

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 diomedea*, *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 expeditions. 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

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

Nippon Kyodo Hogeï 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.

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 personnel 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, experimen-

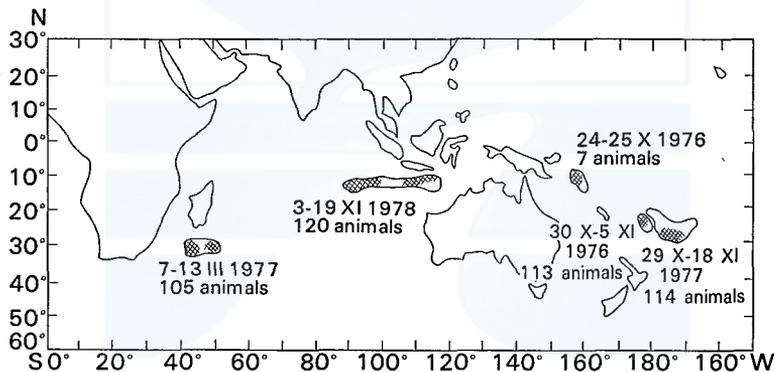


Fig. 1. Catch areas of the Bryde's whales taken by scientific permit in the South Pacific and Indian oceans during the seasons of 1976/77-1978/79. The shaded area indicates heavy concentration of catches.

tal 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).

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 outwestern 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 biased 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.

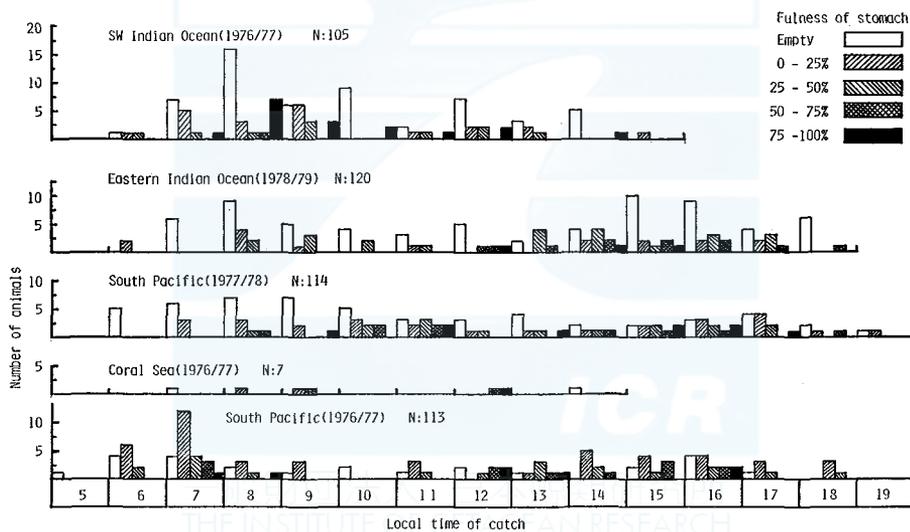


Fig. 2. Change of stomach fulness by the local time of catch in five different whaling areas.

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 biased

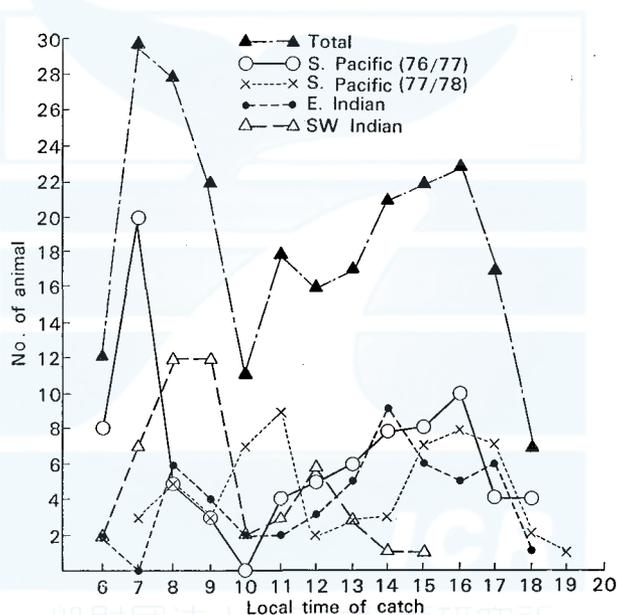


Fig. 3. Diel variation in the number of animals with filled stomach.

in the afternoon toward evening, and a possible nocturnal 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).

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

Euphausiacea :

- Euphausia recurva* Hansen
Euphausia diomedea 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	<i>Euphausia diomedea</i>
	Oct. 30- Nov. 5	20°-23°	S. Pacific	24°25'-27°59' S 177°11'-178°34' E	<i>Euphausia recurva</i> <i>Thysanoessa gregaria</i>
	Mar. 7-13	24.6°-26.6°	SW Indian Ocean	28°23'-31°47' S 43°55'-51°36' E	<i>Euphausia recurva</i> Hatchetfish*
1977/78	Oct. 29- Nov. 18	20.2°-23.4°	S. Pacific	21°15'-29°24' S 179°45' E-170°58' W	<i>Euphausia recurva</i> <i>Thysanoessa gregaria</i> Gonostomatid fish**
1978/79	Nov. 3- Nov. 19	25.8°-30.3°	E. Indian Ocean	9°47'-12°49' S	<i>Euphausia diomedea</i>
				92°02'-118°32' E	<i>Euphausia sibogae</i>
					<i>Pseudeuphausia latifrons</i>
					<i>Thysanopoda tricuspidata</i>
					<i>Vinciguerria nimbaria</i> <i>Auxis thazard</i> 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 euphausiids 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. diomedea*, *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. diomedea*, *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 diversified 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 :				Whaling ground	
	Both	Only		Absent		Unknown
	Male + Female	Male	Female	Male + Female		
<i>E. diomedea</i>	3	1	1			Coral Sea
<i>E. diomedea</i>			6	2	2	E. Indian
<i>E. recurva</i>	6		28	5	11	S. Pacific (76/77)
<i>E. recurva</i>	2		29	5	16	SW Indian
<i>E. recurva</i>			3	30		S. Pacific (77/78)
<i>T. gregaria</i>				11	2	S. Pacific (76/77)
<i>T. gregaria</i>	2	1		35	2	S. Pacific (77/78)
<i>E. sibogae</i>		1	2		4	E. Indian
<i>P. latifrons</i>		1	1	29	2	E. Indian
<i>T'da tricuspidata</i>				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 biased 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 biased to females (Table 6). *E. diomedea* 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 pos-

sible 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 tricuspadata* also did not carry sperm sacs but this species by no means occurred associating with any kind of planktonic eggs.

In summarizing 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 tricuspadata* and *E. diomedea* 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
<i>Auxis thazard</i> (Frigate mackerel)	215	10°14' S 112°12' E	Nov. 9, 1978	<i>Candacia pachydactyla</i> <i>Euchaeta marina?</i> Others*
<i>Vinciguerria nimbaria</i>	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 (<i>P. latifrons</i>) -egg?
Myctophiformes	24-25	11°16' S 97°34' E	Nov. 15, 1978	Copepods**

* Decapoda-megalopa, large cheliped like appendages, Amphipoda-Hyperiididae, *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. Although 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 com-

position except one mixed example with *E. diomedae*.

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 notwithstanding 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

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	
<i>E. diomedae</i>		5			6	11
<i>T. gregaria</i>	10			28		38
<i>Euphausia</i> sp.*	7		1			8
<i>E. recurva</i> + <i>T. gregaria</i>	8			3		11
<i>T. gregaria</i> + <i>E. recurva</i>	1			8		9
<i>E. recurva</i>	38		51****	20		109
<i>E. sibogae</i>					7	7
<i>P. latifrons</i>					29	29
<i>P. latifrons</i> + <i>E. diomedae</i>					2	2
<i>T'da tricuspidata</i>					2	2
<i>Euphausia</i> sp.**					1	1
<i>E. diomedae</i> + <i>V. nimbaria</i>					1	1
Fish larva*** + <i>E. diomedae</i>					1	1
<i>V. nimbaria</i>					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.

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.

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 diomedea*, *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

Food species	Minor components									
	1	2	3	4	5	6	7	8	9	10
1 <i>E. diomedea</i>	6	5							1	
2 <i>E. recurva</i>		51								
3 <i>T. gregaria</i>		38	20	8	3					
4 <i>E. sibogae</i>		1	8	10	28	7				
5 <i>P. latifrons</i>	2				29					
6 <i>T. tricuspidata</i>						2				
7 <i>Euphausia</i> sp.*							1			
8 <i>Euphausia</i> sp.**							7			
9 <i>V. nimbaria</i>								1		
10 Gonostomatids									4	
11 Nyctophiformes	1									1

Major components

Key to the numerals in square

E. Indian	SW Indian
Coral Sea	S. Pacific (1976/77)
S. Pacific (1977/78)	

* 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.

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. diomedea*. 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. diomedea* and *E. sibogae* accounted for 11.3% and 13.2% respectively. The latter two species can be referred 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

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. diomedae*, *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. diomedae*. 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 biased area, the occurrence of *E. diomedae* 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-

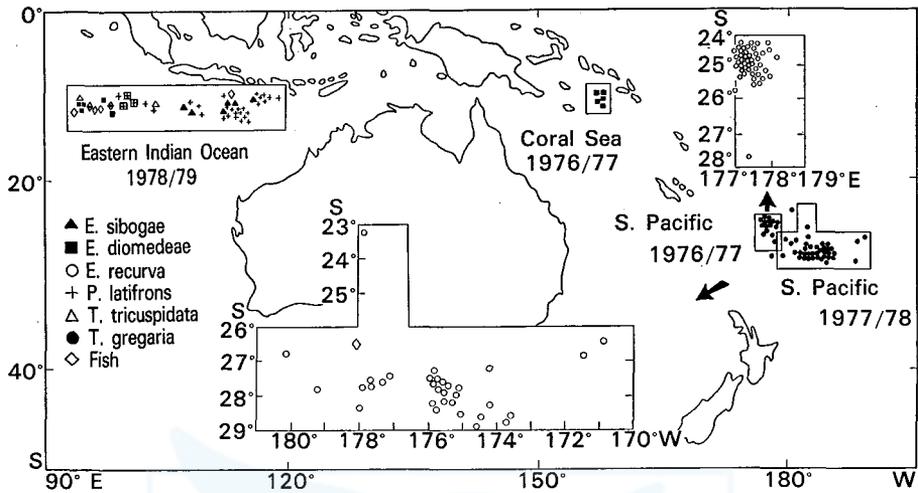


Fig. 5. Distribution of euphausiids and fish that were fed by the southern Bryde's whales.

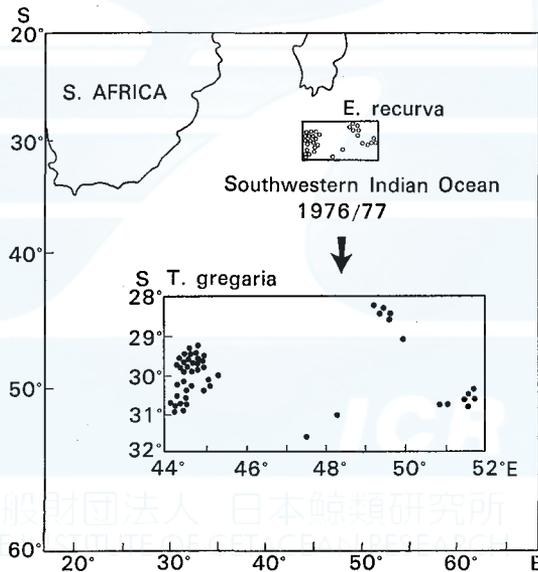


Fig. 6. Distribution of euphausiids that were fed by the southern Bryde's whales.

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 biased 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 con-

siderable 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. diomedae* 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 sparsely in the midst of the eastern Indian Ocean area. Although the reason why food organisms distributed so sparsely is unknown at present, the region well coincides with the area where distinct discontinuity of euphausiid distributions has been demonstrated (Ponomareva, 1972).

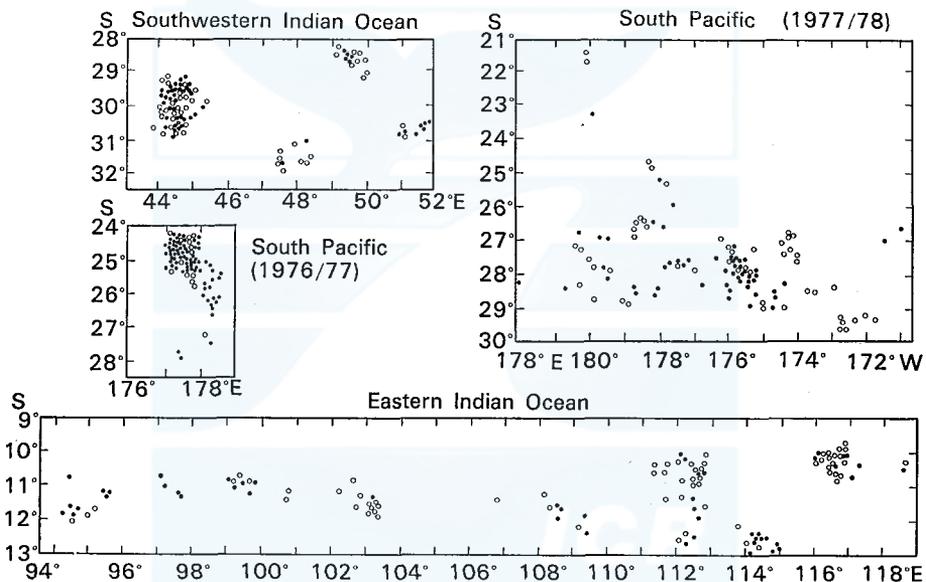


Fig. 7. Catch distribution of Bryde's whales during the seasons of 1976/77-1978/79. Filled and open circles denote the animal of filled and empty stomach respectively.

To summarize 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 bias 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 biased 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 ocellata*) 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 ocellata*) 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 ocellata*, 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 *Maurollicus 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 1st 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. From 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 ichthyophagous animals among all of the balaenopterid whales, i.e., the Bryde's whale seems to feed upon whatever the organisms of greater availability or encount-

ered 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 frequency 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 contents, 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 biased 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. diomedea*, 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. diomedea* and *T'da tricupidata* 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 ichthyofauna 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 fullness, 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 thousands 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 equatorial 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 (Wyrтки, 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 fairly 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. diomedae* 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 Bryde'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 sporadically 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 primary 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. diomedae*, *E. recurva*, *E. sibogae*, *P. latifrons*, and *T'da tricuspidata* may be referred to as the distinct swarm-forming species. Among these members, at least *T'da tricuspidata*, *P. latifrons* and *E. diomedae* 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	2	1	3			3	6	6	3		3	12	
10						2						9					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						

* one stomach by fish food is included.

* one stomach by fish food is included.

** two stomachs by fish food are included.