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 developped 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

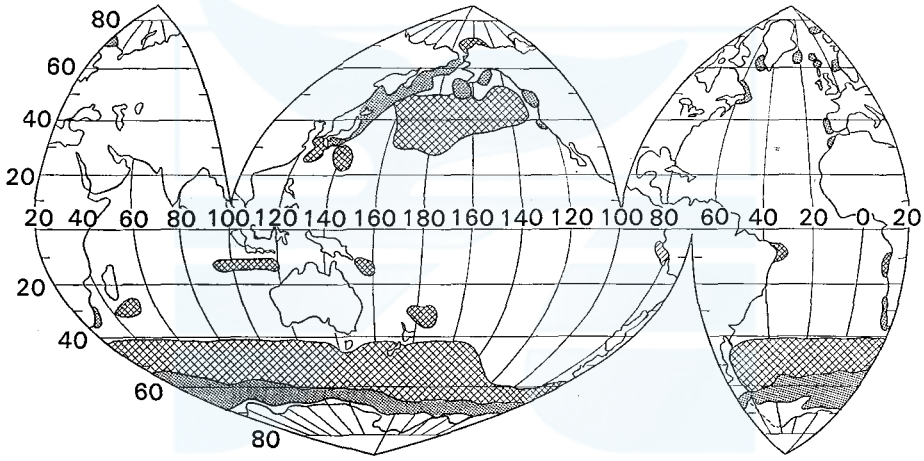

Fig. 1. World whaling grounds for mainly rorquals. The original figure by Mackintosh (1965, Fig. 7) to which recent and some past principal occupations of whaling grounds for sei and Bryde's whales are additionally demonstrated by mesh. The whaling grounds in the mid-latitude offshore waters indicate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

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.

To meet on to their nutritional requirements the baleen whale developed a

quite characteristic apparatus—the baleen plates or whalebone. The sub-triangular 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	Hump-back	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.

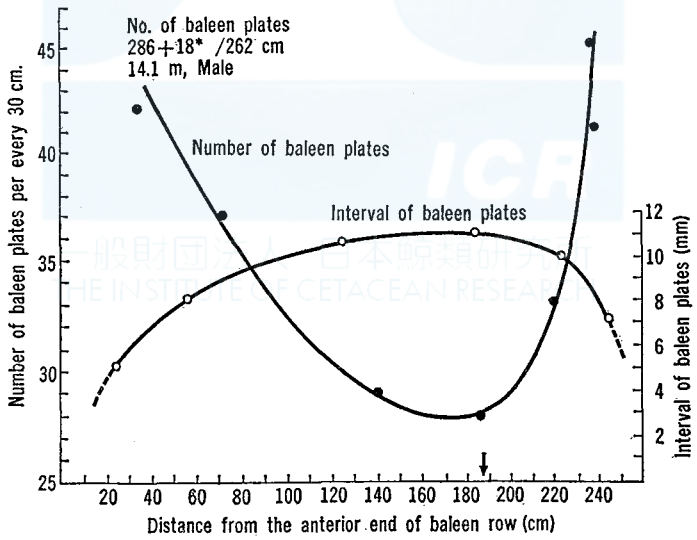

Fig. 2. Variation of the number of baleen plates in sei whale. Arrow shows the spot where maximum length of baleen plates was found (Kawamura, 1974). (* fringes)

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

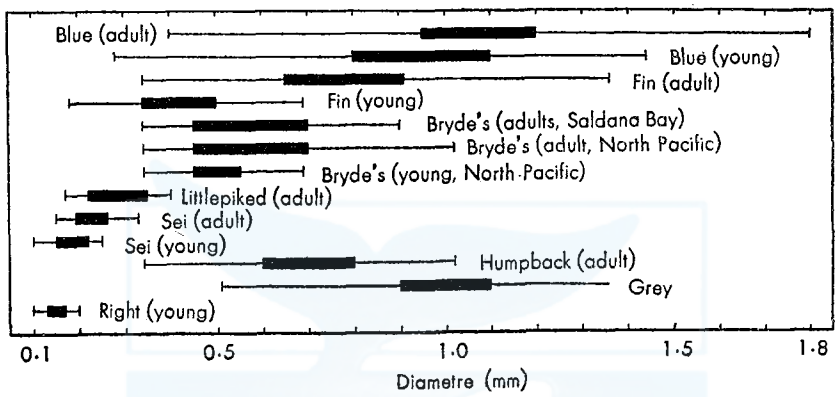

Fig. 3. Diameters of baleen fringes of baleen whales measured at the center position of baleen plates. Black belts show the ranges of dominant sizes of baleen fringes. Adult: whales after the sexual maturity, Young: sexually immature and baleen plates are not chipped (Nemoto, 1959).

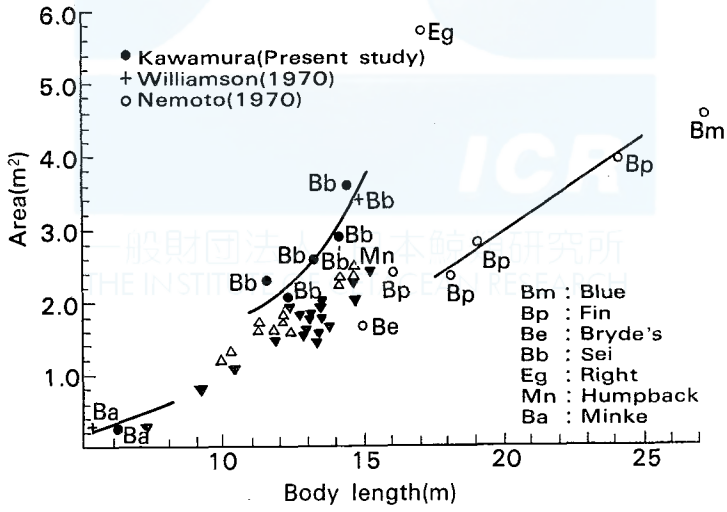

Fig. 4. Total baleen filter area in baleen whales (Kawamura, 1974). Both filled and open triangles show the filter area for the Bryde's whales in the North Pacific and southern oceans respectively (Kawamura, 1978a).

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 dis-

tance 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				
	Blue[1]	Fin	Sei[2]	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*, Nototheni ramsayi, Paralepis* sp., *Tetroganurus curvieri, Lepidotus candatus, Protomyctophum normani, Xenocytus 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	*Calanus tonsus*		*Calanus simillimus*		*Drepanopus pectinatus*		*Euphausia lucens*		*Euphausia vallentini*		*Euphausia superba*		*Euphausia diomedeae*		*Parathemisto gaudichaudii*		*Notolepis coatsi*	
II	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 1964-V	M 164	167	331	50	390	653	1043	37
		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)]	Humpback[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, *Sphenis-cus 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

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

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-

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-

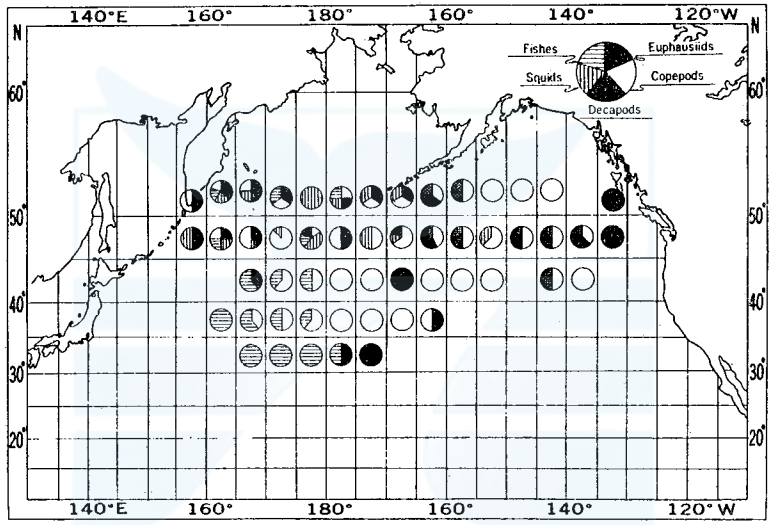

Fig. 6. Approximate occurrence of food organisms of baleen whales in terms of percentage figures in the North Pacific (Nemoto and Kawamura, 1977).

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: *Tarrella 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

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.

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

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"
Arctic[2]	Bear Island		—	—	+	—	—	—	especially in autumn
	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)

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.

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).

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.

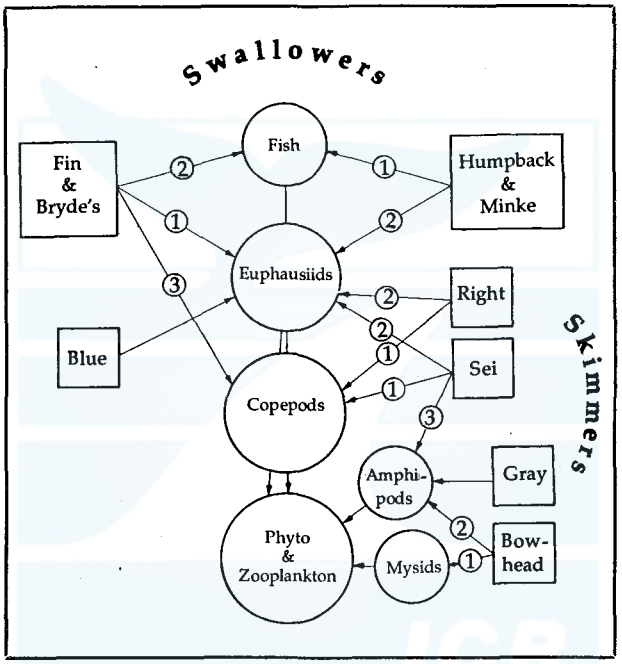

Fig. 7. Schematic food web showing predation by "swallowing" and "skimming" baleen whales on main food sources (Mitchell, 1974).

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 (Ser-

geant 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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REFERENCES

ABE, T. 1957. Notes on fishes from the stomachs of whales taken in the Antarctic. I. *Xenocyttus nemotoi*, a new genus and new species of zeomorph fish of the subfamily Oregosonimae Goode and Bean, 1895. *Sci. Rep. Whales Res. Inst.*, 12: 225–233.

BANNISTER, J. L. and A. de C. BAKER, 1967. Observations on food and feeding of baleen whales at Durban. *Norsk Hvalfangst-Tid.*, 56: 78–82.

BEALE, T. 1839. *The Natural History of the Sperm Whale.* The Holland Press, London, 393 p.

BERRY, A. J., WELLS, D. R. and C. K. NG, 1973. Bryde's whale in Malaysian seas. *Malay Nat. J.*, 26: 19–25.

BERTRAM, G.C.L. 1940. The biology of the Weddell and crabeater seals, with a study of the comparative behaviour of the pinnipedia. *Brit. Mus.* (*Nat. Hist.*) *Sci. Repts. Brit. Graham Land Exped., 1934–1937*, 1: 1–139.

BEST, P. B. 1960. Further information on Bryde's whale (*Balaenoptera edeni* Anderson) from Saldanha Bay, South Africa. *Norsk Hvalfangst-Tid.*, 49 (5): 201–215.

BEST, P. B. 1967. Distribution and feeding habits of baleen whales off the Cape Province. *Investl Rep. Div. Sea Fish. S. Afr.*, 57: 1–44.

BEST, P. B. 1977. Two allopatric forms of Bryde's whale off South Africa. *Rep. int. Whal. Commn* (*Special Issue 1*): 10–38.

BETESHEVA, E. I. 1954. [Data on the feeding of baleen whales in the Kurile region]. *Trans. Inst. Oceanogr. Acad. Sci. USSR*, 11: 238–245. (in Russian)

BETESHEVA, E. I. 1955. [Food of whalebone whales in the Kurile Islands region]. *Trans. Inst. Oceanogr. Acad. Sci. USSR*, 18: 78–85. (in Russian)

BETESHEVA, E. I. 1961. [Feeding of the common whales of the Kurile region]. *Proc. Confer. Ichthyol. Com. Acad. Sci. USSR*, 12: 104–111. (in Russian)

BRODIE, P. F., D. D. SAMEOTO and R. W. SHELDON, 1978. Population densities of euphausiids off Nova Scotia as indicated by net samples, whale stomach contents, and sonar. *Limnol. Oceanogr.*, 23 (6): 1264–1267.

BROWN, S. G. 1968. Feeding of sei whales at South Georgia. *Norsk Hvalfangst-Tid.*, 57 (6): 118–125.

BUDYLENKO, G. A. 1978. On sei whale feeding in the Southern Ocean. *Rep. int. Whal. Commn.* 28: 379–385.

CHITTLEBOROUGH, R. G. 1959. Balaenoptera Brydei Olsen on the West Coast of Australia. *Norsk Hvalfangst-Tid.*, 48 (2): 62–66.

CHRISTENSEN, I. 1975. Preliminary report on the Norwegian fishery for small whales: Expansion of Norwegian whaling to Arctic and Northwest Atlantic waters, and Norwegian investigations of the biology

of small whales. *J. Fish. Res. Bd. Can.* 32 (7): 1083–1094.

CLARKE, R. and A. AGUAYO, L. 1965. Bryde's whale in the Southeast Pacific. *Norsk Hvalfangst-Tid.*, 54 (7): 141–148.

COLLETT, R. 1886. On the external characters of Rudolphi's rorqual (*Balaenoptera borealis*). *Proc. Zool. Soc. London*, XVIII: 243–265.

DALL, W. and DUNSTAN, D. 1957. *Euphausia superba* Dana from a humpback whale, *Megaptera nodosa* (Bon naterre), caught off southern Queensland. *Norsk Hvalfangst-Tid.*, 46 (1): 6–9.

DAWBIN, W. H. 1956. The migrations of humpback whales which pass the New Zealand coast. *Trans. roy. Soc. N.Z.*, 84 (1): 147–196.

DOI, T., OHSUMI, S. and T. NEMOTO, 1967. Population assessment of sei whales in the Antarctic. *Norsk Hvalfangst-Tid.*, 56 (2): 25–41.

DOROSHENKO, N. V. 1978. [Biology of *Balaenoptera acutorostrata* Lacépède 1804 in southern hemisphere]. Abstract of master's thesis, 03.00.08 Zoology. Biology. Pedology Inst., Far Eastern Center, Vladivostok: 3–21.

EARLE, S. A. 1979. Feeding behavior of humpback whales. Abstracts of papers, Committee F, Section FIII, XIV Pacific Science Congr., Khabarovsk, USSR: 129.

GAMBELL, R. 1968. Seasonal cycles and reproduction in sei whales of the southern hemisphere. *Discovery Reports*, 35: 31–134.

GAMBELL, R., BEST, P. B. and D. W. RICE, 1974. Report on the international Indian Ocean whale marking cruise, 24 November 1973–3 February 1974. *IWC/SC/26/37.*

GASKIN, D. E. 1976. The evolution, zoogeography and ecology of cetacea. *Oceanogr. Mar. Biol. Ann. Rev.*, 14: 247–346.

HERDMAN, W. A. Sir, 1971. *Founders of Oceanography and Their Work.* Transl. by K. Hidaka, Tokai Univ. Press, Tokyo, 315 p.

HINTON, M.A.C. 1925. *Reports on papers left by the late Major G.E.H. Barrett-Hamilton relating to the whales of South Georgia.* The Crown Agents for the Colonies, London: 57–209.

HJORT, J. 1933. Whales and whaling. *Hvalradets Skr.*, 7: 7–29.

HJORT, J. and J. T. RUUD, 1929. Whaling and fishing in the North Atlantic. *Rapp. Proc. Verb., Conseil. Intern. Explor. Mer*, 56 (1): 1–123.

HOLLIS, E. H. 1939. Biological report of the United States Bureau of Fisheries. Food and parasites of whales collected during the season 1937–1938. *Norsk Hvalfangst-Tid.*, 1: 13–17.

INGEBRIGTSEN, A. 1929. Whales caught in the North Atlantic and other seas. *Rapp. Explor. Mer.*, LVI (27): 1–26.

IVASHIN, M. V. *et al.* 1972. *Zool. Zh.*, 51: 1715–1723. (Cited from Gaskin, 1976).

JONSGÅRD, Å. 1951. Studies on the little piked whale or minke whale (*Balaenoptera acuto-rostrata* Lacépède). Report on Norwegian investigations carried out in the years 1943–1950. *Norsk Hvalfangst-Tid.*, 40: 209–232.

JONSGÅRD, Å. 1966. The distribution of Balaenopteridae in the North Atlantic Ocean. *In*: K. S. Norris (ed.), *Whales, Dolphins, and Porpoises.* Univ. Calif. Press, Berkeley and Los Angeles, 789 p.

JONSGÅRD, Å. and I. CHRISTENSEN, 1968. A preliminary report on the "Harøybuen" cruise in 1968. *Norsk Hvalfangst-Tid.*, 57: 174–175.

JURASZ, C. M. and V. P. JURASZ, 1979. Feeding modes of the humpback whale, *Megaptera novaeangliae*, in Southeast Alaska. *Sci. Rep. Whales Res. Inst.*, 31: 69–83.

KAWAKAMI, T., HAMABE, M. and R. SAITO, 1973. A preliminary note on the ecology of the Ommastrephid squid *Nototodarus sloani sloani* (Gray) in New Zealand waters-II. *Bull. Tokai. Reg. Fish. Res. Lab.*, 76: 53–69.

KAWAKAMI, T. 1976. The fishery biological study on a squid, *Nototodarus sloani sloani* (Gray), in the New Zealand waters. *Bull. Tokai Reg. Fish. Res. Lab.*, 85: 31–104.

KAWAMURA, A. 1970. Food of sei whale taken by Japanese whaling expeditions in the Antarctic season 1967/68. *Sci. Rep. Whales Res. Inst.*, 22, 127–152.

KAWAMURA, A. 1972. [The position of marine mammals in the marine food chains]. *The Heredity*, 26 (11): 21–31. (in Japanese)

KAWAMURA, A. 1973. Food and feeding of sei whale caught in the waters south of 40°N in the North Pacific. *Sci. Rep. Whales Res. Inst.*, 25: 219–236.

KAWAMURA, A. 1974. Food and feeding ecology in the southern sei whale. *Sci. Rep. Whales Res. Inst.*, 26: 25–144.

KAWAMURA, A. 1975. A consideration on an available source of energy and its cost for locomotion in fin whales with special reference to the seasonal migrations. *Sci. Rep. Whales Res. Inst.*, 27: 61–79.

KAWAMURA, A. 1977. On the food of Bryde's whales caught in the South Pacific and Indian Oceans. *Sci. Rep. Whales Res. Inst.*, 29: 49–58.

KAWAMURA, A. 1978a. On the baleen filter area in the South Pacific Bryde's whales. *Sci. Rep. Whales Res. Inst.*, 30: 291–300.

KAWAMURA, A. 1978b. An interim consideration on a possible interspecific relation in southern baleen whales from the viewpoint of their food habits. *Rep. int. Whal. Commn* 28: 411–419.

KAWAMURA, A. 1980. Food habits of the Bryde's whales taken in the South Pacific and Indian oceans. *Sci. Rep. Whales Res. Inst*,. 32: 1-23.

KAWAMURA, A. and T. KIKUNO, 1980. [On the size composition of *Euphausia superba* that fed by the Antarctic minke whale]. *Geiken Tushin*, 334: 23–34. (in Japanese).

KELLOG, R. 1929. What is known of the migrations of some of the whalebone whales. *Annual Rep. Smithsonian Institution*, 1928.: 467–494.

KLUMOV, S. K. 1961. Plankton and the feeding of the whalebone whales (Mystacoceti). *Trudy Inst. Okeanol.*, 51: 142–156.

KLUMOV, S. K. 1963. Feeding and helminth fauna of whalebone whales (Mystacoceti). *Trudy Inst. Okeanol..*, 71: 94–194.

LAWS, R. M. 1977. Seals and whales of the Southern Ocean. *Phil. Trans. R. Soc. Lond. B.* 279: 81–96.

LIPPS, J. H. and E. MITCHELL, 1976. Trophic model for the adaptive radiations and extinctions of pelagic marine mammals. *Paleobiology*, 2 (2): 147–155.

LOWRY, L. F., Frost, K. J. and J. J. Burns, 1978. Food of ringed seals and bowhead whales near Point Barrow, Alaska. *Canadian Field-Naturalist*, 92 (1): 67–70.

LYTHGOE, J. & G. 1971. *Fishers of the sea.* Blandford Press, London, 320 p.

MACKINTOSH, N. A. 1942. The southern stocks of whalebone whales. *Discovery Reports*, 22: 197–300.

MACKINTOSH, N. A. 1965. *The Stocks of Whales.* Fishing News (Books) Ltd., London, 232 p.

MACKINTOSH, N. A. and J.F.G. WHEELER, 1929. Southern blue and fin whales. *Discovery Reports*, 1: 257–540.

MARR, J. 1962. The natural history and geography of the Antarctic krill (*Euphausia superba* Dana). *Discovery Reports*, 32: 33–464.

MATTHEWS, L. H. 1932. Lobster krill. *Discovery Reports*, 5: 467–484.

MATTHEWS, L. H. 1937. The humpback whale, *Megaptera nodosa*.. *Discovery Reports*, 17: 7–92.

MATTHEWS, L. H. 1938a. The sei whale, *Balaenoptera borealis*. *Discovery Reports*, 17: 183–290.

MATTHEWS, L. H. 1938b. Notes on the southern right whale, *Eubalaena australis*. *Discovery Reports*, 17: 169–182.

MATUURA, Y. and K. MAEDA, 1942. [Biological investigations of whales from the northern Pacific. The right whale]. Hogei Shiryo, 9: 44–45. (in Japanese).

MILLAIS, J. G. 1906. *The Mammals of Great Britain and Ireland.* Longmans, London, 384 p. (Cited from Gaskin, 1976).

MILLAIS, J. G. 1973. From Placentia Bay to Spitzbergen: A naturalist aboard a North Atlantic whaler. *Nature Canada*, 2 (4): 4–8.

MITCHELL, E. 1973. Draft report on humpback whales taken under special scientific permit by eastern Canadian land stations, 1969–1971. *Twenty-Third Report of the Commission, IWC, London:* 138–154.

MITCHELL, E. 1974. Trophic relationships and competition for food in Northwest Atlantic whales. *In*: Burt, M.D.B. (ed.), *Proc. Canadian Soc. Zoologists. Ann. Meet.*, 123–133.

MIZUE, K. 1951. Food of whales (In the adjacent waters of Japan). *Sci. Rep. Whales Res. Inst.*, 5: 81–90.

NEMOTO, T. 1957. Food of baleen whales in the northern Pacific. *Sci. Rep. Whales Res. Inst.*, 12: 33–89.

NEMOTO, T. 1959. Food of baleen whales with reference to whale movements. *Sci. Rep. Whales Res. Inst.*,

14: 149–290.

NEMOTO, T. 1962. Food of baleen whales collected recent Japanese Antarctic whaling expeditions. *Sci. Rep. Whales Res. Inst.*, 16: 89–103.

NEMOTO, T. 1970. Feeding pattern of baleen whales in the ocean. *In*: J. H. Steele (ed.) *Marine Food Chains*, Univ. Calif. Press, Berkeley and Los Angeles, 552 p.

NEMOTO, T. and A. KAWAMURA, 1977. Characteristics of food habits and distribution of baleen whales with special reference to the abundance of North Pacific sei and Bryde's whales. *Rep. int. Whal. Commn (Special Issue 1)*: 80–87.

NISHIMOTO, S., M. TOZAWA and T. KAWAKAMI, 1952. Food of sei whales (*Balaenoptera borealis*) caught in the Bonin Island waters. *Sci. Rep. Whales Res. Inst.*, 7: 79–85.

NISHIWAKI, M. 1959. Humpback whales in Ryukyuan waters. *Sci. Rep. Whales Res. Inst.*, 14: 49–87.

OHSUMI, S. 1979a. Population study of the Bryde's whale in the southern hemisphere under scientific permit in three seasons, 1976/77–1978/79. *IWC/SC/31/Doc.* London, June.

OHSUMI, S. 1979b. Feeding habits of the minke whale in the Antarctic. *Rep. int. Whal. Commn.*, 29, S 13: 473–476.

OHSUMI, S., Y. MASAKI and A. KAWAMURA, 1970. Stock of the Antarctic minke whale. *Sci. Rep. Whales Res. Inst.*, 22: 75–125.

OLSEN, Ø. 1913. On the external characters and biology of Bryde's whale (*Balaenoptera brydei*), a new rorqual from the coast of South Africa. *Proc. Zool. Soc. London*, 1073–1090.

OMURA, H. 1958. North Pacific right whale. *Sci. Rep. Whales Res. Inst.*, 13: 1–52.

OMURA, H. 1975. Osteological study of the minke whale from the Antarctic. *Sci. Rep. Whales Res. Inst.*, 27: 1–36.

OMURA, H. 1977. Review of the occurrence of Bryde's whale in the North Pacific. *Rep. int. Whal. Commn. (Special Issue 1)*: 88–91.

OMURA, H. and H. SAKIURA, 1956. Studies on the little piked whale from the coast of Japan. *Sci. Rep. Whales Res. Inst.*, 11: 1–37.

OMURA, H., T. ICHIHARA and T. KASUYA, 1970. Osteology of pygmy blue whale with additional information on external and other characteristics. *Sci. Rep. Whales Res. Inst.*, 22: 1–27.

OMORI, M., A. KAWAMURA and Y. AIZAWA, 1972. *Sergestes similis* Hansen, its distribution and importance as food of fin and sei whales in the North Pacific Ocean. *In*: A. Y. Takenouti, Anraku, M., Banse, K., Kawamura, T., Nishizawa, S., Parsons, T. R., Tsujita, T., (ed.), *Biological Oceanography of the Northern North Pacific Ocean*. Idemitsu Shoten, Tokyo, 626 p.

OTTESTAD, P. and RUUD, J. T., 1936. (cited from Tomilin, 1967).

PAIVA, M. P. and N. F. GRANGEIRO, 1965. Biological investigations on the whaling season 1960–1963, off Northeastern coast of Brazil. *Arg. Est. Biol. Mar. Univ. Fed. Ceara, Fortaleza*, 5 (1): 29–64. (cited from Budylenko, 1978).

PAIVA, M. P. and B. F. GRANGEIRO, 1970. Investigation on the whaling seasons 1964–1967, off Northeastern coast of Brazil. *Arg. Est. Biol. Mar. Univ. Fed. Ceara, Fortaleza*, 10 (2): 111–126. (cited from Budylenko, 1978).

PERVUSHIN, A. S. 1968. Observations of behaviour and feeding of whalebone whales in the area of the Crozet Islands. *Okeanologia*, 8 (1): 139–145.

PETERS, H. 1955. Über das Vorkommen des Walkrebschens *Euphausia superba* Dana und seine Bedeutung für die Ernährung der sudlichen Bartenwale. *Arch. Fischreiwissenschaft*, 6: 288–304.

PETERS, N. (ed.) 1938. *Der neue Deutsche Walfang*. Hansa, Deutsche Nautische Zeitschrift Carl Schroedter, Humburg, 263 p.

PONOMAREVA, L. A. 1949. [On the food plankton of baleen whales in the Bering Sea]. *Doklady, Acad. Nauk, USSR*, 68 (2): 401–403. (in Russian)

RICE, D. W. 1961. Sei whales with rudimentary baleen. *Norsk Hvalfangst-Tid.*, 50 (5): 189–193.

RICE, D. W. 1977. A list of the marine mammals of the world. *NOAA Tech. Rep. NMFR, SSRF*-711: 1–15.

RICE, D. W. and WOLMAN, A. A. 1971. *The life history and ecology of the gray whale (Eschrichtius robustus)*. Amer. Soc. Mammalogists Spec. Publ., 3, 142 p.

ROBERTS, T. J. 1977. Cetacean records for Pakistan. Studies on cetaceans, Vol. VIII: 95–99.

RØRVIK, C. J., J. JÓNSSON, O. A. MATHISEN and Å. JONSGÅRD, 1976. Fin whales, *Balaenoptera physalus* (L.), off the west coast of Iceland. Distribution, segregation by length and exploitation. *Rit Fiskideildar*, 5 (5): 1–30.

RUUD, J. T. 1937. *Norsk Hvalfangst-Tid.*, 26, 193–194. (cited from Gaskin, 1976)

SALINIKOV, N. E. 1953. [Issledovaniia Kitov Antarktiki]. Investigations of whales in the Antarctic. *Trans. VNIRO*, 25: 54–67. (in Russian).

SCAMMON, C. M. 1874. *The Marine Mammals of the Northwestern Coast of North America*. Dover Publications, Inc., N.Y., 319 p. 1968. (Reprint). Originally published, John H. Carmany and Co., San Francisco, and G. P. Putnam's Sons, N.Y., 1874.

SCHMIDT-NIELSEN, K. 1972. Locomotion: Energy cost of swimming, flying, and running. *Science*, (4045): 222–228.

SCHRAM, F. R. 1977. Paleozoogeography of late Paleozoic and Triassic malacostraca. *Systematic Zool.*, 26 (4): 367–379.

SCORESBY, W. 1820. *An Account of the Arctic Regions. Vol. 2, The Whale Fishery*. Archibald Constable and Co., Edinburgh, 1820. Reprint, Redwood Press Ltd. for David & Charles (Holdings) Ltd., Newton Abbot Devon, 574 p. 1969.

SERGEANT, D. E. and W. HOEK, 1974a. Seasonal distribution of bowhead and white whales in the eastern Beaufort Sea. *In*: J. C. Reed and J. E. Sater (eds) The coast and shelf of the Beaufort Sea. The Arctic Inst. N. America, Washington: 705–719.

SERGEANT D. E. and W. HOEK, 1974b. Biology of the bowhead *Balaena mysticetus* and white whale *Delphinapterus leucas* in the Beaufort Sea. Interim Rep. Beaufort Sea Project Study A4, Victoria, B.C. 1–8.

SLEPTSOV, M. M. 1955. [Biology and fishing of whales in the Far Eastern Seas]. S. E. Kleinenberga (ed.) *Pishepromizdat*. Moskow. Japanese transl. H. Sakiura, *Gieken-Sosho*, No. 1, Whales Res. Inst., Tokyo, 51 p.

SLIJPER, E. J. 1962. *Whales*. Hutchinson & Co., London, 475 p.

SMIRNOV, N. A., 1935. (Cited from Tomilin, 1967).

TOMILIN, A. G. 1967. *Cetacea. Vol. 9, Mammals of the U.S.S.R. and adjacent countries*. Heptner, V. G. (ed.) Israel Prog. Sci. Transl., Jerusalem, 717 p.

TOWNSEND, C. H. 1935. The distribution of certain whales as shown by logbook records of American whaleships. *Zoologica*, 19 (1): 1–50.

UNESCO, 1973. *Check-list of the fishes of the North-eastern Atlantic and of the Mediterranean*. Clofnam I. J. C. Hureau & Th. Monod (ed.), Paris, 683 p.

UNESCO, 1973. *Check-list of the fishes of the North-eastern Atlantic and of the Mediterranean*. Clofnam II. J. C. Hureau & Th. Monod (ed.), Unesco, Paris, 331 p.

WATKINS, W. A. and W. E. SCHEVILL, 1976. Right whale feeding and baleen rattle. *Jour. Mamm.*, 57 (1): 58–66.

WHEELER, A. 1969. *The fishes of the British Isles and North-West Europe*. Macmillan, London, Melbourne, Tronto, 613 p.

WILLIAMSON, G. R. 1975. Minke whales off Brazil. *Sci. Rep. Whales Res. Inst.*, 27: 37–59.

YUKHOV, V. L. 1969. Observations on the cetacea in the Aden Gulf and the north-west part of the Arabian Sea. *In*: Marine Mammals, Nauka, Moscow: 327–328. (cited from Budylenko, 1978).

ZENKOVICH, B. A. 1937. [The food of the Far-Eastern whales.] *Doklady Acad. Sci. S.S.S.R.*, 16 (4): 231–234. (in Russian).