investigations on the structure of each brain component in this dolphin and in higher types are likely to be rewarding. Studies of the quantitative composition of the brain in bats and in other mammals already pointed to the same idea. As for dolphins, there has been a fashionable excitement in the last few years about those aquatic mammals being almost as intelligent, in several respects, as man itself, or even "smarter" than *Homo sapiens* in some. It will take a lot more data on both the qualitative and the quantitative aspects of the dolphin brain to "relocate" such claims into reality, and many, many more observations of their behaviours.

APPENDIX

ON SOME QUALITATIVE FEATURES OF *P. GANGETICA*'S BRAIN

This appendix is made of short remarks A) on a sample of 8 low magnification photographs of the brain sections used for the above quantitative analysis, B) on the gross external morphology of 4 views of another brain of *P. gangetica* and C) on the most obvious features in 9 sections of the brain-stem of the same specimen. The animal used for B) and C) was a female individual 120.5 cm long with a brain weighing 236 g. It was thus a little older and larger only than the specimen P285 mentioned above. It was collected together with the former by the first author in the course of his expedition to Pakistan.

A. *Sections for quantitative analysis*

Demarcations of main areas have been made by following the few photographs published on dolphin brain and, in the absence of relevant pictures from dolphins, by resorting to atlases for various Primates. Photomagnification ×*ca.* 2.

Fig. 2. Front part of the right hemisphere with distended ventricle. Section

1061.

Fig. 3. Plane of emergence of a little distinct paleocortical region, in caudad direction. Section 1506.

Fig. 4. Septal plane. Ventral P reduced. Section 1856.

Fig. 5. Caudad to commissura anterior. P reduced to small lateral area. Tuberculum olfactorium visible ventrally. Section 2206.

Fig. 6. Pontine fibers plane. Emergence of H and a few fimbriae visible. Colliculus superior. Section 2906.

Fig. 7. Colliculus inferior and cerebellar peduncle plane. Nucleus cochlearis. Section 3356.

Fig. 8. Plane at caudal edge of H. Caudal part of colliculus inferior. Maximum extension of O. Section 3506.

Fig. 9. Caudal N. Typical outline of Cetacean C with developed paraflocculus in particular. Section 3956.

B. *Gross external morphology*

Fig. 10. External aspect of the calve brain. A) Dorsal view. The fissural pattern is one of the simplest found among dolphins. The longitudinal sulcus constitutes the main sulcus. B) Ventral view. Olfactory nerve absent; optic nerve very thin; acoustic nerve well developed. The contrast between the last two nerves is especially notweorthy. C) Lateral view of the left half. We cannot engage here into a rediscussion of sulci and gyri nomenclature. There seems to be very little, if anything, new to contribute from the examination of this specimen. For general surface anatomy of dolphin brain, the reader is referred in particular to Gruenberger (1970). D) Median section of the right half. The high development of the colliculi inferiores can be appreciated.

C. *Sections throught the brain-stem*

The internal structure of the brain-stem in *P. gangetica* is illustrated here. The brain-stem was prepared into serial sections which were stained by the Weigert-Par carmin technique (embedding in celloidin, sectioning 30 μm thick). Microscopical study revealed many remarkable peculiarities in the development of the various component structures. The sectional planes shown here are as follows.

Fig. 11. Section through the inferior end of the medulla (ser. no. 120).

Fig. 12. Section of medulla through the cuneate nuclei (ser. no. 255).

Fig. 13. Section through the rostral portion of the medulla at the exit the pharyngeal-laryngeal fibers to nerves IX, X and XI from nuclei ambigui (ser. no. 450).

Fig. 14. Section through the middle of the trapezoid body at the level of the genu of the facial nerve (ser. no. 555).

Fig. 15. Section through the colliculus inferior at the level of the colliculi inferiores commissure (ser. no. 635).

Fig. 16. Section through the middle of the colliculus inferior at the level of colliculi inferiores commissure (ser. no. 690).

Fig. 17. Section through the colliculus superior, brachium of the colliculus inferior and nuclei for the oculomotor nerve (ser. no. 795).

Fig. 18. Section through the colliculus superior, nucleus ellipticus, nucleus interstitialis and tractus opticus (ser. no. 830).

Fig. 19. Section through the thalamic nuclei (ser. no. 900).

ACKNOWLEDGMENTS

We wish to thank Dr F. Yamasaki and Dr T. Kasuya, members of the University of Tokyo Cetacen Research Expedition, for their help in collecting the *Platanista* brains in Pakistan. Mrs H. Rietveld-Fernandez carried out the histological preparation and the photographic work at the Université de Montréal. Financial assistance to both authors for all phases of the research was received from the Japanese Government's Ministry of Education, Science and Culture and the second author's sojourn at the University of Tokyo was also largely funded by the Natural Sciences and Engineering Research Council Canada (grant A0778).

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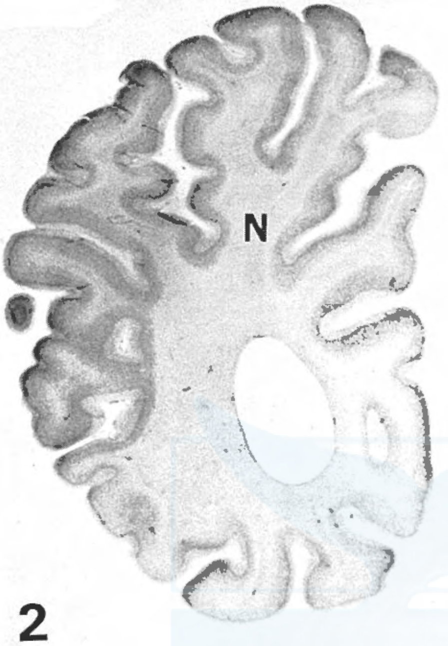

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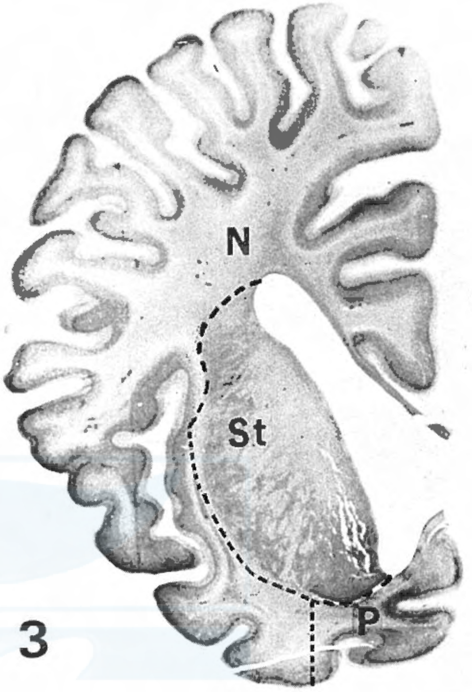

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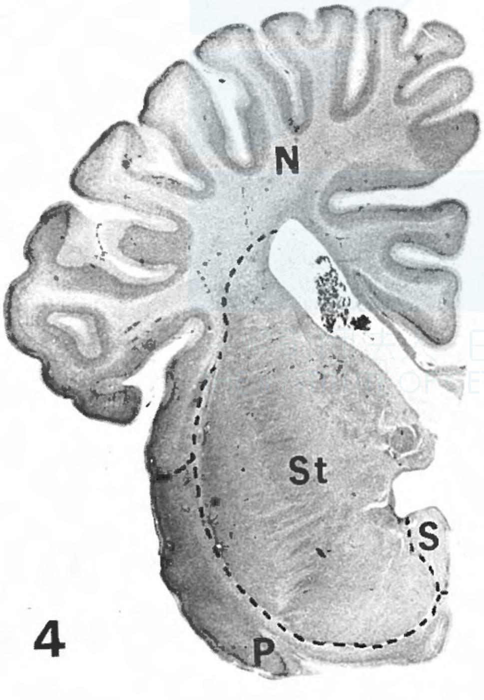

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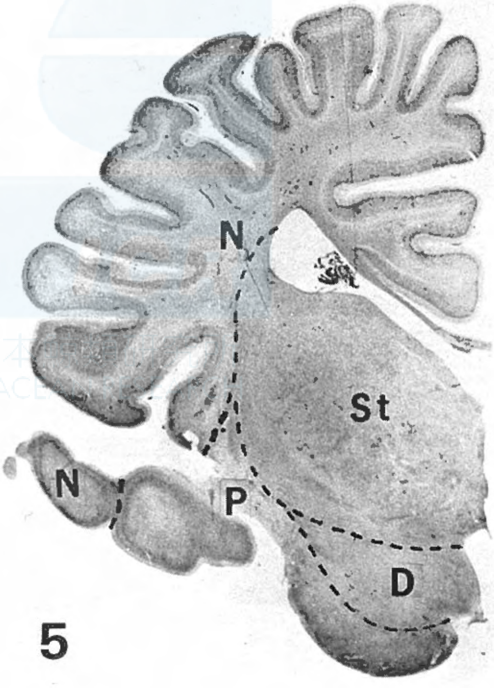

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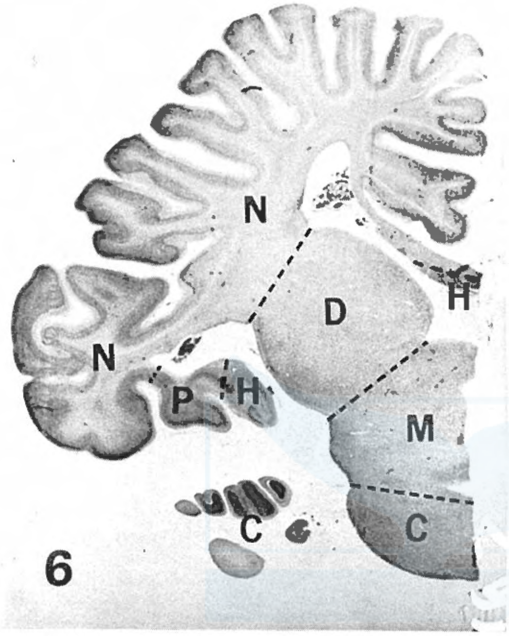
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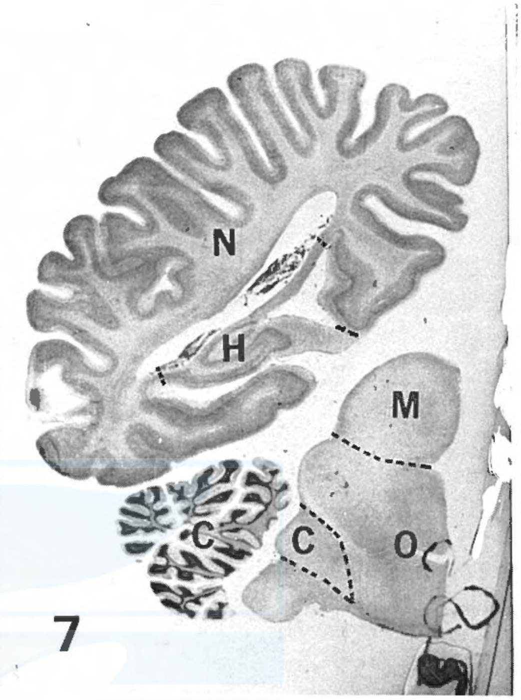
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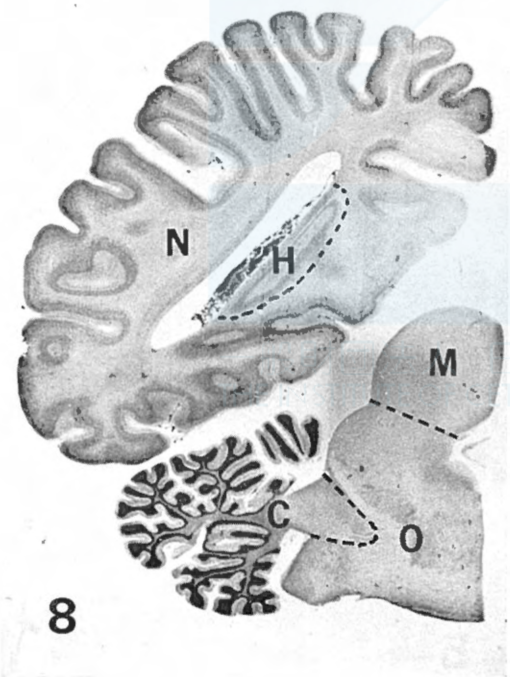
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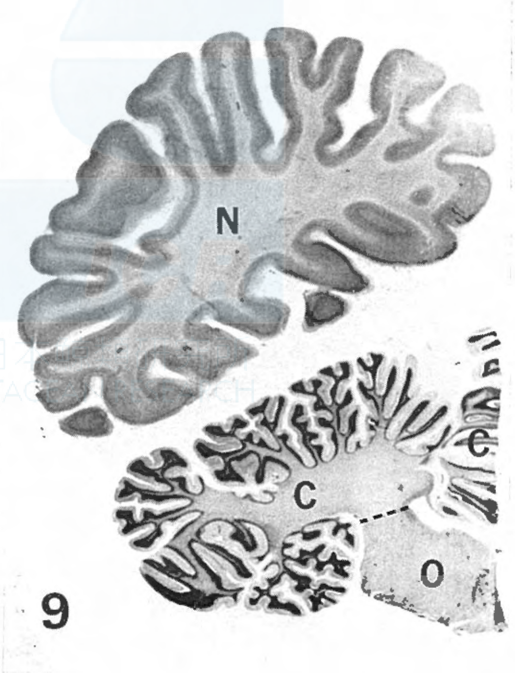
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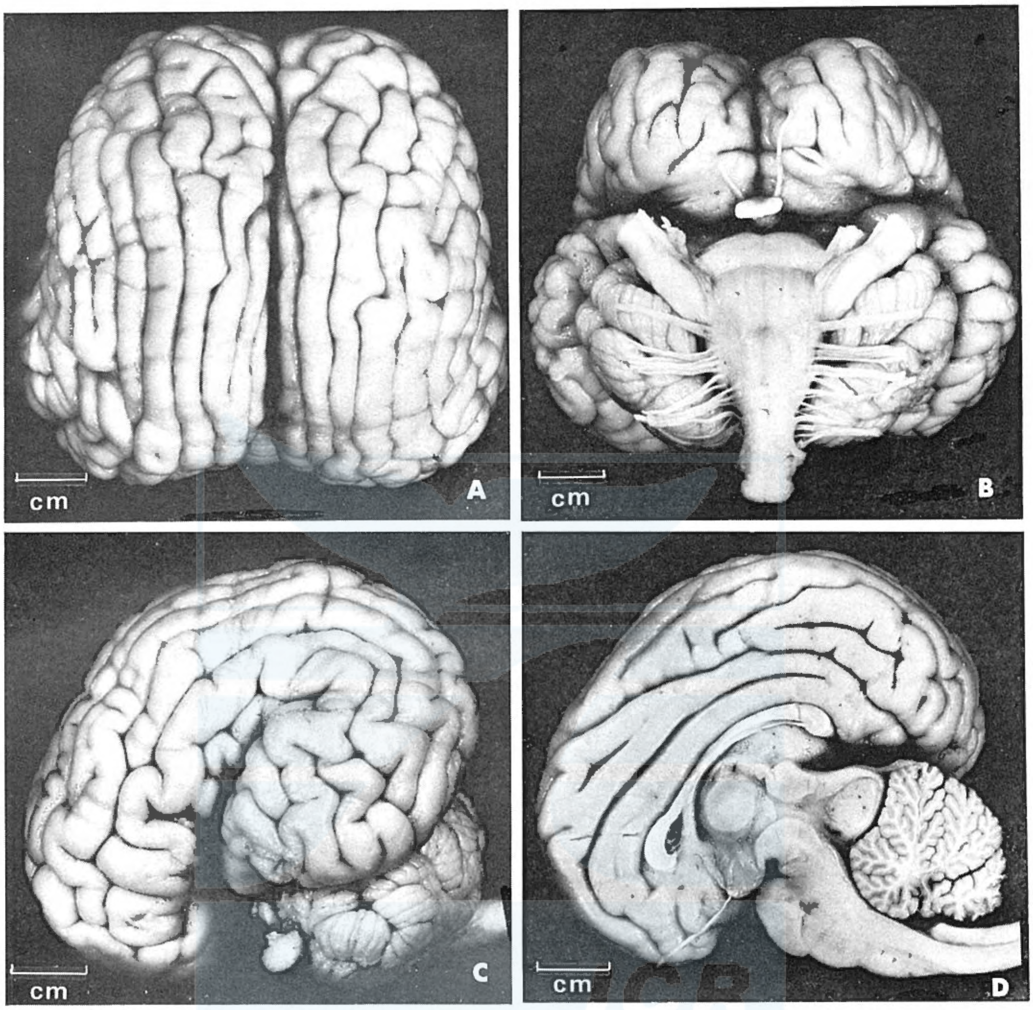
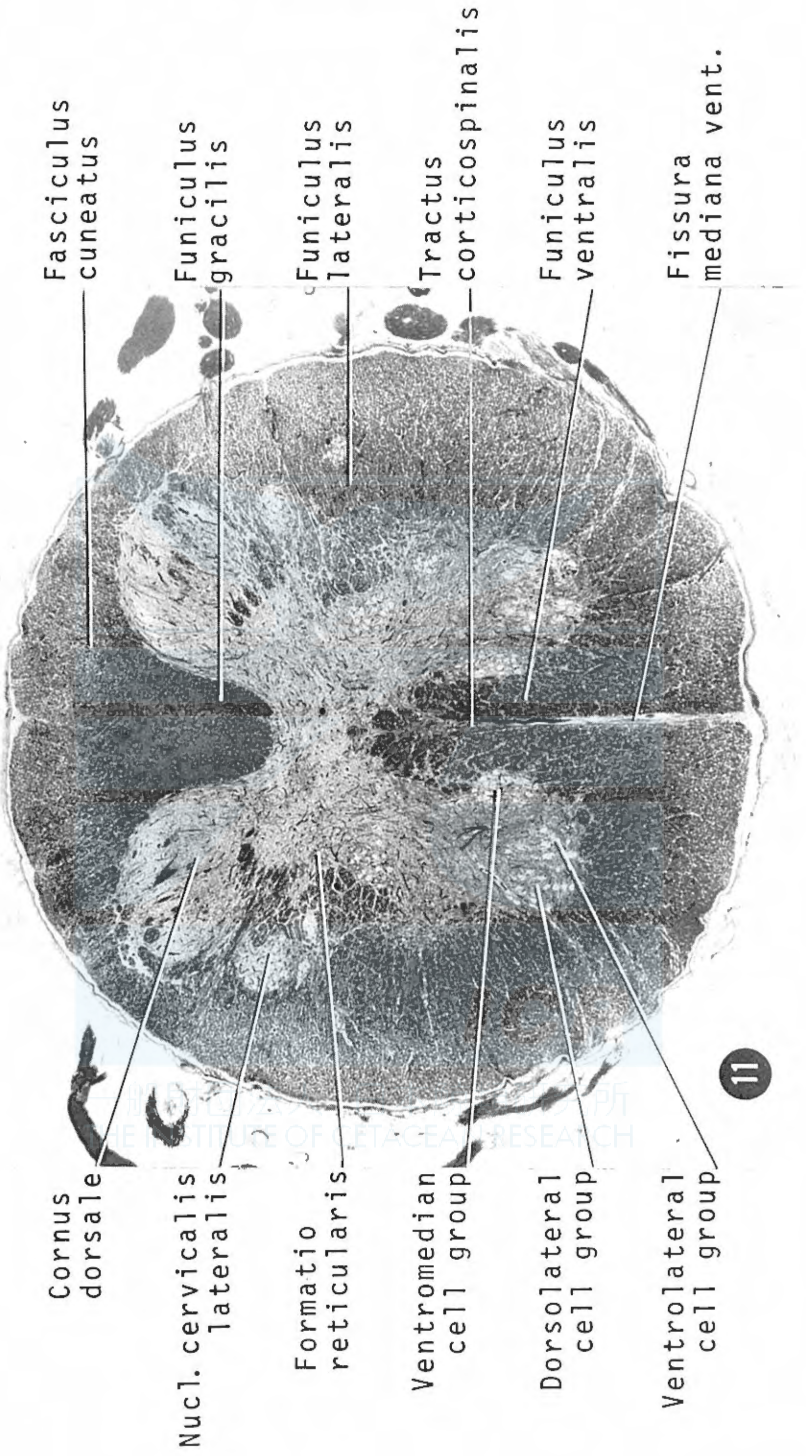


Fig. 10


Fasciculus cuneatus
Funiculus gracilis
Funiculus lateralis
Tractus corticospinalis
Funiculus ventralis
Fissura mediana vent.
Cornus dorsale
Nucl. cervicalis lateralis
Formatio reticularis
Ventromedian cell group
Dorsolateral cell group
Ventrolateral cell group
11

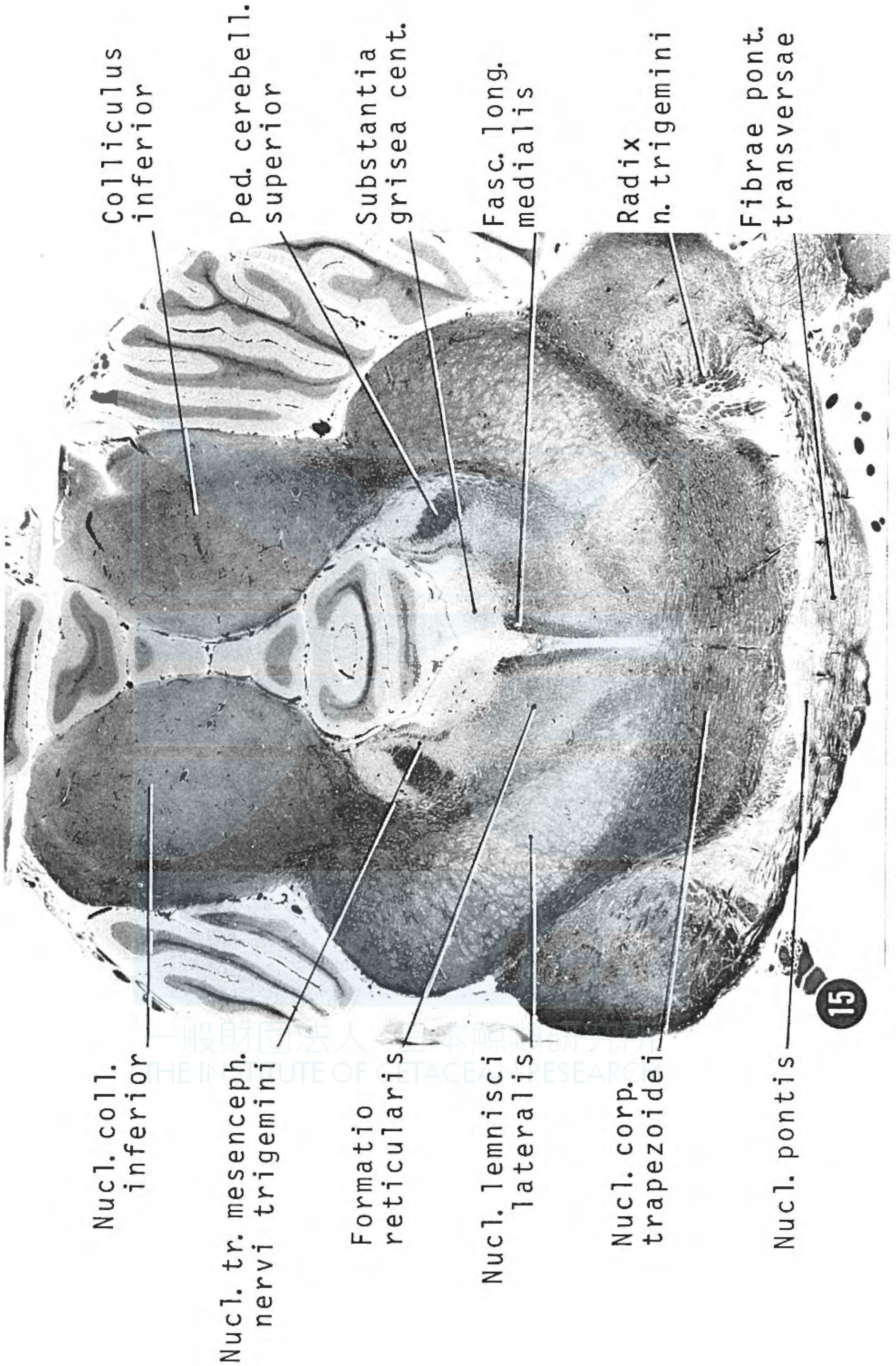

Funiculus dorsalis
Tr. spinalis n. trigemini
Fasc. long. medialis
Formatio reticularis
Decussatio lemniscorum
Nucl. olivae
Nucl. cuneatus
Nucl. tr. spinalis nervi trigemini
Substantia gresea cent.
Dorsolateral cell group
Ventromedian cell group
Tr. corticospinalis

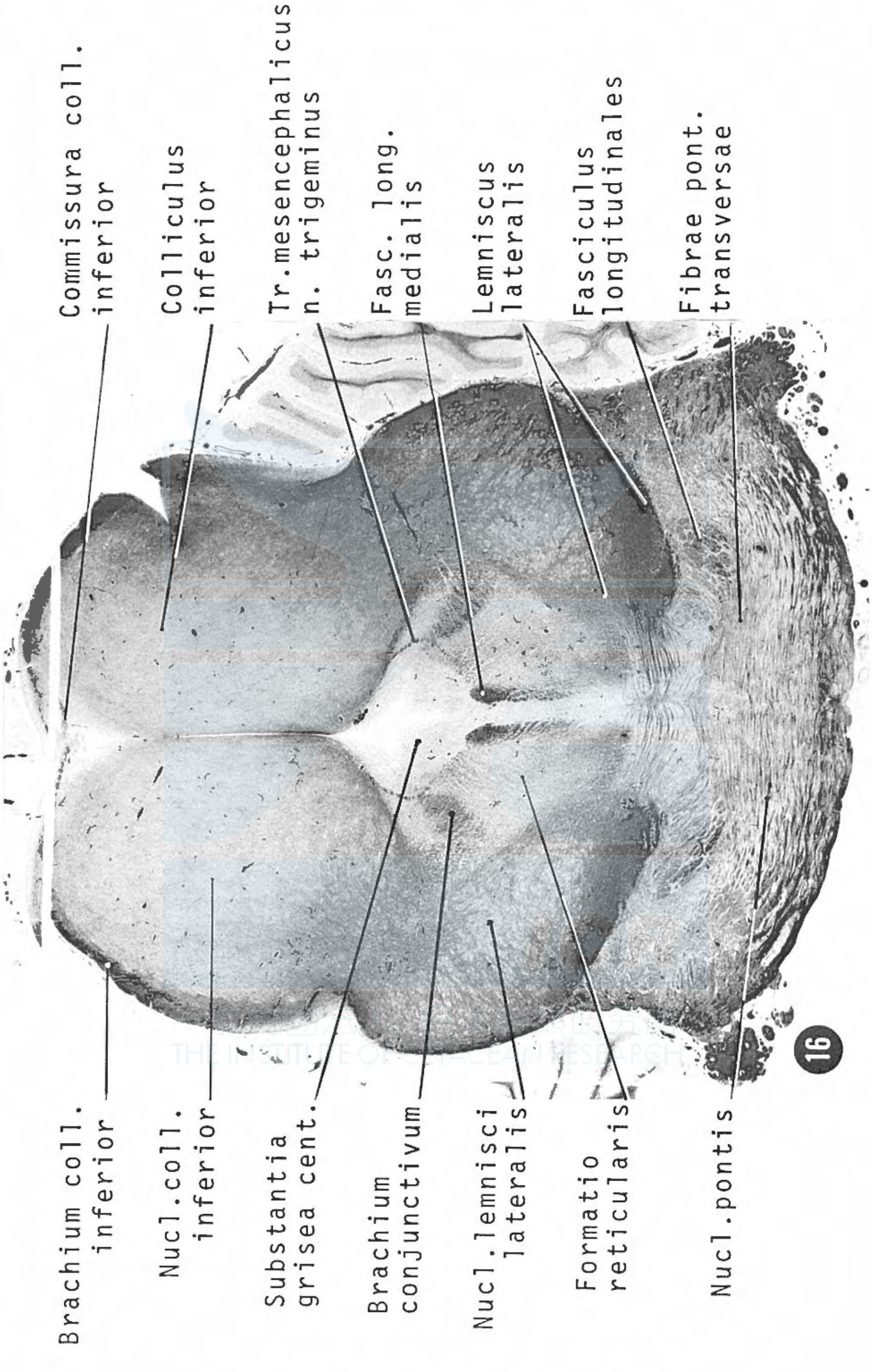
12


Fasc.long.med.
Tr.solitarius
Tr.spinal. n.vestibuli
Nucl.n.trigem.
Corpus restiforme
Fibrae arcuatae int.
Lemniscus medialis
Nucl.dors. n.vagii
Nucl.spinal. n.vestibuli
Nucl.tr.spinal. n.trigem.
Nucl.ambiguus
Nucl.oliv.access. dorsalis
Nucl.olivaris
Nucl.oliv.access. med.-vent.
13


Ped. cerebell. superior
Genu n. facialis
Fasc. long. medialis
Radix n. facialis
Corp. trapezoideum
Tr. corticospinalis
Nucl. vestibul. lateralis
Ped. cerebell. medius
Nucl. oliv. superior
Tr. spinal. n. trigemini
Nucl. cochlear. vent. (pars dors.)
Nucl. corp. trapezoidei

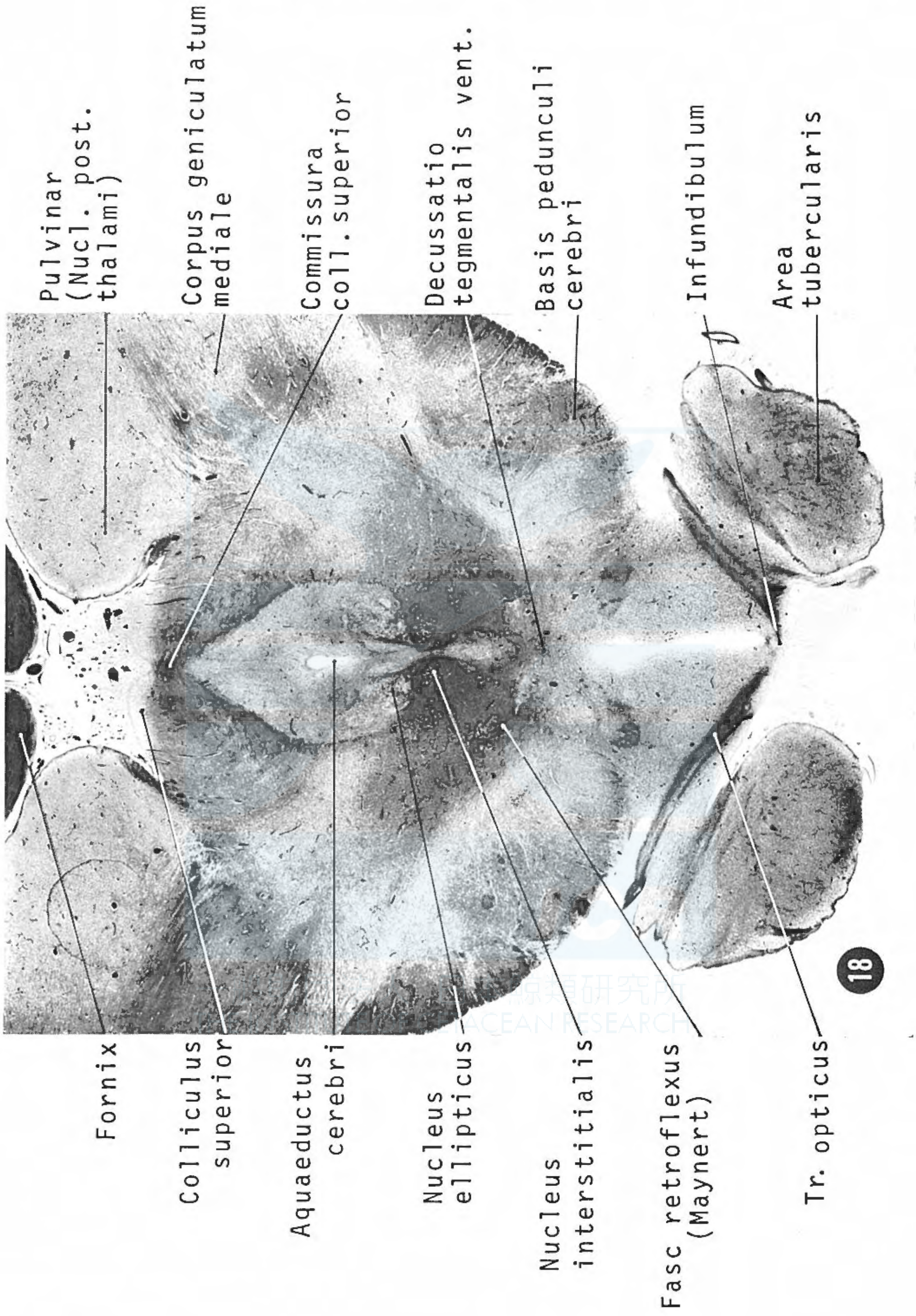
14

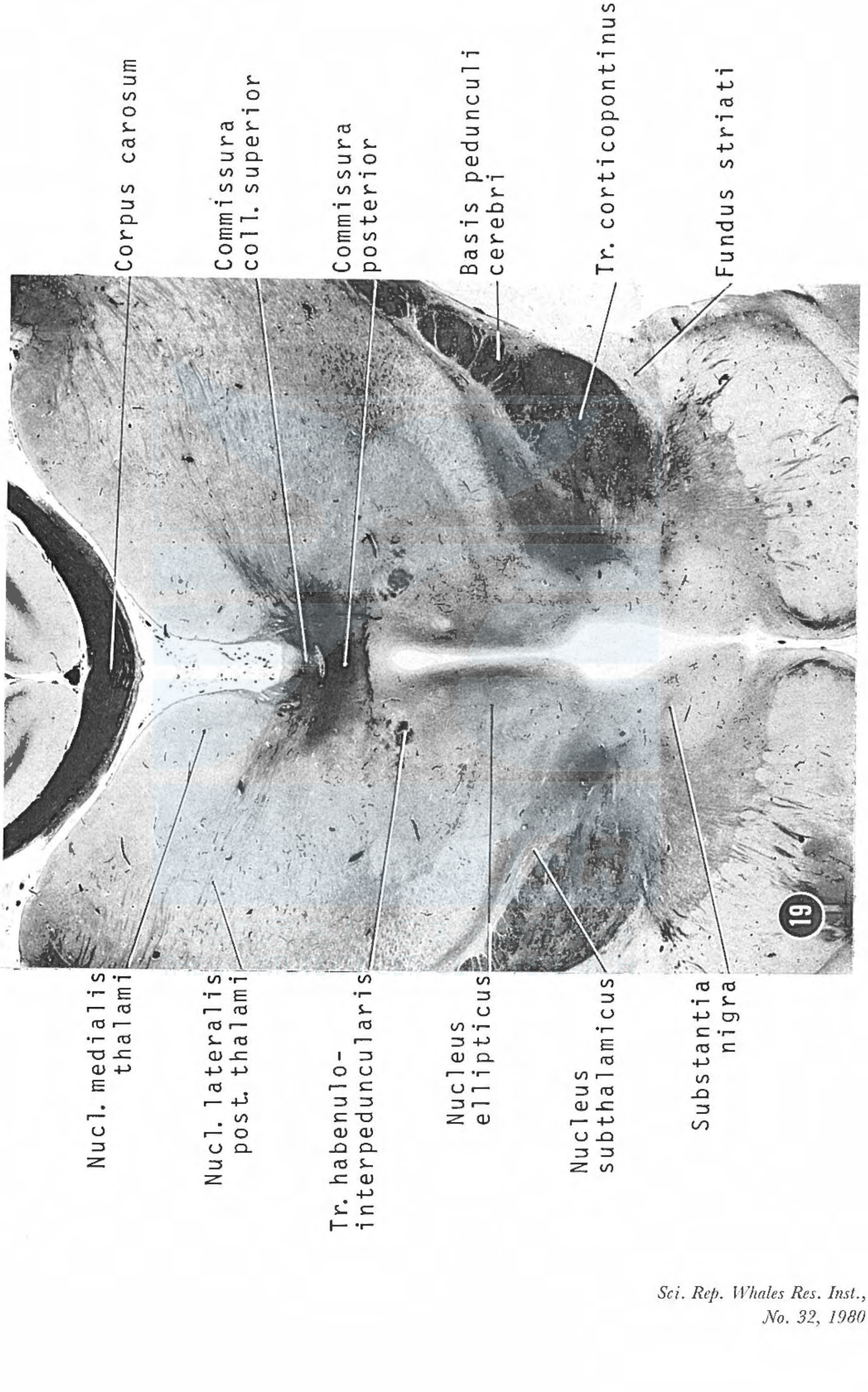

Colliculus inferior
Ped. cerebell. superior
Substantia grisea cent.
Fasc. long. medialis
Radix n. trigemini
Fibrae pont. transversae
Nucl. coll. inferior
Nucl. tr. menceph. nervi trigemini
Formatio reticularis
Nucl. lemnisci lateralis
Nucl. corp. trapezoidei
Nucl. pontis
15


Commissura coll. inferior
Colliculus inferior
Tr.mesencephalicus n. trigeminus
Fasc. long. medialis
Lemniscus lateralis
Fasciculus longitudinales
Fibrae pont. transversae
Brachium coll. inferior
Nucl.coll. inferior
Substantia grisea cent.
Brachium conjunctivum
Nucl.lemnisci lateralis
Formatio reticularis
Nucl.pontis
16


Commissura coll. sup.
Brachium coll. inf.
Lemniscus medialis
Fasc. long. medialis
Basis ped. cerebri
Decussatio brachii conjuctivum
Fossa interpeduncularis
Colliculus superior
Tr. mesencephalicus nervi trigemini
Substantia grisea cent.
Nucl. nervi oculomotorii
Nucleus peripeduncularis
Substantia nigra

17


Pulvinar (Nucl. post. thalami)
Corpus geniculatum mediale
Commissura coll. superior
Decussatio tegmentalis vent.
Basis pedunculi cerebri
Infundibulum
Area tubercularis
Fornix
Colliculus superior
Aquaeductus cerebri
Nucleus ellipticus
Nucleus interstitialis
Fasc retroflexus (Maynert)
Tr. opticus
18


Corpus carosum
Commissura coll. superior
Commissura posterior
Basis pedunculi cerebri
Tr. corticopontinus
Fundus striati
Nucl. medialis thalami
Nucl. lateralis post. thalami
Tr. habenulo-interpeduncularis
Nucleus ellipticus
Nucleus subthalamicus
Substantia nigra
19

A COMPARATIVE MORPHOLOGICAL STUDY ON THE TONGUES OF MANATEE AND DUGONG (SIRENIA)

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ABSTRACT

Tongues of two species of manatee, *Trichechus senegalensis*, and *T. manatus*, and of the dugong, *Dugong dugon*, were observed macro- and light microscopically. The tongue, with an anterior short free tip in both families, was a slender, firm, very muscular structure set rather vertically but with adipose tissues being rather rich in the posterior part. No circumvallate papillae, sulcus terminalis, and foramen caecum could be seen on the dorsum. The lingual apex was rounded in the manatee and truncated in the dugong. While many digitiform, cuticular spines were present in the tip region, in dugong they extended further posteriorly and were shaggier than in manatee. The remainder of the dorsum of the manatee was quite smooth whereas that of the dugong had small elevations, some of which had a bunch of spines. A pair of multifossulate swellings was present on both posterior margins with another pair occurring on the posterior part of the side wall in the manatee. In the dugong, two rows with pits could be seen on either of two regions corresponding to the dorsal swelling in the manatee. Similar pits were also found in a group at the base of the lingual side wall. These structures on the dorsum of both manatee and dugong are homologous to each other, as are those on the side wall. However, those on the dorsum and side wall may exhibit variations in the vallate and foliate papillae, respectively. Taste buds were limited to the thin epithelia of the fossulae of the swelling in the manatee and to the epithelia of the pits in the dugong. Mucous glands, though partially mixed ones, in the manatee and well developed serous glands in the dugong opened into the fossulae and pits, respectively. The posterior glandular portion contained well developed pure mucous glands. The lateral surfaces were studded with round, flat patches in the form of large-sized fungiform papillae, which may act as tactile organ.

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INTRODUCTION

The sirenian order is one of three major mammalian groups (along with cetaceans and pinnipeds) that have adapted to living in water. There are two living sirenian families; manatees (Trichechidae) and dugongs (Dugonidae). Trichechidae has only one genus, and that genus is classified into three species; *Trichechus manatus*, *T. inunguis*, and *T. senegalensis*. On the other hand, among Dugonidae, only one species, *Dugong dugon*, now remains. As sirenians feed on water plants (being entirely vegetarian) in shallow water, their digestive systems are interesting and differ considerably from those of cetaceans or pinnipeds. Not a few morphological observations have been made on the tongues of manatee or dugong (Rapp, 1857; Owen, 1868; Murie, 1870; Gmelin, 1892; Beddard, 1897; Weber, 1904; Gudernatsch, 1907, 1908, 1909; Sonntag, 1922; Aoki *et al.*, 1938; Hill, 1945; Gohar, 1957; Nair *et al.*, 1975; Husar, 1978). However, most of these descriptions excepting Gudernatsch's (1908, 1909) have been very brief and ambiguous, and comparative studies of manatee and dugong tongues have been very scarce. Since we have identified some differing morphological characteristics on the tongues between the two families, the results are reported here and offered as an addition to the knowledge of sirenian tongues.

MATERIALS AND METHODS

Two tongues of the African manatee, *Trichecus senegalensis*, one of the West Indian manatee, *T. manatus*, and three of the dugong, *Dugong dugon*, were used for this study (Table 1). The African manatees (body length 158 cm, male, specimen No. TS-1; and 198 cm, male, TS-2), sent by boat from Africa in a frozen state, were given us by the Ocean Research Institute of the University of Tokyo. The West Indian manatee (body length 282 cm, male, TM-1) was provided by the Yomiuriland Aquarium, Tokyo. One of the dugongs (138 cm, male, DD-1, collected in the Philippines) was imported for scientific research by permission of the Philippine Government, while the other two (204 cm, female, DD-2; and 254 cm, DD-3, collected in Indonesia) were provided by the Okinawa Expo Memorial Park Aquarium, Motobu, Japan. After dissection, the tongues of these animals were fixed with 10% formalin solution in our laboratory. Following gross anatomical observations of the tongues, materials for histological observations were excised from several parts of the tongues and were embedded in paraffin or celloidin. Sections made from these materials were stained with hematoxylin-eosin.

OBSERVATIONS

Gross anatomy

The tongues of the sirenians, both manatee and dugong, observed were firm and hard muscular structures. They were slender when viewed from the dorsal aspect (Figs 1 and 6), and were set rather vertically due to the narrowness of the space between the mandibular rami. There were no median sulcus, vallate papillae, sulcus terminalis or foramen caecum on the dorsum. Since the anterior two-thirds, which was elevated, was divisible from the posterior lower glandular portion, for convenience sake we regarded the anterior and the prosterior as the body and the root of the tongue, respectively, in this study. Measurements of the tongues are shown in the following table.

TABLE 1. MEASUREMENTS OF THE TONGUES OF MANATEES AND DUGONGS OBSERVED

Specimens	Body length (cm)	Sex	Length* (cm)	Breadth** (cm)	Thickness*** (cm)
Trichechus senegalensis					
TS-1	158	male	14	3	2.5
TS-2	198	male	15	3	2.5
Trichechus manatus					
TM-1	282	male	19	4	4
Dugong dugon					
DD-1	138	male	10.5	2.7	2.5
DD-2	204	female	13	3.5	3.5
DD-3	254	female	16	4	4.2

* Whole length from the lingual apex to the base of the epiglottis.

** The widest portion at the posterior of the lingual body.

*** The thickest portion from the floor of the mouth at the mid-part of the body.

The anterior free tip of the tongue, without frenulum, was short, about 1 cm to 1.5 cm in length, and the tongue, ventrally, was extensively attached to the floor of the mouth, indicating that the sirenian tongue may possesses only limited mobility. The tip of the tongue of the manatee was rounded (Fig. 1) while that of the dugong was truncated (Fig. 6). The tongue of sirenians thickened progressively from the anterior to the posterior part of the body, and thinned in the posterior glandular portion, the lingual root (Figs 2 and 7). The mid-part of the dorsum of the body was considerably convex, both lengthwise and transversely in the dorsal direction. In the dugong, a wide longitudinal elevation of about one-third of the lingual width was seen on the mid-part of the dorsum, thus forming lateral strips on either side. In the young dugong, DD-1, the lateral strips were not so marked. The anterior dorsum in the African manatee, approximately 2 cm in extent from the apex, was covered with many hard, digitiform, cuticular spines, each about 2 mm in length and 0.2 mm in thickness, which were anteriorly directed along the cornified hard anterior margin (Fig. 1). Small amounts of fine, soft spines were seen extending almost to the posterior half of the lateral margin. In the West Indian manatee, the anterior margin was rather uneven in appearance, and a few spines, 1 mm or less in length, were seen in several parts along the margin. In both species of the manatee, the dorsum, excluding the anterior spine covered region, was quite smooth, both to touch and the naked eye, and was devoid of the papillous processes seen in other land mammalian tongues. In the dugong, the anterior dorsum of the tongue, about 1.5 cm in extent from the apex, was thickly covered with hard spines quite closely resembling those in the manatee, though far shaggier (Fig. 6). Anterior spines extended to the ventral side of the free tip, being about 5 mm in breadth and having a clear border. Smaller and softer spines than those in the apex region occurred on the anterior fourth of the mid-part and on lateral strips, except at the middle longitudinal elevation. In the case of the young dugong, DD-1, they extended far posteriorly covering almost all of the dorsal surface of the body and were shaggier than those in the apex region. Spines in the dugong were stained dark brown in color, probably by the juices of seaweed. In the dugong, the lingual dorsum had small elevations, 0.2 to 1 mm in diameter, with superficial minute unevenness, especially remarkable along the mid-line area except for the tip region. A bunch of digitiform spines grew on the elevations (Fig. 8), showing the patterns of what Gohar in 1957 called "papillae calici-penicilliformes".

In the manatee, specific areas with many fossulae forming pairs were present near both posterior lateral margins of the dorsum (Figs 1, 3 and 4). There were roughly 25 to 30 rather large fossulae in the area, each area being clearly distinguishable from the neighborhood. These areas formed remarkable swellings, multifossulate swellings, in the African manatee (Figs 1, 3 and 11) but not such remarkable ones in the West Indian manatee (Fig. 4). The swellings, with gradual thinning anteriorly, were slightly opened anteriorly. The swellings in the African manatee were approximately 2 cm long and 0.7 cm wide in the posterior part; was 2.5 cm long and 0.8 cm wide, in TS-1 and TS-2, respectively; and was about 2 cm long and 0.8 cm wide in the West Indian species. Another multifossulate swelling was present on either lateral wall, in the anterodorsal region of the palatoglossal arch (Figs 2 and 5). This lateral swelling was about 0.8 cm across in TS-1, and 1 cm in TS-2, and had about six to eight fossulae*. Since the swelling of this area was rather more poorly developed than that of the dorsal swelling, and since a part of the lateral swelling intermingled with the patches which are mentioned later, the boundary of the lateral swelling was rather inconspicous compared with that of the dorsal swelling. Some fossulae resembling those of the swellings were seen at the lingual margin between the dorsal and lateral swellings. Therefore, at first sight it appeared that both the dorsal and lateral swellings were fused each together into one continuous large swelling**. Fossulae at the swellings were rather elliptic, about 1 mm in minor and 2 mm in major axes, and were arranged in a rather parallel manner in the African manatee. Fossulae located at the posterior part of the dorsal swelling in the West Indian manatee were rather shallow and composed of several minute glandular openings. Many small glandular openings were observable on the dorsum from the region between the middle part of both dorsal swellings to the epiglottis. In the case of African manatee, TS-2, both sides of the dorsum of the root were slightly swollen with rather large openings being observable on their surface.

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* In the West Indian manatee the regions on both sides on which the lateral swellings may be present were not observable, because they were excoriated.

** We described both swellings, dorsal and lateral, as a single swelling in a previous paper (Yamasaki *et al.*, 1980).

On the other hand, in the dugong tongue, two rows with deep pits (three on both sides in DD-1; right, six, and left, seven in DD-2; three on both sides in DD-3) were present near both posterior lateral margins which correspond to the postero-lateral region of the dorsal swelling in the manatee (Figs 6 and 9). The regions with the dorsal pits were not elevated. The pits were round, about 1 mm in diameter. Arranged longitudinally, they opened slightly anteriorly with a separation of about 3 to 4 mm. Small projections could be seen in some pits. Glandular openings, smaller than those of the pits and surrounded by small elevations, were observed on the dorsum from the posteriormost pit to the epiglottis. Three to seven pits, the lateral pits, (seven on the right and six on the left in DD-1; six on the right in DD-2*; three on either side in DD-3) resembling the dorsal pits, were present in a group, a little nearer the dorsal surface adjacent to the anterior region of the palatoglossal arch (Figs 7 and 9). This region was confined to within about 1 cm or less and was not elevated.

In both, manatee and dugong, 20 to 25 round, flat conspicuous patches were seen extending on both sides from about the anterior one-fifth of the tongue almost to the palatoglossal arch in the manatee (Fig. 2), and from the mid-part to near the arch in the dugong (Fig. 7). The patches were rather white in color in the fixed state, 1 to 3 mm in diameter, and slightly elevated. One or more small glandular openings were seen on the surface of some of these patches. Those located at the posterior intermingled regionally with the lateral swelling in the African manatee, and the lateral pits in the dugong. Small glandular openings were seen in the ventral region of these patches, being particularly abundant on the posterior part.

Histology

Though the sirenian tongues observed were extremely muscular, adipose tissues was rich in muscular tissues in the posterior area. Superior longitudinal muscle bundles were rather well developed immediately subjacent to the mucous membrane on the dorsum except in the posterior glandular portion. The epithelium of the dorsum at the spiny apex region was thick, approximately 2 mm or more, but gradually thinned toward the rear. The epithelium of the dorsum along the midline region of the manatee was relatively thin, with the epithelium becoming thick at the lingual lateral margin. The thickness of the epithelium of the side wall was about 1 mm. A superficial layer, about 15 μm, of the epithelium, excluding the rear part, was cornified. Epithelia of the dorsum and side wall of the dugong were not thick when compared with those of the manatee. The spines of sirenians, which were strongly cornified filiform papillae, consisted of a cornified superficial epithelium without a conical elevation of the tunica propria. All spines located posterior of the dorsum were thinner than those in the apex region but were almost the same in histological appearance.

The submucosa beneath the multifossulate swellings in the manatee was oc-

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* Pits on the left could not be counted, because this area was excoriated.

cupied by a lobulated gland mass mostly composed of mucous glands (Figs 11-14). In regions with fossulae, mixed glands which were usually present often opened directly into the fossulae at the relatively upper part (Figs 12 and 14). The gland masses at the mid-part of the dorsal swelling were approximately 7 mm and 8 mm deep in the African manatee and West Indian species, respectively. The gland mass of the lateral swelling (Figs 15 and 16) reached about half the depth (TS-2) or less (TS-1) of that of the dorsal swelling. The gland masses of both the dorsal and lateral swellings fused with each other. The fossulae were approximately 1 mm in depth. The inside wall of the fossula was covered with stratified squamous epithelium of about 50 μm in thickness, without cornification. Secondary papillae were rather poorly developed in this part. This epithelium contained pale flask-shaped structures or irregularly arranged cell masses with occupied almost the total thickness of the epithelium (Fig. 12). These were undoubtedly degenerated taste buds, although they were not clearly confirmed due to their poor condition. Well developed pure mucous glands about 6 mm in depth were present from the front of the multifossulate area to the rear. This mucous gland field extended from the anterior part of the palatoglossal arch to the ventral region of the side wall of the tongue. Capacious ducts were seen in places in the glandular tissues of the tongue (Figs 12 and 13).

On the other hand, in the dugong, pits, both dorsal (Fig. 17) and lateral (Fig. 18), were approximately 3 mm in depth, and surrounded by well developed lobulated pure serous gland masses, clearly distinguishable from the neighboring well developed pure mucous glands (Fig. 17). Wide lumens of gland ducts were observed in these glandular tissues. Since the serous gland mass was fused to the adjacent gland mass, large serous gland areas existed beneath the pits. The gland mass at the dorsum was approximately 14 mm in depth, and that at the side wall was about 10 mm deep. Serous glands opened into the pits and the neighboring mucous glands opened directly onto the dorsum. Some of pits had small projections protruding from their bottoms or walls (Figs 17 and 18). The epithelia of the pits, in which taste buds could be seen, were thin, being about 50 μm in thickness. Taste buds were found grouped together in some places, especially in the lateral pits (Figs 18 and 19). There seemed to be a larger number of taste buds in the pits of the dugong than in the fossulae of the manatee.

Sections of the round patches on the lateral surfaces of the tongues of manatee (Fig. 20) and dugong (Fig. 21) showed a thinning of the epithelium of approximately 100 to 200 μm. Secondary papillae at the patches were relatively short with a superficial 12 to 20 μm of their epithelium having a tendency towards cornification. The lamina propria of this region contained relatively abundant thick nerve fiber bundles (Fig. 22). No taste buds were present at the patches. Mucous glands, comparatively poorly developed in relation to those at the rear part of the dorsum, opened on the surface of some of the patches.

The mucous glands of the rear part of the tongue extended to the palate and pharynx. Those in the dugong were well developed when compared with those in the manatee. Dugong glands also extended down almost to the end of the esophagus. Condensations of lymphoid tissue could not be observed at the lingual root except in one case, African manatee, TS-2, which had some lymphatic nodule-like structures with crypts.

DISCUSSION

The sirenian tongue is difficult to divide strictly into two portions, the body and the root, due to the lack of a row of vallate papillae, sulcus terminalis, and a trace of foramen caecum, which are features seen at the border between the two portions in many land mammalian tongues. Therefore, the whole length of the tongue was measured from the apex to the base of the epiglottis. However, data reported by former investigators have often been unclear as to the posterior measuring point. Measuring points are necessary in the estimation of data showing the length of tongues such as those of sirenians, since they have no border marks between the body and the root as in cetacean tongues (Yamasaki *et al.*, 1976a, 1976b, 1978a, 1978b).

There are some ambiguities among previous descriptions on the manatee and dugong tongues. However, the characteristics of the sirenian tongue observed were 1) comparative smallness in relation to body size, 2) slenderness and vertical thickness, 3) absence of sulci on the dorsum, 4) existence of hard, digitiform, cuticular spines in the apex region, 5) existence of large-sized patches on the side wall, 6) presence of peculiar gustatory organs, varied types of foliate and vallate papillae. Anatomical differences between the two families are summarized and shown in table 2. Items in the table will be compared and discussed.

TABLE 2. ANATOMICAL DIFFERENCES BETWEEN MANATEE AND DUGONG TONGUES

		manatee	dugong
1.	Apex	round	truncate
2.	Spines	existing in the apex region only	extending posteriorly on the body of the tongue
3.	Dorsum	smooth, devoid of papillous projections	full of small elevations with spines
4.	Gustatory organ	forming dorsal and lateral multifossulate swellings	having several pits on dorsum and side wall, forming no swellings
5.	Glands of the gustatory organ	mucous, partially mixed	serous, well developed

The outline of the apex of the manatee tongue is rounded. That of the dugong is truncated, but the bifid tip in the dugong as reported by Hill (1945) could not be observed. Since the apex in the young dugong is round as in the manatee, age and individual differences may be related to its outline. In young dugong, Gohar (1957) observed that the cornified tip of the tongue is smooth but that with advancement in age it develops stiff bristles and becomes rasp-like in appearance. Our observations on a young dugong, whose spines at the tip were very short, is in approximate agreement with his descriptions. Drawings of a conspicuous horny process at the apex pointing anteriad in the dugong tongue were done by Sonntag (1922) and Aoki *et al.* (1938), and the process was described by the latter. However, we could not locate such a process at the tip region in the tongues of either family.

One of the great differences between the two families is the appearance of the dorsum. In the dugong, small epithelial elevations, each with a bunch of spines, spread over the dorsum in contrast with the smoothness of the dorsum of the manatee. Gohar (1957) made very detailed descriptions of the appearance of the dorsum of the tongue of the Red Sea dugong. He stated that no typical circumvallate papillae could be seen, and proposed to call the special type of papillae observed, a bunch of spines on the elevation, "papillae calici-penicilliformes". He looked upon them as a modified form of the circumvallate papillae. We cannot agree that the structure composed of special papillae is a modification of the circumvallate papillae, but we assume that it may be a specially arranged filiform papilla, because of its form, distribution, number and histological features. Vallate papillae have been reported on the posterior part of the dorsum of the manatee by several investigators; Rapp (1857)* in *Manatus latirostris,* Murie (1870)* in *M. americanus,* Gmelin, (1892) in *M. latirostris,* Weber (1904), species unclear. In the dugong, clustered vallate papillae and rudimentary ones have been reported by Sonntag (1922) and Hill (1945)**, respectively. However, Gudernatsch (1909) observed that these papillae were absent in sirenian tongues, and we also could not locate such papilla in our specimens. Gudernatsch (1909) reported "Spiegeln" on the dorsum resembling those on the side wall of *M. latirostris* and he considered them to be fungiform papillae. However, in our specimens we could not find such structures on the dorsum, except for the side wall.

The most characteristic feature of the sirenian tongue is the presence of peculiar gustatory organs, a multifossulate swelling in the manatee and pits in the dugong, with notable differences in the organs being marked between the two families. Several interpretations have been made by former investigators and there has been confusion in terminology among them, especially on the organs of the manatee.

The structures that seem to indicate a dorsal swelling in manatee judging from the descriptions, drawings or figures are:

1. a sieve and tonsil-like plate by Rapp (1857) in *M. latirostris*
2. many fossulate-papillae by Owen (1868)***, species unclear
3. a double set of circumvallate glands by Murie (1870) in *M. americanus*
4. an anterior tonsil by Gmelin (1892) in *M. latirostris* (with a drawing)

those seemingly indicating a lateral swelling are:

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* Rapp (1857) and Murie (1870) might have considered even the patches on the side wall as vallate papillae, since they indicated that the structures extended to the anterior third of the tongue. This distribution almost corresponds to that of the patches of our specimens.

** Hill (1945) reported another group of vallate papillae just anterior to the foremost group in the pit on the side wall in the dugong.

*** Owen (1868) described the structures as extending to the anterior third of the tongue.

1. a simple lateral gustatory organ by Gmelin (1892) in *M. latirostris* (with a drawing)
2. a large papillary plate by Weber (1904), species unclear

and those probably indicating a continual single swelling, dorsal and lateral, are:

1. a large patch of circumvallate papillae (Mayer's organ)* by Beddard (1897) in *M. inunguis* (with drawings)
2. a compact glandular apparatus with gustatory pits by Gudernatsch (1909) in *M. latirostris* (with photographs)
3. a large cushion with numerous fissures (lateral organ)** by Sonntag (1922) in *M. americanus* (with a drawing)

However, the descriptions of the pits in the dugong by former investigators have been clearer than those on the swelling in the manatee, though the pits have been written of with various terms: Gudernatsch (1907, 1908), on the dorsal and lateral pits (with photographs); Aoki *et al.* (1938), dorsal and lateral (with drawings); Hill (1945), dorsal and lateral; Gohar (1957), lateral only (with a drawing); Nair *et al.* (1975), lateral only; Husar (1978) dorsal only. Although detailed observations were made on the gustatory organs in both manatee and dugong by Gudernatsch (1908, 1909), for some reason, no investigators have referred to his articles.

Undoubtedly the multifossulate swelling and pits are a variation of the gustatory organs*** formed by lingual papillae. However, it is difficult to conclude whether they correspond to the vallate or foliate papillae, since neither animal has these two kinds of papillae, at the corresponding regions as seen in other land mammalian tongues. The classification of the lingual papillae is based on their form and distribution. Since the gustatory organs on the dorsum and on the side wall in sirenian tongues are quite similar to each other morphologically, it would be more advisable to clarify the organs by distribution rather than by form. The lateral and dorsal pits of the dugong are clearly distinguishable in their location. As the lateral swelling in the manatee is located in almost the same region as the lateral pits in the dugong, both structures may be considered homologous to each other as indicated by Gudernatsch (1909). Some former investigators have stated that structures corresponding to the lateral swelling (Gmelin, 1892; Weber, 1904; Gudernatsch, 1909) and the lateral pits (Gudernatsch, 1908)**** were primitive type of the foliate papillae. We agree that the structures belong to the foliate papillae, but believe it advisable to consider them a varied type of foliate papillae rather than

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* Mayer's organ is a structure with numerous fissures located on the lateral surface of the elephant tongue. As this structure was first described by Mayer in 1844, it has since been called Mayer's organ in honor of its discoverer (Forbes, 1879). This structure in the elephant tongue consists of the foliate papillae themselves (Shimizu *et al.*, 1960). Therefore, the description by which Beddard (1897) regarded circumvallate papillae as Mayer's organ is inadequate.

** Although Sonntag's description is extremely ambiguous in the use of the term lateral organ, we have judged from his drawing that the organ may have indicated a swelling.

*** Aoki *et al.* (1938) and Gohar (1957) considered the pits of the dugong as merely glandular openings.

**** Gudernatsch (1908) also used the term " remnants " for the structures.

to label them a primitive type of foliate papillae variation. Gudernatsch (1909) observed that the group of gustatory pits on the side wall (=lateral swelling) in the manatee extended to the dorsum, that is, he believed the pits on the dorsum (=dorsal swelling) to be a continuation of those on the side wall. We, however, consider the dorsal swelling in the manatee to be an independent structure from the lateral swelling as is also true in the case of the dorsal pits in the dugong, and believe that the structures on the dorsum in both animals may be a variation of the vallate papillae. In the case of the manatee, the organ is multifossulated and expanded, and swells upwards. In the dugong, on the other hand, the organ grows downwards, with each pit becoming deep instead of being multifossulated. In the manatee, when each swelling, dorsal and lateral, has become well developed with age, the swellings may fuse with each other, and may then be seen as a single continuous large swelling as shown in Beddard's figure (1897).

There have been no descriptions concerning the existence of taste buds in the manatee, and only Gudernatsch reported numerous ones in the dorsal pits (1907) and in the lateral ones (1908) in the dugong. However, though the number of taste buds in the sirenians observed may not be as numerous as those of vegetarian land mammals, they are much more numerous than those in cetaceans (Komatsu and Yamasaki, 1980).

The region with pits in dugong consists of a well developed serous gland mass, while that of the swelling in the manatee is composed of a mass of mucous glands, though partially mixed ones, in agreement with Gudernatsch's descriptions (1908, 1909). In the region having taste buds in the fossulae, mixed glands are found near the upper part of the fossulae in manatee. Serous fluid may be useful in rinsing the fossula or pit having taste buds, particularly in the case of dugong, which feed on sea grasses. It is possible that some enzymes contained in serous fluid may turn the polysaccharide of sea grasses into the small molecules which stimulate the taste buds. Gudernatsch (1909) considered that the manatee's gustatory organ glands showed a far simpler grade of development than those in dugong, based on the poorly developed serous glands in manatee, and stated that marked morphological differences of the gustatory organs between the animals might depend on some biological factors rather than on the difference in food habits. Since this is a very interesting problem and since adaptation for foods cannot be disregarded, further studies are expected.

In the dugong, Gohar (1957) observed that mucous glands containing fewer and smaller serous glands were present under the whole surface of the tongue except for the anterior tip. However, in our observations mucous glands were not present in the lingual body except on the lower part of the side wall, but were present at the root, and serous glands were limited to the pit region. Dugong glands, in particular, are more well developed than those of manatee and extend down almost to the end of the esophagus.

The other characteristic external feature is the presence of patches studded on the lateral surface of the sirenian tongue. Gudernatsch (1908, 1909) called these structures "Spiegeln" in the dugong and manatee, and regarded them as fungiform papillae. In the dugong, Gohar (1957) also described various sized fungiform papillae, whereas Hill (1945) stated that these were absent. We consider the patches in sirenians to be large-sized fungiform papillae. Although they have no taste buds, it is supposed that the structures play the role of sensory organs, probably tactile organs.

Rapp (1857) reported tonsils, which were oval plates having numerous openings and showing a sieve-like appearance, on each side in the posterior part of the tongue in *M. latirostris*. Gmelin (1892) showed anterior* and posterior tonsils in his drawing of the same species. However, it is as yet uncertain whether or not lingual tonsils are present in the sirenian tongue at the corresponding region since only in one case of African manatee have structures which seem to be poorly developed lingual tonsils with crypts been seen.

ACKNOWLEDGMENTS

We are greatful to Doctors M. Nishiwaki, University of the Ryukyus, Naha, Okinawa and T. Kasuya, Ocean Research Institute, University of Tokyo, for kindly supplying the materials for this study. We wish to thank Doctors J. E. Reynolds III, School of Marine and Atmospheric Science, University of Miami, K. Kubota, Institute of Stomatognathic Science, Tokyo Medical and Dental University, and K. Takahashi, Department of Anatomy, Sapporo Medical College, who gave us valuable suggestions and advice for our study. The techinical assistance of Mr S. Ohtani, Histo-Technical Center, Sapporo Medical College, is also acknowledged.

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* As mentioned above, this seems to be the structure corresponding to our dorsal swelling.

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EXPLANATIONS OF FIGURES

Fig. 1. A dorsal view of the tongue of an African manatee (TS-2). The tongue is rather slender as a whole, and its tip is rounded. The tip region is covered with many hard, digitiform, cuticular spines. Dorsal multifossulate swellings, slightly opened anteriorly, forming a pair may be observed near both posterior lateral margins of the dorsum. Numerous small openings of mucous glands are visible on the posterior part of the dorsum. ×1.

Fig. 2. Left side view of TS-2 tongue. The tongue becomes thick posteriorly but thin at the lingual root. A lateral multifossulate swelling is observed in the anterodorsal region of the palatoglossal arch. Some twenty-five round flat patches are present, extending from the anterior fifth of the side wall to near the palatoglossal arch. Small mucous glandular openings are visible from the mid-part to the arch. ×1.

Fig. 3. A higher magnified view of the left dorsal swelling of TS-2 in figure 1. Roughly twenty-five rather oval, large fossulae are obviously visible on the swelling. Numerous glandular openings, far smaller than the fossulae in diameter, are clearly seen from the posterior region of the swelling to the posterior part of the tongue. ×2.

Fig. 4. A left dorsal swelling of a West Indian manatee (TM-1). The swelling, having many large fossulae, is not as remarkable as that of TS-2. ×2.

Fig. 5. A higher magnified view of the lateral swelling of TS-2 tongue in figure 2, showing more than ten oval fossulae. Numerous glandular openings, far smaller than the fossulae in diameter, are observable. ×2.

Fig. 6. A dorsal view of the tongue of a dugong (DD-3). The tongue is rather slender as a whole, with the spine-covered tip region being truncated. Thin, soft spines extend posteriorly, being especially shaggier on the lateral strips. Small elevations are seen on the dorsum. A row of dorsal pits can be seen at both posterior margins (arrows). ×1.

Fig. 7. Left side view of DD-3 tongue. The body of the tongue strongly bows anteroposteriorly, with the root being situated at a lower level to the body. Three lateral pits are observable on the posterior side wall (arrow). About fifteen round flat patches are present on the mid-part of the side wall. ×1.

Fig. 8. Bunches of spines grow on the small elevations at the anterior dorsum of the DD-3 tongue. ×20.

Fig. 9. A higher magnified view of the dorsal pits on the left side of the dorsum of DD-3 in figure 6. Small mucous glandular openings can be seen on the posterior part of the pits. ×2.5.

Fig. 10. A higher magnified view of the lateral pits and patches of figure 7. The pits and patches vary in size. Small mucous glandular openings are observable on the ventral side of the pits and patches. ×2.5.

Fig. 11. A cross section of both dorsal swellings with fossulae in an African manatee (TS-1). Mixed glands are present in the regions with fossulae, whereas in the area between both swellings the submucosa is occupied by pure mucous glands. ×5.5.

Fig. 12. A cross section of two fossulae of a dorsal swelling of TS-1. Several flask-shaped spaces in the epithelium of the side wall of the fossulae may show the remnants of taste buds, the cells of which have sloughed off. Glands are, for the most part, mucous in nature but partially mixed, especially in the upper part of the gland mass. Capacious ducts are seen at points in the glandular tissues. The secondary papillae of the side wall of the fossula are poorly developed. ×15.

Fig. 13. A cross section of a fossula of a dorsal swelling of TS-2. Mucous glands

more developed than those of TS-1 are seen but serous glands intermingle partially at the bottom of the fossula. The thin epithelium of the inner wall of the fossula has exfoliated due to its poor condition. ×15.

Fig. 14. A cross section of two fossulae of a dorsal swelling of the West Indian manatee (TI-1). Well developed glands are mostly mucous in nature, but partially mixed in the upper part of the gland mass. ×15.

Figs 15 and 16. Cross sections of two fossulae (TS-1, Fig. 15) and a fossula (TS-2, Fig. 16) of the lateral swelling. The nature of glands is almost the same as that of the dorsal swelling, but the glands of the lateral swelling are poorly developed as compared with those of the dorsal swelling. These glands are well developed in TS-2 as compared with those in TS-1. ×15.

Fig. 17. A cross section of a dorsal pit of a dugong (DD-3). Small projections can be seen in the pit. The pit is surrounded by well developed serous glands (Sg) which are clearly distinguished from mucous glands (Mg). The epithelium of the pit is very thin. ×7.5.

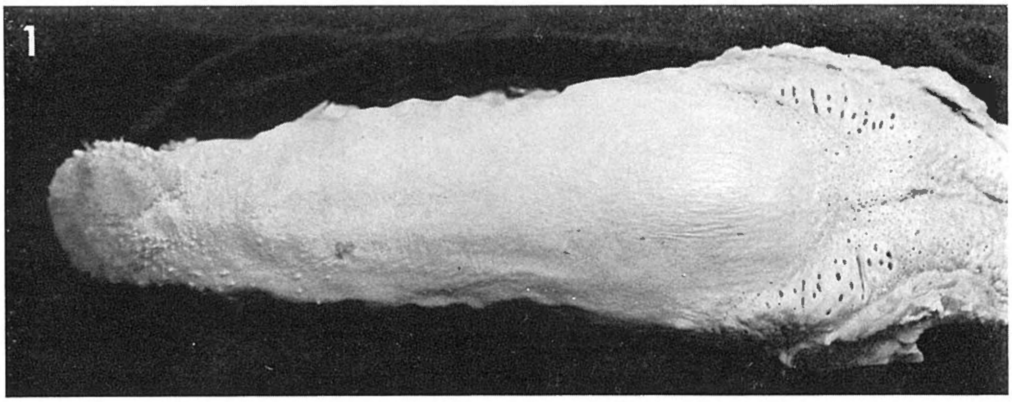
Fig. 18. A cross section of a lateral pit of DD-3. A small projection having taste buds in its thin epithelium can be seen in the pit surrounded by well developed serous glands. ×25.

Fig. 19. A more highly magnified view of a part of the projection in figure 18. Taste buds lie in the thin epithelium of the projection. This figure is taken from the area where taste buds are crowded together. ×300.

Fig. 20. A cross section of two patches of TS-2. The epithelium is rather thin and secondary papillae are poorly developed in the patches as compared with those of the remainder. Mucous glands and a glandular opening can be seen in the lower patch. ×15.

Fig. 21. A cross section of a patch of DD-3. The epithelium is rather thin as compared with that of the remainder. Mucous glands can be seen in places. ×15.

Fig. 22. A more highly magnified view of a cross section of a patch of DD-3. Abundant, rather thick nerve fibers are observable in the submucosa of the patch. ×50.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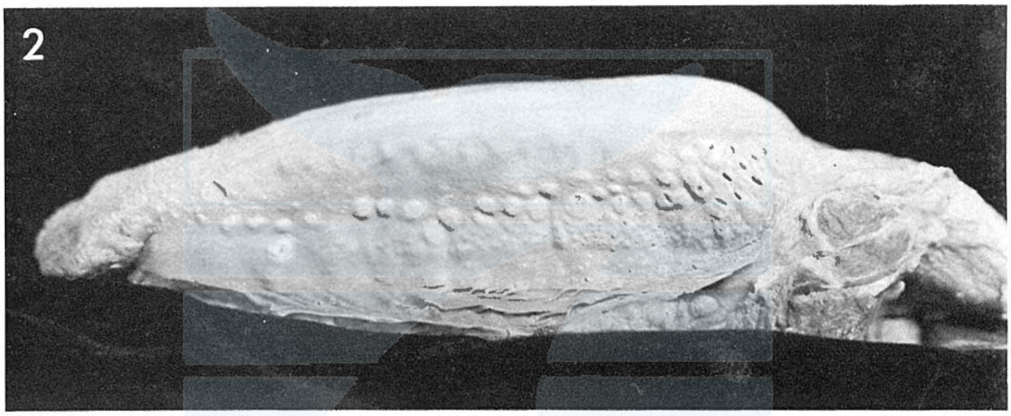
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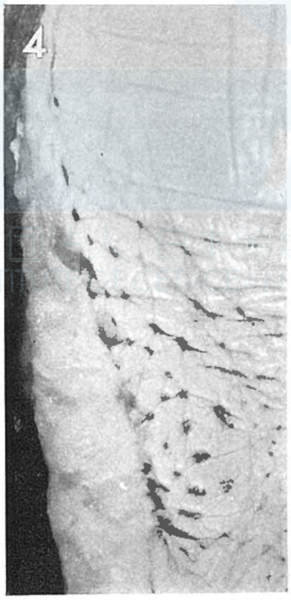
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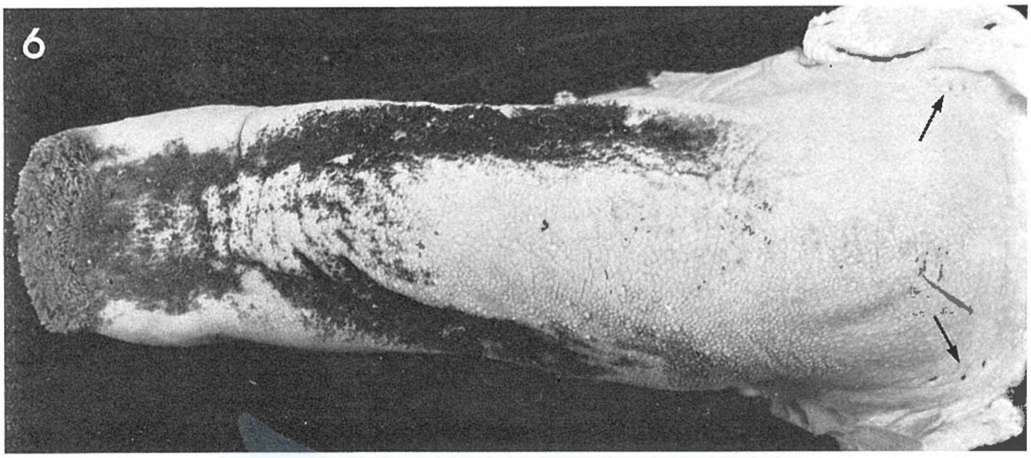

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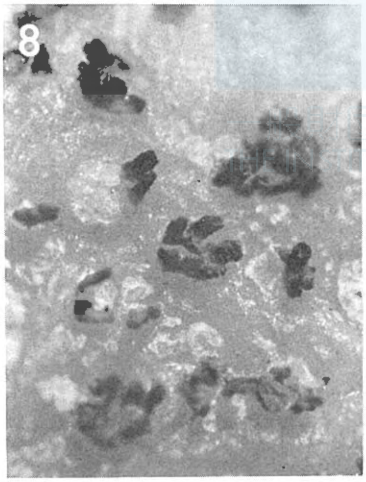

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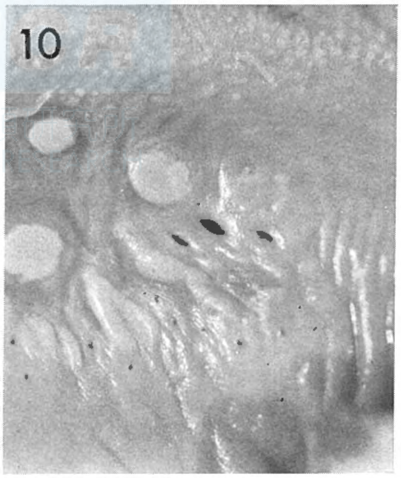

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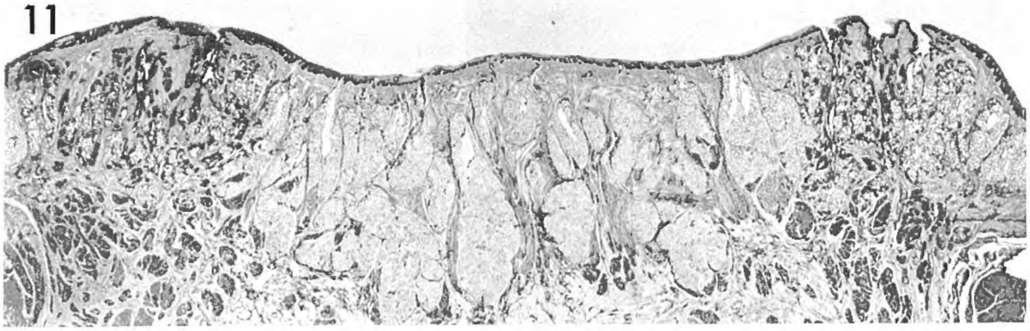

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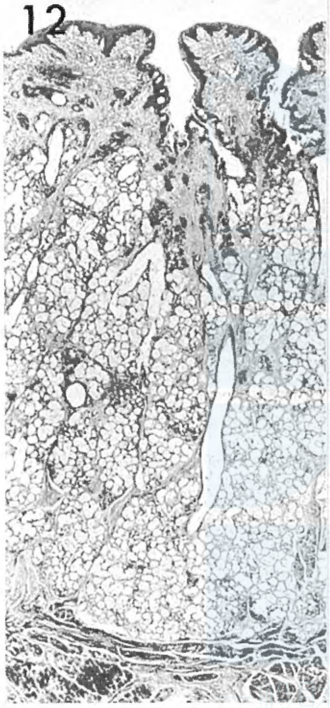

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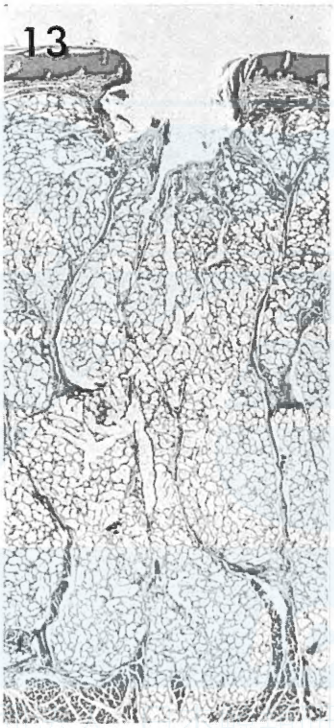

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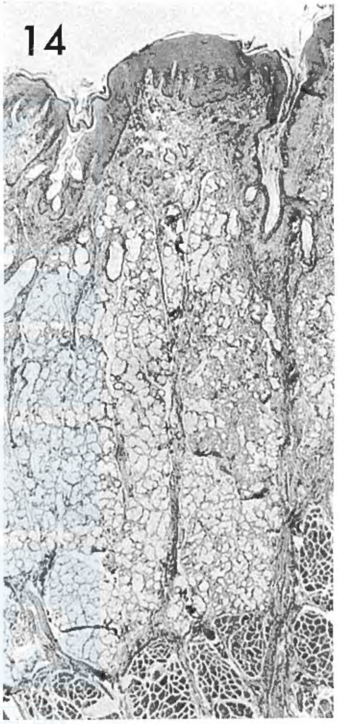

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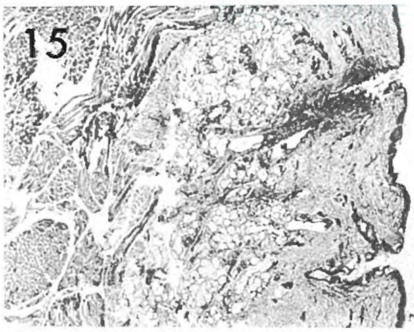

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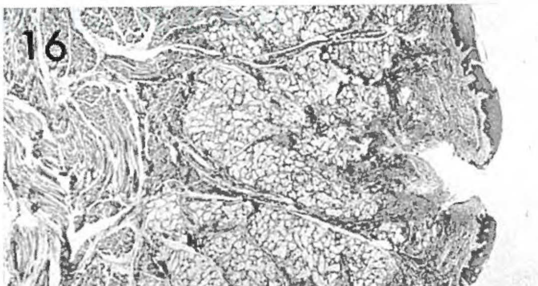

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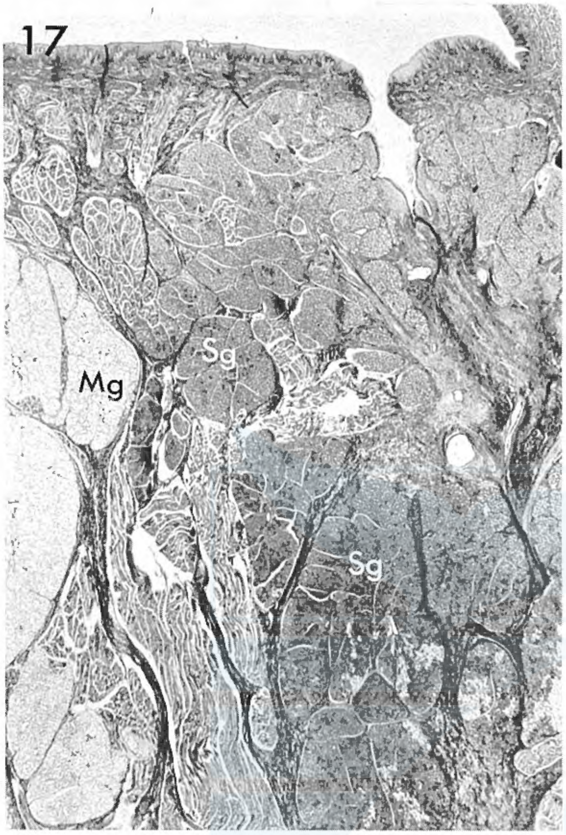

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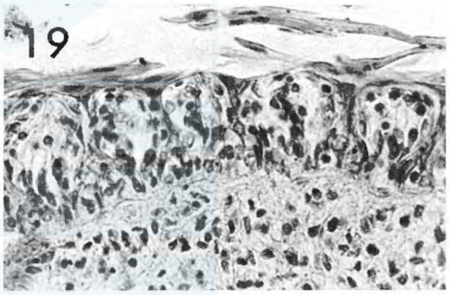

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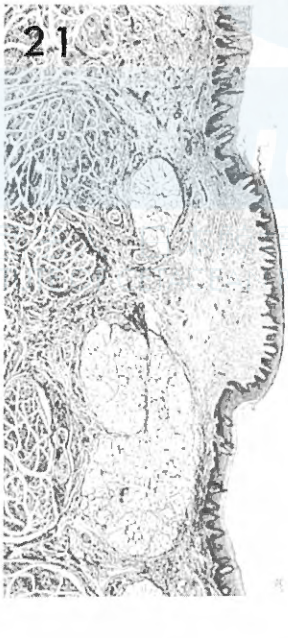

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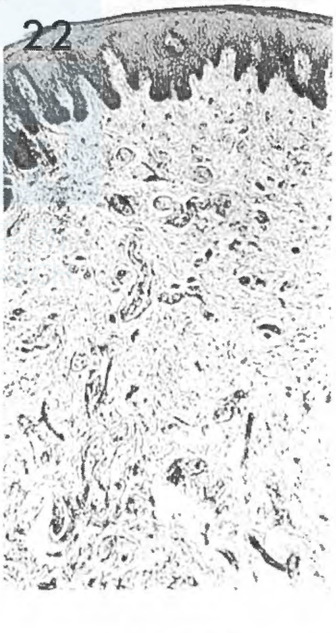

ON A MASSIVE STRANDING OF SHORT-FINNED PILOT WHALE, *GLOBICEPHALA MACRORHYNCHUS* GRAY, 1846, ON MARGARITA ISLAND (VENEZUELA)

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On October 1971 a school of short-finned pilot whales stranded on a large bay from the south of Margarita (El Guamache), a sandy beach with mangrove trees. Altogether, they were 22 animals, measuring between 4 and 6 m. Some specimens were drawn along the coast to the west by the streams as far as a distance of 20 km from El Guamache (Fig. 1).

This species does not seem scarce in the neighbouring area of the Caribbean Sea. Van Bree (1975) in a checklist of Cetaceans from this region quoted strandings on Nevis, Barbados and Guadeloupe and catchings—in St. Lucia, Dominica and St. Vincent. Dr Hernández-Camacho, from Inderena (Bogotá, Colombia) reported to A.C. (oral communication) strandings in the west of the zone: San Andrés island (40 specimens in July 1966) and several ones on Guajira peninsula. Nevertheless, after Dr Fernando Cervigón (Universidad de Oriente, Núcleo de Nueva Esparta) the short-finned pilot whale seems uncommon in Margarita. It arrives as far as 60 miles to the north (Isla Blanca), in oceanic waters. But Margarita is a zone of neritic shelf waters. Always according Dr Cervigón, the best period for permitting to approach pilot whales would be between June and September, when the waters are warmer and there is a depletion of fish and zooplank-

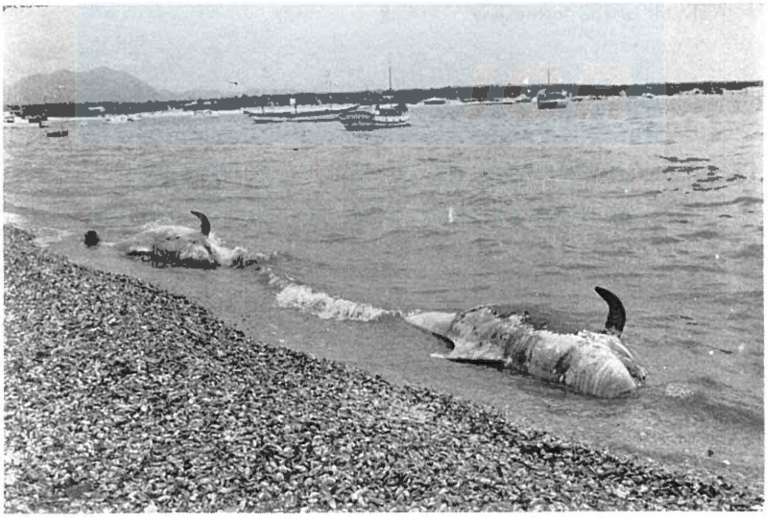

Fig. 1. Two of the stranded specimens.

TABLE 1. SKULL MEASUREMENTS OF THE STUDIED SPECIMENS

	Measurements	Universidad de Oriente (Margarita)			Fundación "La Salle" (Margarita)	
		1	2	3	1	2
1	Total (condylobasal) length	600 mm	550 mm	601 mm	550 mm	567 mm
2	Rostrum length	330 „	298 „	291 „	285 „	301 „
3	Rostrum basal width	242 „	218 „	258 „	231 „	240 „
4	Rostrum width 60 mm anterior to base	244 „	198 „	247 „	210 „	—
5	Rostrum width at middle	210 „	156 „	218 „	171 „	—
6	Rostrum width at 3/4 of the length	158 „	92 „	161 „	134 „	—
7	Maximun premaxillae width	220 „	217 „	180 „	194 „	204 „
8	Preorbital width	413 „	363 „	414 „	380 „	836 „
9	Postorbital width	433 „	384 „	440 „	400 „	406 „
10	Zygomatic width	439 „	384 „	448 „	408 „	419 „
11	Width of braincase across squamosals	285 „	255 „	274 „	268 „	265 „
12	Length temporal fossa	123 „	104 „	126 „	104 „	126 „
13	Height temporal fossa	135 „	100 „	104 „	111 „	111 „
14	Tip rostrum to the nares	412 „	385 „	397 „	382 „	389 „
15	Tip rostrum to the pterygoid bone	350 „	—	351 „	335 „	331 „
16	Length of upper toothrow (right)	120 „	—	122 „	117 „	154 „
17	Length of upper toothrow (left)	133 „	122 „	119 „	111 „	154 „
18	Number of alveoli of the upper jaw (right)	8	9	7	7	8
19	Number of alveoli of the upper jaw (left)	7	9	7	6	8
20	Lower jaw length (left side)	497 mm	444 mm	—	—	—
21	Coronoid length	147 „	136 „	—	—	—
22	Length of the lower jaw symphysis	55 „	59 „	—	—	—
23	Length of the lower toothrow (right)	131 „	113 „	—	—	—
24	Length of the lower toothrow (left)	130 „	105 „	—	—	—
25	Number of alveoli of the lower jaw (right)	8	7	—	—	—
26	Number of alveoli of the lower jaw (left)	8	7	—	—	—

ton. During those months faunistic elements from the Caribbean corral-ine islands arrive as far as Margarita. But the present stranding is the only sure reference.

In July 1977, during a trip to Venezuela, one of us (A. C.) had the possibility of studying osteological remains of the 1971 massive stranding, distributed between the "Centro de Investigaciones Cientificas de la Universidad de Oriente (Núcleo de Nueva Esparta)" and the "Fundacion La Salle", both of them in Margarita. Altogether there were remains from five specimens. Measurements of the skulls are given in Table 1.

In the former center, there is a complete mounted skeleton (number 1). Its vertebral formula is: seven cervical vertebrae (joined), ten dorsal vertebrae, fifteen lumbar vertebrae and twenty three caudal vertebrae. Besides there are two skulls, one of them (number 3) without lower jaw. In "Fundación La Salle" two skulls are kept, both of them without lower jaw, as well.

Skull measurements from Margarita's material have been compared with those

IN MM AND PRECENTAGES AGAINST SKULL LENGTH.

L.A.C. (M.N.H.N.) (Paris)		Universidad de Oriente (Margarita)			Fundación "La Salle" (Margarita)		L.A.C. (M.N.H.N.) (Paris)	
A-3215	A-3216	1	2	3	1	2	A-3215	A-3216
537 mm	560 mm	100%	100%	100%	100%	100%	100%	100%
271 „	294 „	55	54.1	48.4	51.8	53	50.4	52.5
222 „	206 „	40.3	39.6	42.9	42	42.3	41.3	36.7
227 „	193 „	40.6	36	41.1	38.1	—	42.2	34.4
198 „	—	35	28.3	36.2	31	—	36.8	—
138 „	114 „	26.3	16.7	26.8	24.3	—	25.7	20.3
195 „	—	36.6	39.4	29.9	35.27	34.21	36.3	—
368 „	349 „	68.8	66	68.8	69	68	68.5	62.3
—	386 „	72.1	69.8	73.2	72.7	71.6	—	68.9
395 „	389 „	73.1	69.8	74.5	74.1	73.9	73.5	69.4
247 „	260 „	47.5	46.3	45.6	48.7	46.7	46	46.4
125 „	115 „	20.5	18.9	21	18.9	22.2	23.2	20.5
94 „	88 „	22.5	18.1	17.3	20.1	19.5	17.5	15.7
371 „	370 „	68.6	70	66.0	69.4	68.6	69	66
320 „	335 „	58.3	—	58.4	60.9	58.3	59.6	59.8
136 „	142 „	20	—	20.3	21.2	27.1	25.3	25.3
147 „	137 „	22.1	22.1	19.8	20.1	27.1	27.3	24.4
7	8	—	—	—	—	—	—	—
8	8	—	—	—	—	—	—	—
—	483 mm	82.8	80.7	—	—	—	—	86.2
—	144 „	24.5	24.7	—	—	—	—	25.7
—	54 „	9.1	10.7	—	—	—	—	9.6
—	137 „	21.8	20.5	—	—	—	—	24.4
—	149 „	21.6	19	—	—	—	—	26.6
—	10	—	—	—	—	—	—	—
—	9	—	—	—	—	—	—	—

of two skulls coming from Muséum Guadeloupe belonging to the collection of the "Laboratoire d'Anatomie comparée, Muséum National d'Histoire Naturelle" (Paris). True (1889, page 141) says about this that: "a skull in the Paris Museum from Guadeloupe Island, and which is the basis of *Globicephalus guadaloupensis* Gray". The skull figures in van Beneden and Gervais (1880) under the name of *Globicephalus intermedius*. Gray took it as the type of his species *G. guadaloupensis*. Unfortunately, we do not have more details on the skull and it is not possible to say which of the two Paris' skulls is the type of the Gray's species.

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A BRIEF REPORT ON THE BEHAVIOR OF COMMERSON'S DOLPHIN, *CEPHALORHYNCHUS COMMERSONII*, IN PATAGONIAN SHORES

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ABSTRACT

Data on the behavior and movements of Commerson's dolphins at Comodoro Rivadavia's harbor were collected as a preliminary step to future studies on this cetacean. Evidence on prey-species, calving season and ecological preferences are also given in this general account on what is actually known about the natural history of *Cephalorhynchus commersonii* and its position in the harbor's summer community.

Commerson's dolphin, also known as "Tonina Overa" because of its black and white coloration, is a cetacean of about 1.70 m long and very common in the southwestern Atlantic south of 42°S.

It is also frequent in Chilean waters south of 50°S to Drake passage (Aguayo and Torres, 1967; Aguayo, 1975). Strange (1972) and Hamilton (1952) comment its abundance in Malvinas islands and, finally, Angot (1954) reported this species for Kerguelen islands.

This report, although short is considered of relative importance because it gives some general new data for this cetacean as well as for imply considerations that I hope will be of interest for future studies.

Observations were made in the harbor of Comodoro Rivadavia (45°52′S; 67°29′W), Chubut province mostly at the end of the southern pier (Fig. 1) or from the top of the cliffs that lay just in front of the pebble beach of the harbor.

During most of the time it was possible to track dolphins with the unaided eye but sometimes 8×30 binoculars were necessary.

A Heuler stopwatch with an error of 0.2 sec. was used to clock breathing times, and notes were tape recorded or written directly.

Dolphins were tracked during 145 hours in January 1977 and January-February 1980.

The harbor of Comodoro Rivadavia has a mean depth of 5 m and its waters, although of relatively small volume, contain a high number of species in a moderately populated community at least during part of spring and summer.

Most abundant are schools of gregarious fishes such as silversides (*Basilichthys* sp.), Fueguian sardine (*Sprattus fueguensis*) and southern anchovy (*Engraulis anchoita*) all of which are the prey of dolphins, terns (*Sterna* aff. *hirundinacea*), Magellanic penguins (*Spheniscus magellanicus*) and shags (*Phalacrocorax albiventer*).

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There are great kelp beds, especially near the northern pier where Commerson's dolphin appears to be most of the time.

Tidal difference in the area is of about 4–5 m and nothing is known about how this might influence the movements of dolphins. Another disturbance for the cetaceans are long lasting oil patches left in the harbor by tankers and other ships.

Commerson's dolphin usually swims at moderate speeds, about 6–7 knots. When feeding they reach higher speeds and perform several kinds of breaches.

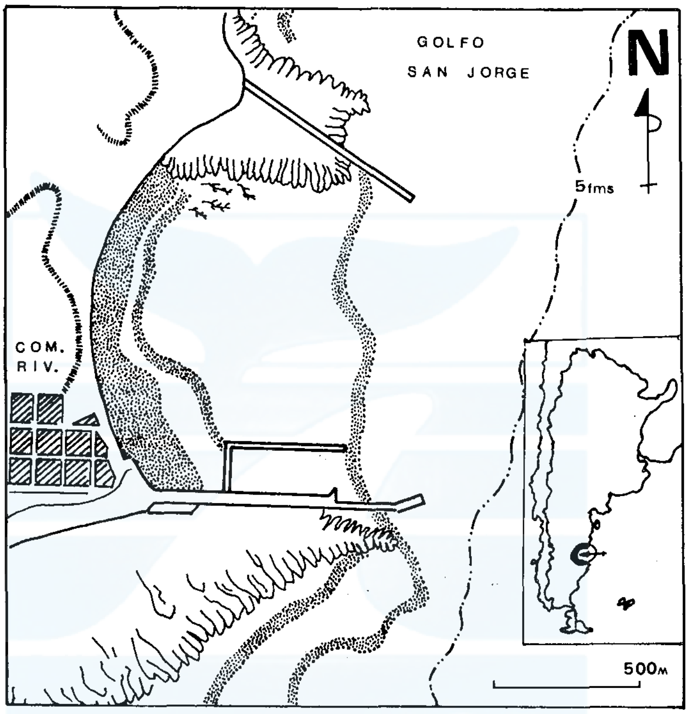

Fig. 1. General view of the harbor area of Comodoro Rivadavia, and its position in Argentine shores.

Generally, movements of this species seem similar to those described by Moreno (1892) who named it *Lagenorhynchus floweri*. From the end of the southern pier it was possible to track with detail this cetacean's slow breathing movements, which are altered when the animal swims at higher speeds, which it frequently does. *C. commersonii* surfaces at an angle of 45°, the tip of the snout first, and then it bends the head backwards, breathes, and then goes underwater with the body curved so that immediately after each breath the dorsal fin is above water, then the animal submerges and the flukes do not come out of the water.

Tracking Commerson's dolphin is very difficult for they usually remain submerged for 15–20 seconds, during which time they swim in a very erratic course, so it is not easy to tell where they will emerge.

From the top of the cliffs dolphins can be seen swimming at a depth of 1 or

1.5 meters, rarely in straight line.

Dolphins were seen in the harbor every day, mainly at the northern pier and the kelp beds. They usually search for fish, two or three meters from shore, and the same distance from the end of the southern pier, where they have been seen at only half a meter when pursuing a school of fish together with Magellanic penguins. These animals also jump very often, making all kinds of breaches. During field studies in 1980 we saw few of them but in the previous season the maximum recorded was 65–70 breathes made by 6 dolphins in only 17 minutes on 9 January 1977 (1317 hs, local time).

In general, a group of Commerson's dolphins breathes two or three times and then they all submerge almost at the same time.

The range of 93 breathing times recorded for several adult dolphins ran from 1 sec. to 1 min. 37 sec. ($\bar{x}$: 14.2 sec, SD: 18, 1 sec.) and 54 for calves: from 1 sec. to 48 sec. ($\bar{x}$: 12, 6 sec, SD: 11, 6 sec.).

We recorded 52 interbreathing times from a captive pair of adult dolphins for several days in an artificial pool which extended from 3 sec. to 23 sec. with a mean of 14.8 sec and a standard deviation of 15.1 sec, six hours after their capture, which is in accordance with breathing times recorded in free-living animals. The simultaneous inmersions of both cetaceans, and the almost imperceptible difference between them when this was not the case, was also seen in the pool.

Inhalation follows exhalation without an intertime. The spout is not visible even at close range.

Cephalorhynchus commersonii usually swims in groups of 2 to 4 animals although schools of 6–7 animals are seen. The greatest group sighted in the harbor of Comodoro Rivadavia was one of about 20 adult dolphins and 11 calves on 25 January 1977 (1500 hs, local time). They also congregate in higher numbers when swimming at the bow of a ship.

This schooling behavior is similar with that described by Baker (1978) for *Cephalorhynchus hectori* in New Zealand waters, and mainly by Aguayo (1975) for *C. commersonii.*

The dolphins are often in several groups of three or four that move as independent unities for a long time. We cannot say if these groups form part of a larger stock.

Almost nothing is known about the social behavior of this species. On the side of an adult male 1.58 m long captured on February 1980, we found scars distributed in three series; they appear to have been made by another animals of the same species. This could be the result of "social fighting", probably for females as suggested by McCann (1974).

Cases of "social facilitation" were seen: several dolphins begin to breach, being followed after few minutes by other animals.

When some Commerson's dolphins were carefully caught for a German zoo, we could see that other dolphins began to swim slowly near the captive ones. Acoustic distress signals from those entangled in the net might have attracted the others. We saw this every time when we succeeded in netting a dolphin.

It is interesting that no dolphins tried to evade the net by jumping over it. Every time they seek an exit, they do so underwater, never at the surface. Being adapted to the aquatic environmet, it is proper that when they feel danger they look for safety in the water where they can use echolocation. This case is similar to that of the Pacific tuna-porpoise problem in which *Stenella* species almost never escape from the net by breaching over it.

Rather frequently the bibliography mentions several species of cetaceans swimming together with pinnipeds, sea birds etc, but few if any of these references describe *interspecific relations* between them.

Commerson's dolphins although seen almost every day in the company of Magellanic penguins, terns and shags, never seemed to interact with these species. For example, on 11 February 1976, during field studies carried out at the San José gulf I sighted a lonely Commerson's dolphin swimming a hundred meters from a school of three Burmeister's porpoises, *Phocoena spinipinnis*, without noticing any kind of mutual interest (Würsig *et al.*, 1977).

At Comodoro Rivadavia, *Cephalorhynchus commersonii* usually swims close to terns, southern sea lions and Magellanic penguins, but we never could detect interspecific activity. Also, we did not see collaboration between terns and the dolphins in the capture of schooling fishes as was described by Würsig and Würsig (1979) in dusky dolphins, *Lagenorhynchus obscurus* and sea birds at the San José gulf, where they feed on southern anchovies, *Engraulis anchoita*. A probable explanation of this would be that in the San Jose gulf dolphins and birds need to "drive" fishes in a compact mass to be able to feed efficiently on them, because of the extension of the gulf. Commerson's dolphins and their prey species live during summer in a relatively restricted area of shallow water where there is no need such collaboration. This would not be the case in southern, more open waters, where something similar to the situation reported by Würsig and Würsig (op. cit.) may occur.

Little data was gathered on the ecology of *C. commersonii*.

Harmer (1922) reported krill and squids from a single animal from Puerto Stanley, Malvinas islands. Although we did not record stomach contents, from the behavior of dolphins and the capture of several hundreds of Fueguian sardines (*Sprattus fueguensis*) after the dolphins feeding activity, we conclude that this fish, probably together with silversides and southern anchovies, are the prey-species of the Commerson's dolphins in the San Jorge gulf, at least during spring and summer. The distribution of *S. fueguensis*, on the other hand, is exactly the same as that of the cetaceans (López, 1963).

Dolphins congregate in protected areas such as Comodoro Rivadavia harbor, the Ria Deseado (Santa Cruz province) and Rio Gallegos (Santa Cruz). We suppose that, as baleen whales do, they look for quiet and protected areas for calving. Dolphins are seldom seen in wide beaches as, for example, Rada Tilly south of Comodoro Rivadavia and Bahia Solano, north of it, nor are sea birds and sea lions. They might prefer harbor waters because there it would be easier to feed on schooling fishes where it is not neccesary to drive them, as was said above.

We never saw dolphins feeding at the center of the harbor, only close to the beach and piers. Würsig and Würsig (1979) reported the way *Lagenorhynchus obscurus* feed on *E. anchoita* at the sea surface, using it as a "wall" to which fishes are confined. It is very probable that Commerson's dolphins at Comodoro Rivadavia use the beach and piers in the same way as dusky dolphins utilize the sea surface. In the case of *L. obscurus*, generally several tens of animals drive the fishes, together with sea birds; but this does not happen with *C. commersonii*, usually not more than ten animals feed at a given time.

Commerson's dolphins spend much time swimming in kelp beds, this has been reported also by Harmer (1922) for Malvinas islands. If the cetaceans profit from this, we do not know.

Goodall (1978) reported the capture of two pregnant females on the first days of December, 1977, one of which calf was born on the beach. Another animal (RNP 634) with a near term foetus was captured on 12 December 1977.

In Comodoro Rivadavia's harbor, at the middle of January we begun to see calves with the adults. The newborn calf is completely brown, as it grows it becomes greyish and then the black and white areas begin to appear, being at first gray instead of white and darker where it will be black. At the middle of February 1980, we still see calves. A census made on 28 January on the whole harbor area, showed a minimum of 18 dolphins, two of which were calves, one of them very small. This means an adult-calf ratio of 8: 1. A similar census carried out on 25 January 1977 showed a minimum of 50 adults and 11 calves, with a ratio of 4.5: 1.

Goodall (1978) reported 105 animals of her own from Tierra del Fuego, collected mainly between 1974 and 1978, which means a mean stranding of 21 animals per year. Mitchell (1975) mentioned a report made by James G. Mead on this species in Patagonian shores in which the author suspected an annual mortality of near 100 cetaceans in the whole coast.

We have no way of knowing the exact number of animals entangled in fishermen's nets for the moment, so this is the only source of information we have on the matter at present.

Commerson's dolphin is one of most common cetaceans in Patagonian shores. The first impression we got is that it appears to occupy a very similar ecologic niche as *Lagenorhynchus obscurus* north of the San Jose gulf, both animals preying on schooling fish. If these cetaceans intermingle on Argentine shores is something we hope to study in the future.

The calving season takes place in early summer, and it appears that dolphins prefer quiet areas, although sometimes they are seen in more open waters. This could be because calves need special water conditions and there might be a preference by adult dolphins for areas in which is easier for them to feed.

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A REVIEW OF FOOD OF BALAENOPTERID WHALES

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ABSTRACT

In order to elucidate what species among so many kind of marine organisms are likely to be consumed largely by the balaenopterid whales, the existing evidence on the food habits of baleen whales is reviewed. To meet with this primary purpose the report was mainly focussed on to describe qualitative aspects of food species having been known to date from the notable whaling grounds over the world rather than documenting quantitative subjects. One of interesting facts noticed throughout the contribution was that there exists fairly intense diversity in the assembly of food species composition by regions such as; northern hemisphere vs. southern hemisphere, Pacific region vs. Atlantic region, inshore waters vs. offshore waters, embayed waters vs. open waters, where the former usually shows more diversed complexity than the latter. The fact however suggests that although the composition of food species locally varies over the various whaling grounds, the food organisms as taxonomical groups are very similar one another even in locally isolated whaling grounds when the food organisms and their assemblies are considered by the family or genus basis. In this connection many evidences given in the text may suggest that the balaenopterid whales as a whole may substantially live on quite simply compositioned forage assembly in comparison with tremendous variety of organisms existing in the marine ecosystems. One of important aspects of the baleen whales food must be found in their characteristics of forming dense swarms, schools, and/or aggregations in the shallower enough layers to be fed by the whales. The present and past status of larger baleen whales as the mighty monarch through their evolutional pathways may entirely depend upon the spatial distribution pattern of possible food organisms, *i.e.* the animal aggregations.

CONTENTS

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INTRODUCTION

This contribution firstly prepared in response to the request by the CRC Press Inc., U. S. A. under the title, "Diets for Balaenopteridae" as one of the contents should be included in the "Handbook Series in Nutrition and Food". In December 1979, however, the publisher informed me that they were unable to include this contribution in the volume to be published near future due to excess holds of contributions submitted. In response to this situation, submission of article was switched to the *Scientific Reports of the Whales Research Institute* No. 32, 1980 by courtesy of Dr Hideo Omura, the Director of the Whales Research Institute, Tokyo.

Since the main purpose of this article was subjected to describe the known evidence on the food habits of balaenopterid whales, the viewpoint was mainly focussed on to collect and give qualitative information in a manner of encyclopedia rather than documenting quantitative and logical discussion. On the other hand, the evidence around food and feeding habits of larger whales from the ecological viewpoint has been well documented by Nemoto (1959) and later by Gaskin (1976). The former treated largely the case found in the North Pacific and its environs, while the latter covered nearly all kind of whale species occurring over the world oceans, and summerized widely scattered evidences into a very comprehensive knowledge from the viewpoint of evolutional ecology.

At present, it may be considered that the whaling is at its lowest but somewhat stationary activities being operated in very limited regions, and that the kind of food items taken by baleen whales does not seem to increase so largely as the past several decades when both whaling ground and whale species changed drastically from year to year. Since the study by Gaskin (1976), however, some additional evidence has been known through the study of Bryde's whales from the tropical seas (e.g. Kawamura, 1977), and these are considered to be added as a recently known evidence to the general knowledge of food habits of baleen whales.

This contribution aims to present simply what kind of organisms are likely to be taken selectively by the larger whales occurring over the world oceans. Different from treating materials by the organic carbon basis, qualitative knowledge by species basis must be characteristic and indispensable factors in elucidating the structure and function of marine ecosystems since the amount of organisms annually consumed by the larger whales is undoubtedly so enormous as estimated the case in the antarctic krill, *Euphausia superba* (e.g. Laws, 1978). As the biological environmental factors local food condition strongly relates to the movements and migration of whales (Kellog, 1928; Nemoto, 1959; Kawamura, 1975). One of another important aspects of the dietary habits is the state and condition of stomach contents actually observed in carcasses, which indicate ecological characteristics of food organisms such as individual density, biology of animal aggregation and patchy distributions, neither of these are hardly known by the conventional net samplings (Omori *et al.*, 1972; Kawamura, 1974; Brodie *et al.*, 1978). In this connection, the baleen whales and their feeding characteristics as discussed by Klumov (1962) can be considered really functional and effective 'biological sampler' for marine zooplankters and micronektonic organisms.

Each evidence given in the text may indicates that considerably diversified food habits are exhibited by locality, seasons, and by each whale species even in a taxon, Balaenopteridae. Ever known facts on the food and feeding ecology may indicate guide lines which suggest a possibly existing inter- and intraspecies relationships between larger whales and small planktonic or nektonic organisms of lower trophic ladder.

In order to unify the family name of food organisms under the similar forms, such expression as euphausiids, for example, in the tables quoted elsewhere in the text was changed into Euphausiacea without notifying this in each corresponding table.

THE BALAENOPTERID WHALES

The order Cetacea is comprised of two suborders, Mysticeti and Odontoceti. The former is the baleen or whalebone whales, which includes three taxonomical families, *i.e.*, Eschrichtiidae, Balaenopteridae, and Balaenidae, while the Odontoceti, the toothed whales are comprised of five families (Table 1).

As it is suggested by the common name, all member of mysticete whales that are known as the baleen whales or whalebone whales, are furnished with subtriangular horny baleen plates in the upper mandible as the filtering apparatus instead of tooth in collecting forages although the shape and structure of baleen plates vary considerably by each family and species. As relatively large mouth proportion, say, about 1/5 long of their total body length suggests, the mysticete whales could be considered the greatest 'filter-feeders' or 'strainers' among all animal ever lived on this earth. It is their mouthful row of baleen plates that make mysticete whales to be the quite distinct animals both in biological and ecological aspects, especially in gathering their food more powerfully in the aquatic environment. Of three mysticete families, the Balaenopteridae is the representative taxon which includes so-called great whales or 'rorquals' *i. e.*, the blue, fin (finback), sei, Bryde's, minke whales and humpback whale.

Apart from two another families, the balaenopterid whales are supposedly best adapted animals to aquatic environments, and distributed widely throughout the world oceans. Their habitat is usually found in the pelagic waters while two others, Balaenidae and Eschrichtiidae, are common in the pelagic to neritic waters. Sometimes these whale group invade deeply into the inlets and lagoons. Because of their well adapted structure to the aquatic environments, the balaenopterid whales could perhaps have been maintained their largest populations than any other mysticete families in both northern and southern oceans, which undoubtedly due to their powerful, and consequently more advantageous feeding habits as filter-feeders in fulfilling the daily nutritional requirements. Because of their gracefully devellopped but mysterious way of life, the great whales have long attracted scientific interests, and their dietary habits must have been refered to as one of those mysteries. Inversely, it was unfortunate for the animals of distinct zoological characteristics, that they were doomed later to be the target of modern whaling, but it was also the beginning of intensive harvest of those giants over the world oceans.

TABLE 1. THE MEMBER OF MYSTICETI (MYSTACOCETI: BALEEN WHALES)

Scientific name	Common name
Family Balaenidae	
Balaena mysticetus	bowhead
Balaena glacialis glacialis	northern right whale, black right whale, right whale
Balaena glacialis australis	southern right whale, black right whale, right whale
Caperea marginata	pygmy right whale
Family Eschrichtiidae	
Eschrichtius robustus	gray whale
Family Balaenopteridae	
Balaenoptera musculus[1]	blue whale
Balaenoptera physalus	fin whale
Balaenoptera borealis	sei whale
Balaenoptera edeni[2]	Bryde's whale
Balaenoptera acutorostrata[3]	minke whale
Megaptera novaeangliae	humpback

1) There exists a subspecies, pygmyblue whale, *B. musculus brevicauda*, which is an endemic species in the southern ocean (Omura, *et al.*, 1970).

2) The name *B. brydei* is still valid relating to the identity of two forms of this animal (Omura, 1977).

3) *B. bonaerensis* has been used for the southern animals. Between *B. acutorostrata* and *B. bonaerensis* there are morphological and biological differences by a magnitude of hardly separable (Ohsumi *et al.*, 1970; Omura, 1975, but see also Doroshenko, 1978). But, Rice (1977) proposes three subspecies, *B. a. acutorostrata*, *B. a. davidsoni*, *B. a. bonaerensis*.

Because immediate ancestry animals for the mysticete whale are unknown at present, it is very hard to suppose that at the beginning of adaptive radiation what made the land-dwelling animals driven so as to invade into the aquatic environment during the Oligocene to Miocene periods. However, it seems to be one of the best way for the ancestry animals evolving toward the aquatic animals that feed mainly on the abundant minute crustaceans which undoubtedly had been widely obtainable over the epicontinental shallow seas since the suturing of the supercontinent Pangaea in the Permo-Triassic periods onward (Schram, 1977), and subsequent rapid evolution might perhaps be accelated by the increased marine production by upwelling of the sea, although the latter is a hypothesis at the present state (Lipps and Mitchell, 1976).

Although each food item for the balaenopterids may show geographical and seasonal variations along with the abundance of suitable food even within the same whale species, the filter-feeder as an adaptation to aquatic environments must be perhaps an great advantageous way of life in competing for food with many kind of another animals. Among so many diversed species composition with the variety of radiation in the phocid seals, the crabeater seal, *Lobodon carcinophagus*, for example, is the unique animal. The complexed teeth and its general arrangements in this animal serve as the sieve in collecting minute crustaceans such as *Euphausia superba* in the Antarctic waters (Bertram, 1940). The unquestionably larger population size of *L. carcinophagus* presumably indicates the successful evolutional pathways of this animal through out the order Carnivora (Kawamura, 1972).

The balaenopterid whales are really cosmopolitic animals that undertake a large scale seasonal migrations of several thousands kilometers, which connect between feeding and breeding grounds while the balaenid whales, *Balaena mysticetus*, *Balaena glacialis glacialis*, *B.g. australis* and *Caperea marginata* are considered somewhat neritic and/orendemically established species. Although the famous gray whale, *Eschrichtius robustus* migrates for a great distance of such as between Lower California and the Arctic Ocean, this animal must be considered really neritic and bottom or benthos feeders (Rice and Wolman, 1971), which enable them to feed any time and place enroute their migrations though the major feeding seems to occur in the high arctic regions. The balaenopterid whales as fully developed planktono- and ichthyophagous animals complete their migration by utilizing deposited lipids as an energetic sources. As it has been pointed out by many workers, the balaenopterids usually do not or can not feed while they are far outside from the proper feeding grounds, but recent observations (Gambell *et al.*, 1974; Kawamura, 1975, 1977) strongly suggest the feeding activity of baleen whales even in the warmer seas. This again suggests the balaenopterid whales to be the most fully adapted filter-feeders among many others since they can deposit possibly enough amount of lipids for the nutritional requirements in addition to that used in metabolism during four to five month stay in the feeding grounds.

BALEEN PLATES AND FEEDING

An adaptation of the balaenoptrid whales as the filter-feeder and, despite their ingenious structure in harvesting those minute planktonic crustaceans, the gross daily nutritional and energetic requirements are enormous although the energy cost for locomotion as an aquatic animals would be very smaller than any other terrestrial animals (Schmidt-Nielsen, 1972; Kawamura, 1975). For instance, the southern fin whale is estimated to consume only 0.022 kcal/gram body weight/km (Kawamura, 1975). As it is supposed generally in the food items for the balaenopterid whales, there seems to be difficult in obtaining suitable amount of food over the vast oceans except those spacially very limited places so-called the feeding grounds. The baleen whales, from the beginning of their ancestory evolution towards aquatic animals, are largely dependent upon the organisms occurring with large biomass and forming dense swarms in the upper subsurface waters (Hjort, 1933). Although the planktonic crustaceans, small gregarious fish, fish larvae, and some others like squids may occur widely in the oceans, there are only very limited groups of possible food organisms being actually utilized by the baleen whales. The productivity of oceans shows quite biassed aspect in its distributions. The rich primary production which finally links to the rich secondary production is usually found in the colder seas of north and south latitudes higher than 40° latitudes and in the upwelling regions. The famous feeding ground ever known for baleen whales, therefore, may be regarded as the most possible and easiest place in locating aggregations and/or schools of prey organisms (Fig. 1). As mentioned before, the evidence that the baleen whales under breeding migrations rarely feed is certain to some extent, but this actually seems to be the result due to absolute scarceness of prey in the warmer seas where they give birth to a calf and mate. Whenever the whales may encounter to the place where large but local food stocks are available they undoubtedly prey upon them voraciously (Kawamura, 1977). This suggests that poor feeding activity of baleen whales during the breeding migrations does not seem to be the result of their ecological and physiological characteristics but due rather simply to the poorer standing stocks of possible food organisms in the breeding grounds or warmer sea regions.

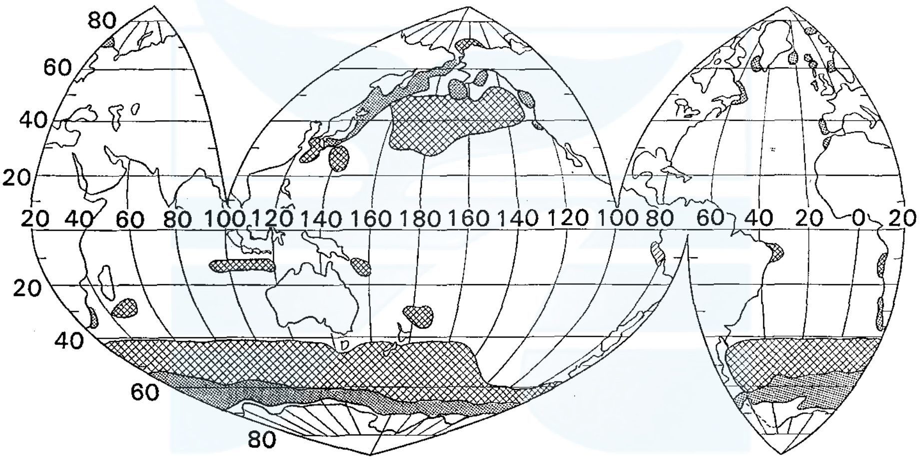

Fig. 1. World whaling grounds for mainly rorquals. The original figure by Mackintosh (1965, Fig. 7) to which recent and some past principal occupations of whaling grounds for sei and Bryde's whales are additionally demonstrated by mesh. The whaling grounds in the mid-latitude offshore waters indicate the catch place of Bryde's whales during exploratory fishing (1976/77–1978/79) under scientific permit (see Kawamura, 1977, 1980; Ohsumi, 1979).

To meet on to their nutritional requirements the baleen whale developed a quite characteristic apparatus—the baleen plates or whalebone. The subtriangular baleen plates with fine inner fringes and their curtain like arrangements in two sets of row on the upper jaw form a fuge filtering or straining apparatus to sieve off some several cubic meters of water containing the aggregation of food organisms. An importance of well developed baleen plates and the row is obvious. Once the baleen filter was damaged by some reasons such as the infection of parasites (Rice, 1967), the animal may sometime become very poorly nutritioned being caused by far little food ingestion due to less effective feeding apparatus.

In the balaenopterid whales the baleen plates usually count 260–400 in number on one of two sides of upper jaw. Each baleen plate is arranged closely one to the next to form a comb-like row with an intervals of about 0.5–1.3 cm although

TABLE 2. AVERAGE NUMBER OF BALEEN PLATES IN ONE OF TWO SIDES IN THE NORTH PACIFIC AND ANTARCTIC BALEEN WHALES (Nemoto, 1959; Ohsumi *et al.*, 1970)

	Blue	Fin	Bryde's	Little piked	Sei	Humpback	Right	Gray
North Pacific								
Range	300-400	300-400	260-370	260-300	320-380	300-370	230-260	130-180
Approximate mean	360	355	300	280	340	330	245	160
Antarctic and southern hemisphere								
Range	260-400*	260-480*	250-280	261-359	300-410*	300-370*	220-240*	—
Approximate mean	320	360	—	289	345	—	—	—

* After the data by *Discovery* research since 1929.

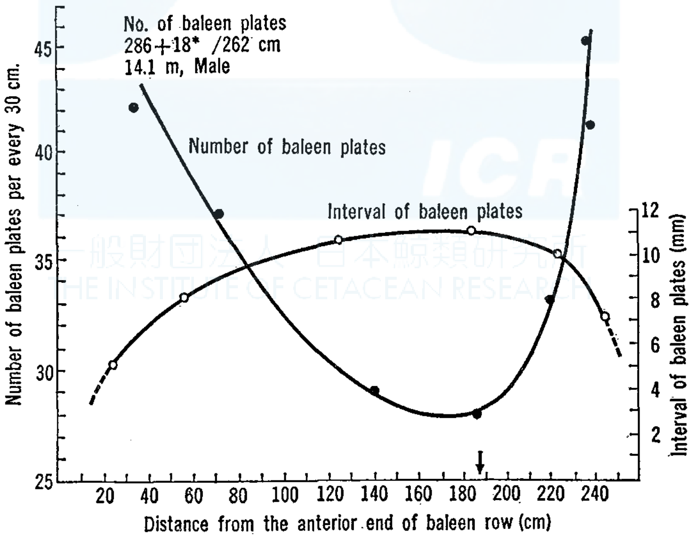

Fig. 2. Variation of the number of baleen plates in sei whale. Arrow shows the spot where maximum length of baleen plates was found (Kawamura, 1974). (* fringes)

the number of baleen plates and their intervals to the next may vary in details with species and the age of animals (Kawamura, 1974). (Table 2, Fig. 2). Usually, the younger the animal, the more thickly intervaled in baleen plate arrangements. One of baleen row measurements as found in the southern sei whale is demonstrated in Fig. 2. The inner fringe of baleen plate is furnished with fine horny bristles (=fringes) of about 3–5 cm long which, by overlapping one to the other, to form the sieving meshes or 'fibrous mat' as called by Gaskin (1976) that directly concerned with retaining the food organisms on them. The thickness of baleen bristles

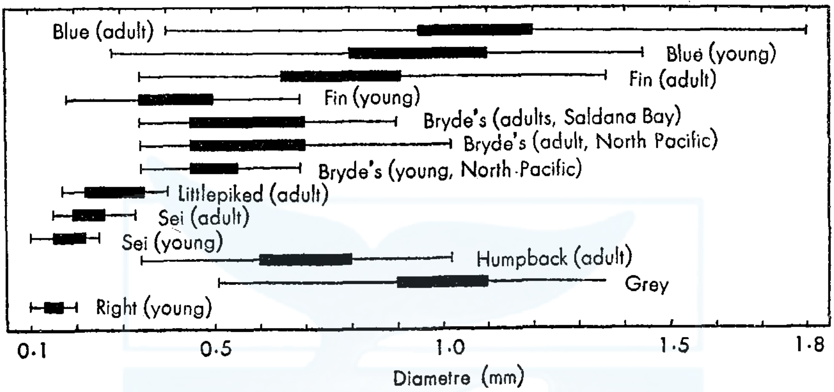

Fig. 3. Diameters of baleen fringes of baleen whales measured at the center position of baleen plates. Black belts show the ranges of dominant sizes of baleen fringes. Adult: whales after the sexual maturity, Young: sexually immature and baleen plates are not chipped (Nemoto, 1959).

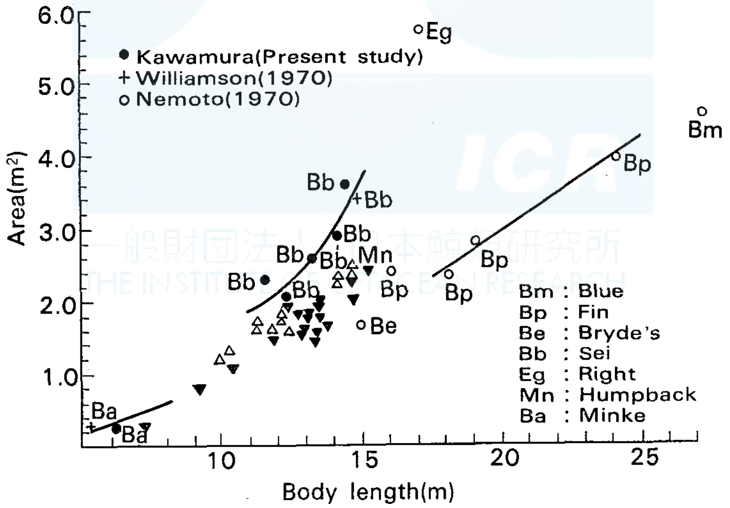

Fig. 4. Total baleen filter area in baleen whales (Kawamura, 1974). Both filled and open triangles show the filter area for the Bryde's whales in the North Pacific and southern oceans respectively (Kawamura, 1978a).

in terms of their diameter also varies with whale species; then the coarsest filter among the balaenopterids may be found in blue whale whilst the finest one in sei whale (Fig. 3). Further details on the baleen filter can be consulted to Nemoto (1959, 1970), and Kawamura (1974).

As the figures and tables clearly show, the general morphological character of filtering apparatus in the mysticete whales varies from family to family, and from species to species, although a greater variation may be found in the family Balaenopteridae. The whole structure and the function of filtering apparatus is closely related to those above shown individual characteristics. Among all above mentioned the average along with maximum length of the baleen plates may decides the total filter area of animals, which may finally characterize the food and feeding habits of each whale species (Fig. 4).

Putting together these figures and tables, it is noticed that the balaenopterid whales as a taxonomical group may be recognized from both eschrichtiids and balaenids by distinguishing relative shorter but finer filtering apparatus. Although there are several another morphological characteristics relating to the dietary habits of whales, the author believes that the structure of filter itself and its total but actually functional filter area is among all the most important agents that determine the feeding habits of each whales species. Further but more general details on this subject may be consulted to Scoresby (1820), Ingebrigtsen (1929), Mackintosh (1965), Slijper (1962), Nemoto (1970), Kawamura (1974) and Gaskin (1976).

FEEDING TYPES

The morphological characteristics of filtering apparatus in baleen whales may extremely well related to the feeding types and feeding behavior, which largely determine the kind or the group of principal prey organisms although the latter again varies with the geographic regions.

Two different feeding types employed in baleen whales have been proposed, (Nemoto, 1959, 1970): *i.e.*, swallowing and skimming types, or swallowers and skimmer (Mitchell, 1974), both of which were perhaps derived from the field observations by Ingebrigtsen (1929), although Hjort (1933) noted swallowers as to "play" against the so-called skimmers. His description is so suggestive as to imagine the whales feeding, and considered worth to be quoted; he (Ingebrigtsen, 1929) describes, " During whaling operations in 1905 I had the opportunity of seeing that the humpback is far more intelligent than other species of whale. It employed two methods of capturing " krill " when the latter was on the surface of the water. One was to lie on its side on the surface and swim round in a circle at great speed, while it lashed the sea into a foam with flukes and tail and so formed a ring of foam. The frightened " krill " gathered together in the circle. This done the humpback dived under the foam-ring and a moment later came up in the centre to fill its open mouth with " krill " and water, after which it lay on its side, closed its mouth, and the catch was completed."

" The other method ", Ingebrigtsen (1929) continues, " was to go a short distance below the surface of the water, swimming a ring while at the same time it blew off. The air rose to the surface like a thick wall of air bubbles and these formed the " net ". The " krill " saw this wall of air bubbles, were frightened into the centre, and then the manoeuver of the first method was repeated."

" When the whale lay on its side and shut its mouth the rifled belly formed an enormous distended bag before it was contracted and the water pressed out between the whaleboneplates."

" When one saw that enormous bag, which was many times larger than the real mouth from the gullet to the nose one could understand that the humpback, fin-back, sei-whale and blue-whale have the rifled belly from the point of the chin to the middle of the body, solely in order to be able to take in an enormous quantity of water containing food. With the straight jaws and rather straight palatal region possessed by these 4 whales as compared with the right whales, which have curved jaws and palatal region, there would be little room for water in the mouth, if there was taut, smooth blubber under the chin and belly, as its the case with the right whales, the Greenland whale and the North Cape whale." He also describes, " The blue-whale, fin-back and humpback turn over, often with part of the head above water, when feeding." Very recently Jurasz and Jurasz (1979) observed the humpbacks in Alaskan waters use three different feeding methods, *i.e.*, lunge feeding, bubblenet feeding, and flick feeding depending on the school mode of available feed. In the lunge feeding there also noticed that the method includes variations of 'lateral', 'vertical', and 'inverted' lunge feeding.

" The sei-whale, on the contrary, 'skims' the food. It swims at great speed through the swarms of copepods, with half open mouth, its head above water to just behind the nostrils. The copepods rush in with the water and are filtered from the water by the whale-bone plates. When a suitable mouthful of copepods has been taken the whale dives, shuts its mouth and swallows the food. It is especially in the evening and early in the morning, when the copepods are most at the surface, that 'skimming' takes place." (Ingebrigtsen, 1929).

The balaenopterids are usually known as to perform a swallowing type feeding. The whale engulps a mouthful of food containing water by the aid of ventral grooves, and sieve off through the slit of baleen row by giving a pressure on the water with its tongue. Then the food organisms retained on the baleen filter are swallowed through throat and oesophagus of several inches across. Recently Gaskin (1976) showed a series of very clear figures of feeding in balaenopterid whales. As it is noticed in Figs 3 and 4, the sei whale shows rather closer feeding habits to the balaenid whales with relatively finer baleen bristles and larger filter area, and is considered to demonstrate both skimming and swallowing types of feeding (See also Table 3). Although the humpbacks as quoted above usually perform the swallowing type feeding, there are clear indication of occasional bottom feeding that is suggested by a significant occurrence of demersal fish and crustaceans along with large amounts of 'fine pebbles' in the stomach (Zenkovich, 1936 cited from Gaskin, 1976). The minke whale as Norwegian call them " Vaaghval " (=Bay whale) sometimes enters deeply into the river, inlets and the bay such as the Thames, St. Lawrence,

TABLE 3. FEEDING TYPES IN THE MYSTICETI WHALES
(Nemoto, 1970; Mitchell, 1974)

- Swallowing type or swallowers
  - blue whale and pygmy blue whale
  - fin whale
  - Bryde's whale
  - humpback whale
  - minke whale
  - Antarctic minke whale
- Skimming type or skimmers
  - right whale (northern and southern right)
  - Greenland whale (bowhead)
  - pygmy right whale
- Skimming and swallowing type
  - sei whale
  - gray whale

TABLE 4. THE ORDER OF SELECTION OF THE FOOD IN BALEEN WHALES*
(Nemoto, 1970) (=shows equivalence, and >shows the dominance to the left)

Blue whale	Euphausiacea
Fin whale	Euphausiacea=Copepoda (large)=Gregarious fish>Copepoda (small)>Cephalopoda (squids)
Bryde's whale	Euphausiacea=Gregarious fish>Copepoda (small)
Sei whale	Copepoda≧Amphipoda≧Euphausiacea=Swarming fish=Cephalopoda (squids)
Humpback whale	Euphausiacea=Gregarious fish>Demersal fish and crustacean
Minke whale	Swarming fish=Euphausiacea>Copepoda
Right whale	Copepoda>Euphausiacea>Planktonic Pteropoda

* slightly changed from the original.

freshwater tributaries of Puget Sound (Tomilin, 1967). Pebbles and grand particles in the stomach suggest that the minke as well as the humpbacks feeds at the bottom occasionally. The balaenids, the right whale group, as known by their enormously long baleen plates with finest filter meshes but no ventral grooves perform a really way of skimming type of feeding (Scoresby, 1820; Watkins and Schevill, 1976). (Table 3).

The difference in feeding types of whales may characterize the group and/or the species of food organisms in the order of more preferable feeding. Generally speaking, the swallowing type of feeding performed by the balaenopterids is considered more suitable for harvesting the larger and faster swimming prey organisms while the skimming in the near surface water by largely opened mouth would allow to entrap a really small and weak swimmers of planktonic organisms such as ctenophores, pteropods, chaetognaths and copepods. (Scoresby, 1820; Hjort and Ruud, 1929; Watkins and Schevill, 1976). Table 4 gives one of such differences as having been proposed by Nemoto (1970) where he calls these trends as the order of selection of the food in baleen whales. These, however, must be regarded as a largely generalized idea, which sometimes seems to be hardly applicable in actual cases mostly by the difference of ecologically heterogenious ocean systems to which the whales come to concentrate and feed. One of typical examples of local differences may be found in the dietary habits of the balaenopterids demonstrated between the Antarctic and the North Pacific feeding grounds (Gaskin, 1976; Nemoto and Kawamura, 1977).

KIND OF FOOD ORGANISMS

One of well known whales food is the krill, *Euphausia superba* Dana in the Antarctic Ocean. *E. superba* predominates over the southern oceans, and is not only the food of baleen whales but also the food of almost all larger animals, seals, seabirds, fish, squids and perhaps of some benthic animals occurring on the shelf and underwater ridges. One of comparative study relating this subject was given by Salinikov (1953). *E. superba* that is called as the Antarctic krill, certainly build up those gigantic blue whale of weighing hundred tons and keeps growing the enormous biomass of various whale stocks. Undoubtedly, *E. superba* can be literally regarded as the key species in the Antarctic marine ecosystems. (Marr, 1962; Laws, 1977).

There are, however, many evidences on the food items of baleen whales occurring over the world oceans although the place of events somewhat biassed by localities since our knowledge on the diet of larger whales largely depends upon the whaling operations through which we can examine the carcasses of whales, but this is also restricted by the whaling regulations for locality, seasons and whale species inclusive. Being due to these limited source for the informations, there are vast sea regions such as Arabian Sea left under complete lack of knowledge concerning the whales food. It seems, therefore, to be reasonable to describe the evidence on the food habits of whales by the localities where the whaling of an appreciable extent have had been and/or have been took place.

Southern Seas

a. *Antarctic and Subantarctic*

During earlier days of the Antarctic whaling in the South Georgian waters there had been reported only *Euphausia superba* and some ‘ shrimp ’ as the whales food (Hinton, 1925). It might be simply due to the whale species hunted in those years of the 1920s’–1930s’, when the blue whale, *Balaenoptera musculus* and fin whale, *B. physalus* were the main target of whaling. However, several years later, Peters (1938) found fish, *Palarepis coregonoides* and squid, *Onichoteuthis banksii* as food of blue and fin whales in addition to *E. superba*, and more later Peters (1955) added the following species for the Antarctic balaenopterids being based on the German whaling expeditions during 1936/37–1938/39; *Euphausia recurva*, *Thysanoessa macrura*, *Cyllopus spezialis*, *Parathemisto gaudichaudii*, *Eusirus antarcticus*, *Calanus propinquus*, and *C.* (=*Calanoides*) *acutus*.

In accordance with the change of main harvestable whale species since the

TABLE 5. STOMACH CONTENTS OF BALEEN WHALES CAUGHT BY JAPANESE PELAGIC WHALING FROM 1961 TO 1965 IN THE ANTARCTIC (Nemoto, 1970)

Food species	Whale species				
	Blue1)	Fin	Sei2)	Humpback	Minke
Euphausiacea	517	16158	5936	7	88
Euphausiacea & others	4	18	4	—	—
Copepoda	2	—	2472	—	—
Amphipoda	6	9	1514	—	—
Munida (Decapoda)	—	—	75	—	—
Pisces	—	76	31	—	—
Cephalopoda (squid)	—	—	5	—	—
Vacant	674	18878	16145	2	10
No. of whales examined	1203	35139	26182	9	98

1) mainly subspecies *Balaenoptera musculus brevicauda* distributed in the lower Antarctic.
2) catch for 1966 season is included.

TABLE 6. FOOD ORGANISMS FOUND IN THE STOMACH OF BALAENOPTERID WHALES IN THE SOUTHERN OCEANS (Abe, 1957; Nemoto, 1959, 1962, 1970; Brown, 1968; Kawamura, 1970, 1974; Budylenko, 1978)

Euphausiacea:	*Euphausia superba**, *E. crystallorophias*, *E. vallentini**, *E. lucens*, *E. similis**, *E. recurva*, *E. frigida*, *E. spinifera*, *Thysanoessa gregaria*, *T. macrura**, *T. vicina*, *Thysanopoda actifrons*
Copepoda:	*Calanus tonsus**, *C. simillimus**, *Clausocalanus laticeps**, *Drepanopus pectinatus**, *C. propinquus*, *C. acutus Calinocalanus macrocarinatus*
Amphipoda:	*Parathemisto gaudichaudii f. compressa**, *f. bispinosa**, *f. intermediate*
Decapoda:	*Munida gregaria**, *Penaeus* sp.
Pisces:	*Gymnospelus nicholsi*, *Myctophum subasperus*, *M. punctatum*, *Scomberesox saurus**, *Notolepis coatsi**, *Vinciguerria attenuata**, *Notothenia ramsayi*, *Paralepis* sp., *Tetroganurus curvieri*, *Lepidotus candatus*, *Protomyctophum normani*, *Xenocyttus nemotoi*, *Engraulis australis**, *Scomber* sp.
Cephalopoda:	*Octopoda* sp., *Oegopsida* sp., *Onychoteuthis banksii*
Pteropoda:	*Clione sulcata*, *C. antarctica*
Chaetognatha:	*Eukrohnia hamata*
Tunicata:	Species name is not stated

* Important food species.

commencement of modern whaling in the Antarctic onward (blue-fin-humpback-sei/fin-sei-sei/minke-minke) (Kawamura, 1974), a considerable amount of knowledge on whales food have been accumulated. Table 5 is one of the summerized figures which covers blue, fin, sei, humpback, and minke whales. It may clearly be noticed that the blue, fin, and minke whales as typical swallowing type feeder mainly feed upon euphausiids while sei whale alone shows a stronger preference for copepods and amphipods in addition to euphausiids, *i. e.*, the former is considered really stenophagous and the latter is euryphagous at least in the Antarctic feeding grounds.

Finding no significant differences in the structure of baleen plate of the North Atlantic sei whale to that of the Antarctic, Tomilin (1967) considered that the sei whale firstly evolved as the microplanktophagous filter-feeder in the North Atlantic since there had been known only *E. superba* as the food of sei whale from the Antarctic, and he (Tomilin, 1967) concluded that the sei must be a species appeared recently in the Antarctic regions. A part of this consideration, however, it does not seem to be agreeable because the sei actually feeds on so many kind of minute crustaceans in the Antarctic as well as in the North Atlantic although the evidence from the palaeozoogeography supports the origin of balaenopterids somewhere in the North Atlantic regions (Gaskin, 1976).

TABLE 7. KIND OF FOOD ORGANISMS OCCURRED IN THE STOMACH OF SEI, FIN AND PYGMY BLUE WHALES TAKEN IN THE ENVIRONS OF CROZET ISLANDS (Pervushin, 1968).

Kind of food organisms	Sei	Fin	Pygmy blue
Euphausia frigida	+	+	+
Euphausia vallentini	+	+	+
Calanus propinquus	+	−	−
Calanus acutus	+	−	−
Calanus simillimus	+	−	−
Myctophum punctatum	+	−	+
*Onychoteuthis banksii**	+	−	+

*Identification by Yu. A. Filippova.

TABLE 8. FOOD SPECIES OF SEI WHALES IN THE ANTARCTIC (Doi *et al.*, 1967)

Season	Euphausiacea	Copepoda	*Munida*	Amphipoda	Pisces	Cephalopoda (Squids)
1964/65	3688 (5)	19	10	109 (2)	13 (3)	—
1965/66	767 (7)	2173 (7)	65	1136 (2)	2	5

Number of concurrent food in brackets.

The species of food organisms known to date from the Antarctic region are as given in Table 6. Looking at the table, we are surprised at the greater diversity in the composition of diet in balaenopterid whales, and item of food organisms turns more diversified features when the adjacent waters to the Antarctic are included. Actually, Budylenko (1978) shown a total of eighty-two food species having been found in the southern sei whales. However, it must be took in mind that the majority of them are found in sei whale alone, and also it is only a few food species that actually occurs largely with significant nutritional importance in each individual stomach. The very rare food species are also included in the table. The subspecies of blue whale, *B. musculus brevicauda* (pygmy blue whale) (Omura *et al.*, 1970) occurring in the Kerguelen/Crozet waters feeds solely upon *Euphausia vallentini* (Nemoto, 1962), but Pervushin (1968) reported *E. frigida* and some another organisms (Table 7). However, the food habits of this animal shifts to *E. recurva* and/or *E. diomedeae* in the South African waters (Bannister and Baker, 1967).

At present, minke whale, *Balaenoptera acutorostrata bonaerensis* (Rice, 1977) is only the harvestable whalebone whales in the Antarctic waters. The stomach con-

TABLE 9. COMPOSITION OF FOOD ORGANISMS IN THE STOMACHS OF SOUTHERN SEI AND FIN WHALES DURING THE ANTARCTIC SEASON, 1969/70 (Kawamura, 1974)

I / II	*Calanus tonsus*		*Calanus simillimus*		*Drepanopus pectinatus*		*Euphausia lucens*		*Euphausia vallentini*		*Euphausia superba*		*Euphausia diomedeae*		*Parathemisto gaudichaudii*		*Notolepis coatsi*	
	Sei	Fin	Sei	Fin	Sei	Fin	Sei	Fin	Sei	Fin	Sei	Fin	Sei	Fin	Sei	Fin	Sei	Fin
C. tonsus	203[1)]	3													1			
C. simillimus			5[2)]		1													
Th. vicina	2																	
Th. gregaria	1									1								
Th. sp.	1	1																
E. lucens	3						2	1										
E. vallentini	1								10	38								
E. superba											8	8						
E. similis										1								
E. diomedeae														1				
Th. actifrons	1																	
P. gaudichaudii	19		1							1				1	20	2		
Penaeus sp.	4																	
S. saurus	1																	
V. attenuata	1																	
N. coatsi																		1

I & II: Order of dominancy.

1) Including a mixture with *Pseudochirella* sp. in the Order II.

2) Including a mixture with a few individuals of *P. gaudichaudii*, *E. vallentini*, *Th. gregaria* and *E. hamata* in the Order II.

Note: Finding a few specimens of *Parathemisto gaudichaudii* at South Georgia, Mackintosh and Wheeler (1929) considered that this species were eaten almost accidentally along with *E. superba*. More later, Mackintosh (1942) discussed the food habits of South Georgian baleen whales and stated that *P. gaudichaudii* consisted a wholly insignificant part of the diet, and Brown (1968) confirmed this again in sei whale. But he (Brown, 1968) found two species of myctophids, *Electrona* (*Elampa*) *subasper* and *Electrona* (*Protomyctophum*) *normani*. Table 9, however, strongly demonstrates that the importance of *P. gaudichaudii*, copepods and euphausiids other than *E. superba* in the subantarctic waters.

tents of this animal were consisted of *Euphausia superba*, *E. spinifera* and *Calanus tonsus* (Ohsumi *et al.*, 1970). However, more later study suggests that *E. superba* may be considered to be solely responsible food organisms of the minke whale (Ohsumi, 1979b), and Kawamura and Kikuno (1980) found but a single occurrence of *Thysanoessa macrura* out of 381 minke whale stomachs examined.

Among the balaenopterid whales the Bryde's whale alone does not seem to enter into the so-called Antarctic region, and none of information is available at the present state.

Although there are considerable number of food species in Table 6, the occurrence of different food species largely depends upon the characteristics of their own zoogeography, and this may be noticed by comparing Tables 7 and 8. For the filter-feeders one of the important aspects of ecological characteristics is that the prey organisms should be an aggregate or school forming animals. This has been deduced from the finding that the stomach contents of each animal are really monotonously or even monospecifically compositioned (Table 9). As it is noticed in Table 9, the stomach contents of whales are usually composed of one or two predominant food species, and those with no asteriks in Table 6 are mostly considered as a temporal migrants or occasional contaminants when the major food species were preyed. To look at Tables 6 and 9, it is considered that the most important and staple food of the southern balaenopterids counts only a several numbers of planktonic crustacean species, most of which are the herbivorous and/or omnivorous creatures. At the sametime, it can be considered from the ecological viewpoint that the marine production and the energetic flows in the Antarctic ecosystem are structured under relatively simple pathways, a very short circuited flux between primary production and higher consumers.

TABLE 10. INCIDENCE OF WHALES WITH FOOD IN THE STOMACH IN THE SOUTH AFRICAN AND ANTARCTIC WATERS (Gambell, 1968)

		Sei				Fin			
		Food present	Empty	Total	% feeding	Food present	Empty	Total	% feeding
Durban[1)]	1962	33	56	89	37	45	97	142	32
	1963	3	79	82	4	16	129	145	11
	1965	13	24	37	35	5	7	12	42
Cape Province[2)]	1962	122	138	260	47	11	13	24	46
	1963	351	281	632	56	13	30	43	30
South Georgia	1960-I to	M 164	167	331	50	390	653	1043	37
	1964-V	F 276	149	425	65				
Antarctic pelagic (Area II)	1961-II & 1962-III	186	16	202	92	336	72	408	82

1) Bannister & Baker (1967).
2) Best (1967).
M and F in the table indicate male and female respectively.

b. *South African waters*

The balaenopterid whales visit the South African waters and its environs on their way to and from the Antarctic feeding grounds. Usually those temperate to subtropical waters are considered only the migratory passages for the baleen whales and consequently, very little feeding activity is expected (Mackintosh and Wheeler, 1929). However, in some regions of under the influence by the Agulhas and Benguela Current systems where relatively rich marine production or standing stocks of both planktonic and nektonic animals are expected to form a fishing grounds, the migrating whales may stay and feed to some extent (Table 10). Because of its geographical and oceanographical characteristics, even the temperate/tropical whale species, the Bryde's may come and concentrate in those offshore and inshore waters (Best, 1960, 1967). As it is suggested by the annual catching season in Saldanha Bay during the austral winter (chiefly from May to October), the stomach of whales shows what are the nutritional sources during the 'off season' of the Antarctic whaling.

There are rather few available data concerning the dietary habits of whales in the South African waters except one fine piece by Best (1967), in which a very comprehensive results are given being based on the investigations during 1962–1963. By examining a total of 1085 stomachs, Best (1967) demonstrated that about an half of the stomachs of baleen whales visited the South African waters of lying in mid latitudes (36°30′–32°40′ S) was repleted considerably with many kind of food organisms (Table 11). The species of prey by a taxonomical groups found in the whales stomach were given in Table 12. It is clearly shown in the Table 12 that

TABLE 11. NUMBER OF WHALE STOMACHS EXAMINED AND FEEDING CONDITION IN THE SOUTH AFRICAN WATERS (Best, 1967)

	1962		1963	
	A	B	A	B
Sei	260	47	632	55.4
Fin	24	45.8	43	30.2
Bryde's	30	100	89	83.1
Blue	0	0	2	0*
Humpback	1	0	3	0
Minke	0	0	1	0

A: Number of whale stomachs examined.
B: Number of stomachs with food in percent figures.
* a few megalopa larvae was found.

TABLE 12. FREQUENCY OF OCCURRENCE OF ORGANISMS IN BALEEN WHALE STOMACHS, DONKERGAT 1962 AND 1963 (combined) (Bannister and Baker, 1967; Best, 1967)[1]

Species	Sei	Fin	Bryde's	Pygmy blue[3]	Hump-back[3]
Euphausiacea					
Euphausia lucens	54	3	18		
Euphausia recurva	33	9	5	1	1
Euphausia diomedeae					
Thysanoessa gregaria	7	2	1		1
Euphausia spinifera	3	2			
Nematoscelis microps?	1				
Nematoscelis megalops?	1				
Nyctiphanes capensis	1	1	1		
Copepoda					
Calanus tonsus	72	1			
Calanoides carinatus	59	1			
Clausocalanus arcuicornis forma *major*	56				
Nannocalanus minor	14	1			
Euchirella rostrata	14				
Centropages chierchiae	10				
Oncaea media	3				
Corycaeus sp.	4				
Corycaeus speciosus	1				

Continued...

TABLE 12. Continued.

Species	Sei	Fin	Bryde's	Pygmy blue[3)]	Humpback[3)]
Candacia bipinnata	2				
Centropages brachiatus	2				
Scolecithrix danae	2				
Undeuchaeta major	1				
Eucalanus attenuatus	1				
Metridia lucens	1				
Temora turbinata	1				
Pleuromamma borealis	1				
Oncaea venusta?	1				
Paracalanus parvus?	1				
Calanus tenuicornis?	1				
Pisces					
" Mackerel "[2)]	2				
Scomberesox saurus	1		1		
Hygophum hygomi	1				
Myctophum humboldi	1				
Engraulis capensis			24		
Trachurus trachurus			10		
Sardinops ocellata			10		
Maurolicus muelleri			3		
Lestidium sp.			3		
Scombrid sp.			1		
Amphipoda					
Hyperia macrophthalma	2				
Vibilia armata	2				
Brachyscelus rapacoides	1				
B. crusculum	1				
Primno macropa	1				
Platyscelus serratulus	1				
Phronima semilunata?		1			
Pteropoda					
Cavolinia gibbosa	2				
Ianthina ianthina	1				
Ianthina globosa?	1				
Styliola subula	1				
Diacria trispinosa	1				
Megalopa larvae	14				
Velella sp.	1				

1) Retabulated (data by Best (1967) and Bannister & Baker (1967)).
2) These fish were not examined by a biologist.
3) Data at Durban, 1962–1963 by Bannister & Baker (1967).

the diet of whales is extremely variable in species composition as the evidence found from such a spacially small scale feeding grounds. Especially, the compositions for copepods, amphipods, and pteropods are of great complexity. The sei feeds mainly upon copepods as well as found in the Antarctic waters while fin and Bryde's feed mostly upon euphausiids though the latter shows more stronger trends of prefer-

TABLE 13. PERCENT BY VOLUME OF DIET COMPONENTS IN SEI, BRYDE'S, AND FIN WHALES IN THE SOUTH AFRICAN WATERS (Best, 1967)

	1962		1963		
	Sei	Bryde's	Sei	Bryde's	Fin*
Euphausiacea	64.0	2.5	73.0	53	94.1
Copepoda	31.0	—	23.5	—	3.8
Megalopa larvae	4.6	—	3.0	—	—
Pisces	0.2	97.5	0.2	47	—
Other organisms	—	—	0.2	—	—
Amphipoda	—	—	—	—	2.0

* 1962 and 1963 combined.

TABLE 14. SPECIES COMPOSITION OF DIET OF BRYDE'S WHALES OFF DONKERGAT (Best, 1977)

Species	Inshore form (number of stomachs)	Offshore form (number of stomachs)
Pisces		
Engraulis capensis	25	0
Trachurus trachurus	11	0
Sardinops ocellata	10	0
Maurolicus muelleri	0	3
Lestidium sp.	0	3
Scomberesox saurus	0	1
Scombrid sp.	0	1
Euphausiacea		
Euphausia lucens	0	18
Euphausia recurva	0	5
Nyctiphanes capensis	1	1
Thysanoessa gregaria	0	1

ing fish diet (Table 13).

Finding new rorqual species, *B. brydei*, Olsen (1913) reported the two instances of very unusual food items where sharks up to 2 feet long was found in a stomach, and on another occasion there was found no less than 15 Jackass Penguins, *Spheniscus demersus* and one Cape Gannet "malagass", *Sula capensis*. These are, however, considered to be taken accidentally while the whale was feeding on fish school, and those stomach contents are presumably spit out later.

More recently, Best (1977) studied more about the Bryde's whale occurring in the same locality and showd a obviously different dietary habits between two possible allopatric forms; the offshore and inshore forms. His data demonstrate that there exists stronger ichthyophagous form with more coarser baleen filter, and the other is planktonophagous form ,with finer, more sei-whale-like baleen filter. The former corresponds to the inshore form and the latter to the offshore form. Their dietary characteristics which are chiefly due to the difference in occurring water masses are clearly observed in Table 14.

Because of very little whaling operatons in pelagic waters through the tropics, information around the dietary habits of baleen whales seem to scarcely found. Land based whaling off Angola, the west coast of Africa was once reported but there does not seem to exist any appreciable data about the stomach contents of whales. Along the Somalian coast both Bryde's and pygmy blue whales feed directly on fish, but species name is unknown (Yukhov, 1969). Another existing few information suggests that the blue whale along the African coast feed euphausiids, *Nyctiphanes africanus* and *Euphausia lucens* (Mackintosh and Wheeler, 1929), and the humpbacks may feed the lobster-krill, *Munida gregaria* (Matthews, 1937), although there is an indication of non-feeding activity of whales on the whole (Ottestad and Ruud, 1936).

The variety and diversity of whales food items around the South African waters may lead to a consideration that the baleen whales may feed upon those variable organisms which occur with a larger biomass if not largely but even spacially limited distribution in such a local waters of well outside from their main feeding grounds in the Antarctic Ocean.

c. *Australian and New Zealand waters*

The humpbacks had been the main baleen whale species hunted in the Australian and New Zealand waters. According to Dawbin (1956) the humpbacks on the northward migration through the New Zealand waters usually feed little. In some localities, however, there occurs very dense swarms of neritic species of euphausiids such as *Nyctiphanes australis*, on which the humpbacks feed occasionally. *N. australis* is an important food species largely fed by the squid, *Nototodarus sloani sloani* around the southern New Zealand waters (Kawakami *et al.*, 1973; Kawakami, 1976). In the Cook Strait, New Zealand, humpbacks also take the late larval form of " Glimothea " of galatheid decapods, *Munida gregaria*, the same prey fed by the balaenopterids in the Patagonian waters. The Bryde's whale visited Hauraki Gulf off North Island of New Zealand has been reported to feed on mugilid fishes called ' Mullet ' but its scientific name is unknown (Gaskin, 1976). Sei whale, on the other hand, feed largely on *Calanus tonsus*, *Clausocalanus laticeps* and *Parathemisto gaudichaudii* around southern New Zealand toward Tasmania (Kawamura, 1974).

In the western Australian waters, the food of humpbacks changes to *Euphausia spinifera* and *E. hemigibba* (Dall and Dunstan, 1957). However, Hollis (1939) reported the occurrence of *Pseudeuphausia latifrons*, herring-like fishes tentatively been identified as *Clupea fimbriata* and a few larval stomatopods in the three out of fifty-five stomach samples of humpback whales taken in Shark Bay off the west coast of Australia, although the latter two food items were found in the mouth cavity of a female animal. The anchovy, *Engraulis australis* and unknown species of young mackerel also have been known as main food of Bryde's whales off southern West Australia. In these waters, however, the baleen whales can be considered feed little during June to October as Hollis (1939) notes, " apparently the whales were not feeding in this locality ", and empty stomach usually contained only heavy green flocculent substance or " chunks " of dark green gelatinous material from the squamous epithelium of alimentary tract (Hollis, 1939).

d. *South Pacific and its environs*

According to Budylenko (1978), Smirnov (1935) reported that the sei whale stomachs from the tropical zone of the Pacific contained " fish ". One of few available data is that on the food and feeding habits of the southern Bryde's whale caught in the Coral Sea and South Pacific regions (Kawamura, 1977, 1980). According to Kawamura (1977), a total of 120 Bryde's whales (7 in the Coral Sea, and 113 in the South Pacific between New Zealand and Fiji Islands) were caught during October-November, 1976 and found that 75% of the stomachs over the regions contained food with various state. One of another pelagic catches of the Bryde's whale off southern coast of Madagascar, was found that 46.7% of stomachs examined out of 105 were also filled with food. The compotition of stomach contents was completely different from that expected, *i. e.*, they were solely comprised of euphausiids, *E. diomedeae*, *E. recurva*, and *Thysanoessa gregaria* in the South Pacific animals while there were only first two species in the Madagascar animals. Table 15 shows one of results found by Kawamura (1980). It is again noteworthy that the feeding of baleen whales may takes place wherever the appropriate prey are found, and so goes even in the tropical waters of generally poor in the first two stages of productivity.

e. *Brazilian waters*

Since the commencement of whaling off Costinha, Brazil in 1910 onward, a total of about 11,243 balaenopterid whales have been caught until 1974 (William-

TABLE 15. NUMBER OF STOMACHS BY THE KIND OF FOOD ORGANISMS (Kawamura, 1980).

	1976/77			1977/78	1978/79	Total
	S. Pacific	Coral Sea	SW Indian	S. Pacific	E. Indian	
E. diomedeae		5			6	11
T. gregaria	10			28		38
Euphausia sp.*	7		1			8
E. recurva+*T. gregaria*	8			3		11
T. gregaria+*E. recurva*	1			8		9
E. recurva	38		51****	20		109
E. sibogae					7	7
P. latifrons					29	29
P. latifrons+*E. diomedeae*					2	2
Thysanopoda tricuspidata					2	2
Euphausia sp.**					1	1
E. diomedeae+*V. nimbaria*					1	1
Fish larva***+*E. diomedeae*					1	1
V. nimbaria					4	4
Gonostomatid fish				1		1

* Probably *E. recurva.*

** Probably *E. sibogae.*

*** Larval forms of Myctophiformes.

**** Mixture with one individual of hatchet fish is included.

son, 1975). The abundant species as found in catch statistics are minke, sei, and humpbacks yet there is no existing data about the diet of these animals. The minke whales which have currently been caught about 700 annually do not seem feed extensively in the Brazilian waters, but a short description stating; "The stomachs of nearly all the whales are empty. A little krill is found in the stomachs of about 3% of the whales" (Williamson, 1975). Unfortunately, however, Williamson (1975) did not give the scientific name for this 'krill'. However, feeding of baleen whales off tropical Brazilian coast does not seem to take place to an appreciable extent (Paiva and Grangeiro, 1965, 1970).

Indo-Pacific

a. *Arabian and Malaysian seas*

Although the Bryde's whale occurs and strands occasionally in the Arabian Sea regions (e.g. Roberts, 1970) and Malaysian seas (e.g. Berry *et al.*, 1973), there seems to exist no information about the dietary habits of whales.

Northern Seas—North Pacific

a. *North Pacific and Bering Sea*

The baleen whales occurring in the North Pacific of higher than 50°N and Bering Sea regions have been studied extensively along with that in the Antarctic since there have been heavy exploitation of whale stocks by the factory ship operattions. Since the studies by Ponomareva (1949), Betesheva, (1954, 1955, 1961), Nemoto (1957, 1959) and several more Russian workers as compiled in Tomilin (1967), the main whaling grounds shifted southward year by year far south down to 20°N in 1972 by an ammendments of whaling regulations and measures, from which many kind of prey organisms have been introduced (Omori *et al.*, 1972; Kawamura, 1973) In accordance with these general trends, it became rather that clear an overall composition of whales diet shows considerable complexity covering various taxonomical groups of food organisms over the whole North Pacific and Bering Sea regions. It can be stressed here that the relative importance of fish and/or squid diet among many others in the northern seas is hardly comparable to that in the southern hemisphere. When we see the structure of ecosystem through the viewpoint of nature in food chain arrangements, for example, the shape of the El-

Fig. 5. Two deformed schemata for the Eltonian pyramid (Nemoto and Kawamura, 1977).

tonian pyramids could be expressed two schematically different types (Nemoto and Kawamura, 1977) as shown in Fig. 5. The proposed schemata demonstrate that most of the principal food organisms in the North Pacific are consisted of both omnivorous and carnivorous species while the herbivores largely form main diet of baleen whales in the southern oceans (Fig. 6). The feeding grounds of baleen whales, when viewed from the structure of trophic levels in the sea are not substantially equivalent from one to the another.

An overall food items for the North Pacific balaenopterid whales are given in Table 16. To see the Table 16 along with Fig. 6, it may be noticed that relatively higher occupation of fish and squid in the whales diet in the North Pacific is cha-

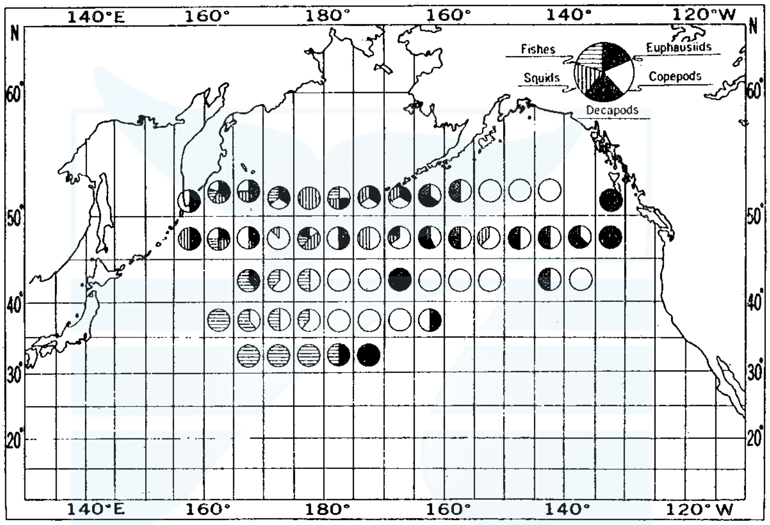

Fig. 6. Approximate occurrence of food organisms of baleen whales in terms of percentage figures in the North Pacific (Nemoto and Kawamura, 1977).

TABLE 16. STOMACH CONTENTS OF BALEEN WHALES CAUGHT BY JAPANESE PELAGIC OPERATIONS FROM 1952 TO 1971* IN THE NORTH PACIFIC (Nemoto and Kawamura, 1977).

Food species	Blue	Fin	Sei	Bryde's	Right	Humpback
Euphausiacea	97.6%**	64.1%**	12.6%**	88.9%	—	77.3%
Euphausiacea & copepoda	1.1%	3.4%	0.0%	—	—	0.6%
Euphausiacea & others	—	0.3%	—	—	—	3.9%
Copepoda	1.3%	25.5%	82.7%	—	100.0%	0.6%
Copepoda & others	—	0.0%	0.1%	—	—	—
Pisces	—	5.0%	3.4%	11.1%	—	17.2%
Pisces & others	—	—	0.0%	—	—	—
Cephalopoda (Squids)	—	1.7%	1.2%	—	—	0.3%
Empty	504	10064	9665	82	0	150
No. of whales examined	971	29575	21713	109	9	458

* Exclusive of data in 1966.
** Including *Sergestes similis*.

racteristic yet the importance of both euphausiids and copepods as staple food is unchanged. As it was observed in the South African waters, and possibly in the Antarctic, both Bryde's and humpback whales prefer strongly to feed fish than any other members of the Balaenopteridae. On the contrary, sei whale that performs both skimming and swallowing types of feeding shows a considerably wider ranges of selecting the preferable prey organisms.

Each group of prey organisms which represent both the northern North Pacific and the Bering Sea is shown in Table 17.

TABLE 17. FOOD OF THE BALAENOPTERID WHALES IN THE HIGHER LATITUDES OF THE NORTHERN NORTH PACIFIC AND BERING SEA (Sleptsov, 1955; Nemoto, 1957, 1959; Tomilin, 1967; Kawamura, 1973).

Euphausiacea:	*Euphausia pacifica, Thysanoessa inermis, T. longipes, T. spinifera, T. raschii*
Copepoda:	*Calanus cristatus, Calanus plumchrus, C. finmarchicus, Metridia lucens*
Mysidacea:	*Gnathophausia gigas* (larva)
Decapoda:	*Pandalus borealis, Sergestes simillis*
Pisces:	*Clupea pallasi, Mallotus catervarius, Theragra charchogramma, Colorabis saira, Pleurogrammus monopterigius, Gadus macrocephalus, Eleginus gracilis, Sebastodes polispinis, Boreogadus saida*
Cephalopoda (Squids):	*Ommastrephes sloani pacificus*, many others & larva
Pteropoda:	*Limacina* sp. *Clione* sp.

Of those food organisms given in Table 17, the most important euphausiid species from their frequency occurrence are considered to be *Thysanoessa inermis* and *T. longipes* as well as their similar situation in the North Atlantic waters (see Table 25). It is noteworthy that the genus *Thysanoessa* in the North Pacific and Bering Sea region is extremely important while the genus *Euphausia* represents largely in the southern oceans. In connection with this, the geographically biassed distribution of food species must be considered: *i.e.*, *T. inermis* predominates in the northern side of the Aleutian Chains of especially eastern half of the region of under consideration while *T. longipes* may predominate in the southern side of the Aleutian Chains. However, the humpbacks in Glacier Bay, Lynn Canal and Frederick Sound, Southeast Alaska were found to feed mainly on *Euphausia pacifica*, herring, *Clupea herengus*, and/or capelin, *Mallotus villosus* (Jurasz and Jurasz 1979). Similar geographical changes may perhaps be found in the copepod food. In general, the distribution of food organisms shows a considerable locally biassed concentrations according to the zoogeographical characteristics in distribution pattern by each prey species, and the idea may be extended further over the almost all groups of food organisms.

In the coastal waters of higher latitudes in the Bering Sea the fish food becomes more important than in the pelagic waters. The fin, humpbacks and minke *B. acutorostrata davidsoni* (Rice, 1977) in the Gulf of Anadyr, Olyutorsky Bay, Kronotsky Bay and the Peter the Great Bay, feed chiefly on herring, capelin, saffron cod, and *T. inermis*. Both humpbacks and finbacks have been reported to feed largely on *Thysanoessa spinifera* and its egg masses, and the latter was especially abudant in

TABLE 18. WEIGHT OF STOMACH CONTENTS OF FIN WHALES TAKEN IN THE BERING SEA (constructed from Ponomareva, 1949, Table 1).

Date	Body weight (ton)	Food species					Weight of stomach contents (kg)	Index of stomach fulness
		Ti	Tr	Tl	Cc	Ct		
				Kommandorsky region				
16 VI	36.0	+	–	+	–	–	170.0	470
16 VI	37.2	+	–	+	–	–	212.5	570
18 VI	36.6	–	–	–	–	+	255.0	690
21 VI	37.8	+	–	+	+	+	425.0	112
25 VI	50.25	–	+	–	–	–	127.1	250
26 VI	31.14	+	–	–	–	–	85.0	270
27 VI	25.76	+	–	–	–	–	68.0	340
28 VI	43.56	+	–	+	–	–	255.0	580
4 VII	37.8	+	–	+	–	–	212.5	560
4 VII	55.38	+	–	–	–	–	85.0	150
5 VII	36.0	+	–	+	–	–	34.0	97
10 VII	28.86	+	–	–	–	–	38.2	120
13 VIII	28.86	–	–	–	+	–	63.7	200
6 X	52.5	+	–	+	–	–	340.0	640
				Olyutorsky Bay				
14 VI	42.9	–	+	–	–	–	68.0	150
14 VI	43.76	–	+	–	–	–	51.0	110
15 VII	37.2	–	+	–	–	–	136.0	36
19 VII	37.1	–	+	–	–	–	85.0	230
20 VIII	36.6	+	–	+	–	–	297.5	810
20 VIII	43.56	+	–	+	–	–	233.7	530
20 VIII	37.2	–	+	–	–	–	170.0	450
20 VIII	31.32	+	–	+	–	–	27.5	400
20 VIII	36.6	+	–	+	–	–	85.0	230
20 VIII	31.86	–	+	–	–	–	25.5	80
8 IX	30.60	–	+	–	–	–	106.2	340
8 IX	42.24	–	+	–	–	–	106.0	200
9 IX	37.80	–	+	–	–	–	170.0	450
9 IX	52.50	–	+	–	–	–	340.0	640

Ti: *Thysanoessa inermis*, Tr: *Th. raschii*, Tl: *Th. longipes*, Cc: *Calanus cristatus*, Ct: *Calanus tonsus* (= *Calanus plumchrus*).

the humpback stomach (Hollis, 1939). He (Hollis, 1939) believes that over a short period of time the euphausian egg may be of some importance as whales food. The blue whale were found to feed *T. inermis* and *Nematoscelis megalops* both in Avachinskii Bay and Kronotsky Bay (Tomilin, 1967). Another food items which are absent from the Chukchi Sea animals are sand lance (*Ammodytes personatus*), amphipod (*Anonyx nugax*), euphausiid (*Nematoscelis megalops*) and copepod (*Calanus cristatus*). Ponomareva (1949) reported that both *Thysanoessa inermis* and *Th. longipes* were the dominant food assembly in the Olyutorsky and Commandorsky regions. For these sea regions in 1947, Ponomareva (1949) gives following percentage figures where she suggests the increase of copepod food towards autumn:

June: *Th. longipes* (35%), *Th. inermis* (30%), *Th. raschii* (15%), *Calanus cris-*

tatus (10%) and *Euphausia lanei* (=*E. pacifica*) (10%)

July-October: *Th. longipes* (30%), *Th. inermis* (33%), *Th. raschii* (12%) and *Calanus cristatus* (25%)

In connection with relative occurrence of each food species, there exists one of very few indispensable data on the amount of stomach contents which enable us to consider the actual importance of food species (Table 18).

The knowledge on the Chukchi Sea animal is very limited since there seem to have been a sporadic whale catches, and the following prey organisms may be seen in the stomachs of humpbacks, but fin whales have been reported to feed *T. raschii*, *T. inermis*, and *Eualus gaimardi* during August-September (Tomilin, 1967).

Food of the Chukchi Sea humpbacks:

Mysis oculata
Thysanoessa longipes
Pandalus goniurus
Eualus gaimardi
Capelin (*Mallotus villosus*)
Saffron cod (*Eleginus glacilis*)
Arctic cod (*Boreogadus saida*)

The food item for the humpbacks includes considerable number of demersal fish and crustaceans, which strongly suggests the animal may perform the bottom feeding in the shallower coastal regions.

b. *Far Eastern Seas*

Because of the geographical and topographical complexities, there have been reported a large variety of whales food species from many localities.

In the Kurile region the fin shows a greater variety of food items, and euphausiids, cephalopods and fish having been reported, *i.e.* *Thysanoessa raschii*, *T. inermis* and *Euphausia pacifica*, *Podonema longipes*, *Ommastrephes sloani pacifica* (squid), and fish, Pacific saury (*Colorabis saira*), anchovy (*Engraulis japonica*), and walleye pollock (*Theragra charchogramma*) (Betesheva, 1954, 1955), but later she (Betesheva, 1961) added *Calanus tonsus* (=*C. plumchrus*) *C. cristatus* and *Pleurogramma* sp. as food of fin whales in the Kurile region.

Sei whale, on the other hand, feeds largely on copepod, *Calanus plumchrus* but feeds also on *T. raschii*, capelin (*Mallotus villosus*), sand lance (*Ammodytes personatus*) and sardine (*Sardinella melanosticta*) (Zenkovich, 1937). Japanese whaler says that the minke whale in the pelagic Okhotsk Sea regions feed exclusively upon the herring (*Clupea pallasi*) and walleye pollock (*Theragra charchogramma*). They says that the operation of herring fishing boat in those waters is the obvious indications for locating a fishable concentrations of minke whale. The humpbacks may show a similar diet to minke whale but have been reported *Euphausia pacifica*, walleye pollock and even the pink salmon (*Oncorhynchus keta*) (Tomilin, 1967), while the blue whale feeds on *Calanus cristatus* and *E. pacifica* (Sleptsov, 1955).

Russian investigations (Sleptsov, 1955; Klumov, 1963), suggest both euphausiids and fish are the most important diet for the baleen whales occurring in the Far

TABLE 19. FOOD OF BALEEN WHALES IN THE PELAGIC AND COASTAL WATERS IN KURILE REGION DURING 1947-1954 (Sleptsov, 1955)

Whale species	No. of stomach examined	Vacant	*Calanus*	Euphausiacea	Ca+ Eu	Eu+ Cep*	Pisces	Cep+ Pisces	Cephalopoda (Squids)
Fin	196	12	2	52	23	18	64	10	15
Sei	42	8	6	2	3	—	5	6	12
Blue	15	—	—	7	2	—	6	—	—
Minke	12	—	—	4	2	—	6	—	—
Humpback	12	—	—	—	—	—	4	5	3
Total	277	20	8	65	30	18	85	21	30

* Cephalopoda (squid).

TABLE 20. SPECIES COMPOSITION OF FISH DIET OF THE BALAENOPTERID WHALES IN THE FAR EASTERN SEAS (Sleptsov, 1955; Tomilin, 1967)

Clupea harengus pallasi (herring)
Eleginus navaga gracilis (saffron cod)
Osmerus eperlanus dentex (Arctic smelt)
Mallotus villosus socialis (capelin)
Theragra chalcogramma (walleye pollock)
Ammodites hexapterus hexapterus (*A. personatus?*) (sand lance)
Gadus morhua macrocephalus (Pacific cod)
Sebastodes glaucus (rock fish)
Pleurogrammus monopterigius (Atka mackerel)
Sardinops melanosticta (Far eastern sardine)
Oncorhynchus keta (chum salmon)
Boreogadus saida (Arctic cod)
Cololabis saira (Pacific saury)
*Podonema longipes** (a morid fish)

* *Laemonema longipes* (by K. Amaoka).

Eastern Seas, Okhotsk Sea, Kurile, off eastern Kamchatska and subarctic region of the coastal Pacific (Table 19). Although Sleptzov (1955) did not mention the species name of food crustaceans in Table 19, it may be supposed that *Thysanoessa inermis*, *T. raschii*, *Calanus tonsus* (=*plumchrus*), *C. cristatus* and *C. pacificus* would represent the stomach of whales. Later investigation (Klumov, 1963), however, revealed the following prey organisms from the balaenopterid whales;

Copepods: *Calanus glacialis*, *Eucalanus elongatus*, *Metridia ochotensis*, *M. pacifica*
Fish: sardine (*Sardinops sagax*), anchovy (*Engraulis mordax*, and *E. japonica*), capelin (*Mallotus villosus*)
Squid: *Loligo opalescens* and *Gonatius fabricii*

One of characteristics in the dietary habits of whales in the Far Eastern Seas as suggested in Table 20 is the more extensive diversity in the species composition of fish diet than in the pelagic waters of the North Pacific and Bering Sea. Occurrence of gregarious fish in the Far Eastern Seas is an important fact as the trophic environment where even the planktonophagous fin and blue whales feed largely on those fish schools. The balaenopterids known as the stenophagous animal show a distinct euryphagous food habits than any other feeding grounds.

TABLE 21. LATITUDINAL CHANGES OF THE DIET COMPOSITION FOR THE BALAENOPTERID WHALES IN THE NORTH PACIFIC (Nemoto and Kawamura, 1977).

Latitude (N)	Occurrence of food item in percentage				
	Euphausiacea	Copepoda	Pisces	Cephalopoda (Squid)	Decapoda
30°-35°	14	—	86	—	—
35°-40°	5	55	40	—	—
40°-45°	9	59	23	—	9
45°-50°	23	44	6.5	16	10.5
50°-55°	31.5	37	8.5	17	6

c. *Subarctic to Subtropics of the Pacific regions*

As well as the case in the South Pacific the existing informations in the region are again very scarce but one reports the occurrence of " small fish " from the sei whale in the tropical Pacific (Smirnov, 1935 cited from Tomilin, 1967). As Fig. 6 demonstrates the diet of baleen whales in the mid to lower latitudes of the North Pacific may largely be represented by a gregarious fish and copepods though a pelagic shrimp, *Sergestes similis* occurs largely in the stomachs of fin and sei whales, and the sergestid shrimp is considered to make up the staple local food over the mid latitudes of the eastern North Pacific (Omori *et al.*, 1973). An overall trends of latitudinal changes in the dietary composition is given in Table 21. In the lower latitudes, say, south of 40°N, there also exhibits the changes in occurring whale species from sei to Bryde's whales. In accordance with an increase of Bryde's whale among the balaenopterids toward the tropics, the preferable feed item also changes

TABLE 22. FOOD ORGANISMS OF SEI WHALE CAUGHT IN THE SOUTHERN NORTH PACIFIC WHALING GROUND DURING MAY-AUGUST 1972 (Kawamura, 1973).

- Copepoda
  - *Calanus cristatus*
  - *Calanus plumchrus*
  - *Calanus pacificus*
- Euphausiacea
  - *Euphausia recurva*
  - *Euphausia pacifica*
  - *Euphausia diomedeae*
  - *Euphausia tenera*
  - *Thysanoessa inermis*
  - *Thysanoessa spinifera*
  - *Nematoscelis difficilis*
  - *Nematoscelis gracilis*[1]
- Decapoda
  - *Sergestes similis*
- Pisces
  - *Scomber japonicus*
  - *Sardinops melanosticta*
  - *Engraulis japonica*
  - *Cololabis saira*
  - *Maurolicus muelleri*
  - *Pseudopentaceros richardsonii*
- Cephalopoda
  - *Gonatus* sp.[2]
  - *Berryteuthis anonychus*[2]

1) Identification is doubtful due to ill conditioned specimens.
2) Identification by T. Kubodera.

to some extent. The food composition for sei whale over the subarctic to temperate waters between 30°–50°N of approximately 160°E–170°W is given in Table 22, and the recent unpublished data by Kawamura on the stomachs of Bryde's whale in the lower latitudes revealed the followings as newly known organisms that must be added to the dietary list of the balaenopterids (mostly Bryde's) in the southern North Pacific regions (Kawamura, 1973);

Fish: *Vinciguellia nimbaria*
Gasterosteus acreatus acreatus
Scomber tapeinocephala
Pleurogrammus azonus
Tarletonbeania taylori
Ranzania laevis
Amphipods: hyperiids (larvae)
Squids: *Berryteuthis anonychus*
Gonatus sp. (young)

In the waters around Bonin Islands (about 25°N), the stomachs of sei and Bryde's whales are mainly consisted of fish and euphausiids. From the investigations through February to May during 1947–1949 along with data from another sources (Mizue, 1951), Nemoto (1959) reported the following food items:

Euphausiids: *Euphausia similis*
Euphausia recurva
Fish: *Yarrella microcephala* (Gonostomatidae)
Myctophum asperum (Myctophidae)

In addition to above mentioned food items, *Ranzania typus* (Molidae) and two sternophychid fish, *Argyropelecus* and *Polyipnus* sp. were found occasionally (Nishimoto *et al.*, 1952). In the pelagic waters, slender mola, *Ranzania laevis* is largely found in stead of *R. typus* (Kawamura, unpublished data). It is noteworthy that there occurs no copepod food in the Bonin Island waters although a possible occurrence of copepod such as *Candacia* sp. as a constituents of whales food has been pointed out but no evidence have been reported to date.

In Monterey Bay, California, fin whale was found to contain " enormous quantity of codfish," and the blue whale in the waters off the port of San Quentin pursued for the school of sardines and prawns (Scammon, 1874). After mentioning the animalculae, the ' right whale food ' or ' brit ' for bowhead whale in the northern waters, Scammon (1874) continues about the minke, " when roaming about the inland waters of lower latitudes, they often shoot along the shallow borders of the bays in search of the myriads of small fry on which they mainly sustain themselves ". In the eastern Pacific off Mexican coast, Pacific red crab, *Pleuroncodes planipes* (Galatheidae) is known as food of sei and blue whales (Matthews, 1938a), but the prey changes to *Euphausia pacifica*, *Thysanoessa spinifera* and possibly *Calanus plumchrus* in the more northern Pacific coast. The fin whale off Vancouver Island has been reported to feed *Euphausia spinifera*, herring, and squid, *Gonatus fabricii* (Tomilin, 1967). Kellog's description by citing Cornwall (1928) made us confirm the occurrence of *G. fabricii* in these waters (Kellog, 1929).

The balaenopterids in the waters off Peruvian coast are believed to take anchovy, *Engraulis ringens* and some euphausiids but details are unknown (Gaskin, 1976). There seems to exist little information concerning baleen whales food in the Pacific coast along South America. Clarke and Aguayo (1965) found only ' fluid ' in the first and second stomachs of Bryde's whale taken at Caleta Molle, Iquique on the coast of Chile, but Budylenko (1978) suggested that sei whale feeds but slightly along the Chilean coast.

As it was described in the South African waters, it is noticed in Table 22 that there are very distinct similarity in the species composition of whales food, *i. e.*, a largely diversed food composition over the tropical to temperate waters throughout the southern and northern hemispheres.

d. *Coastal waters of Japan and East China Sea regions*

The region includes the traditionally famous ' Japan Grounds ' (Beale, 1839). Today, it is called Sanriku region situated in the Pacific side of northern Japan, and is the most important fishing ground for the land based whaling. The information of whales food, however, is somewhat scarce due to few comprehensive study worked out because the catches in coastal whaling are usually very sporadic. Mizue (1951), however, examined the stomachs of some balaenopterid whales as shown in Table 23. The krill in this region is represented by *Euphausia pacifica* along with less important two *Thysanoessa* species while it changes to *T. inermis* and *T. longipes* in far more northern regions adjacent to Hokkaido. Only *Calanus pacificus* forms the main copepod food in the Sanriku region though it may change to *Calanus plumchrus* in the more northern grounds. Squids are mostly composed of *Ommastrephes sloani pacificus* on which sei whale feed extensively. Sardine in Table 23 actually means the anchovy, *Engraulis japonica.* During April to May in the Sanriku grounds there occurs large school of young sand lance, *Ammodytes personatus*, and the minke whale pursues for them. In accordance with their northward bound migration along the Pacific coast of Japan, the minke also follows after them up to the Hokkaido region. Both *Engraulis japonicus* and *Ammodytes personatus* are the most

TABLE 23. FOOD OF BALEEN WHALES IN THE SANRIKU WHALING GROUND, OFF PACIFIC COAST OF NORTHERN JAPAN (Mizue, 1951).

	Blue	Fin	Sei*	Humpback
Krill	16	43	253	2
Sardine	—	1	103	—
Saury	—	—	25	—
Mackerel	—	1	1	—
Rock fish	—	—	2	—
Squid	—	—	10	—
Octopus	—	—	1	—
Empty	11	41	547	4

* Sei+Bryde's.

important food items of minke whale in the coastal waters of Japan (Omura and Sakiura, 1956), but *Euphausia pacifica* must be added in the waters along southwestern Japan Sea. However, the sei during summer largely feed on young mackerel, *Scomber japonicus*.

TABLE 24. FOOD OF FIN WHALES IN THE EAST CHINA SEA AND ITS ENVIRONS (Nemoto, 1959).

		July	August	September	October
1955	*E. pacifica*	6	22	18	—
	Empty	4	65	76	7
	Unknown	—	3	10	14
1956	*E. pacifica*	2	20	5	—
	Flying fish[1]	—	1	—	—
	Blind eel[2]	—	—	1	—
	Empty	3	9	25	—
	Unknown	49	63	47	19

1) very little quantity.
2) *Eptatretus burgeri*.

In the Okhotsk Sea coast of Hokkaido, Nemoto (1959) describes both *Euphausia pacifica* and *Thysanoessa inermis* with occasional contamination by *T. raschii* for fin whales caught off Abashiri, Hokkaido. Later observations, however, revealed that minke whale feeds on *E. pacifica* and squid, *Ommastorephes sloani pacificus* and fin whale caught far off shore region fed *Thysanoessa inermis*, which increases its importance gradually toward Sakhalin regions.

In the southern Japan around Kyushu the Bryde's whale frequents its offshore waters and feeds *Euphausia similis* during May but gradually shifts to anchovy, *Engraulis japonica* during the summer season. (Nemoto, 1959).

Not so many are known for the East China Sea regions but the following brief informations (Nemoto, 1959) (Table 24). The Bryde's whale which perhaps the northern counter part of the inshore form found in the South African waters (Omura, 1977), feeds mostly on anchovy, *E. japonica* and three kinds of horse mackerels, *Trachurus japonicus*, *T. declivis*, and *T. argenteus* though the first two are more prefered by the whales.

In the adjacent waters of Korean coast, the Yellow Sea and Japan Sea, it has been known that the fin and minke whales feed on euphausiids with occasional occurrence of squid. The corresponding euphausiid species has been believed to be *Euphausia pacifica*. There is single record of the fish, *Clupanodon punctatus* from the fin whale in the Yellow Sea. (Nemoto, 1959).

The humpbacks in the Ryukyuan waters seems to feed little but a few records indicate *Euphausia similis* and *Pseudoeuphausia latifrons* to be the possible whales food (Nishiwaki, 1959).

Northern Seas—North Atlantic

a. *Northeast Atlantic*

According to Gaskin (1976), Allen (1916) earlily reported *Thysanoessa inermis* as food of North Atlantic humpbacks. As Hjort and Ruud (1929) reviewed on the fishing and whaling industries in the North Atlantic, the shelf region around the Norwegian Sea and the Greenland Sea has been exposed to the extensive whaling of the blue, fin, sei, and humpback whales since the beginning of this century. Norwegian whalers have been aware of the importance of food plankton (=krill) abundance in relation to their catch (Hjort and Ruud, 1929). The krill undoubtedly correspond to one of the largest euphausiid species, *Meganyctiphanes norvegica* and several others such as *Thysanoessa inermis*, *T. raschii*, and *T. longicaudata*. Since there also largely occurs copepods and two amphipod species, *Themisto libellula* and *Parathemisto oblivia* in addition to euphausiids, the latter crustaceans group may also likely to be fed by the baleen whales.

Although Hjort and Ruud (1929) did not mention about the whales food in the Greenland waters, they showed the following items as having been found in the whales treated at Aukra Island, off the coast of Möre, Norwegian Sea during 1925–1928. A total of 619 baleen whales were examined (366 fin, 252 sei and 1 blue) and found the enormous amount of plankton food among many animals during January-August.

The food items found were:

1. Herrings (especially ' large ' or spring herrings)
2. Euphausiids (krill)
   a. " Stor-krill " (large krill) corresponds to *Meganyctiphanes norvegica*
   b. " Smaa-krill " (small krill) mostly *Thysanoessa inermis*
3. Rod-aate " (copepods) mainly consisted of *Calanus finmarchicus*

According to Hjort and Ruud (1929), Sars (1874) states that the food of blue whale in the waters of Finmarken was exclusively comprised of " loddle " or capelin, *Mallotus villosus* and *Thysanopoda* (=*Thysanoessa*) *inermis*, while fin whales follow after spawning shoals of capelin (*M. villosus*) off the coast of Finmark (Jonsgård, 1966). The herring does not seem to be fed by the blue whale but both humpback and minke take herring largely in this waters. In the Davis Strait, the fin feeds herring and *Thysanoessa inermis* during winter (January-March) but it changes to smaller euphausiids and *Calanus finmarchicus* in the spring (April-May) and then shifts to *Meganyctiphanes norvegica* from May to August (Tomilin, 1967). In addition to above mentioned food items, followings are the fish food of greater importance in the North Atlantic; cod, mackerel, sand lance, dog fish, whiting, and pollock. Although the food item may varies with season and whale species, capelin, *M. villosus* must be an another important whales food in the Finmarken waters.

One of characteristics of the marine distribution in the North Atlantic is the occurrence of very small copepod called " swamps " (Millais, 1973), *Temora longicornis* as food of baleen whales as well as the food of herrings in the Irelandic waters (Collet, 1886; Millais, 1906; Herdman, 1971), and in the Newfoundland waters

TABLE 25. STOMACH CONDITIONS OF MINKE WHALE AROUND THE NORWEGIAN WATERS (constructed from Jonsgård, 1951).

Region	Area	No. of obs.	Stomach contents					
			Empty	Fish[1]	Krill+Copepod/Krill+Fish			Milk
Arctic	Barentz Sea	94	2	14		78[2]		
Norwegian waters		105	33[3]	56		14[3]		1[3]
	Lofoten	(75[3]+20)	(33[3])	(27[3])	(7[3])		(7[3])	(1[3])
	Vestraalen	(9)						
	Helgoland	(1)				1		
		199	35	70	(77)	93	(16)	1[4]

1) Cod, "skrei"
2) Krill, *Thysanoessa inermis*
3) Vestfjord proper
4) Calf, 16 feet 10 inches

TABLE 26. FOOD OF MINKE WHALE IN THE NORWEGIAN COASTAL WATERS (constructed from Jonsgård, 1951[1])

Region	Area	No. of obs.	Herring	Herring+others	Capelin	Haddock	Cod	Other species	Remarks
Vestfjord	Røst	20	12	3	—	—	—	5	0-group herring "musse"
Vesteraalen	Outside	9	9	—	—	—	—	—	I-group herring "bladsild" especially in autumn
Arctic[2]	Bear Island		—	—	+	—	—	—	
	Spitzbergen		+	—	—	—	+	—	Large herring, small cod
	Barentz Sea		+	—	—	+	—	—	I-group herring "bladsild" large haddock

1) Jonsgård notes that "the truth is evidently that minke whales prefer krill when this animal abounds, but they resort to a great variety of shoaling fishes wherever these are met with."
2) No actual number of animals examined is stated.

where blue whale takes this species (Tomilin, 1967). *T. longicornis* have never been found as the whales food over any another whaling grounds in the world. In addition to crustaceans, there have been reported the pteropod molluscus which is considered to be *Clione limacina* and/or *Limacina helicina.* (Hjort and Ruud, 1929; Peters, 1938).

To see these food items by each whale species, it can be said that the sei in the coastal banks and slopes region feeds almost exclusively on *Calanus finmarchicus*, while the fin feeds herrings, *Calanus finmarchicus* and two euphausiid species above mentioned. The abundance of migrating whales into the whaling grounds in Möre region is closely related to the abundance of these food organisms, *i. e.*, there can be expected richer whale migrations into the whaling ground in the years of more abundant food distribution. The whales food as mentioned above may changes by whale species and also by the seasons. The fin whales during January-March, for instance, feed either herrings or *Thysanoessa* species, while they feed *Calanus finmarchicus* and *T. inermis* in April towards early May. During August, the season of " summer fishing " (Hjort and Ruud, 1929) as they call, the fin survives exclusively on *Meganyctiphanes norvegica*.

According to Christensen (1975) the food items of the North Atlantic minke whales *B. acutorostrata acutorostrata* (Rice, 1977) in the Barents Sea and off East Greenland were largely consisted of capelin, but they changed to sandeels and krill, *Thysanoessa inermis* in the waters off West Greenland. One of interesting evidensces found in the North Atlantic to the Arctic waters is greater variable dietary items of minke whale by season and localitites as shown in Tables 25 and 26. The minke in these waters, however, feeds generally on herring in spring along the Norwegian coast, while it feeds mainly on capelin during summer in the northern waters along with gadoid fishes such as cod, whiting, and coalfish (Jonsgård, 1951). Although there may exist some confusion regarding the identity of food animals, Jonsgård (1951) gave fourteen possible fish species as the food of minke whale; herring, sprat, mackerel, cod, coalfish, haddock, ling, pollock, whiting, Norway haddock, catfish, salmon, capelin and sand-eel (Table 27). He (1951) also suggested the occurrence of copepods (*Calanus*), krill (Euphausiacea), small shrimp or ' aate ', and even mature cod ' skrei ' and big gadoid fishes. Gravel and stones up to the size of an egg are occasionally found (Jonsgård, 1951).

TABLE 27. POSSIBLE FISH FOOD FOR THE NORTH ATLANTIC MINKE WHALES (Jonsgård, 1951). THE SCIENTIFIC NAME CORRESPONDING TO THE COMMON NAME WAS BASED ON WHEELER (1969), LYTHGOE (1971) and UNESCO (1973)

Common name	Scientific name
Salmon	*Salmo salar*
Capelin	*Mallotus villosus**
Herring	*Clupea harengus**
Mackerel	*Scomber scombrus*
Sand lance	*Gymnammodytes cicerellus*
Cod	*Gadus morhua**
Coalfish	*Pollachius virens* (=*Gadus virens*)
Haddock	*Melanogrammus aeglefinus* (=*G. aeglefinus*)
Norway haddock	*Sebastes marinus*
Pollock	*Pollachius pollachius*
Whiting	*Merlangius merlangius**
Sprat	*Sprattus sprattus**
Ling	*Molva molva*
Catfish (Wolf fish)	*Anarhichas lupus**
Dog fish	*Scyliorhinus caniculus*

* UNESCO (1973) recommends trinominal nomenclature for these fishes.

In the region of southern slopes of the Norwegian Sea—the Norway—Shetland—Faroe Island area—three euphausiids, *M. norvegica*, *T. inermis* and *T. longicaudata* occur with larger quantity. Although Hjort and Ruud (1929) did not show the whales food in this region, it may be supposed that the fin whale occurring off

Faroe Island feeds above three euphausiids. The similar dietary situation could be supposed to the northern slopes of the Norwegian waters.

In the Icelandic waters there has been reported an appreciable number of the blue, fin, sei and humpback whales come to concentrate and feed. The coincidence of their concentration with the pronounced abundance of krill distribution suggests the possible whales food to be *Thysanoessa inermis* and *Meganyctiphanes norvegica*. Reviewing the fin whale fishery off the West Coast of Iceland, Rørvik *et al.* (1976) described, " In all the investigated years, 1925–1928, the fin whales were eating herring, small krill (*Thysanoessa inermis*) or copepods, mainly *Calanus finmarchicus*, from the middle of January to the early part of May ". From May to the middle of August, " . . . . the fin were feeding exclusively on the large krill, *Meganyctiphanes norvegica* ". However, the greater part of the fin whales food seems to change to capelin, *M. villosus* toward the eastern Greenland. (Jonsgård and Christensen, 1968).

Towards south closer to the temperate North Atlantic there seems to increase in the variety of fish food among many others, especially the fish belonging to gadoids, clupeids and scombroids and they may become important particularly in the coastal waters (Gaskin, 1976).

b. *Northwest Atlantic*

From temperate to subarctic waters along the eastern coast of North America there exists one of two places where the large number of the balaenopterid whales come to concentrate and feed during the warmer season. Composition of the whales food in this region is generally comprised of similar animal communities to that known in the northeastern Atlantic waters, where copepods, euphausiids, and gregarious fish predominate in the whales stomachs. In the region of Bay of Fundy, copepods, euphausiids, herring and mackerel are said to begin rise into the surface during the summer, and the fin whale being attracted to those possible prey organisms begin to gather in the region (Gaskin, 1976). Although the diet of baleen whales may generally go similar way over the whole North Atlantic, yet there seems to exist qualitative differences from localities and seasons.

The baleen whales food as revealed by the Canadian workers gives a comprehensive knowledge about whales food (Mitchell, 1974). By examining both fin and sei whales at Blandford, Nova Scotia, and sei at Dildo and Williamsport, Newfoundland between 1965 and 1972, Mitchell (1974) found the following food species: krill, copepods, sand lance, mackerel, herring, squid and ' fish ' for the Nova Scotian animals, whilst the food in Newfoundland animals was composed of capelin, sand lance, lantern fish, krill, white fish, and cod. Although Mitchell (1974) did not give the scientific name for copepods and krill, they were perhaps comprised of *Thysanoessa inermis*, *Meganyctiphanes norvegica*, *Calanus finmarchicus*, and *Temora longicornis*. One of distinct differences existing between two locations are the complete lack of capelin from the diet in the Nova Scotian animals. The capelin comprises the main diet of fin whales of mostly 80–100% through May to November in the Newfoundland. On the other hand, the same whale species in the Nova

Scotian waters feed largely on krill possibly be comprised of *M. norvegica* and several *Thysanoessa* euphausiids through May to November in more than 80% of animals, but the sei alone feeds largely on copepods (60–80%) between June and October. Brodie *et al.* (1978) reports that of 67 stomachs of fin whale taken in the Nova Scotian waters 63 were full of krill, *Meganyctiphanes norvegica,* three contained copepods and one was full of young herring. The importance of krill, *M. norvegica* as food of fin whale is clear in the northwestern Atlantic region. To see the whales food as shown in the two above localities, it is observed that both krill and copepods are the most important food items in the Nova Scotian waters. Both sand lance and mackerel are also fed by the fin whale but none of them by the sei whale.

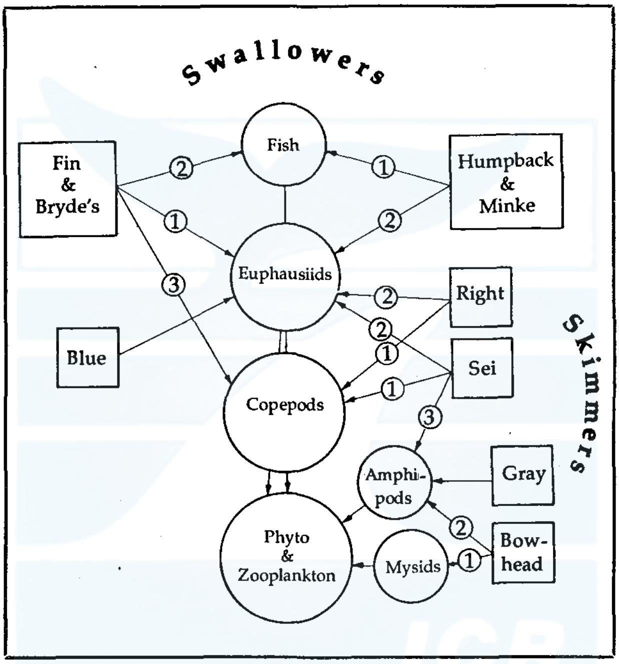

Fig. 7. Schematic food web showing predation by " swallowing " and " skimming " baleen whales on main food sources (Mitchell, 1974).

Lantern fish and white fish may come to the next importance in the Newfoundland especially in October through November. The humpback whales taken at Nova Scotia (Blandford) and Newfoundland (Williamsport and Dildo) were found to feed capelin, sand lance, white fish, mackerel and krill (Mitchell, 1973). Of those prey items, both capelin and krill are considered to be the main diet of humpbacks in the Canadian Atlantic waters. Generally, it can be considered that there exists a considerably different feeding grounds in the northwestern Atlantic region whereas its expansion is spacially very limited. One of such feeding grounds may largely depends upon the planktonic crustaceans in the formation of feeding ground while the another one depends upon the small to medium sized gregarious fish species (Fig. 7).

Summerizing addendum

In summerizing the review, it may be said that although the main subject of this article was confined to deal with the diet of " balaenopterid whales ", the food of the balaenids—right, bowhead, and pygmy right whales as stenophagous animal is generally consisted of very similar food items with that found in the balaenopterids while the eschrichtiid whale alone shows quite different aspects from the above two taxonomical groups. As mentioned in the morphological characteristics of the baleen filter, the balaenid whales obviously perform " skimming " and feed preferably on smaller, weak powered swimmers of crustaceans such as copepods even in such waters of rich euphausiid distributions as known in the the southern oceans, where an another problem—competion for food between southern right and sei whales may arise. (Kawamura, 1978b).

The bowhead, however, by their extraordinal biological, ecological, and zoogeographical distinctions, feeds rather complicated prey organisms. In his marverous book, "*An Account of the Arctic Regions* ", Scoresby (1820) demonstrated a fantastic plate showing the food organisms of bowhead whales, in which he introduced; *actiniae*, *cliones*, *sepiae*, *medusae*, *cancri* and *helices*. He also added *squllae* or shrimp from the different observations. To see Scoresby's plate XVI (Scoresby, 1820), several additional food organisms may be observed; that is, two kinds of chaetognaths and a kind of both planktonic tunicates possibly belong to *Oikopleura* and gammarid amphipods. Although it is difficult to interprete each organisms from the Scoresby's descriptions, Hjort and Ruud (1929) identified some groups of whales food being based on the figures in the Scoresby's plate and found:—

1. The four ctenophores: *Beroe cucumis*, *Pleurobrachia pileus*, *Mertensia ovum*, and *Bolina septentrionalis*
2. The two pteropods: *Clione limacina* and *Limacia helicina*
3. The two or three crustaceans: *Hymenodora glacialis*, *Calanus hyperboreus*, and possibly *Themisto libellula*

These organisms, however, seem to be unlikely as the staple food of bowhead, and it was concluded later that their main food in the Atlantic Arctic region must be a copepod, *Calanus finmarchicus* as illustrated very likely in the Scoresby's plate (Ruud, 1937). Euphausiids may also be included in the diet of Atlantic bowead whale. In the Alaskan waters the bowhead feeds copepods, *Calanus glacialis* and *C. hyperboreus* during their Bering Sea/Chukchi Sea migrations although the benthic gammarids are likely to be taken supplementary. Very recently, Lowry *et al.* (1978) examined two female bowhead whales caught in the vicinity of Point Barrow, Alaska. The stomach contents analysis revealed that the Alaskan bowhead feeds mainly on *Thysanoessa raschii*, gammarid amphipods, *Gammarus zaddachi*, *Acanthostepheia behringiensis*, *Monoculoides zernovi*, and *Rozinante fragilis*, and hyperiid amphipod, *Parathemisto libellula*. Of those above mentioned food species, *T. raschii* made up 90.3% of the total volume. Lowry *et al.* (1978) also found an unidentifiable carapace of shrimp and even a small pebble in the stomach. According to Sergeant and Hoek (1974a), however, " nothing is yet known of the nature of the food of bowheads " in the Franklin Bay region, Canadian Arctic, but they (Sergeant and Hoek, 1974b) suggested that *Calanus hyperboreus*, *Parathemisto libellula*, *Thysanoessa inermis* and *Th. raschii* are the most possible food organisms of bowheads in the Cape Lambton and Cape Parry regions in the Beaufort Sea.

Scoresby (1820) writes the way of feeding by the bowhead whale, the largest skimmers ever existed as follows: " When the whale feeds, it swims with considerable velocity below the surface of the sea, with its jaws widely extended. A stream of water consequently enters its capacious mouth, and along with it, large quantities of water insects; the water escapes again at the sides; but the whalebone, which, from its compact arrangement, and the thick internal covering of hair, does not allow a particle the size of the smallest grain to escape ".

Right and pygmy right whales are the dwellers of the subarctic and/or subantarctic regions where the most highest marine production is usually expected. There have been reported that these animals as microplanktonophagi feed exclusively on copepods which predominate in theirown habitat: *Calanus finmarchicus*, *Thysanoessa inermis* and pteropods but lesser extent in the North Atlantic waters, but this assemblage changes to *Calanus plumchrus* (Matuura and Maeda, 1942), *C. cristatus*, and possibly *Metridia* sp. in the North Pacific and Okhotsk Sea. They may also feed *Calanus pacificus* and *Euphausia pacifica* in the more southen waters from northern Japan to the boreal regions of the North Pacific (Omura, 1958). The southern counterpart, *Eubalaena glacialis australis* (=*E. australis*) feeds both euphausiids and copepods in the subantarctic waters. Their main prey animal, however, must be *Calanus tonsus*, *Calanus simillimus* and *Euphausia vallentini* as it is supposed by the occupation of thier main feeding (=whaling) grounds during the austral summer (Townsend, 1935; Kawamura, 1978b). There also have been reported that *Euphausia superba* is taken in the Antarctic proper, whereas the food species change to Grimothea larva of *Munida gregaria* in the waters off Patagonian coast (Matthews, 1932; 1938b).

Very little is known for the pygmy right whale. It has been reported that the animal as their finer baleen fringes suggest was found containing several number of *Calanus* species in the South Atlantic waters (Ivashin *et al.*, 1972).

The composition of baleen whales food in the North Atlantic waters as has been reviewed in this article seems to be somewhat monotonous assemblages when it was compared with that found in the North Pacific and its environs. It may be unlikely to consider these differences simply due to the faunistic characteristics in the community composition of food animals, but it was the result possibly due to the limited material sources from the less exploitation of whale stocks in the pelagic waters using the whaling factories in the North Atlantic regions. There is no reason therefore, to believe the greater difference in the biological environments concerning the diet of baleen whales between the North Pacific and the North Atlantic oceans.

The dietary habits of great whales as well as their general biology have long been a mythological subject but the modern whaling accompanied with a extensive biological works gradually unvailed the mystery of whales one after another during the past several decades and, perhaps some more will be found but gradually in the next.

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A REVIEW OF SPERM WHALE FOOD

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ABSTRACT

Papers on the food of sperm whales caught in various parts of the world hitherto published were reviewed, and the outline of the informations obtained are as follows:

The composition of the items in the sperm whale food is various according to region, season, year, etc., depending on the composition of the food animals inhabiting the area. The most important food items are squids, followed by fishes.

Among squids, numerically important species are histioteuthids, gonatids, onychoteuthids and octopoteuthids. In addition to these squids, cranchiids are also very important in some regions. Seeing their importance from the view point of weight, the important species are octopoteuthids and histioteuthids nearly all over the world except some regions, and onychoteuthids, architeuthids and ommastrephids are important in some regions.

Though the species of fishes in the food of sperm whales are various, they are less important than squids. They are rather important in the northeastern part of the North Pacific, New Zealand waters and the northern part of the North Atlantic.

The important fishes as the food of sperm whales are rock fishes, cod, sharks, rag fish, skate, dory-type fish, ling, lumpsucker, etc., though the degree of the importance of them are different according to region.

Sperm whales sometimes attack and catch large squids, e.g. *Architeuthis* sp. and *Moroteuthis robusta* of 2–3 m in mantle length, and also large fishes of 1–3 m in total length such as sharks *Cetorhinus maximus*, *Somniosus* sp. etc., *Dissostichus mawsoni*, etc.

The amount of the stomach contents of sperm whales has been considered less than 300 kg, and the foods consumed in a day have been considered differently by person as 2–3 tons or 1 ton. And also there is another estimate: 300 kg and 200 kg for average-sized male and female sperm whale respectively. The total weight of squids eaten by sperm whales in a year has been estimated to be 110–320 million tons.

INTRODUCTION

The sperm whale (*Physeter macrocephalus* Linnaeus) has 20–28 teeth in each side of the lower mandible, the diameters of which attain 10 cm (Nishiwaki 1965). These teeth have the function to attract and catch cephalopods, particularly the large squids, which are the staple food of the sperm whales. Fishes are, as Clarke, R. (1956) said, subsidiary, but not negligible, items of food.

The foods of sperm whales in various regions have long been studied by many

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TABLE 1. OCCURRENCES OF SQUIDS AND FISHES IN THE STOMACHS

Locality	Number stomachs observed	Number stomachs with food	Number and percent (of the stomachs			
			Squid		Octopus	
			No.	%	No.	%
Japan	555	338	323*	96	10	3
Japan	1365	809	725	90	16	2
	1379	818	788	96	3	0
	2744	1627	1513	93	19	1
Japan	65	65	65	100	—	—
Kuriles	360?	360?	>250*	>69	—	—
Kuriles (Okhotsk)				13–100		
(Pacific)				4– 97		
Kamchatka		21				
Bering Sea						
(Komandorskiye)	67	67	66 (50)	99 (75)		
(Aleutorskiye)	29	26	21 (14)	81 (54)		
(Northern)	14	14	10 (5)	71 (36)		
(Total)	110	107	97 (69)	91 (64)		
Bering Sea and Aleutian coast						
(-180°)		256	240	94		
		148	129	8		
(180°–160°W)		612	434	71		
		125	116	93		
Coast of Alaskan Gulf						
(160°–130°W)		139	45	32		
British Columbia	50	≦50	35	≧70		
Central California	128	54	52	96	6	11
New Zealand	133	118	95	81		
Iceland	57	49	27	55		
Azores	39	28	28?	100?		
Antarctic		56				
”	129	115				
South Georgia and South Africa	74	63	63	100		

scientists. A detailed review of their results was made by Berzin in 1971. Since then the several researches on this problem have been made, especially on squids (Clarke, M. R. 1972, 1977; Clarke, M. R. *et al.*, 1974, 1976; Kawakami, 1976; Okutani *et al.*, 1976, 1978). Recently the taxonomic studies of squids by beaks have been developed by Clarke, M. R. *et al.* and the studies on the food of sperm whales have advanced with a lot of beak samples removed from the stomachs of sperm whales caught in various parts of the world, and their results were summed up (Clarke, M. R., 1977, 1980).

I have again reviewed the published reports on the foods of sperm whales in

OF SPERM WHALES TAKEN FROM DIFFERENT PARTS OF THE WORLD

with food) stomachs with				Number and percent (of the stomachs observed) empty stomachs		Remarks	Source
Fish		Others					
No.	%	No.	%	No.	%		
5	1	—	—	217	39		Omura 1950
68	8	—	—	556	41	Males	Mizue 1951
25	3	2	0	561	41	Females	
93	6	2	0	1117	41	Total	
—	—	—	—	0	0		Kawakami 1976
110**	30	—	—	0?	0?	*: Only squid	Betesheva and Akimushkin 1955
						**: Including squid remainders	
	57-100						Tarasevich 1963
	13- 50						
4	19						Tomilin 1957
17 (1)	25 (1)			—	—	In parentheses, for only squids or fishes	Berzin 1959
12 (5)	46 (19)			3	10		
9 (4)	64 (29)			—	—		
38 (10)	36 (9)			3	3		
16	7					1960	Okutani and Nemoto 1964
19	13					1963	
178	29					1960	
9	7					1963	
94	68					1963	„
≦45	90?						Pike 1950
33	61	1	2				Rice 1963
93	79			15	11		Gaskin and Cawthorn 1967
48	98	8	14	8	14	Males	Roe 1969
4	14	0?	0?	11	28	Both sexes	Clarke, R. 1956
7	13					Males	„
6	5			14	11	Males	Korabelnikov 1959
7	11	—	—	11	15	Both sexes	Matthews 1938

various regions, and summarised them. But I could not fully refer to Dr Clarke's latest paper (1980) as I could get it only after the completion of this manuscrpt.

RELATIVE IMPORTANCE OF SPECIES IN THE FOOD OF SPERM WHALES

The frequencies of occurrence of various food items of sperm whales are different according to the region, season, year, etc., and also it may be varied by sex, age, or body length, but various species of cephalopods predominate almost always and

TABLE 2. RATIO OF OCCURRENCE OF SQUIDS AND FISHES IN THE STOMACHS OF SPERM WHALES TAKEN FROM DIFFERENT PARTS OF THE WORLD

Locality	Ratio of occurrence in percentage		Sex of whales	Year observed
	Squid	Fish		
Japan	98	2		1948-49
Japan	91	9	Males	1946-48
	97	3	Females	,,
	94	6	Total	,,
Japan	100	0		1772
Kulile Islands	69	31		1951-52?
Bering Sea				
(Komandorskiye)	80	20		1957
(Aleutorskiye)	64	36		,,
(Northern)	53	47		,,
(Total)	72	28		,,
Bering Sea and Aleutian Coast				
(-180°)	94	6		1960
	87	13		1963
(180-160°W)	71	29		1960
	93	7		1963
Coast of Alascan Gulf				
(160-130°W)	32	68		1963
British Columbia	≧44	56≧		1948-49
Central California	61	39		1959-62
New Zealand	51	49		1963-64
Iceland	36	64	Males	1967
Azores	87≧	≦13	Both sexes	1949
South Georgia and South Africa	90	10	Both sexes	1932-35

Notes: 1) The ratios were calculated with the numbers of stomachs having squid and fish.
2) Sources are the same as those in Table 1.

everywhere.

The composition of the food items in sperm whale depends on the composition of the food animals inhabiting the area where the whales take food (Berzin 1971), but it does not always represent the fauna of the area. This may be thinkable from the fact that species composition of the families is different between net samples and whales' stomach contents, and many of those taken by nets are smaller species and not young specimens of the large species sampled by whales (Clarke, M. R., 1977).

The most important food items of sperm whales are cephalopods, followed by fishes as are shown in Tables 1 and 2. In addition to cephalopods and fishes, crabs, shrimps, krill, lobsters, colonial tunicates, jelly-fishes, sponges, starfishes, sea cucumbers, vibrissae, gorgonians, etc. were reported from the stomachs of sperm whales (Mizue 1950, Clarke, R. 1956, Tarasevich 1963), but these are not considered to be the normal food items.

The families and species of cephalopods and fishes reported as the food of sperm whales by many scientists are summarised in Appendix Tables I and II.

Cephalopods as the food of sperm whales

As are shown in Appendix Table I, the cephalopods consist of 36 genera (about 56 species) belonging to 19 families, of which only 5 genera (about 6–7 species) belonging to 4 families are octopods and vampyromorph, and the other 31 genera (about 50 species) belonging to 15 families are decapods. Thus squids are of far greater impotance than octopods almost everywhere. But in the littoral waters, the significance of octopods for sperm whales is sometimes greater, especially of those which have a pelagic mode of life, e. g. *Amphitretus* sp. and *Alloposus mollis*. They are sometimes found in 50% of the total number of stomachs examined (Berzin, 1971).

Most decapods in Appendix Table I are pelagic species except *Loligo* sp. which is the littoral species and was found in the stomachs of sperm whales in the northeastern part of the Atlantic (Clarke, R., 1956). This may be a very rare example. *Octopus* spp. are also littoral species and were reported from the stomachs of sperm whales caught in the littoral waters of the North Pacific (Berzin, 1971).

It is noteworthy, as Berzin (1971) stated, that some of the species inhabiting the surface waters in some regions, e. g. *Todarodes pacificus* which is the widespread and abundant species in the western part of the North Pacific and serves as food for the most varied pelagic animals (including baleen whales), do not form a part of the sperm whales' diet.

The data on the compositions in numerical and weight percentages of families of cephalopod constituents in sperm whale food are available in the waters around Japan, Kurile Islands, California, New Zealand, Peru and Chile, Iceland, Azores, Vigo and Madeira as are shown in Table 3.

The numerically important species of cephalopods are as follows: In the Japanese waters, *Histioteuthis dofleini* is the most important and *Octopoteuthis* sp., *Moroteuthis robusta* and *Ommastrephes bartrami* are also important (Omura, 1950; Mizue, 1951; Berzin, 1971; Kawakami, 1976; Okutani *et al.*, 1976, 1978). In the Kurile Islands waters, the species belonging to Gonatidae such as *Gonatopsis borealis*, *Gonatus magister* and *Gonatus fabricii*, *Galiteuthis armata* and *Histioteuthis* sp. are important (Betesheva and Akimushkin, 1955; Berzin, 1959, 1971; Tarasevich, 1963). In the Okhotsk Sea, *Gonatus fabricii* is important (Tarasevich, 1963; Berzin, 1971). In the Bering Sea and the adjacent waters, *Moroteuthis robusta*, the species belonging to Gonatidae such as *Gonatopsis borealis*, *Gonatopsis makko*, *Gonatus magister* and *Gonatus fabricii*, and *Galiteuthis armata* are important (Berzin, 1959, 1971; Okutani and Nemoto 1964). Off British Columbia and California, *Moroteuthis robusta*, *Gonatopsis borealis* and *Gonatus fabricii* are important (Pike, 1950; Rice, 1963; Berzin, 1971; Fiscus and Rice, 1974; Clarke, M. R., 1979). In the Tasmanian and New Zealand waters, *Moroteuthis* sp. and *Onychoteuthis* sp. are important (Gaskin and Cawthorn, 1967; Berzin, 1971; Clarke, M. R., 1977). Off Peru and Chile, *Histioteuthis* sp., *Chiroteuthis* spp., *Octopoteuthis* sp. and *Dosidicus gigas* are important (Berzin, 1971; Clarke, M. R. *et al.*, 1976; Clarke, M. R., 1977). In the eastern North Atlantic, *Histioteuthis bonelli* is the most important and followed by *Taningia danae* (Clarke, R., 1955, 1956; Clarke, M. R., 1962, 1977; Keil, 1963; Roe, 1969; Berzin, 1971;

TABLE 3. COMPARISON IN NUMERICAL AND WEIGHT PERCENTAGE BY

Family	Japan		Kurile Ialands			California
	(1976)	(1977)	(Okhotsk)	(Pacific)		
Enoploteuthidae	0.1	—	—	—	—	—
Octopoteuthidae	11.1	19.9	—	3.4	1.5	—
Onychoteuthidae	11.4	3.9	3.2	8.4	8.8	42.9
Cycloteuthidae	—	—	—	—	—	—
Gonatidae	1.3	4.0	64.5	50.2	59.5	17.9
Psychroteuthidae	—	—	—	—	—	—
Lepidoteuthidae	0.1	—	—	—	—	—
Architeuthidoe	0.2	—	6.8	3.1	3.8	—
Histioteuthidae	30.4	38.2	1.0	10.9	4.4	—
Ommastrephidae	14.5	0.5	—	0.1	—	—
Chiroteuthidae	—	1.3	—	2.1	5.0	—
Cranchiidae	3.7	5.6	8.7	25.2	11.2	—
Pholidoteuthidae	—	—	—	—	—	—
Unidentified squid	27.0	26.5	—	—	1.5	39.3
Vampyroteuthidae	—	—	—	—	—	—
Octopodidae	—	—	2.0	0.9	0.5	—
Alloposidae	—	—	—	—	1.6	—
Amphitretidae	—	—	—	—	1.5	—
Others	—	—	—	—	0.7	—
Total	100.0	100.0	86.2*	114.3*	100.0	100.0
Source**	(1)	(2)	(3)	(3)	(4)	(5)

Notes 1) The values in parentheses are the percentage by weight.

2) *: These values are calculated by the present author in the same way as the original author did.

FAMILY OF THE CEPHALOPOD CONSTITUENTS IN SPERM WHALE FOOD

New Zealand	Peru, Chile	Iceland		Azores	Vigo	Madeira
		Complete collection	Mixed sample			
—	5.5	0.2	0.3	—	2.9	1.0
(—)	(2.6)	(0.1)			(0.3)	(0.3)
—	9.2	3.4	6.8	39.1	14.3	0.5
(—)	(1.9)	(25.3)			(83.0)	(14.2)
70.7	0.1	0.8	3.3	1.8	—	—
(89.7)	(0.1)	(5.9)			(—)	(—)
—	—	0.6	0.7	—	—	—
(—)	(—)	(0.4)			(—)	(—)
—	3.2	0.3	12.9	—	—	—
(—)	(1.4)	(0.1)			(—)	(—)
—	0.1	0.1	0.2	—	—	—
(—)	(0.1)	(0.0)			(—)	(—)
—	—	—	1.0	—	5.7	1.3
(—)	(—)	(—)			(2.3)	(4.0)
—	—	0.2	0.3	—	1.4	1.7
(—)	(—)	(3.4)			(6.6)	(40.6)
13.3	50.3	73.9	60.5	59.1	67.2	88.3
(1.0)	(56.3)	(46.5)			(5.6)	(36.1)
8.0	4.1	0.1	0.3	—	—	—
(5.6)	(31.7)	(0.0)			(—)	(—)
—	16.1	0.1	—	—	—	—
(—)	(1.0)	(0.0)			(—)	(—)
—	0.8	1.9	3.3	—	5.7	—
(—)	(0.5)	(0.6)			(0.1)	(—)
—	—	0.1	0.7	—	—	—
(—)	(—)	(0.0)			(—)	(—)
8.0	7.6	15.8	7.0	—	—	—
(3.7)	(1.1)	(10.1)			(—)	(—)
—	3.2	—	—	—	—	—
(—)	(3.3)	(—)			(—)	(—)
—	—	—	2.6	—	—	—
(—)	(—)	(—)			(—)	(—)
—	—	2.8	—	—	2.9	0.8
(—)	(—)	(7.5)			(2.1)	(1.5)
—	—	—	—	—	—	—
(—)	(—)	(—)			(—)	(—)
—	—	—	—	—	—	—
(—)	(—)	(—)			(—)	(3.4)
100.0	100.0	100.0	100.0	100.0	100.0	100.0
(100.0)	(100.0)	(100.0)			(100.0)	(100.0)
(6)	(7)	(8)	(8)	(9)	(10)	(11)

3) **: (1) Okukani *et al.* 1976 (2) Okutani and Satake 1978 (3) Tarasevich 1963 (4) Betesheva and Akimushkin 1955 (5) Rice 1963 (6) Gaskin and Cawthorn 1967 (7) Clarke, M. R. *et al.* 1976 (8) Clarke, M. R. and MacLeod 1976 (9) Clarke, R. 1956 (10) Clarke, M. R. and MacLeod 1974 (11) Clarke M. R. 1962, amended by Clarke, M. R. 1974.

Clarke, M. R. and MacLeod, 1974). In the Indian Ocean, histioteuthids are the most important (Matthews, 1938; Berzin, 1971; Clarke, M. R., 1972, 1977). In the Antarctic, onychoteuthids and cranchiids are very important (Matthews, 1938; Korabelnikov, 1959; Berzin, 1971; Clarke, M. R., 1977).

The data on the amount of squids as the food of sperm whales are rather numerous (Clarke, M. R., 1962; Clarke, M. R. and MacLeod, 1974, 1976; Clarke, M. R. *et al.*, 1976), but most of them have not been treated quantitatively (Table 3).

According to Clarke, M. R. (1977) who reported the quantitatively important squid families estimated by the beaks removed from the stomachs of sperm whales, octopoteuthids, including the large *Taningia danae*, are important in all regions except the Antarctic and off Peru and Chile, and histioteuthids, including several species, are important everywhere expect the Antarctic. In addition to them, onychoteuthids, architeuthids, ommastrephids such as *Dosidicus gigas*, *Todarodes* sp., *Ancistrocheirus* of enoploteuthid, and pholidoteuthids are also important in some regions.

Fishes as the food of sperm whales

Though the species of fishes obtained from the stomachs of sperm whales are various as are shown in Appendix Table II, namely 55 genera (about 68 or more species) belonging to 49 families, the occurrence prortion of fishes in the food is not so large as squids, and is different by region and year like cephalopods as are shown in Table 1. The ratios of occurrence of squids to fishes in the food of sperm whales by region are shown in Table 2. In the North Pacific the fish occurrence is between 1% and 68% of the stomachs having fishes and/or squids in them (Omura, 1950; Pike, 1950; Mizue, 1951; Betesheva and Akimushkin, 1955; Tomilin, 1957; Tarasevich, 1963; Rice, 1963; Okutani and Nemoto, 1964). It is only 1–9% in the Japanese waters, 31% in the Kurile Islands waters, 6–47% in the western part of the Bering Sea and Aleutian coast west of 180°, 7–29% in the Bering Sea and Aleutian coast between 180° and 160°W, 68% off the coast of Alaskan Gulf, not less than 56% off British Columbia and 39% off California. In the Bering Sea and Aleutian coast west of 180° it is, as is shown in Table 2, 6–13% according to Okutani and Nemoto (1963), but it is 20%, 36% and 47% in the waters of Komandorskiye, Aleutorskiye and northern part of the Bering Sea respectively according to Berzin (1959). Thus fishes as the food of the sperm whales mostly predominate in the eastern waters along the Alsakan Gulf and the east Bering Sea as was stated by Okutani and Nemoto (1964), and in the northern part of the both sides of the North Pacific.

In the New Zealand waters the sperm whales take squids and fishes in nearly the same ratio, but about one third of them feed both fishes and squids, and the ratio of fishes to squids by weight was 1: 1.69 (Gaskin and Cawthorn, 1967).

In the Iceland waters of the Atlantic, fishes occur in 98% of the sperm whale stomachs with food, in which 54% contain both squids and fishes (Roe, 1969), and the occurrence ratio of squids to fishes is 36: 64. In the Azores waters fishes occur in 13% or less (Clarke, R. 1956). For the sperm whales in the North Atlantic, fishes are more important in the northern part of the Ocean.

TABLE 4. COMPARISON IN NUMERICAL PERCENTAGE OF THE FISHES IN SPERM WHALE FOOD

Fishes	Japan	Japan	British Columbia	California	New Zealand	Iceland
Lamprey	—	—	2.2	—	—	—
Shark	—	3.2	—	25.0	6.9	6.3
Skate	—	—	20.0	54.2	—	3.1
Rag fish	—	—	35.6	—	—	—
Sardine	—	4.3	—	—	—	—
Salmon-like fish	—	—	6.7	—	—	—
Lanternfish	—	—	—	4.2	1.7	—
Conger eel	—	—	—	—	13.8	—
Saury	—	6.5	—	—	—	—
Dory-types	—	—	—	—	29.3	—
South kingfish	—	—	—	—	12.1	—
Groper	—	—	—	—	15.5	—
Anarrhichus minor	—	—	—	—	—	3.1
Ling	—	—	—	—	20.7	—
Rock fish	80.0	55.9	35.6	—	—	25.0
Sablefish	—	—	—	8.3	—	—
Lingcod	—	—	—	8.3	—	—
Lumpsucker	—	—	—	—	—	31.3
Cod	20.0	30.1	—	—	—	18.8
Angler fish	—	—	—	—	—	12.5
Total	100.0	100.0	100.0	100.0	100.0	100.0
Source	Omura 1950	Mizue 1951	Pike 1950	Rice 1963	Gaskin and Cawthorn 1967	Roe 1969

Note: The percentages were calculated with the numbers of stomachs in which the fish were found by the present author.

In the waters of South Georgia and South Africa, the fishes occur in 11% of the sperm whales' stomachs with food (Matthews, 1938), and in the Antarctic, in 5–13% (Clarke, R., 1956; Korabelnikov, 1959) (Table 1).

Thus, generally speaking, the occurrence proportion of fishes is not so large as squids, and in many cases fishes are found mixed with squids. These conditions are various according to the region, and the regions where fishes are rather important are the northern and the northeastern parts of the North Pacific, the New Zealand waters and the northern part of the North Atlantic.

The data on the composition in numerical percentage of fish constituents in sperm whale food are available in the waters of Japan, British Columbia, California, New Zealand and Iceland as are shown in Table 4. The important fishes in each region are rock fish and cod for the Japanese waters, rock fish and rag fish for the British Columbian waters, skate and shark for Californian waters, dory-type fish and ling for the New Zealand waters, and lumpsucker and rock fish for the Iceland waters.

THE FEEDING TIME OF SPERM WHALES

It may be thinkable that sperm whales actively feed during night when squids come up to the surface, and do not move about so actively in the daytime, judging from the catch data of the Antarctic whaling (Matsushita 1955), but Okutani and Nemoto (1964) and Clarke, M. R. (1980) found no evidence for special feeding time in the North Pacific and off Durban respectively.

THE SIZE OF FOOD ANIMALS EATEN BY SPERM WHALES

Squids

Though the size of cephalopods usually eaten by sperm whales does not appear so large, sperm whales are considered to attack sometimes the gigantic squids. This is considerable from the large scars up to 20 cm in diameter on the skin of sperm whales caused by large suckers of squids, and also from the reports of huge fragments of squids vomitted by dying whales or recovered among the stomach contents, although Roe (1969), who recorded the sucker scars of 1.7–11.5 cm in diameter, doubted whether the very large scars such as 11.5 cm in diameter had been, in fact, caused by squids, and considered it was possible that they were old sucker scars which had stretched as the whale had grown (Matthews, 1938; Roe, 1969; Berzin, 1971).

TABLE 5. SIZES OF SQUIDS FROM STOMACHS OF SPERM WHALES EXAMINED AT HORTA IN 1949 (Quoted from Clarke, R., 1956)

Sizes of squids Length group	Standard length	Male whales		Female whales	
		No. of squids	%	No. of suids	%
Small	0.6 to 0.9 m	41	59	28	67
Medium	0.9 to 1.5	26	37	13	31
Medium-large	1.5 to 1.8	2	3	0	0
Large	1.8 to 2.4	1	1	1	2
Total		70	100	42	100
Average size of squids		0.95 m		0.92 m	

Kondakov (1940) considered that the suckers as large as 20 cm in diameter might belong to *Architeuthis* of 18 m in total length. The large *Architeuthis* whose total length and weight were 10.5 m (mantle length was 2 m), 184 kg, and 12 m, 200 kg were actually removed from the stomachs of sperm whales from the Azores in 1955 and from the Antarctic in 1964 respectively (Clarke, M. R., 1955; Berzin, 1971). An architeuthid 2.4 m in mantle length was obtained from the stomach of the sperm whale in the Azores waters (Keil 1963). In addition to these architeuthids, *Moroteuthis robusta* of 2.9 m, 2.4 m and 2.4 m long were reported from the stomachs of the sperm whales caught off Kommandorskiye Islands, off British Columbia and in the Antarctic respectively (Pike, 1950; Clarke, R., 1956; Berzin, 1971).

As the large scars and scratches are usually found on the head of male whales, and females are smaller in body length than males, it is often considered that male sperm whales take larger squids than females (Matthews, 1938). Clarke, M. R. (1980) also considered that males favour larger species than females by a χ^2 test of the data of the sperm whales off Durban. But there is also another opinion that males and females take food of the same size as shown in Table 5 (Clarke, R. 1956).

The size of the food items in the diet may be different according to the ground, and an example of the difference was shown by Clarke, R. (1956) as follows: The average standard length of squids from the sperm whales caught in the Azores was 0.94 m and that of the Antarctic (*Moroteuthis ingens*) was 1.3 m.

Fishes

Fishes are, as stated above, generally not so important food for sperm whales as squids, but sometimes large fishes 1–3 m in body length have been removed from the stomachs of sperm whales as follows: a 3 meter shark, the species of which was unidentified, was reported off South Africa (Chabb, 1918; fido Berzin 1971), a basking shark *Cetorhinus maximus* 2.5 m long, at the Azores (Clarke, R., 1956), a green shark *Somniosus* sp. 2.1 m long, another shark *Squalus acanthias* 1.3 m long, and *Alepisaurus aesculopius* 1.3 m long, in the Kurile waters (Betesheva, 1961; fido Berzin 1971), fishes belonging to Notothenidae up to 1.5 m long and a ray *Raja griseocandata* 1.1 m long, near Tierra del Fuego (Semskii, 1962, fido Berzin 1971), *Dissostichus mawsoni* up to 1.7 m long (as a rule 1.2–1.4 m), near the Balleny Island (Berzin, 1971), fantailed ragfish *Icosteus aenigmaticus* 1.3 m long, off British Columbia (Pike, 1950).

THE WEIGHT OF DOOD OF SPERM WHALES

The weight of food in a stomach of sperm whales

The weight of food in a stomach of sperm whales may be different according to the size of whales, and is generally considered to be less than 300 kg. According to Betesheva and Akimushkin (1955) and Betesheva (1961), it did not exceed 200 kg. Other data showed that stomachs contained 201–500 squid (*Gonatus fabricii*) (Berzin, 1971), the weight of which may be calculated as 80–200 kg, supposing the average weight of this squid is 400 g. The weight of fresh food of the sperm whales in the Cook Strait region of New Zealand was reported to have varied from 12.7 to 105 kg (Gaskin and Cawthorn, 1967).

On the difference of the quantity of food for male and female sperm whales, there are two different opinions. The quantity of food of sperm whales in the Japanese waters was not different between males and females (Mizue, 1950), but the uncomplete data from the Azores suggested (not concluded) that females were feeding rather less heavily than males, and this might be explained as follows: females are hampered to feed heavily by calves which cannot dive deep (Clarke, R., 1956).

The amount of sperm whale food consumed in a day and in a year

The food of sperm whales consumed in a day was considered to be at least 2–

3 tons of squids for a sperm whale 13–14 m long by Sleptsov (1952), and one ton a day by Berzin (1971).

Clarke, M. R. (1977) considered the amount of food consumed in a day by sperm whales would be 2–4% of their body weight and calculated as 300 kg and 200 kg for males and females respectively, supposing the average body weights were 15 tons and 5 tons for males and females respectively. As he stated that the weight of sperm whales is between 8 and 50 tons, if the largest whale is considered, the amount of food consumed in a day will be one ton.

The total weight of cephalopods eaten by sperm whales each year has been estimated by Clarke, M. R. (1977) to be over 110 million tons on the basis of the data on estimated number of whales and estimated weight of food consumed by whales, and also as a muximum figure the amount of cephalopods eaten was estimated to be 320 million tons, accepting a value of 15 tons for the average whale and a consumption of 3.5% of body weight per day as well as an average calorific value of 75% of that for mascular squids.

NUTRIENT DISPERSAL BY SPERM WHALES

This problem has scarecely been studied. Sperm whales seem to eat food actively near the surface during night as stated above, but it may be true that they certainly eat several midwater species and also eat species in spawning condition on the bottom. Therefore, it could be considerable that sperm whales probably carry nutrient upwards by eating deepsea squid and defaecating near the surface as Clarke, M. R. (1977) stated.

Many families of cephalopods are said to have large amount of ammonia in their tissues and coelom, and 53–78% of the number of cephalopods consumed by sperm whales are said to be ammonical squid (Clarke, M. R., 1977), which are probably not good for human food as they are.

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APPENDIX TABLE I. THE CEPHALOPODS FOUND IN THE STOMACHS OF SPERM WHALES BY AREA*

Family Genus Species	Pacific					Atlantic			Indian	Antarctic				Off S. Afr.[8]
	NW[1]	N[2]	NE[3]	SW[4]	SE[5]	NE[3]	SW[4]	SE[5]	S[6]	Pac	Atl	Ind	Ant[7]	
Loliginidae	−	−	−	−	−	−	−	−	−	−	−	−	−	−
Loligo forbesi	−	−	−	−	−	+	−	−	−	−	−	−	−	−
Enoploteuthidae	−	−	−	+	−	−	+	+	+	−	−	−	−	−
Ancistrocheirus lesueuri	+	−	−	−	+	+	−	+	+	−	−	−	−	−
Octopoteuthidae	−	−	−	+	+	+	+	+	+	−	−	−	+	−
Octopoteuthis longiptera	+	−	+	−	−	−	+	−	−	−	−	−	−	−
O. spp.	+	−	−	−	+	+	−	−	−	−	−	−	−	−
Taningia danae	+	−	−	−	+	+	−	−	−	−	−	−	−	−
=Cucioteuthis unguiculata	−	−	−	−	−	+	−	−	−	−	−	−	−	−
Onychoteuthidae	+	+	+	+	−	−	−	+	+	−	−	−	+	−
Onychoteuthis banksii	+	+	+	−	−	+	−	−	−	−	+	−	+	−
O. spp.	+	−	+	+	−	−	−	−	−	−	−	−	−	−
Moroteuthis robusta	+	+	+	−	−	−	−	−	+	+	−	−	−	+
M. lönbergii	+	−	−	−	−	−	−	−	−	−	−	−	−	−
M. ingens	−	−	−	−	−	−	−	−	+	−	−	+	−	−
M. robsoni	−	−	−	−	−	+	−	−	−	−	−	−	−	−
M. knipovitchi	−	−	−	−	−	−	−	−	−	−	−	−	+	−
M. sp.	−	−	−	+	+	−	−	−	+	−	−	−	−	−
Tetronychoteuthis dussumierii	−	−	−	−	−	+	−	−	−	−	−	−	−	−
T. sp.	−	−	−	−	−	+	−	−	−	−	−	−	−	−
Kondakovia longimana	−	−	−	−	−	+	−	−	−	−	−	−	−	−
K. sp.	−	−	−	−	−	−	−	−	−	−	−	−	+	−
Cycloteuthidae	−	−	−	+	−	−	+	−	+	−	−	−	−	−
Cycloteuthis akimushkini	−	−	−	−	−	+	−	−	−	−	−	−	−	−
C. sp.	−	−	−	−	+	−	−	−	−	−	−	−	−	−
Gonatidae	+	+	+	−	+	+	−	−	−	−	−	−	+	−
Gonatus fabricii	+	+	+	−	−	+	−	−	−	−	−	−	−	−
G. berryi	+	−	−	−	−	−	−	−	−	−	−	−	−	−
G. antarcticus	−	−	−	−	+	−	−	−	+	−	−	−	−	−
G. sp.	+	−	−	−	−	−	−	−	−	−	−	−	−	−
Berryteuthis magister	+	−	−	−	−	−	−	−	−	−	−	−	−	−
=Gonatus magister	+	+	+	−	−	−	−	−	−	−	−	−	−	−
Gonatopsis borealis	+	+	+	−	−	−	−	−	−	−	−	−	−	−
G. makko	+	+	−	−	−	−	−	−	−	−	−	−	−	−
G. octopedatus	+	−	−	−	−	−	−	−	−	−	−	−	−	−
Mesonychoteuthis hamiltoni	−	−	−	−	−	−	−	−	+	−	−	−	−	−
Psychoteuthidae	−	−	−	+	−	−	−	−	−	−	−	−	−	−
Psychoteuthis sp.	−	−	−	−	+	−	−	−	−	−	−	−	−	−
Lepidoteuthidae	−	−	−	+	−	+	+	−	−	−	−	−	−	−
Lepidoteuthis grimaldii	+	−	−	−	−	+	−	−	−	−	−	−	−	−
L. sp.	−	−	−	−	−	+	−	−	−	−	−	−	−	−
Architeuthidae	−	−	−	+	−	+	−	+	−	−	+	−	−	+
Architeuthis japonica	+	−	+	−	−	−	−	−	−	−	−	−	−	−

Continued . . .

APPENDIX TABLE I. Continued.

Family Genus Species	Pacific					Atlantic			Indian	Antarctic				Off S. Afr.[8]
	NW[1]	N[2]	NE[3]	SW[4]	SE[5]	NE[3]	SW[4]	SE[5]	S[6]	Pac	Atl	Ind	Ant[7]	
A. physeteris	−	−	−	−	−	+	−	−	−	−	−	−	−	−
=*Dubioteuthis physeteris*	−	−	−	−	−	+	−	−	−	−	−	−	−	−
A. sp.	−	−	−	+	−	+	−	−	+	−	+	−	−	−
Histioteuthidae	+	−	+	+	+	+	+	+	+	−	−	−	+	−
Histioteuthis dofleini	+	−	−	−	−	+	−	−	−	−	−	−	−	−
=*Stigmateuthis dofleini*	−	−	+	−	−	−	−	−	−	−	−	−	−	−
H. sp.	−	−	−	−	+	+	−	−	−	−	−	−	−	−
=*S.* sp.	−	+	−	−	−	−	−	−	−	−	−	−	−	−
=*Calliteuthis* sp.	−	−	−	−	−	+	−	−	−	−	−	−	−	−
H. meleagroteuthis	−	−	−	−	−	−	−	−	−	−	−	−	−	−
=*Meleagroteuthis separata*	+	+	+	−	−	−	−	−	−	−	−	−	−	−
H. bonelliana	−	−	−	+	−	+	−	−	+	−	−	−	−	−
H. bonellii	−	−	−	−	−	+	−	−	−	−	−	−	−	−
H. cookiana	−	−	−	+	−	−	−	−	−	−	−	−	−	−
Ommastrephidae	−	−	+	+	+	−	−	−	+	−	−	−	+	−
Todarodes sagittatus	−	−	−	−	−	+	−	−	−	−	−	−	−	−
T. sp.	−	−	−	−	−	−	−	−	+	−	−	−	−	−
Nototodarus sloani	−	−	−	+	−	−	−	−	−	−	−	−	−	−
Ommastrephes bartrami	+	−	−	−	−	−	−	−	−	−	−	−	−	−
=*Stenoteuthis bartrami*	+	−	−	+	−	−	−	−	+	−	−	−	−	−
Dosidicus gigas	−	−	−	−	+	−	−	−	−	−	−	−	−	−
=*Ommastrephes gigas*	−	−	−	−	+	−	−	−	−	−	−	−	−	−
Symplectoteuthis sp.	−	−	−	−	+	−	−	−	−	−	−	−	−	−
Chiroteuthidae	−	−	+	+	+	−	−	−	+	−	−	−	−	−
Chiroteuthis calyx	+	−	−	−	−	−	−	−	−	−	−	−	−	−
C. veranyi	+	+	+	−	−	−	−	−	−	−	−	−	−	−
C. spp.	−	−	−	−	+	+	−	−	−	−	−	−	−	−
Mastigoteuthidae	−	−	−	+	−	−	−	−	−	−	−	−	+	−
Mastigoteuthis sp.	−	+	−	−	−	−	−	−	−	−	−	−	−	−
Cranchiidae	−	−	+	+	+	+	−	+	+	−	−	−	+	−
Cranchia scabra	+	−	−	−	−	−	−	−	−	−	−	−	−	−
Taonius pavo	+	+	+	−	−	+	−	−	−	−	−	−	−	−
T. megalops	−	−	−	−	+	+	−	−	−	−	−	−	−	−
T. spp.	+	−	−	−	−	−	−	−	−	−	−	−	−	+
Galiteuthis armata	+	+	+	−	−	+	−	−	−	−	−	−	−	−
G. sp.	+	−	−	−	−	−	−	−	−	−	−	−	−	−
Phasmatopsis cymoctypus	−	−	−	−	−	+	−	−	−	−	−	−	−	−
P. sp.	−	−	−	−	+	−	−	−	−	−	−	−	−	+
Mesonychoteuthis hamiltony	−	−	−	−	+	−	−	−	−	−	−	−	+	−
Pholidoteuthidae	−	−	−	+	−	−	−	+	+	−	−	−	−	−
Pholidoteuthis sp.	−	−	−	−	−	+	−	−	+	−	−	−	−	−
P. ? boschmai	−	−	−	−	−	+	−	−	−	−	−	−	−	−
Vampyroteuthidae	−	−	+	−	+	−	−	−	−	−	−	−	−	−
Vampyroteuthis infernalis	−	−	−	−	+	−	−	−	−	−	−	−	−	−

Continued . . .

APPENDIX TABLE I. Continued.

Family Genus Species	Pacific					Atlantic			Indian	Antarctic				Off S. Afr.[8]
	NW[1]	N[2]	NE[3]	SW[4]	SE[5]	NE[3]	SW[4]	SE[5]	S[6]	Pac	Atl	Ind	Ant[7]	
Vampyroteuthis sp.	–	–	–	–	+	–	–	–	–	–	–	–	–	–
Octopodidae	+	–	+	+	+	+	–	–	+	–	–	–	–	–
Octopus vulgaris	+	–	–	–	–	–	–	–	–	–	–	–	–	–
O. gilbertianus	+	–	+	–	–	–	–	–	–	–	–	–	–	–
O. sp.	–	–	+	–	–	–	–	–	–	–	–	–	–	–
Paroctopus gilbertianus	+	–	–	–	–	–	–	–	–	–	–	–	–	–
Alloposidae	–	–	–	–	–	+	–	–	–	–	–	–	+	–
Alloposus mollis	+	–	+	–	–	+	–	–	–	–	–	–	–	–
A. sp.	–	–	–	–	–	+	–	–	–	–	–	–	–	–
Amphitretidae	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Amphitretus sp.	+	–	–	–	–	–	–	–	–	–	–	–	–	–

Notes:

* The list has been drawn up on the basis of data from the works listed in the chapter "REFERENCE." The bar in the table only shows that the shecimen was not reported by this name.

1) Northwestern part of the Ocean.
2) Northern part of the Ocean.
3) Northeastern part of the Ocean.
4) Southwestern part of the Ocean.
5) Southeastern part of the Ocean.
6) Southern part of the Ocean.
7) The part of the Ocean was not reported.
8) Off South Africa.

APPENDIX TABLE II. THE FISHES FOUND IN THE STOMACHS OF SPERM WHALES BY AREA*

English name	Family Genus Species	Pacific						Atl.	Ind.	Antarctic			
		NW[1]	N[2]	NE[3]	SW[4]	SE[5]	Pac[6]	NE[3]	S[7]	Pac	Atl	Ind	Ant
Lamprey	Petromyzonidae	–	+	+	–	–	–	–	–	–	–	–	–
Pacific lamprey	*Entophenus tridentatus*	–	+	–	–	–	–	–	–	–	–	–	–
	Scyliorhinidae	–	–	–	–	–	–	–	–	–	–	–	–
Brown cat shark	*Apristurus brunneus*	–	–	+	–	–	–	–	–	–	–	–	–
	Cetorhinidae	–	–	–	–	–	–	–	–	–	–	–	–
Basking shark	*Cetorhinus maximus*	–	–	–	+	–	–	+	–	–	–	–	–
	C. sp.	–	–	–	–	–	–	+	–	–	–	–	–
Blue shark	Carchariidae	–	–	–	–	–	–	–	–	–	–	–	–
	Carcharias glaucus	–	–	–	–	–	–	+	–	–	–	–	–
Shark	Squalidae	+	–	–	–	–	+	–	–	–	–	–	–
Spined dog fish	*Squalus acanthias*	+	+	–	–	–	–	–	–	–	–	–	–
	=*Koinga kirki*	–	–	–	+	–	–	–	–	–	–	–	–
	Dalatiidae	–	–	–	–	–	–	–	–	–	–	–	–
Green shark	*Somniosus* sp.	+	–	–	–	–	–	–	–	–	–	–	–
Greenland shark	*S. microcephalus*	–	–	–	–	–	–	+	–	–	–	–	–
Black shark	*Dalatias licha*	–	–	–	–	–	–	+	–	–	–	–	–
	D. sp.	–	–	–	+	–	–	–	–	–	–	–	–
Shark	Echinorhinidae	–	–	–	–	–	–	–	–	–	–	–	–
	Echinorhinus cooki	–	–	–	+	–	–	–	–	–	–	–	–
	E. sp.	–	–	–	+	–	–	–	–	–	–	–	–

Continued...

APPENDIX TABLE II. Continued.

English name	Family Genus Species	Pacific						Atl.	Ind.	Antarctic			
		NW1)	N)2	NE3)	SW4)	SE5)	Pac6)	NE3)	S7)	Pac	Atl	Ind	Ant
Shark, Pacifice angel shark	Squatinidae	−	−	−	−	−	+	−	−	−	−	−	−
	Squatina californica	−	−	+	−	−	−	−	−	−	−	−	−
Shark		+	−	−	−	−	−	+	−	−	−	−	−
Ray, Long nose skate	Rajidae	−	+	+	−	−	−	−	−	−	−	−	−
	Raja smirnovi	+	−	−	−	−	−	−	−	−	−	−	−
	R. rhina	−	−	+	−	−	−	−	−	−	−	−	−
	R. griseocaudata	−	−	−	−	−	−	−	−	−	+	−	−
	R. sp.	+	+	−	+	−	−	+	−	−	−	−	−
	Chimaeridae	−	−	−	+	−	−	−	−	−	−	−	−
Round-herring	Dussumieridae	−	−	−	−	−	−	−	−	−	−	−	−
	Etrumeus micropus	+	−	−	−	−	−	−	−	−	−	−	−
	Clupeidae	−	−	−	−	−	−	−	−	−	−	−	−
Sardine	*Sardinops melanosticta*	+	−	−	−	−	−	−	−	−	−	−	−
	Engraulidae	−	−	−	−	−	−	−	−	−	−	−	−
	Engraulis japonicus	+	−	−	−	−	−	−	−	−	−	−	−
Salmon	Salmonidae	−	−	−	−	−	−	−	−	−	−	−	−
	Onchorhynchus gorbusha	+	−	−	−	−	−	−	−	−	−	−	−
Salmon like fish		−	−	+	−	−	−	−	−	−	−	−	−
Lantern fish	Myctophidae	−	−	−	−	−	−	−	−	−	−	−	−
	Myctophum humboldti	−	−	−	+	−	−	−	−	−	−	−	−
	Tarletonbeania crenularis	−	−	+	−	−	−	−	−	−	−	−	−
	Alepisauridae	−	+	−	−	−	−	−	−	−	−	−	−
	=Plagiodontidae	−	+	−	−	−	−	−	−	−	−	−	−
	Alepisaurus aesculapius	+	+	−	−	−	−	−	−	−	−	−	−
	=Plagyodus aesculapius	−	+	−	−	−	−	−	−	−	−	−	−
	A. spp.	−	−	−	−	−	−	+	−	−	−	−	−
Large eel	Anguillidae	−	−	−	−	−	−	−	−	−	−	−	−
	Anguilla sp.	−	−	−	−	−	−	+	−	−	−	−	−
Conger eel	Congridae	−	−	−	+	−	−	−	−	−	−	−	−
Eel		−	−	−	+	−	−	−	−	−	−	−	−
	Scombresocidae	−	−	−	−	−	−	−	−	−	−	−	−
Saury	*Cololabis saira*	+	+	−	−	−	−	−	−	−	−	−	−
Dory-like fish	Trachichthidae	−	−	−	−	−	−	−	−	−	−	−	−
	Hoplostethus sp.	−	−	−	+	−	−	−	−	−	−	−	−
John Dory	Zeidae	−	−	−	−	−	−	−	−	−	−	−	−
	Zeus faber	−	−	−	+	−	−	−	−	−	−	−	−
Porcupine fish	Diodontidae	−	−	−	−	−	−	−	−	−	−	−	−
	Diodon sp.	−	−	−	−	−	−	−	+	−	−	−	−
Mackrel	Scombridae	−	−	−	−	−	−	−	−	−	−	−	−
	Scomber japonicus	+	−	−	−	−	−	−	−	−	−	−	−
	S. tapeinocephalus	+	−	−	−	−	−	−	−	−	−	−	−
	=S. japonicus tapeinocephalus	+	−	−	−	−	−	−	−	−	−	−	−

Continued . . .

APPENDIX TABLE II. Continued.

English name	Family Genus Species	Pacific						Atl.	Ind.	Antarctic			
		NW1)	N2)	NE3)	SW4)	SE5)	Pac6)	NE3)	S7)	Pac	Atl	Ind	Ant
Tuna	Thunidae	–	–	–	–	–	–	–	–	–	–	–	–
Yellow fin tuna	*Thunus albacares*	–	–	–	–	–	–	+	–	–	–	–	–
	Sphyraenidae	–	–	–	–	–	–	–	–	–	–	–	–
Barracuda	*Sphyraena* sp.	–	–	–	–	–	–	+	+	–	–	–	–
	Acinaceidae	–	–	–	–	–	–	–	–	–	–	–	–
Southern king fish	*Rexea solandri*	–	–	–	–	–	–	–	–	–	–	–	–
	=*Jordanidia solandri*	–	–	–	+	–	–	–	–	–	–	–	–
	Histiopteridae	–	–	–	–	–	–	–	–	–	–	–	–
	Pseudopentaceros richardsoni	–	+	–	–	–	–	–	–	–	–	–	–
	Serranidae	–	–	–	–	–	–	–	–	–	–	–	–
Groper	*Polyprion oxygeneios*	–	–	–	+	–	–	–	–	–	–	–	–
	Anarrhichadidae	–	–	–	–	–	–	–	–	–	–	–	–
	Anarrhichas minor	–	–	–	–	–	–	+	–	–	–	–	–
	Ophidiidae	–	–	–	–	–	–	–	–	–	–	–	–
Ling	*Genypterus blacodes*	–	–	–	+	–	–	–	–	–	–	–	–
Rock fish	Scorpaenidae	+	+	+	+	–	–	–	–	–	–	–	–
Red fish	*Sebastes flammeus*	+	–	–	–	–	–	–	–	–	–	–	–
	S. iracundus	+	–	–	–	–	–	–	–	–	–	–	–
	S. alutus	–	+	–	–	–	–	–	–	–	–	–	–
	S. mentella	–	–	–	–	–	–	+	–	–	–	–	–
	S. marinus	–	–	–	–	–	–	+	–	–	–	–	–
	S. ruberrimus	–	–	+	–	–	–	–	–	–	–	–	–
Rock fish	*S. rober*	+	–	–	–	–	–	–	–	–	–	–	–
	=*Sebastodes rober*	–	–	–	–	–	–	–	–	–	–	–	–
	S. sp.	+	+	–	–	–	–	–	–	–	–	–	–
	Helicolenus papilosus	–	–	–	+	–	–	–	–	–	–	–	–
	Anoplopomidae	–	–	–	–	–	–	–	–	–	–	–	–
Sable fish, Black cod	*Anoplopoma fimbria*	–	–	+	–	–	–	–	–	–	–	–	–
	Hexagrammidae	–	–	–	–	–	–	–	–	–	–	–	–
	Pleurogrammus monopterigius	–	+	–	–	–	–	–	–	–	–	–	–
	P. sp.	+	–	–	–	–	–	–	–	–	–	–	–
Greeling, Ling cod	*Ophiodon elongatus*	–	–	+	–	–	–	–	–	–	–	–	–
Large gobies	Cottidae	+	+	–	–	–	–	–	–	–	–	–	–
	Myoxocephalus jaok	+	–	–	–	–	–	–	–	–	–	–	–
	M. verrucosus	+	+	–	–	–	–	–	–	–	–	–	–
	M. sp	–	+	–	–	–	–	–	–	–	–	–	–
	Agonidae	–	+	–	–	–	–	–	–	–	–	–	–
	Percis japonica	–	+	–	–	–	–	–	–	–	–	–	–
	Cyclopteridae	–	+	–	–	–	–	–	–	–	–	–	–
Lumpsucker	*Cyclopterus lumpus*	–	–	–	–	–	–	+	–	–	–	–	–
	Aptocyclus ventricosus	+	+	–	–	–	–	–	–	–	–	–	–
	Moridae	–	–	–	–	–	–	–	–	–	–	–	–
	Podonema longipes	+	–	–	–	–	–	–	–	–	–	–	–
Cod (fish)	Gadidae	+	–	+	–	–	–	–	–	–	–	–	–
	Gadus macrocephalus	+	–	–	–	–	–	–	–	–	–	–	–

Continued . . .

APPENDIX TABLE II. Continued.

English name	Family Genus Species	Pacific						Atl.	Ind.	Antarctic			
		NW1)	N2)	NE3)	SW4)	SE5)	Pac6)	NE3)	S7)	Pac	Atl	Ind	Ant
Pacific cod	=*G. morhua macrocephalus*	+	+	−	−	−	−	−	−	−	−	−	−
	G. morhua	−	−	−	−	−	−	+	−	−	−	−	−
	G. aeglefinus	−	−	−	−	−	−	+	−	−	−	−	−
	=Melanogrammus aeglefinus	−	−	−	−	−	−	+	−	−	−	−	−
	Pollachius virens	−	−	−	−	−	−	+	−	−	−	−	−
Walleye pollack	*Theragra chalcogramma*	+	−	−	−	−	−	−	−	−	−	−	−
	Eleginus gracilis	+	−	−	−	−	−	−	−	−	−	−	−
	E. gracilis navaga	+	−	−	−	−	−	−	−	−	−	−	−
Southern poutassou	Gadidae	−	−	−	−	−	−	−	−	−	−	−	−
	Micromesistius australis	−	−	−	−	−	−	−	−	−	+	−	−
	Nototheniidae	−	−	−	−	−	−	−	−	−	−	−	−
	Dissostichus eleginoides	−	−	−	−	−	−	−	−	−	+	−	−
	D. mawsoni	−	−	−	−	−	−	−	−	+	−	−	−
Macrurid	Coryphaenoididae	−	−	−	−	−	−	−	−	−	−	−	−
	=Macruridae	−	+	−	−	−	−	−	−	−	−	−	−
	Coryphaenoides pectoralis	+	−	−	−	−	−	−	−	−	−	−	−
	=*Laemonema longipes*	−	+	−	−	−	−	−	−	−	−	−	−
	C. sp.	−	+	−	−	−	−	−	−	−	−	−	−
	=*Macrurns* sp.	−	+	−	−	−	−	−	−	−	−	−	−
	Hemimacrurus acrolepis	+	−	−	−	−	−	−	−	−	−	−	−
	Icosteidae	−	−	−	−	−	−	−	−	−	−	−	−
Fan-tailed rag-fish	*Icosteus aenigmaticus*	−	−	+	−	−	−	−	−	−	−	−	−
Brown ragfish	*Acrotus willoughbyi*	−	−	+	−	−	−	−	−	−	−	−	−
Angler fish	Lophiidae	−	−	−	−	−	−	−	−	−	−	−	−
	Lophius piscatorius	−	−	−	−	−	−	+	−	−	−	−	−
Large (bathy pelagic) angler fish	Ceratiidae	−	−	−	−	−	−	−	+	−	−	−	−
	Ceratias holboelli	−	−	−	−	−	−	+	−	−	+	+	−
	Himantolophidae	−	−	−	−	−	−	−	−	−	−	−	−
	Himantolophus groenlandicus	−	−	−	−	−	−	+	−	−	−	−	−
	Oneirodidae	−	−	−	−	−	−	−	−	−	−	−	−
Angler fish	*Oneirodes* sp.	+	−	−	−	−	−	−	−	−	−	−	−

Notes:

* The list has been drawn up on the basis of data from the works listed in the chapter "REFERENCE." The bar in the table only shows that the specimen was not reported by this name.

1) Northeastern part of the Ocean.
2) Northern part of the Ocean.
3) Northeastern part of the Ocean.
4) Southwestern part of the Ocean.
5) Southeastern part of the Ocean.
6) The part of the Ocean was not reported.
7) Southern part of the Ocean.

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