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Food and helminth fauna of whalebone whales (Mystacoceti) in the main whaling regions of the world ocean

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about the numerous investigations of Soviet scientists and the recent works published by Japanese zoologists on this problem. Hence his data are quite incomplete. Moreover, in his summary, Schubert does not present any comparative studies on the feeding of whalebone whales in various areas of the World Ocean, or any generalizations.

The majority of the works on this subject treat only of the qualitative aspect of the feeding. As a rule, the lists of the sources of food contain only the main, abundant forms. Very little attention was paid to the quantitative aspect chiefly because of some technical difficulties, since the empty stomach of a large whalebone whale, fin whale of an average size caught in whaling (18-19 m in the northern hemisphere and 20 - 22 m in the southern), weighs about one ton, and the stomach filled with food weighs sometimes about two tons. The stomach of a blue whale weighs still more. Hence the determination of the weight or volume of the food in the stomach of a whale is extremely difficult and complex, especially when working on a floating whaling base, where the dressing of a whale on a small area simply prevents the scientists from doing research of this kind.

Some other aspects of the feeding of whales also were not adequately treated. In particular, until the present, the problem has not yet been solved whether the concentration (biomass) or the "density" of the accumulation of food organisms (plankton, for instance) may be regarded as food, i.e. the food organisms sufficient enough to attract

groups of whalebone whales (or individual specimens) [95]
and to enable them to obtain food in the amount which would satisfy their need for a 24-hour period of time. True, we made theoretical estimations in this regard back in 1956 and published them in 1961 (Klumov, 1961). However, we still lack the data which would experimentally corroborate our figures.

The problem of the 24-hour-long feeding, the orientation of the whales in search for and the discovery of food aggregations of zooplankton or other food organisms on vast areas of individual regions of the ocean still have to be solved. We do not know yet how the whales behave while feeding on plankton of the highest concentration. Instrumentally, no depth has been recorded to which the whalebone whales descend while searching for food and while feeding. Many details on the interrelation in regard to the distribution of whales and their feeding grounds have to be determined. The problem pertaining to individual hunting grounds of whales, their boundaries, size, etc., still remains to be specified. In short, in the domain of the study of the feeding of whales, there are many unsolved problems, which are of great importance not only to the scientist, but which are also important from the practical viewpoint, as they determine the behavior and distribution of these animals within the foraging range.

In the present article, we do not propose to answer all the problems stated above and to fill the gaps present.

Our aim is considerably more unpretentious: we want to present, on the strength of the material at hand, a summary of the material on the food objects of whalebone whales for the main whaling areas of the World Ocean and to state a few working hypotheses and some considerations in regard to individual aspects of the ecology of their feeding. We have come to these considerations not only because of the study of some data found in literature, but mainly because of the personal observations in recent years (1951 - 1956) in the north-west of the Pacific Ocean.

In 1951, assisted by the Ministry of Fisheries of the USSR and the late P.P. Shirshov, Director of the Institute of Oceanology of the Academy of Sciences of the USSR, we organized an expedition for studying the cetaceans. For several seasons, this expedition did research in the waters near the Kuriles, on the side of the Sea of Okhotsk and on the side of the Pacific Ocean of the Kurile Range, and in the Bering Sea, first aboard the whaling vessel "Shkval" (1951) and later aboard the "Krylatka" and "Nerpa" trapping schooners of the "Dal'kitzvertrest" (at present called the Board of the Far-East Whaling Flotillas) assigned for this purpose. A.V. Lavrov, N.N. Martynov, and B.M. Yefimov, the directors of the trust mentioned above, were of great help to us.

The research workers and laboratory technicians, organized in shore detachments, investigated the sea. In addition, they observed and gathered biological material at shore whaling enterprises located on the Kurile Islands.

The participants of this expedition, including the present writer, collected vast material in regard to the qualitative composition and the feeding of the Far-East cetaceans, including the feeding of fin whale and sei whale; to a lesser extent, right ("Japanese"*) whale, blue, humpback and Minke whales (Klumov, 1956b, 1957, 1958, 1961, 1962). The treatment of the material obtained was entrusted to I.I. Akimushkin (Cephalopoda) and Ye.I. Betesheva (plankton and fish). Their work was published as follows: Akimushkin, 1954, 1955a, 1955b, 1957, etc.; Betesheva, 1954, 1955; Betesheva and Akimushkin, 1955. Yu.A. Filippova and I [96] jointly treated the collections pertaining to the feeding of Pacific right whales.

Besides taking samples on feeding (taken at shore whaling enterprises during the dressing of whales by I. Akimushkin, Ye. Betesheva, Ye. Buzinov, V. Gerasimov, V. Gudkov, G. Derviz, N. Zarenkov, I. Zelenova, Ye. Ivanova, L. Kl'ashtorin, T. Pokrovskaya, N. Sergiyenko, A. Skr'abin, V. Sokolov, S. Uspensky, Ye. Chuzhakina, by me personally, and others, the behavior of the whales in the sea was observed. Some of these** were used while preparing this paper.

A number of foreign works on the feeding of whales used in this article were translated by T.N. Pokrovskaya.

I would like to express my deepest gratitude to all those persons mentioned above, who facilitated the expedition,

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* Verbatim. Used without quotes, the species refered to is Pacific right whale. Translator.

** "samples"? "observations"? or "samples and observations"? Translator.

collected the material and passed on to me their observations.

METHODS OF STUDYING THE FEEDING OF WHALES

The distribution of the source of food for the cetaceans during the summer of foraging period, the location of places of greatest concentration, i.e. the dislocation of foraging fields, are for the most part the factors which also determine the distribution of the whales in a particular area. The knowledge of the general law and all the seasonal changes affecting the distribution of the animals serving as food for whales is the decisive factor that cuts down the unproductive time wasted in locating the whales and, in the end, in raising the efficiency of catches. This is why a detailed and thorough study of the feeding of whales and the determination of the law in regard to the distribution of food objects is a very important factor of the program on the study of the biology of these animals not only from the viewpoint of science, but also mainly from the point of view of commercial practice.

The feeding of whales should be studied systematically and the study could be divided into several stages.

The first stage provides for the study of the qualitative composition of the whales: the determination of the food objects for each species of the whales individually by geographical zones or microregions; making lists of all the animals which serve as prey for whales and singling out the basic, guide forms; establishment of the differences in the collection of prey in regard to various age (or size) and sex groups of a particular species of whale; establishment of seasonal differences in the feeding of whales. If the material for study has been collected for years, also the changes in regard to the selection of the most important sources of food (especially the guide forms) in regard to individual years should be established.

The animals used as food for whales are usually determined from the remains, and sometimes from some small fragments of their bodies. It is important to be able not only to identify the species correctly, but also to establish its size and weight. In this regard, the establishment of a standard collection is of great help. For this purpose, they preserve not only whole organisms, but also the individual parts of the latter, especially the remains which are difficult to digest (skeletons of fish and individual bones, including otoliths, beaks of squids, etc.), which quite frequently are discovered in the stomachs of whales.

Once the lists of prey are established and the guide forms of the animals used as food by individual species of whales are known, once the seasonal changes in the correlation of these forms are clarified, then the scientist will be able to turn to the second stage of his studies [97]

When the stomach and the intestines are dressed for taking samples of food, special attention should be paid to the presence of endoparasites; these should be collected and preserved for further studies. Other organs of whales, too, should be investigated: the heart, lungs, kidneys, liver, the uterus in the females, head brains, eyes, etc. The presence of helminths should be noted, and so also the degree of the infestation - the number of the endoparasites of each species in each organism- and they should be fixed.

Stage two includes the study of the quantitative aspect of the feeding of whales: the weight or volume of the stomach's content and also, if at all possible, the number of the animals eaten by the whale (the question is about large animals, such as fish, squids, etc.). They establish the correlation between individual objects of the feeding of whales in regard to volume, weight or quantity (in the latter case, the size or weight of the animal is a must, as it is impossible to compare one Pacific saury with one lancetfish). The degree of the filling of the stomach of whales caught in various areas and during various seasons of the year is examined. They also note the number of whales with empty stomachs; determine age and sex differences in the amount of the food found in the stomach. The filling of the stomachs of whales caught during various periods of the 24-hour period reveals the whales' activities during a 24-hour period and their daily norm, and also their seasonal changes.

In order to determine the 24-hour-long activity of a whale, the content of its stomach should be taken into consideration and also special observations of the feeding of the whales in the sea, on feeding grounds[1], should be made. At the same time instruments can be used to determine the depth of the whales' submersion while in search of food. P. Scholander (1940) developed a special apparatus for this purpose. A similar apparatus, but of a slightly different type (better than that of Scholander in regard to its application) was developed in the Laboratory of Marine Techniques of the Institute of Oceanology, Academy of Sciences, USSR; however, it still has to be tested.

While observing the whales on their feeding grounds, they tag them for further studies to be done later (upon the accumulation of material) in regard to the boundaries of individual "hunting sections".

Stage three of the investigations is connected with the study of the biology and the source food of itself. First of all, the boundaries and the peculiarities of prey within the foraging area of whales should be established, and so also their quantitative distribution, laws of the vertical microdivision of the biomass in the water (Klumov, 1958, 1961); conditions, causes, places and terms for the formation of accumulations; laws of seasonal changes in the life of the prey, and a number of other problems of their biology and behavior.

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1. It is desirable to conduct thoroughly representative catches of the zooplankton, to determine its composition, the depth of the distribution of the layer of maximum, and also to catch a whale while in the act of feeding, on a given feeding ground, and to compare the correlation of the composition of the plankters in regard to the species both in nature and in the whale's stomach (Klumov, 1961).

While studying the quantitative distribution of zooplankton by detailed observations of the feeding of whales on feeding grounds, the scientists determine the minimum amount of the biomass which, for whales, may be regarded as the "food biomass" (Klumov, 1958, 1961).

<u>Stage four</u> makes provisions for the establishment of food links between the whales and their food objects, the rate at which the latter are eaten by all their predators, the degree of the whalebone whales among themselves and with other animals which feed on zooplankton, and, [98]
finally, the establishment of links in regard to the distribution of the whales and the distribution of their food objects during the summer foraging season, and later during the entire annual cycle.

<u>The fifth</u> and last stage is completely independent and at the same time closely related to all the findings pertaining to the feeding of the cetaceans. The question here is about the experimental works on the physiology and reflexology of search and capture of food and on digestion, which in our country were not studied because of the lack of a technically well-equipped base even in regard to small cetaceans (dolphins).

The data on the rate of the digestability of food by the cetaceans, on their 24-hour-long activity and norm, and on many other aspects, obtained experimentally by means of a series of experiments would be absolutely reliable and could help in many ways to solve and clarify a number of very important aspects of the biology of the cetaceans.

The sequence of the enumerated five stages is generally preserved while the material is being treated. This also holds true in regard to some individual stages in research in the field, when it is possible to gather the material for all stages of field research mentioned above. Such is, in brief, our scheme of a subsequent study of the feeding of the cetaceans.

For years, while doing field research work on the study of the cetaceans in the Far East (1951-1956), we* were not able to carry out the planned research completely, as our work, for reasons beyond our control, was interrupted in 1953-1954. However, the initial stages of the planned study of the cetaceans had already been carried out and the corresponding material collected.

The material on the content of whales' stomachs was gathered at all coastal observation stations located on the Kuriles where all the captured whalebone whales were examined and average samples to be treated in laboratories were taken. In order to obtain the qualitative characteristics of the whales' feeding, the content of the stomachs was either weighed or measured volumetrically and later converted into weight units, or the food objects were counted, if they were large (fish, squids).

While taking samples of the content of whales' stomachs, we deemed it necessary to study their habitat as thoroughly as we could.

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* "We" refers to the author himself. Translator.

We organized this type of work for the first time in the expedition of 1951. Later the same techniques were used in our expeditions that followed, until the study of the whales in the Far East was completed in 1956. For years (1951 - 1956), the whole complex of elementary oceanological research (measuring the water temperature, determining the salinity, the direction and the force of currents, etc.) was studied by means of special vessels used in expeditions, according to standard horizons up to 1,000 m. Before the quantitative distribution of the food objects of the whalebone whales was studied, for years, we took pictures, once or twice, of the plankton in the areas where these whales were hunted. The plankton was taken by the standard Dzhedy* net (gauze No. 38) or an ichtyoplankton net (diameter 80 cm, gauze No. 15). In spite of the imperfection of the techniques used (Klumov, 1961) and the inability to determine accurately the vertical microdistribution of the food plankton, i.e. the horizon in which the maximum layer of the zooplankton is concentrated (Klumov, 1956b, 1958, 1961), the average data obtained for the layer 0 - 100 m allowed us to clarify, if even very roughly, the comparative distribution of the biomass of the plankton on a large area of the north-west of the Pacific Ocean. This research permitted us to determine approximately the distribution of the feeding grounds of whales, to compare the data with the seasonal distribution of fin whales and right whales, and also to compare the qualitative composition and the /99/

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* "Juday plankton net"? Translator.

quantitative correlation of individual prey within the whale's stomachs and on the feeding grounds. In some cases, these comparisons yielded interesting material and enabled us to come to interesting conclusions pertaining to the whales and their capacity to select food.

Detailed analyses of the stomach content of whales, which were carried out for several years by the mentioned expedition of the Institute of Oceanology of the Academy of Sciences of the USSR in the north-west of the Pacific Ocean, and also the investigations conducted recently by Japanese scientists (Mizue, 1954; Nishimoto, Tozawa and Kawakami, 1954; T. Nemoto, 1957, 1959, 1960; etc.) have served as a basis for a compilation of most complete lists of the food objects of whalebone whales inhabiting the northern half of the Pacific Ocean. We lack similar data on other important hunting grounds of whales in the World Ocean, such as the Antarctic and the northern half of the Atlantic Ocean (especially the latter), as nobody did there thorough research similar to ours in the northern half of the Pacific Ocean. As regards the Antarctic, there are the old materials of the Committee Discovery, insignificant material published by Japanese scientists, and some published by Soviet zoologists (Sal'nikov, 1953; Korabel'nikov, 1957). In other respects we have at our disposal only individual remarks on the feeding of whales and their source of food, information scattered in enormous literature on the description of the biology of whales and whaling. This sparseness and heterogeneity of the material has affected the incompleteness of the lists which we compiled in regard to the source of food of whalebone whales found in the northern part of the Pacific Ocean, Antarctic and the waters adjacent to it, and the Northern Atlantic.

While compiling the lists, we became confronted with the irregular knowledge of the feeding of whales not only in regard to geographical areas, but to the species ones as well. For instance, the feeding of right whales has scarcely been studied in detail; the feeding of fin whales was studied better than that of sei whales; in its turn, the feeding of the latter was studied better than that of grey whales, etc. This mixed character of the degree of the study of the feeding of whales in regard to species and geographical areas impeded greatly the comparison and the analysis of the material and caused the generalization to be preliminary, since new, more detailed data on other, earlier unexplored areas, may greatly change the conclusions made in the present paper on the basis of the known preservations and collections[1].

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1. The lists of food objects of the whalebone whales are based on the literature of our country at hand and foreign literature, and also some ~~fund~~ materials of the Institute of Oceanology of the Academy of Sciences of the USSR, Pacific Institute of Fishing and Oceanography (TINRO) and the All-Union Institute of Marine Fishing and Oceanography (VNIRO), as well as observations of individual persons.

It should be stressed that in order to compile /100/ lists of the source of food of the whalebone whales, such immense numbers of literary sources and material collections as well as observations of individual persons were used that practically it is impossible to quote the published or collected works on every food object of each individual species of the whalebone whales, as in doing so we would make the present work too wearisome. This is why we limit ourselves only to a general, far from being complete, list of the bibliography used. Only in cases when the problem treats of certain pr_ey which might be of a particular interest or doubt, the author is mentioned and reference is made to his work or observations.

All the data taken from literature, and also reports of individual persons are presented in tables, individually for each species of the whalebone whales, in the corresponding chapter.

The prey for whalebone whales is presented in a systematic order in the tables, along the ascending line, i.e. from simpler to rather more complex organisms. Food objects of some whales (fin whales and sei whales, for instance) for the northern half of the Pacific Ocean reach quite impressive numbers- about forty various animal species the majority of which are secondary as the source of food and do not play any significant role in regard to whale's feeding, as they were taken by the whales accidentally. The whales of a local pod inhabiting a certain area of the World Ocean, a certain micro-region, their "hunting ground", have their delicious food, found in abundance and typical of this area. As a rule, the number of basic food objects is small, and even in various areas of the northern half of the Pacific Ocean, it varies. This circumstance hampers the singling out of basic, guide forms of prey for a certain species of whales. Nevertheless, we have made an attempt to clarify this problem. This singling out is based upon the frequency of the occurrence of the prey in the stomachs of the whales and also upon the quantitative evaluation of this occurrence.

FEEDING OF WHALEBONE WHALES

Right Whales

Feeding

Our material on the feeding of the Pacific right whales in the northern half of the Pacific Ocean, and also the data found in literature on all the right whales in other areas were summed up and presented in detail as an independent section on the feeding of the Pacific right whales in a special work written in 1958 and published in 1962 (Klumov, 1959, 1962).

Our data indicate that in all places where right whales are found, they are noted for their capacity to select food. In the northern hemisphere -Northern Atlantic and the northern half of the Pacific Ocean-, in their distribution, the right whales are closely connected with the planktonic crustaceans of the group of Calanoida(Table 1.)

On the other hand, in the southern hemisphere, in the Antarctic waters, the right whales, like all the other whalebone whales, feed almost exclusively on Euphausia superba, which is the most abundant form of zooplankton found in the surface layer and is the basis for the life of almost all marine animals inhabiting the mentioned area of the World Ocean. Their distribution is confined to this Euphasia superba. [101] As far as other forms of zooplankton discovered in the stomachs of right whales of the southern hemisphere are concerned, only the larval stage of Munida gregaria (Grimothea) was recorded. It is true that during the entire history of the whaling of the right whales inhabiting the southern hemisphere, only a few stomachs of whales were opened and their content studied.

The main food of right whales (Eubalaena glaicalis glacialis and Balaena mysticetus) in the Northern Atlantic is Calanus finmarchicus and to a considerably lesser extent Thysanoessa inermis and pteropod mollusks Clione limacina and Limacina helicina.

Calanus finmarchicus, which in the Northern Atlantic forms 80.46% of the average-annual biomass (Zenkevich, 1947) is distributed primarily in the surface layer, 0 - 25 m, and especially in the layer of 0 - 10 m (Bogorov, 1938). It does not move vertically, to the extent of being noticed, during the summer season (this is characteristic also of the mature E. superba in the Antarctic waters!), and its volume in the surface layer remains almost unchanged during a 24-hour period.

Table 1

COMPOSITE TABLE OF FOOD OBJECTS OF RIGHT WHALES (EUBALENA* GLACIALIS) IN MAIN WHALING AREAS OF THE WORLD OCEAN

(According to Klumov, 1962)

Antarctic and adjacent regions: the waters of South Africa and Patagonia	North Atlantic	North of the Pacific Ocean
Crustaceans	Crustaceans	Crustaceans
Grimothea (post - larvae Munida gregaria	Calanus finmarchicus Thysanoessa inermis	Calanus plumchrus Calanus cristatus
		(Calanus glacialis**) (Calanus pacificus)
Euphausia superba	Mollusks, Gastropods	Parathemisto japonica Euphausia pacifica
	Clione limacina	
	Limacina helicina	

* "Eubalena"? Translator.

** In the works of all the authors involved in research previously, this species was called "Calanus finmarchicus".

Because of their enormous size, the right whales do not descend lower than to 15 - 20 m, only seldom reaching a depth of 25 m. As a rule, they are found in the 0 - 10 m layer where they also find their food. Thus, the feeding of the right whales on Calanus sp. in the northern hemisphere may be explained by two main reasons: (1) the inability of the whales to discover food and to capture prey at depths over 20 - 25 m and (2) the abundance of prey forming concentrated aggregations with an abundant biomass in the upper layer of water. Proceeding from these, in our estimation correct positions, it becomes evident why Thysanoessa inermis in the North Atlantic, which sometimes forms quite dense accumulations in the northern part of this area, is, nevertheless, a very important food component of the right whales inhabiting this area. This Euphausia usually inhabits depths of more than 25 m, rising to the surface layer only from time to time, and only for a short period of time. Incidentally, it should be noted that the average annual biomass of Euphausia 9 forms in the North Atlantic only 5.3% of the total biomass of the zooplankton (Zenkevich, 1947).

The main prey for the right whales in the [102] northern half of the Pacific Ocean are also representatives of the group Calanoida. To begin with, these are Calanus plumchrus and C. cristatus.[1] As regards the feeding of

1. B..Mednikov (1961) points out that in the north-west of the Pacific Ocean, predominant are the following three species of Calanus: C. cristatus, C. plumchrus, and Eucalanus bungii. They are sharply predominant over others and form 87.5% of the entire biomass of the zooplankton in the 0 - 50 m layer.

the Pacific right whales, we may ascertain the change of these main food components, which may be explained by the seasonal propagation of the mentioned Calanus sp. and the feeding grounds of the whales. During May - June, in the south of the Kurile waters, we discover in the stomachs of the Pacific right whales basically Calanus cristatus, which at the end of July is replaced by C. plumchrus (Table 2). However, with the advent of the whales to the north, along the Kurile Range, C. cristatus, it seems, no longer can serve as food for the Pacific right whales, as its accumulations in the waters around the northern Kurile and Commander islands still are present in July; later on, in this place, it submerges to greater depths as is the case in the area of the southern Kuriles, where the surface waters are heated considerably earlier than in the north-west of the Pacific Ocean and the south-west part of the Bering Sea. This is why C. plumchrus substitutes C. cristatus as prey for the Pacific right whales in the north of the Pacific Ocean approximately one month later than in the south- in the waters near the Japan and near the Kuriles.

There is no doubt that also the Calanus sp. of the group C. finmarchicus become important food components, especially in the north-east of the Pacific Ocean and the south-east of the Bering Sea. However, specialists on planktonology have not come to one definite conclusion as to the reality of some species of this group, their habitat, and the boundaries of their distribution in the northern half of the Pacific Ocean. Until now, the question has not been answered whether the Calanus sp. inhabiting the Bering Sea and the Sea of Okhotsk belongs to the species Calanus finmarchicus or to the species C. glacialis, which was recently identified by V.A. Yashnov (1955). Could it not be that both species of Calanus mentioned above inhabit the Bering Sea and the Sea of Okhotsk?

K.A. Brodsky, while quoting in one of his most recent works (1959, p. 1544) Yashnov's statement (the work was written in 1955) that C. glacialis was discovered in all seas in the Far East of our country, writes: "This has to be verified. We assume that even if this species should reach the seas in the Far East, it is most probably confined to the north-east of the Bering Sea and to the northern parts of the Sea of Okhotsk and the Sea of Japan". In his personal report of January 29, 1960, K.A. Brodsky wrote: "... all the specimens you have sent to me should be assigned to C. finmarchicus, and not to C. glacialis.

Is there C. glacialis in the Far East? This question should be investigated. However, judging from the data at hand, C. glacialis is restricted in its distribution only by the northern part of the Sea of Bering and, perhaps, the Sea of Okhotsk and the Sea of Japan".

In Brodsky's work published earlier (1957, p. 184), he presents a map of the distribution of C. finmarchicus containing the boundaries of the area which, according to him, is occupied by the mentioned Calanus sp. from the seas in the

Analysis of the Stomach Content in Ten Pacific (Japanese) whales Taken in the Kurile waters in 1955

Таблица 2

Table 2

Анализ содержимого желудков десяти японских китов, добытых в прикурильских водах в 1955 г.

(По Клумову, 1962) (According to Klumov, 1962)

№ п.п. / Current No.	Пол кита / Sex	Длина кита, м / Length, m	Дата добычи / Date of capture	Количественная характеристика содержимого желудка	Состав пищи / Food	Наличие гельминтов / Presence of helminth parasites	Примечание / Note
1	Самка	18,30	17 мая / May	Не исследовано / Not investigated	Проба не взята / No sample taken	Анализ не производился / Not analysed	
2	Самец	17,00	1 июня / June	Около 12 л / About 12 l	Calanus cristatus	Гельминты не обнаружены / Helminths not discovered	
3	Самка	16,30	19 июня	Около 75 л / " 75 l	То же / Ditto	То же / Ditto	
4	Самец	17,06	13 июля / July	Около 150 л	Calanus plumchrus	6 экз. Tetrabothrius ruudi / specimens	
5	Самка	17,40	22 июля	Содержимое не измерено / Not weighed	Проба не взята / No s. t.	Много Bolbosoma nipponicum в тонких кишках / Numerous ... in small intestines	
6	Самец	10,75	22 июля	То же / Ditto	Молоко и немного Calanus sp. (plumchrus?) / Milk + some	Не обнаружены / Undiscovered	
7	Самец	16,60	10 августа / August	13 л / 13 l	Calanus plumchrus, V стадия / stage	13 экз. Tetrabothrius ruudi, 10 экз. Bolbosoma nipponicum в тонких кишках / specimens ... in small intestines	Пища была только в III отделе желудка / Food present only in 3rd comp. of stomach
8	Самец	16,60	10 августа	Содержимое не измерено / Not weighed	Calanus plumchrus (основа пищевого комка), Parathemisto japonica / (prime ...)	В тонких кишках 4 и в толстых 1 экз. Bolbosoma nipponicum / in small intestines 4 & in large 1 specimen	При разделке кита желудок порезан, и количество пищи не могло быть определено / During processing, stomach cut & the amount of food could be determ.
9	Самка	11,35	11 августа	Слабое наполнение / Slightly filled	То же / Ditto	3 экз. Bolbosoma nipponicum в тонких кишках / in small intestines	Отмечено попадание гарпуна в желудок; в желудке была кровь / Harpoon struck stomach; blood in stomach
10	Самка	17,80	28 августа	То же / Ditto	Calanus plumchrus	Не обнаружены / Not discov.	
11	Самка *	11,58	23 мая 1956 г. / May	Почти пустой / Almost empty	C. plumchrus, C. pacificus **, Euphausia pacifica	То же / Ditto	
12	Самец *	12,40	30 июня 1956 г. / June	То же / Ditto	C. plumchrus, C. cristatus, C. pacificus **	» »	

* Киты № 11 и 12 добыты японцами; данные взяты из работы Х. Омура (1957).

Whales No. 11 & 12 taken by japanese; data taken from H. Omura's work (1957)

** Омура (1957) называет этих калянусов — C. finmarchicus. Однако, судя по месту убоя этих китов (см. текст), это могли быть только C. pacificus.

Omura (1957) calls them ... however, judging from the place where these whales were killed (see text), these could be only C. pacificus.

Far East. This area, according to K.A. Brodsky, encompasses the entire north of the Sea of Bering, north of 60° n.lat.; then, proceeding southward, it sharply decreases and occupies only a narrow coastal strip along the Koryak coast and the eastern coast of Kamchatka, the Sea of [104] Okhotsk, and the northern part of the Sea of Japan (Fig. 1).

In the waters near the Kuriles, judging from the data in this map, C. finmarchicus is absent, as it is the case also in the south-east of the Bering Sea, where during two years (1955 and 1956) we found large aggregations of the crustaceans of this group (superspecies, Yashnov, 1955), during winter months, as will be stated later.

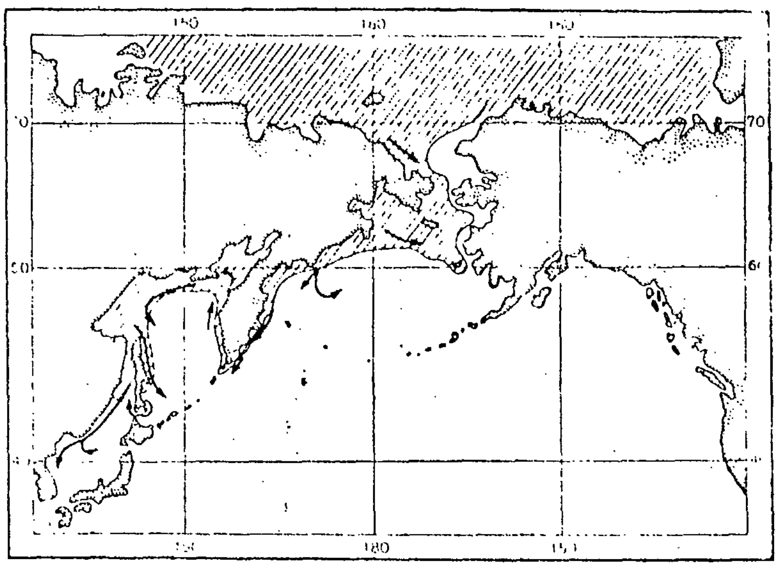

Рис. 1. Область распространения Calanus finmarchicus (заштрихована) в массовом количестве. Стрелками показано направление холодных течений (по К. А. Бродскому, 1957)

Fig. 1. Area of distribution of abundant Calanus finmarchicus (shaded). Arrows indicate the movement of cold currents (after K.A. Brodsky, 1957).

V.G. Bogorov and M.Ye. Vinogradov (1960), using the research carried out aboard the "Vit'az'" as a basis and supporting Brodsky's idea that *C. finmarchicus* does occur only in the coastal areas, present a map on the distribution of this *Calanus* sp. in the waters near the Kuriles, recording its presence along almost the entire range, from the southern termination of Kamchatka to Boussole Strait inclusively. The authors mentioned above state that the southern boundary of the distribution of *C. finmarchus* runs through Boussole Strait and that this species does not run beyond that boundary. However, Z. Nakai, noted Japanese expert on plankton (1954), writes that aggregations of *C. finmarchicus* are found "...almost everywhere in the coastal waters of Japan...". In their work on the plankton in the north-west of the Pacific Ocean (spring, 1958), R. Marumo, M. Kiota, and O. Asaoka, Japanese scientists, indicate (1960) that *C. helgolandicus* occurred constantly on a large area east of the coasts of the northern part of Honshu Island and the eastern shores of Hokhaido Island, approximately 140 to 165° e.long and 35 to 52° n.lat. in a number sometimes exceeding 250 specimens per 1 cu.m. Similar indications about the presence of *C. finmarchicus* and *C. helgolandicus* in the waters around Japan and the north-west of the Pacific Ocean are found in works of Japanese planktonologists.

K.A. Brodsky, however, states (oral report) that [105] the Japanese planktonologists definitely committed an error in regard to the classification as *C. helgolandicus* does not occur in the Pacific Ocean, while *C. finmarchicus* is a poikilothermic animal and cannot migrate as far south, to the shores of Japan, where the temperature of the water surface during spring and summer, acording to the data of our expedition, is 17 - 20, and even 27°C. All this area of the Pacific Ocean, according to K.A. Brodsky, is inhabited by another form of Calanus, namely C. pacificus which in its morphological characters is close to C. finmarchicus..

V.A. Yashnov (oral report), while agreeing with the idea that the south of the northern half of the Pacific Ocean is inhabited by C. pacificus, considers at the same time that this species is a vicariate of the North-Atlantic C. helgolandicus, which it resembles in many respects. This is why, says V.A. Yashnov, the Japanese scientists mistake C. pacificus for C. helgolandicus. As regards the distribution boundaries of C. finmarchicus, V.A. Yashnov quite convincingly proves its absence in the northern half of the Pacific Ocean and the terminal seas. The actual data gathered in the North Atlantic aboard the expedition vessel "Mikhail Lomonosov" and treated by V.A. Yashnov reveal that C. finmarchicus is a surface, boreal, but by no menas a poikilothermic form, contrary to the abyssal, Arctic (poikilothermic) C. glacialis, which is distributed north of the convergence zone. Contrary to C. glacialis, C. finmarchicus is distributed in the zone south of the convergence zone, and also in the Gulf Stream zone; it also penetrates into the Barents Sea. It is likely that it is carried by the currents into the Kara Sea, where it dies, apparently, within a very short period of time (Yashnov, 1961, Fig. 2, 3). According to Yashnov, C. glacialis, an Arctic form widely distributed in the Arctic Sea, found its way to the Pacific Ocean through Bering Strait. From the Bering Sea, this Calanus sp. spread south only along the system of cold currents, which, as is generally known, move, on the whole, along the shores of Asia and the Kurile-Island-arch. It is namely this circumstance used by V.A. Yashnov for explaining the distribution of Calanus glacialis via a comparatively narrow strip along the western shores of the Bering Sea, the Sea of Okhotsk, and the northern part of the Sea of Japan, and also the Kurile Range, including Boussole Strait. Consequently, all the points mentioned earlier by scientists as places where C. finmarchicus occurred should be assigned to C. glacialis, and the points noted by Japanese planktonologists for C. helgolandicus and partly C. finmarchicus (Nakai, 1954, etc.) should be ascribed to the occurrence places of C. pacificus. The latter remark, excepting the data by K.A. Brodsky and V.A. Yashnov, is confirmed also by other investigations, in particular, by the investigations and materials collected by the "Vit'az'" and treated by V.G. Bogorov, M.Ye. Vinogradov, Ye.A. Lubny-Gertsyk, and other scientists.

C. pacificus is discovered in small numbers up to the Aleutian Islands and the southern part of the Bering Sea, to which places it is transported by the currents, although here it does not live long and, no doubt, does not multiply.

The penetration of C. finmarchicus from the North Atlantic into the Pacific Ocean, via the basin of the Arctic Ocean is impossible, according to V.A. Yashnov, because of the natural temperature barrier, as this form is boreal.

Thus, in summing up all the contradictory viewpoints in regard to the distribution of the Calanus sp. of the group Calanus finmarchicus in the northern half of the Pacific Ocean, we should agree with V.A. Yashnov and K.A. Brodsky and consider that: [107]

a) C. finmarchicus and C. helgolandicus are absent in the waters of the northern half of the Pacific Ocean;

b) C. glacialis inhabits the northern part of the Bering Sea and the coastal zones of the Bering Sea, the Sea of Okhotsk, and the northern part of the Sea of Japan, and also a comparatively narrow strip of the Kurile waters on both sides along the Kurile Range to Boussole Strait inclusively, within the zone of cold currents;

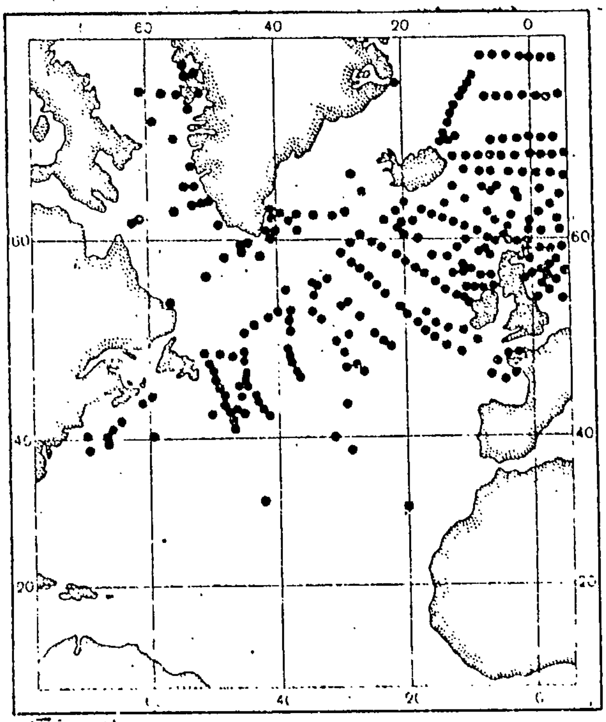

Fig.2. Рис. 2. Распространение Calanus finmarchicus s. str. в Северной Атлантике (по В. А. Яшнову, 1961)

Fig.2. Distribution of Calanus finmarchicus s.str. in North Atlantic (After V.A. Yashnov, 1961).

c) C. pacificus inhabits the southern part of the northern half of the Pacific Ocean, reaching in its extent the north of the Aleutian Islands and the south of the Bering Sea, to which places it probably is being carried by warm currents, where it, apparently, dies (the termination of its range of distribution).

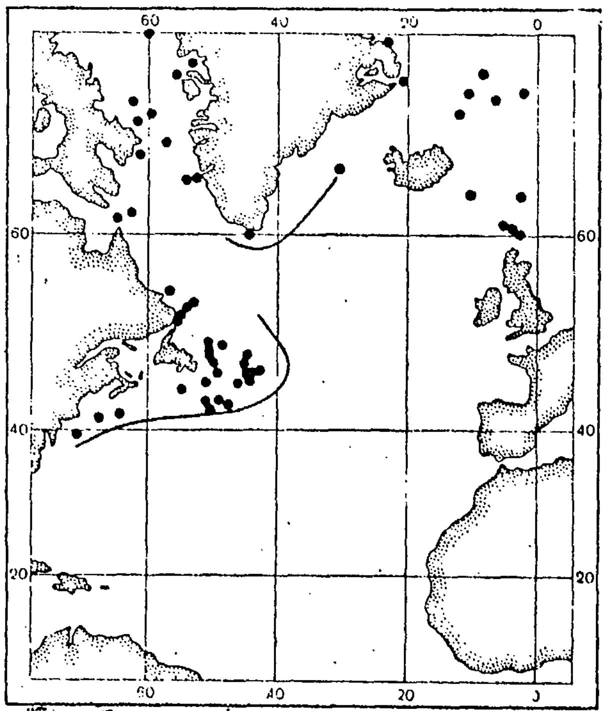

Fig. 3
Рис. 3. Распространение Calanus glacialis в Северной Атлантике. Тонкие линии — зоны конвергенции (по В. А. Яшнову, 1961)

Fig. 3. Distribution of Calanus glacialis in North Atlantic. Thin lines indicate convergence zones (according to V.A. Yashnov, 1961).

Having considered the above-said, we attempted to compile a schematic map on the distribution of the mentioned Calanus sp. We realise that it is only preliminary and should be supplemented and verified (Fig. 4). Nevertheless, it may be used as a guide.

In spite of the specifications made, two questions still remain to be clarified:

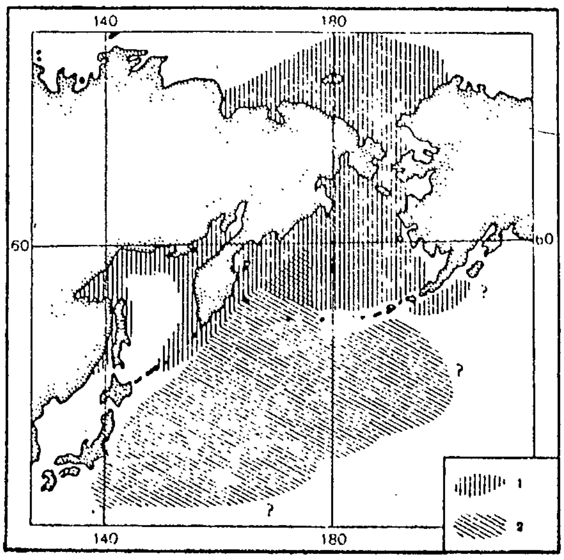

Рис. 4. Схема распространения Calanus glacialis (1) и Calanus pacificus (2) в северной половине Тихого океана (ориг.)

Fig. 4. Distribution of Calanus glacialis (1) and Calanus pacificus (2) in the northern half of the Pacific Ocean (orig.).

1. Our observations (Klumov, 1957) indicate that the ice which is formed during the winter in the northern half of the Sea of Okhotsk, due to an essential annual wind condition, is carried out into the Pacific Ocean during the spring (April - May, and even in June when the weather stays cold for a long period), via the Kurile straits Boussole, Vries, and Catherine. Quite frequently, this ice reaches also the Pacific coast of Hokkaido Island along its entire extent. Here this ice is joined by the ice formed during the winter in Izmena Strait (Kunashir Island) and along the northern coast of Hokkaido Island, which also is being floated into the Pacific Ocean via Izmona and Nemuro straits.

During severe winters, when a powerful ice sheet [108] is formed in the Sea of Okhotsk (for instance, in the winter of 1955/56), the ice fields and crushed ice were carried out in large amounts to the Pacific Ocean via the southern Kurile straits. They were noticed there by the crews of the second whaling flotilla in April and May, 1956. This crushed ice and ice fields covered sometimes the ocean surface some 30 - 40 miles long and 5 - 8 miles wide, i.e. they occupied an area of 150 - 300 sq. miles; there were several similar areas covered with ice sheets in the southern waters near the Kuriles.

The ice which is carried from the Sea of Okhotsk into the ocean chills a narrow local strip of the ocean, if even for a short period of time (1.5 - 2 months). It is only natural to assume that planktonic organisms, including *C. glacialis*, may be carried out with ice into the Pacific Ocean. However, this species cannot live long in the area of the Pacific Ocean, as the environment here does not correspond to the ecological requirements of this animal. It is difficult to imagine that this crustacean might form large aggregations in this new zone. Most probably one might discover here only individual "spots" or scanty specimens.

From the above-said, it is very difficult to solve the problem: What is then "*Calanus finmarchicus*" which was extracted by the Japanese scientists from the stomachs of two right whales (Pacific right whales) caught in the Pacific Ocean about 200 miles east of the shores of Hokkaido Islands, 39 - 41° latitude (Omura, 1957)? K.A. Brodsky is, most probably, right (oral report) in considering that, judging from the place where those two whales were caught, it must have been *Calanus pacificus*. Considering our observations of the ice carried out from the Sea of Okhotsk into the Pacific Ocean, into the zone adjacent to the southern Kuriles and Hokkaido Island, and also the possibility that *C. glacialis* might be carried out with it, we have included into our table on the feeding of right whales also both *Calanus* species mentioned above. However, since the feeding of the Pacific right whales on these *Calanus* sp. has documentally not been substantiated, their names in Table 1 appear in brackets, although we personally do not have any doubts that during a certain time of the year both these *Calanus* forms serve as prey for the right whales inhabiting the northern half of the Pacific Ocean, and form, along with *C. cristatus* and *C. plumchrus*, the main food of these huge animals.

2. As already mentioned, K.A. Brodsky (1957, 1959) does not indicate the presence of *C. finmarchicus* or *C. glacialis* for the south-east of the Bering Sea. However, while doing research aboard the expedition vessel "Nerpa" (summer and fall, 1955 and 1956, in the south-east of the Bering Sea, in the area located between the islands of the Pribylov and Aleutian ranges, about 170° w.lon.), we discovered in August-October aggregations of *Calanus* sp. Upon our request, this *Calanus* sp. was identified by Brodsky as *C. finmarchicus*.

V.A. Yashnov told us that the material on the plankton from the south-east of the Bering Sea had never been studied by Russian and Soviet scientists and that our collections of plankton are the first from that most interesting area. V.A. Yahsnov also stated that there are no reasons whatsoever to doubt the accuracy of the identifications of this material by K.A. Brodsky. However, he does not admit even the thought of the fact that *C. finmarchicus* might have penetrated into the Pacific Ocean and become localized only in the south-east of the Bering Sea, forming there annual aggregations with the average biomass for [109] the 0 - 100 m layer, as we had established it, about 500 mg/cu.m.*

The fact that the aggregations of *Calanus* sp. in the mentioned area are annual (although subject to annual oscillations of the biomass) is corroborated by the following observations.

At first we mentioned that the right whales possess a definite capacity to select their food, preferring in the northern hemisphere the Calanoida to all the other food objects. Our data indicate (Klumov, 1959, 1962), that, in their spread, the (Pacific) right whales are connected first of all with the presence of mass aggregations of *Calanus* sp. (*Calanus cristatus*, *C. plumchrus*, *C. glacialis*, and *C. pacificus*).

Townsend (1935), using the treatment of the log-books of the American whaling vessels for 1785 - 1913, i.e. 128 years, as a basis, has compiled a map of the killing of right whales according to months. We have selected the data on three months (August - October) (Fig. 5).

Thus, the areas with aggregations of the calanids we discovered in the south-east of the Bering Sea are also the places where the Pacific right whales have been distributed for almost the past two centuries. On the other hand, constant observations of right whales near 170° w.lon. between the Aleutian Range and the Pribylov Islands in fall (August-October) bears witness, no doubt, to the fact that the

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* I would like to express my gratitude to K.A. Brodsky and V.A. Yashnov for the identification of the material on the ~~on the~~ calanids and the consultation on the problem regarding the distribution of this interesting group located in the Pacific Ocean.

aggregations of the calanids here are formed every year, they exist a long time, and are confined to certain places, i.e. they are important locally.* This mutual corroboration makes the facts presented authentic indeed.

Having considered the abovesaid, Calanus glacialis should be included in the list of the food of the Pacific right whale as a presumable prey, as we lack the actual substantiation of this fact.

While dealing with this topic, we would like to draw the attention of our readers to the conservatism of right whales, which, apparently, is common to all the cetaceans.

As a result of extremely intensified whaling, the right whales near the shores of the North-American continent were almost completely destroyed back at the end of the past century. At the beginning of the twentieth century, the population of the right whales practically did not exist. By

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* It should be stressed that the initial cause of annual aggregations of the calanids in the area described are the hydrological conditions, which facilitate the annual development of the mentioned crustaceans. Apparently, in this zone, between the Pribylov and the Aleutian islands, the chilled water rich in biogenic elements rises. The origin of this water is still unknown, i.e. we do not know yet whether it comes from the Chukchi Sea or has as its origin natural bottom, rising to the surface as a result of a vertical circulation.

that time, there might have been some twenty to thirty animals. Unprofitable hunting, and then the decree prohibiting [111] the killing of these whales (the international agreement in 1936) facilitated the preservation of the animals which still remained. The population began to increase very slowly. At the present time, the population of the American right whales still remains small. Since the enforcement of the decree, a few generations came into being. However, the character of their migration, their feeding grounds, judging from Townsend's (1935) and Omura's maps (1958), and also from the data by Gilmore (1956), have not changed. The "unconditioned reflex of place" (Klumov, 1955) regulates as ever the behavior and movement of these whales, as seen from the actual data (see Fig. 5, 7).

According to Gilmore (1956), the wintering grounds of the right whales of the American population have become reduced. Now they do not reach 20° n.lat. in the south, as was the case in the nineteenth century. From our point of view, however, this fact may be explained by the small number of the population.

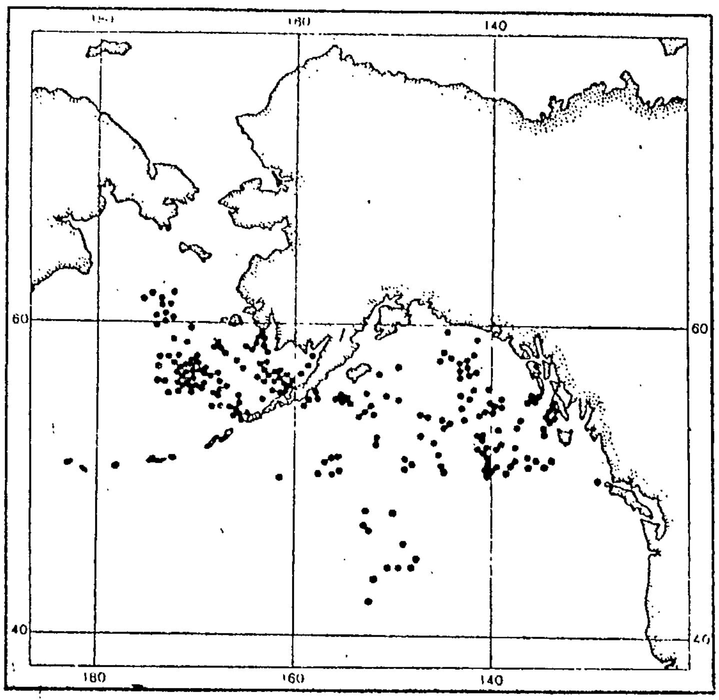

Рис. 5. Распределение добычи гладких (японских) китов в августе, сентябре и октябре за 128 лет (1785—1913 гг.). По Таунсенду (1935)

Fig. 5. Distribution of catches of Pacific right whales in August, September and October during 128 years (1785 - 1913). After Townsend (1935).

The quantitative characteristics of the feeding of the right whales of the southern hemisphere and North Atlantic are lacking, and no data are found in literature on this problem. As regards the right whales of the northern half of the Pacific Ocean, the material we collected indicates that the maximum volume of food discovered in the stomach of a Pacific right whale was 150 l of C. plumchrus. None of the ten Pacific right whales captured (Klumov, 1959, 1962) contained a large amount of food, and no stomach was filled fully (see Table 2). According to an approximate estimation, the stomach of a large Pacific right whale is so big that it could contain 2 - 3 tons of food at one time.

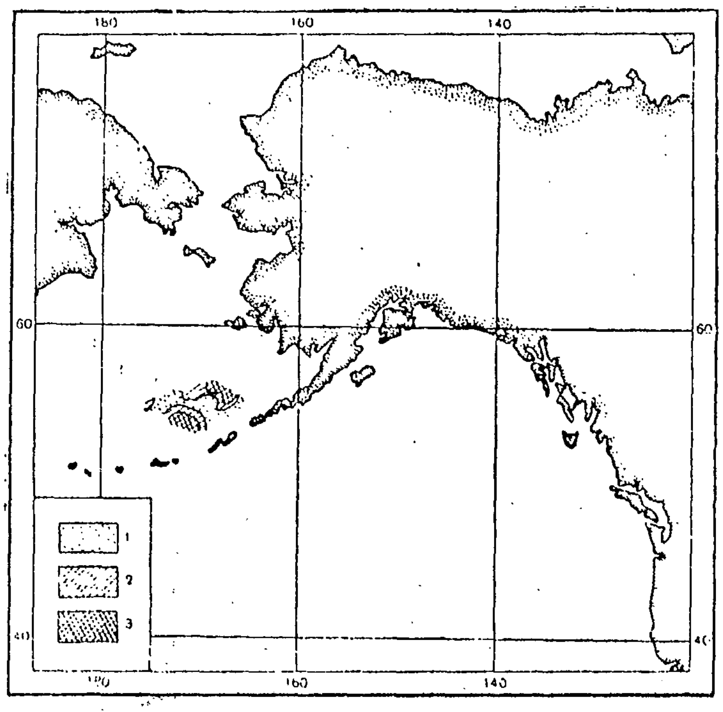

Рис. 6. Биомасса Calanus glacialis в районе постоянных наблюдений японских китов в октябре 1956 г.
1 — менее 100 мг/м³; 2 — 100–200 мг/м³; 3 — 200–500 мг/м³.
По данным экспедиции Института океанологии АН СССР (ориг.). Составлено Ю. А. Филипповой.

Fig. 6. Biomass *Calanus glacialis* in the area of constant observations of the Pacific right whales in October, 1956.

1- less than 100 mg/cu.m.; 2- 100-200 mg/c.m.; 3- 200-500 mg/cu.m.

According to the data of the Expedition of the Institute of Oceanology of the Academy of Sciences of the USSR (orig.). Compiled by Yu.A. Filippova.

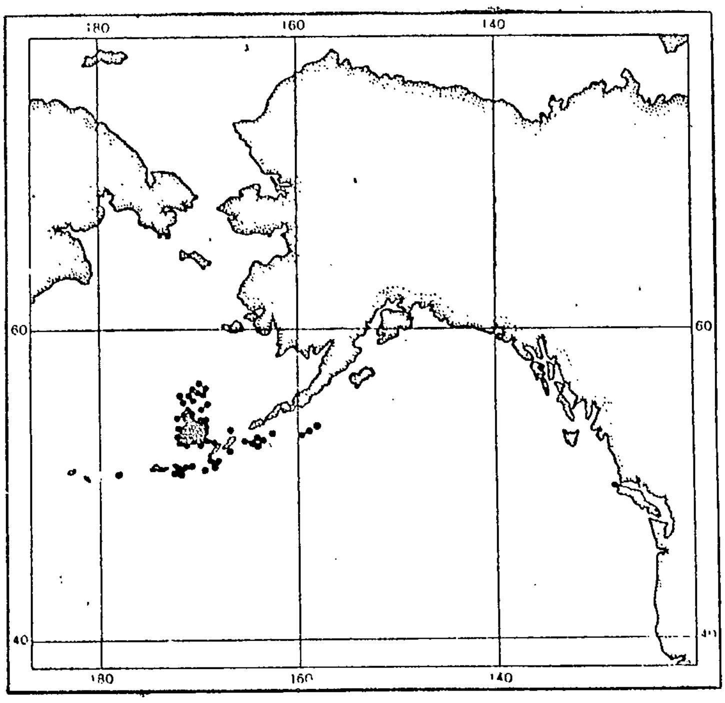

Рис. 7. Наблюдения японских китов в 1946—1957 гг. японским китобойным флотом (по Омура, 1958)

Fig. 7. Observations of Pacific right whales in 1946 - 1957 by Japanese whaling fleet (After Omura, 1958).

Our estimations indicate (Klumov, 1961) that whales of the suborder Mystacoceti, in order to maintain their energy balance and to accumulate food reserves for winter, require about 35 - 40 g per every kilogram of their live weight for a 24-hour period. Judging from this, a Pacific right whale 16 - 17 m long and weighing about 100 tons needs 3 - 4 tons of food.

Our material allow us to establish the age and size of the young of the Pacific right whales at the time these young turn to independent feeding.

A newly-born right whale, including Pacific right whale, measures 5 to 6 m in length. During the first six months, it increases its size almost twice. The termination of the lactation period and change to independent feeding in the northern half of the Pacific Ocean takes place in August - September, at which time the young is six-seven months old and 10.5 - 11 m long (Klumov, 1959, 1962). We discovered in the stomach of a suckling (captured on July 22nd, 1955), besides its mother's milk (which formed the main bulk of the food), a small amount of Calanus sp.; and in the stomach of another young whale, 11.35 m long (of the same generation and captured on August 11th, 1955), the food usual for adult whales (see Table 2).

HELMINTH FAUNA

The researcher studying the food of the cetaceans, while examining the stomach and intestines of the animal, is inevitably faced with the endoparasites of these animals. In this connection, we would like to stress once more how important it is to collect and study the helminthofauna of the cetaceans: the better we understand the helminthofauna of these animals, the more material we get to judge their distribution, their migratory paths, their biology, feeding, migration, formation of local pods, etc., and, perhaps, their origin, in connection with the study of the phylogeny of their parasites.

V.A. Dogel*, while discussing the importance of the helminthofauna of the animals whenever faced with zoogeographical problems, wrote that every endoparasite "... characterizes much better certain natural biotypes than its host. This seems to be incredible, but it is so. Indeed, every free organism is connected with a specific biotype and biocoenosis with a direct live thread itself. Most of the parasites are attached to their biotype, may coexist with it by means of two to three live threads, i.e. their intermediate and terminal hosts. Hence the attachment of the parasites to the definite combinations of biotic and abiotic conditions should be more intimate. Like a tag, the parasite indicates in the given biotype the presence of a complete complex of animals without which its presence in the biotype is unthinkable" (Dogel, 1947, p. 487).

Academician K.I. Skr'abin wrote the following in the foreword to Delamure's** book on the helminthofauna of the sea mammals: "Generalization of the data on the helminthofauna of certain animals may serve as supplementary material for solving the problem about the distribution on the globe of corresponding groups of hosts, while the study of parasitic worms of strictly endemic, relic animals allows us, in some cases,

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* Transliterated from Russian. Translator.

** S.L. Delamure. Transliterated from Russian. Translator.

to clarify the origin of the mentioned hosts" (Delamure, 1955, p. 3). These words of Academician K.I. Skr'abin and Professor V.A. Dogel help us to understand better the role of a detailed study of the helminthofauna of each individual whale. Incidentally, it should be noted here that the helminthofauna of the cetaceans in the World Ocean has been studied quite inadequately and quite unevenly both in regard to the species and geographical regions. In particular, the helminths of the cetaceans of the North Atlantic seem to have been studied least of all. The data on the helminthology of the sea mammals compiled by S.L. Delamure (1955) is the only one in the world literature and it facilitates, undoubtedly, the work of the zoologists studying the pinnipeds and cetaceans. However, almost ten years have elapsed since, and this list is, to some degree, obsolete, although it has not lost its significance. Moreover, we need now the data on the helminthology of the cetaceans in regard to individual geographical (natural) microregions. This is very important. This approach will enable us to discover new interesting laws. Without a detailed study of the helminthology of the cetaceans and pinnipeds for individual geographical microregions, it is impossible to determine the distribution of the helminths and their hosts, the entire progress of the development of causations and causes of their origin in regard to the helminthofaunas of marine animals of individual provinces.

While solving the problems raised, we cannot study the helminthology of individual species of the cetaceans (or pinnipeds) independently from a thorough research of the biology and ecology of the whales themselves and the conditions of the microregions in which they are found. It is important and mandatory to study not the species as such, but every individual specimen, under concrete conditions of its habitat. We also must know the developmental cycles of the helminths of marine mammals, if only the abundant ones, typical of a given area. This detailed study is the next stage of the common work of the helminthologists and zoologists studying marine mammals.

To study the helminthofauna of the cetaceans, we invited helminthologist A.S. Skr'abin to take part in our expedition. He collected vast material; he personally carried out 254 almost complete helminthological investigations of large whales, including nine Pacific right whales (ten were captured, in accordance with a special permission) (Klumov, 1959, 1962). A.S. Skr'abin generalized all the collected material and presented it in the form of a dissertation, - a compendium on the helminths of marine mammals of the northern part of the Pacific Ocean (Skr'abin, 1956, 1958, etc.).

While examining the internal organs of the Pacific right whales (lungs, heart, liver, kidneys, stomach, intestines, the urino-genital system, etc.), A.S. Skr'abin did not discover any endoparasites in three whales (out of nine). One whale (No. 6, Table 2) was a suckling; its stomach contained milk and some Calanus sp. This young was at the stage when it would switch to independent feeding. Cestode Tetrabothrius ruudi was detected in two whales (No. 4 and 7), and the Acanthocephale Bolbosoma nipponicum, not detected yet by anybody in right whales, was discovered in four whales (No.No. 5, 7, 8 and 9, see Table 2). A.S. Skr'abin has noted a rather weak infestation* of the Pacific right whales inhabiting the northern half of the Pacific Ocean (Skr'abin, 1958, 1959).

In his article, Omura (1957) notes that, in spite of a thorough investigation of two Pacific right whales caught in the Pacific Ocean by Japanese whaling vessels and studied by the scientists of the Japan Whaling Institute and also the scientists of the Faculty of Medicine of the Tokyo University, no endoparasites were discovered (see Table 2). Thus, these data also corroborate the idea that the Pacific right whales are not heavily infested by helminths. In this connection, we would like to express a hypothesis, which seems to have some grounds. [114]

Most of the helminths (if not all) make their way into the body of whales via intermediate hosts, i.e. animals which serve as food for whales. When we compare the number of the food objects of whalebone whales with the number of endoparasites discovered in them, we may assume that the greater the variety of the food of a given whale, the more helminths it has. For instance, the right whales of the northern half of the Pacific Ocean are known to have 6 food objects and 3 species of endoparasites; the corresponding figures for blue whales are 15 and 6, for sei whales 38 and 13, and for fin whales, 40 and 15.

Pacific right whales possess a finely developed capacity of selecting their food, and they prefer the Calanoida to all other groups of the zooplankton. This restriction in regard

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* "on the part of these parasites"? Translator.

to the aspect of food and, apparently, the weak infestation of intermediate hosts, i.e. the Calanoida, is the basic reason for the extremely weak infestation of the right whales by these parasites.

For the blue whales, we discovered 15 food objects, i.e. considerably more than for the right whales, although some of these objects are not constant. The number of helminths in the blue whales, compared with those discovered in the Pacific right whales, is also somewhat greater. Unfortunately, we[1] were not able to separate our data on the food objects of the sei whales, as we had at our disposal only two species of whales. Presented here is the information on the sei whales (Balaenoptera borealis) and Bryde's whales, while the number of the helminths is given only for the sei whales of the northern half of the Pacific Ocean. Having considered the aforesaid, we may maintain that the number of the prey of the sei whales is smaller than that of the fin whales, apparently, 25 - 30 species. Consequently, in summing up, we obtain two series rising parallel to one another, which also allow us to assume that the more varied the food of the whalebone whales, the more food objects used by them, the greater the variety of the helminths in them.

The comparative data on the helminthofauna of the right whales of the genus Eubalaena are represented as follows:

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1. Reference to the author himself. Translator.

Antarctic and adjacent waters	North of the Pacific Ocean
Ogmogaster sp. ☆☆	Tetrabothrius ruudi ☆☆☆
Priapocephalus grandis ☆	Bolbosoma nipponicum ☆☆☆
Tetrabothrius affinis ☆☆☆	Bolbosoma turbinella ☆

The data on the helminthofauna of the right whales of this genus in the Arctic Ocean are lacking.

A comparison of the helminthofaunas of the right whales of the northern half of the Pacific Ocean and of the southern hemisphere reveals that they lack common species of helminths. This is natural, of course, as the populations mentioned do not communicate with one another and do not winter in the areas of tropic waters where their geographical ranges are overlapping, as is the case in other whalebone whales. Moreover, the right whales of the southern hemisphere and the northern part of the Pacific Ocean do not share common food objects. As may be seen from Table 1, the former whales feed almost /115/ exclusively on E. superba, while the Pacific right whales live almost exclusively on the Calanus sp. At the same time we cannot but admit that the right whales inhabiting the Antarctic and the waters of the northern half of the Pacific Ocean, on the same grounds, along with other whalebone whales, communicating with these and feeding, to some degree, on the same prey (especially the right whales of the southern hemisphere), could have almost the complete set of the helminths

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☆ /S.L. Transliterated. Translator/ Delamure's data (1955)

☆☆ /H. Translator/ Matthews' data (1938)

☆☆☆ Skr'abin's data, obtained during our expedition.

characteristic of these species. Besides the reasons already stated which explain the lesser infestation of the right whales by these parasites, we should point to the small number (density) of the population of the right whales and lack of large aggregations. Observations have revealed that the right whales occur for the most part in pairs or groups of 3 - 5 specimens at a considerably large distance from one another. It is also possible that some physiological peculiarities of the right whales ("internal medium") also may be factors preventing the spread of a number of helminths and hampering their normal existence and propagation.

When we compare the helminthofauna of the Pacific right whale and Greenland whale[1*] (Eubalaena glacialis sieboldi and Balaena mysticetus, respectively), we also do not discover a common species of the endoparasites (Table 3). This indicates the dissociation of the geographical ranges of these two species of right whales, although their feeding, no doubt, is more like that of the Pacific right whales and other whalebone whales inhabiting temperate and subarctic waters of the Pacific Ocean.

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[*] 1. It belongs, apparently, to the Atlantic population.

Table 3

HELMINTHOFAUNAS OF GREENLAND WHALE AND PACIFIC RIGHT WHALE

Greenland whale	Pacific right whale
Lecithodesmus goliath ☆	Tetrabothrius ruudi ☆☆
Ogmogaster plicatus ☆☆☆	Bolbosoma nipponicum ☆☆
Phyllobothrium delphini ☆	Bolbosoma turbinella ☆
Crassicauda crassicauda ☆	
Bolbosoma balaena ☆☆☆	

☆ After Delamure (1955); data on the helminthofauna of Greenland whale in regard to its entire geographical range; however, we think that the helminths were discovered in the whales belonging to the North-Atlantic population.

☆☆ Data of our expedition (Skr'abin, 1959).

☆☆☆ After Tomilin (1957).

CONCLUSION

1. Right whales inhabiting the World Ocean reveal everywhere that they are capable of selecting food, regardless of their habitat. In each area they inhabit, their food is limited to a small number of food objects. In the northern hemisphere, the chief source of the food of the right whales are representatives of the group of the Calanoida; in the North Atlantic, this is chiefly Calanus finmarchicus, and in the northern half of the Pacific Ocean, Calanus plumchrus and Calanus cristatus. In the southern hemisphere, on the other hand, in the Antarctic waters, the main food of the right whales form the representatives of the group of the Euphausiacea, primarily Euphasia superba. The actual material studied allows us to consider the right whales as the typical stenophagous animals with a very small variety of foods. Right whales feed only on the representatives of the plankton which form large aggregations in the surface waters of the ocean.

2. Narrow specialization of right whales could evolve only if the conditions for feeding were stable - presence of constant abundant aggregations of zooplankton, with the biomass playing a very important role; there is no doubt that the "density" of these aggregations was the most important factor. It seems then that these two factors - stability of the food reserves and formation of mass aggregations of zooplankton in the upper layers of water- were decisive in affecting the evolution and development of a number of trophic adaptations in right whales: formation of disproportionately large head (more than

30% of the body length), enormous mouth, a perfect baleen sieve with long whalebone plates (up to 2.6 m), dense and soft fringe (35 - 40 cm long), and other adaptive devices which facilitate the capturing of an enormous volume of food.

To locate aggregations of food plankton of a required concentration in vast areas of the ocean, whalebone whales, including right whales, possess one more extremely important capacity; they are equipped with a perfect sound-detector by means of which they search for food and waste very little time (Klumov, 1957, 1961). There is no other explanation as to how these huge animals whose 24-hour-long need for food is extremely great can exist.

3. Investigations aimed at the clarification of the quantitative aspect of right whales did not yield positive results, as the maximum volume of food recorded in these whales reached only 150 l (whale, No. 4, Table 2). However, calculations (Klumov, 1961) allowed us to come to the conclusion that during a period of 24 hours whalebone whales require 35 - 40 g food per 1 kg of their body weight. Thus, adult whale weighing 100 t or somewhat more should consume 3 - 4 t of zooplankton during a 24-hour period.

4. Geographical variability in the feeding of right whales the Calanoida in the northern hemisphere and Euphausiacea in the southern) - complete resemblance in their morphological characters and, in particular, their baleen sieve (Klumov, 1959, 1962) and other trophic adaptations acquired in their evolutionary process- allow us to state the following hypothesis.

Right whales, having originated somewhere in the northern hemisphere, perhaps in the northern half of the Pacific Ocean, began to spread after a certain evolutionary stage was complete and they had adapted themselves completely to feeding on fine planktonic organisms which concentrated in upper water layers. It seems that the distribution of right whales (we are talking about the genus Eubalaena) took place during the Quaternary period. At the time of the maximum glaciation, the right whales penetrated into the South Arctic Ocean; during the interglacial warm time, they passed from the Pacific Ocean to the North-Atlantic waters via the Antarctic Ocean. Thus, their isolation was not prolonged, and hence the isolated populations, separated by enormous areas, did not produce any sharp, well discernible morphological differences (Klumov, 1962). This seems to be the only logical explanation why the right whales inhabiting the southern hemisphere, the North Atlantic Ocean, and the northern half of the Pacific Ocean hardly differ from one another in any morphological characters, and only slightly so in regard to their biology.

Under the new conditions, in the Antarctic Ocean, [117] in which aggregations of fine planktonic organisms were lacking in the surface layer, the right whales were forced to turn to feeding on rather larger animals (Euphausia superba) which formed mass and quite dense concentrations in surface waters. Their baleen sieves, however, remained unchanged, since these whales have not yet lived long enough under new conditions, in order to develop some new adaptive characters. It is also possible that earlier the right whales inhabiting the southern hemisphere fed at first on planktonic animals which were finer than now (representatives of the group Calanoida), which later might have been displaced by the contemporaneous form of the zooplankton in the Antarctic waters, i.e. E. superba[1]. This is the more probable as even now the Calanoida form quite large aggregations in the aforesaid waters (Naumov, 1959); however, these aggregations are confined only to depths more than 25 m and therefore are inaccessible to the right whales. The lack of the Calanoida in the surface waters may be explained not only by their displacement by a more massive and active form, but also by the fact that here they do not find conditions suitable for their existence.

5. Distribution of right whales in the areas of their summer stay (feeding grounds) is closely connected with the distribution of the aggregations of their food objects (feeding grounds). In the southern hemisphere, the distribution of the right whales is connected with the distribution of E. superba, and in the northern hemisphere, with the Calanoida; in the North Atlantic, with C. finmarchicus, and in the northern half of the Pacific Ocean,

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1. Taylor's well-known principle (Geptner /Transliterated from Russian. Translator/, 1936) according to which the more primitive forms are pushed aside or displaced by more progressive, more specialized and young forms of intruders, which are introduced or originate in the territory under investigation.

first of all, with *C. plumchrus* and *C. cristatus*, and also with *C. glacialis*.

6. The chief rivals of the right whales in the southern hemisphere are all the whalebone whales there, some seals (crab-eating seal*, Weddel's seal*, and, to a lesser degree, Ross' seal*), all the species of penguins and other marine birds inhabiting that region, and also a few marine pelagic fishes and animals of the Arctic waters which feed almost exclusively on *Euphausia superba*. However, the rivalry between the animals feeding on the above crustacean is not too pronounced because of the abundance of *E. superba*. A very large portion of the zooplankton remains unused. We estimated (Klumov, 1954) that within the area that surrounds Antarctica and located south of 60° s.lat., the whales, seals, marine birds and fishes eat up during the season of the development of the plankton here slightly more than 200 mln. t of zooplankton (almost exclusively *E. superba*); all the remaining mass of the zooplankton - about five billion t- remains unused.

The main rivals of the right whales in the northern hemisphere are: the sei whales which gladly feed on the Calanoida, and a large group of marine birds feeding on plankton, such as *Oceanodroma furcata* and *O. leucorrhoa*, *Fulmarus glacialis*, *Puffinus griseus* and *P. tenuirostris*, partly *Rissa tridactyla*, and some others; less important are the feeders on the Calanoida. The pelagic fishes running in schools (such as herring, Pacific saury, some salmonids, etc). Moreover, pelagic squids, especially *Ommatostrephes sloanei-pacificus* and *Loligo opalescens* in the Pacific

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* Literal translation. Translator.

Ocean, too, are rivals of the right whales, although to a lesser degree, if compared with the animals listed above.

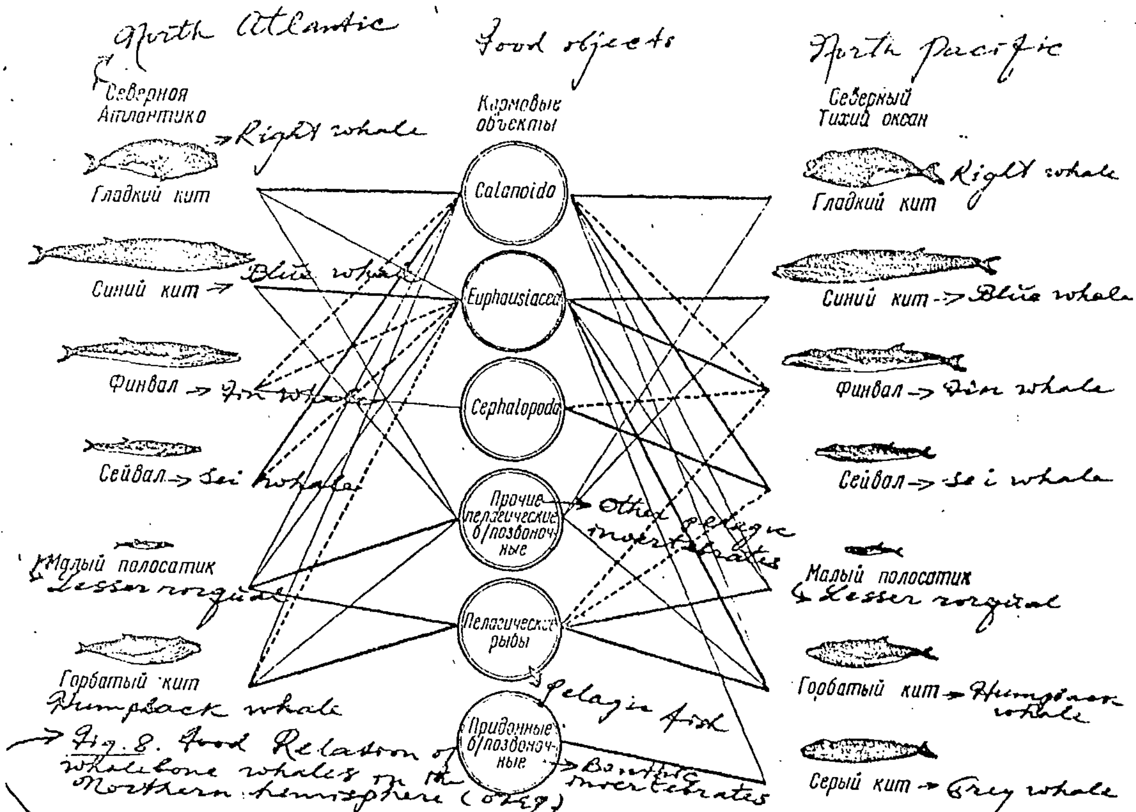

Fig. 8. Food Relation of whalebone whales in the Northern hemisphere (orig.)

Рис. 8. Схема пищевых связей усатых китов в Северном полушарии (ориг.)

Жирной линией обозначена постоянная сильная связь, пунктиром — связь средней степени, тонкой линией — слабая связь

Thick line indicates constant close relation; dotted line - average relation; thin line - weak relation

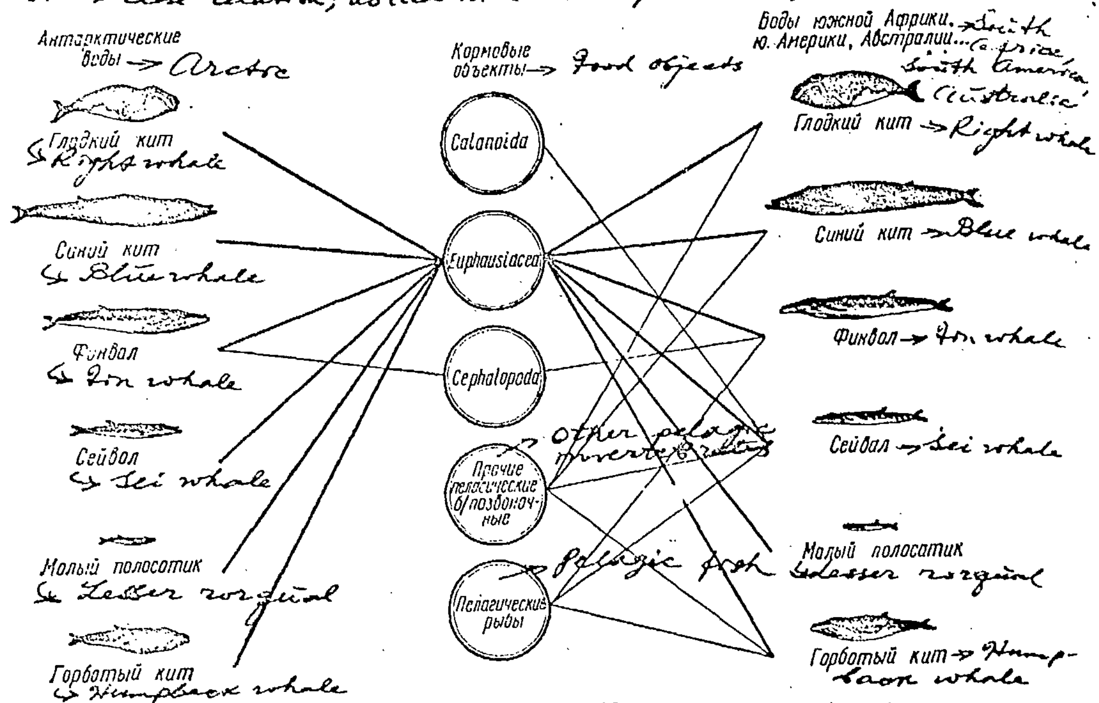

Рис. 9. Схема пищевых связей усатых китов в Южном полушарии (ориг.)

Жирной линией обозначена постоянная сильная связь, тонкой линией — слабая связь

Fig. 9. Food Relation of Whalebone Whales in the Southern Hemisphere (orig.).
Thick line indicates constant close relation; thin line, weak relation

While evaluating the degree of the rivalry of the right whales in regard to food, it should be noted that their population is so small in the northern hemisphere that one cannot speak about any competition. Moreover, not all the mentioned animals feeding on small forms of the zooplankton of the surface waters form numerous populations. For instance, the salmonids of the northern half of the Pacific Ocean and the Clupeidae at present are subject to great reduction because of the numerous catches on the part of the Japanese fishermen. B.M. Mednikov has estimated (1961) that all the populations of the salmonids in the northern half of the Pacific Ocean use during the entire year only 5% of the total volume of the zooplankton in this vast area. During the years of expansive development, the greater part of the zooplankton here remains, it seems, unused. Thus, the increase in the competition for food on the part of the right whales may take place only during the years when the zooplankton, and, in particular, the Calanoida develop poorly. [118]

These data, we believe, allow us to understand the causes of the development of the stenophagous state in the right whales and also the development of the conditions under which, during the evolutionary process, the sharply expressed selective capacity of these whales was formed.

6. Having considered also the resemblance in regard to the feeding of the right whales and some already mentioned marine planktophagous birds, we would note that these birds, under conditions of the northern half of the Pacific Ocean, may serve as guides to the aggregations of food

plankton, and hence to the regions in which the (Pacific) right whales might be encountered.

7. Detailed presentation of the food links of the right whales is far from being completely developed, as many details pertaining to the feeding of the prey for these whales have yet to be clarified. And this is namely the field where supplementary and thorough research should begin. Comparative data on the food links of the whales with the basic animals used as their source of food are given in Fig. 8 (for the northern hemisphere) and in Fig. 9 (for the southern hemisphere). These figures indicate that the food relation of all whalebone whales in the Antarctic waters is confined to the Euphausiidae, as they are the simplest. These relations are somewhat more complex in the subpolar and the antiboreal regions of the southern hemisphere, and they become more complex still in the northern hemisphere, since there, the analogue of E. superba, which forms aggregations of the denseness as does the mentioned crustacean in the southern hemisphere, is lacking.

Fig. 8 and 9 indicate that the food links of the right whales are, perhaps, the simplest, because of the distinct capacity of these animals to select their food.

8. The point of origin of the whalebone whales, in particular, the Minke whales, is considered to be the waters of the North Atlantic, as fossil remains of large cetaceans have been known only from North Africa (Romer, 1939). The waters of the North Atlantic are also considered to be the cradle of the development of most of the Pinnipedia, in

particular, the Phocidae (Boetticher, 1934; Scheffer, 1958).

It seems, however, that there was yet another hearth where the marine mammals originated; it was located in the northern waters of the Pacific Ocean. And there is no unanimous agreement on the part of the scientists on the place of origin of the Otariidae. Some scientists (Botticher, 1934; Geptner, 1936; Scheffer, 1958) consider that it is possible to imagine that these seals originated and spread in the waters of the Antarctic Ocean; others (Romer, for instance, 1939) are completely in favour of the northern half of the Pacific Ocean. Kellog has shown that the primitive ancestor of the eared-seals Allodesmus kernensis [120] was also distributed in the Lower Miocene near the coasts of what is now known as California. In the structure of its skeleton, in spite of the peculiarities, this species shares many similar features with the contemporaneous eared-seals, i.e. sea-lion (Eumetopias), sea-lions (Zalophus), the southern fur seals (Eumetopias), and even walrus (Odobaenus).

In our opinion, the second viewpoint is more accurate as, first of all, almost all the known fossil remains of the ancestors of the Otariidae have been discovered along the coast of the Pacific Ocean and, secondly, it is the northern half of the Pacific Ocean namely where we find the largest number of endemic, including relic forms which indicate that in this area there was, beyond any doubt, a large and important center of origin and the primary location of the spread of a large group of the most diverse animals, the representatives of both the terrestrial and the marine faunas. Suffice it to say that Beringia* was the main centre of origin and spread of Arctic animals "... which produced the main bulk of the inhabitants of the mainlands" (Tugarinov, 1929, p. 679). V.G. Geptner (1936, p. 383) also speaks about the presence "... of a strong centre where various forms (of animals. S.K.) originated in the area of Beringia, whence they moved gradually southward."

Steller's sea cow, for instance, originated undoubtedly in the north of the Pacific Ocean; so did the ribbon seal (Histriophoca fasciata) of the family of true seals and the Kamchatka beaver (or sea otter),- these wonderful endemic animals of the mentioned waters; a whole group of dolphins (Phocoenides, Lissodelphis, etc.) endemic of this region; and, finally, grey whales (which, by the way, resemble closely the right whales), which, although in the ancient times they inhabited the North Atlantic, were of undoubted Pacific origin.

We are entitled to regard all the right whales as the animals which originated in the Antarctic. Among the Pinnipedia, the analogue to the Greenland whale is the walrus. Having considered the present distribution, paleontological data, and other material (the geology of land, the history of the evolution), we may assume that the walrus and the Greenland whale originated in the basin of the Arctic Ocean, most probably in the waters close to

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* Verbatim. The suffix "ia" is used similar to the the formation of countries- Bulgaria, Yugoslavia, etc.- and large territories- Siberia, for instance. Translator.

the northern Pacific Ocean, or perhaps even in the latter. This is the more probable since the walruses, as has been established by paleontologists (Romer, 1939), evolved from old forms (Prorosmarus), which were very close to the eared-seals, and the latter had their ancestor (Allodesmus kernensis) in the Pacific Ocean, near California. The eared-seals which originated in the north of the Pacific Ocean from where they spread into the southern hemisphere, should be regarded as the analogues of the right whales of the genus Eubalaena. The Pinnipedia mentioned above and the right whales penetrated into the southern hemisphere at various times. However, they could have moved along the same paths.

The aforesaid facts and analogues, as well as the paleontological finds of the remains of the ancestors of the whalebone whales in the deposits along the coast of California by Morrice and described by Kellogg (1931), and a number of other data (in particular, the structure and the adaptation of the baleen sieve to the feeding on the Calanoida) allow us to consider that the right whales of the genus Eubalaena originated in the waters of the northern half of the Pacific Ocean. One of the bases for this assumption is the data on the analysis of the helminthofauna of the right whales in the northern half of the Pacific Ocean and the southern hemisphere.

If we compare the helminthofauna of the right whales of various populations, we note that at present they lack contact in regard to one another. As already noted (see Tabl. 4 and 5), a comparison of the helminthofaunas of Eubalaena [121] *glacialis australis* and *Eubalaena glacialis sieboldii*, and also a comparison of the helminthofaunas of *Balaena mysticetus* and *Eubalaena glacialis sieboldii* (unfortunately, the data on the composition of the helminthofauna of the right whales of the North Atlantic are lacking) corroborate this hypothesis, as these whales do not share even a single species of the endoparasites. Moreover, the infestation of the right whales by these parasites is very insignificant).

It is possible that while being either sterile or possessing originally a small series of endoparasites, the right whales of the genus *Eubalaena* penetrated the waters of the Antarctic Ocean, having come from the northern half of the Pacific Ocean (the initial area of their distribution). It seems that this penetration may be confined to the period of the first mass glaciation, i.e. to the relatively not too distant past. Once in the southern hemisphere, these whales (if they were not sterile) "lost" here, apparently, all their endoparasites, as the latter might have not found the conditions necessary for their development (intermediate hosts), and the number of these newcomers was so insignificant (at least during the first time of their penetration to these areas) that the infestation might have disappeared. Later the right whales of the southern waters acquired a small number of helminths which are characteristic of the Antarctic waters (see p. 114 [*]), which also were distributed among other whalebone

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[*] In the original. Translator.

whales here. In the first instance, we might mention *Priapocephalus grandis* and *Tetrabothrius affinis*; the origin of the former is undoubtedly connected with the Antarctic Ocean. The third endoparasite discovered in them is *Ogmogaster* sp. (apparently, *O. plicatus*). It originated in the North Atlantic whence it was carried via the Antarctic waters in the rorquals (this will be stated below, in the chapter on the analysis of the material on the blue whales).

Moreover, it is very important to note that the Australian right whales (*Eubalaena glacialis australis*) were found to contain the commensal nematode *Odontobius ceti* (Roussel de Vauzeme, 1834, after Delamure, 1955) on the baleen plates; it is undoubtedly of Antarctic origin, and it is quite widely distributed among the whalebone whales in the southern Arctic waters, and discovered here in the blue whales and fin whales.[1] What is of special interest, however, is the fact that this nematode is not present in the right whales (*Eubalaena glacialis sieboldii*) of the northern half of the Pacific Ocean.

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1. We believe that it is possible to predict fairly accurately that this nematode will also be discovered in humpback whales, sei whales, and lesser rorquals, if these whales of the Antarctic waters are thoroughly checked. The lack of reports of this nematode in the aforesaid whales is, we believe, due to the insufficiently thorough investigations of their baleen apparatus on the part of the zoologists and helminthologists while collecting the biological data under field conditions.

Odontobius ceti was discovered by our expedition (Skr'abin, 1959) in the north-west of the Pacific Ocean in the blue whales and the fin whales of the Asiatic population. A.S. Skr'abin has examined the baleen plates of five fin whales and five blue whales and discovered the mentioned nematode in both species of whales in 100% of the cases "... in a great number". He also examined thoroughly the baleen apparatus of nine (Pacific) right whales and did not discover *O. ceti* in any of them. This confirms that the distribution of the right whales of the genus *Eubalaena* went from the north of the Pacific Ocean to the southern hemisphere, while the route of the blue whales and fin whales, on the other hand, was from the southern hemisphere to the Pacific Ocean. This question will be treated later, in the corresponding chapters of this work.

BLUE WHALES

Feeding

Before World War II, the blue whales were the main object of whaling in the Antarctic Ocean, and they formed about 90% of the world catch (Table 4). After World War II, the number of the animals killed has sharply dropped, while in other regions of the World Ocean it has remained, on the average, at the same level as it was before the war (Table 5).

Table 4

Catches of Blue Whales According to Individual Regions of the World Ocean Before World War II (individual animals)

Year	Southern hemisphere: Antarctic & South Georgia	South Africa South America, Australia	Northern hemisphere: Arctic & North Atl.	northern half of Pacific Ocean	Total
1929	12847	-	-	-	-
1930	17898	-	-	-	-
1931	29410	-	-	-	-
1932	6488 ☆	-	-	-	-
1933	18891	-	-	-	-
1934	17349	89	25	-	-
1935	16500	162	10	-	-
1936	17731	294	31	-	-
1937	14304	225	57	66	14652
1938	14923	56	15	41	15035
1939	14081	30	26	15	14152
1940	11480	28	1	51	11560

☆ The sharp decrease in whaling is due to the conjuncture of the world market- the drop in price for blubber because of the vast amount of the latter obtained in previous years.

The study of the biology of the blue whales, including their feeding, was quite intensive in the pre-war years, and, in spite of the sharp decrease in catches, it was extremely intensive after the war. This is why the feeding habits of the blue whales and the quantitative composition of their food have been much better studied than those of the right whales.

Table 6 shows a list of the food objects of the blue whales by the basic whaling regions of the World Ocean. Our information on the feeding of the blue whales is most incomplete for the North Atlantic, for which the studies to this effect were conducted in the nineteenth century and at the beginning of this century, and then only in passing, and not as a special subject. Recently, no observations of any kind were conducted in regard to the study of the feeding of the blue whales, and no information on them was published, although it has been known that A. Jonsgard, the Norwegian scientist, studied the whalebone whales, including also blue whales which were taken in the North Atlantic, mainly near the coasts of Norway (Jonsgard, 1955).

The data on the feeding of the blue whales occurring near the Pacific coast of South America, and also near the Atlantic coast of Brazil, although individual catches of these whales take place every year in the regions just mentioned, are lacking completely.

The feeding of the blue whales of the Antarctic waters and the northern half of the Pacific Ocean has been studied as well, it seems, and quite thoroughly. [124]

Table 5

Recent Catches of Blue Whales in Individual Regions

of the World Ocean (individual animals)

Year	Southern hemisphere		Northern hemisphere		Total
	Antarctic & South Georgia	South Africa, South America, Australia	Arctic & North Atlantic	northern half of Pacific Ocean	
1949	7625	59	79	19	7782
1950	6182	59	54	18	6313
1951	7048	106	53	71	7278
1952	5130	169	15	122	5436
1953	3870	193	15	140	4218
1954	2697	94	11	207	3009
1955	2176	164	13	142	2495
1956	1614	214	9	150	1987
1957	1512	109	11	143	1750
1958	1690	175	5	125	1995
1959	1192	95	6	149	1442
1960	1239	☆ 9	☆☆ -	☆ 86	☆ 1334
1961	1744	151	-	92	1987

☆ Data incomplete

☆☆ Data lacking

Table 4 and Table 5 are compiled from the following sources: Norsk Hvalfangst - tidende 1951 - 1961, International Whaling Statistics, vol. I - XXXIX, K. Schubert (1955) et al.

Table 6

Composite Table of Food Objects of Blue Whales (Balaenoptera musculus) in Main Whaling Regions of the World Ocean

Antarctic and adjacent waters (South Africa, Patagonia, etc.)	North Atlantic	Northern half of the Pacific Ocean
Crustacea	Crustacea	Crustacea
Grimothea (post - larvae Munida gregaria)	Temora longicornis	Calanus sp.
Parathemisto gaudichaudi	Mysis oculata	Calanus plumchrus
Euthemisto sp.	Themisto libellula	Themisto sp.
Euphausia superba	T. abyssorum	Nematoscelis difficilis
E. vallentini	Thysanoessa inermis	Euphausia pacifica
E. crystallorophias	T. longicaudata	Thysanoessa inermis
E. recurva	Meganyctiphanes norvegica	T. longipes
E. lucens		T. raschii
Thysanoessa macrura		T. spinifera
Nyctiphanes africanus	Mollusca Gastropoda	Mollusca Gastropoda
	Clione limacina	Clione limacina
	Limacina helicina	Limacina helicina
Mollusca Cephalopoda		Cephalopoda
Onychoteuthis banksii		Ommatostrephes sloanei-pacificus
Pisces		Pisces
Paralepis coatsi		Sardinops sagax melanosticta
P. coregonoides		Mallotus villosus socialis
Myctophum sp.		Ammodytes h. hexapterus
Harpodontidae (gen. sp.)		
Nototheniidae (gen. sp.)		

The main and almost exclusive food of the blue whales in the Antarctic is considered- and justly so- Euphausia superba, the accumulations of which in the Antarctic Ocean are enormous. Marr (1956) has shown that E. superba becomes concentrated in the waters located south of the line of the Atlantic convergence, directly adjacent to the mainland (Fig. 10), within 63 - 65° s. lat., and only in the western part of the Atlantic sector of the Antarctic Ocean its concentrations exceed the boundaries of the mentioned latitude, stretching north in this relatively small area (10 to 60° w.long.) to 52° s.lat.

To a lesser extent, the blue whales of the Antarctic region feed, besides on E. superba, also on Thysanoessa macrura, E. vallentini, and E. crystallorophias, and on one cephalopod mollusk, Onychoteuthis banskii. The feeding of the blue whales on this squid is sporadic and it is irregular, being rather a deviation.

Unfortunately, it is impossible to arrange the food objects of the blue whales (see Table 6) in the Antarctic and adjacent waters according to local herds, as this would require the initial data on the food organisms. It is quite probable that E. superba may not be the primary source of food for the blue whales of some local herds of the Antarctic population, and in the regions where it does not form large accumulations (see Fig. 10), it may be replaced by some other Euphausia organisms[1]. This remark is especially true in regard to the local herds which have their summer feeding grounds north of the Antarctic convergence, south of which are found aggregations of *E. superba* (see Fig. 10). Our studies of the feeding of the sperm whales which belong to various herds of the Asiatic population (north-west of the Pacific Ocean) in which a difference in regard to their prey was established (Klumov, 1959) allow us to form such a hypothesis. This hypothesis is corroborated even to a large extent by an interesting work by T. Ichihara (1961), a Japanese scientist, in which he has described a local Kerguelen herd of blue whales which form part of the Antarctic population. These whales fed exclusively on *E. vallentini* and stayed in the area around Kergeulen Island ($48^{\circ}50'$ s.lat. and $68^{\circ}30'$ - $70^{\circ}45'$ w.long.).

The prey indicated in the left column of Table 6 were discovered in the stomachs of the blue whales taken in the waters adjacent to South Georgia (*Parathemisto gaudichaudi*, *Grimothea*, etc.), towards the shores of South Africa (*Euphausia lucens*, *E. recurva*, *Nyctiphanes africanus*, etc.), South America (Patagonia), and in other regions; they all were discovered in small amounts.

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[1] For instance, we know (Nemoto, 1959) that in the region between 80 and 140° w.long., and also between 40 and 60° e.long. (in Antarctic sectors I and VI), quantitatively *Thysanoessa macrura* was more numerous than *E. superba* not only in the ocean, but also in the stomachs of the whalebone whales.

As regards fish, which sometimes were discovered in the stomachs of the blue whales of the Antarctic herds (a few specimens in each), they were captured by the whales, according to the unanimous agreement of scientists, when these animals were swallowing the zooplankton; hence they cannot be regarded as the common food of whales.

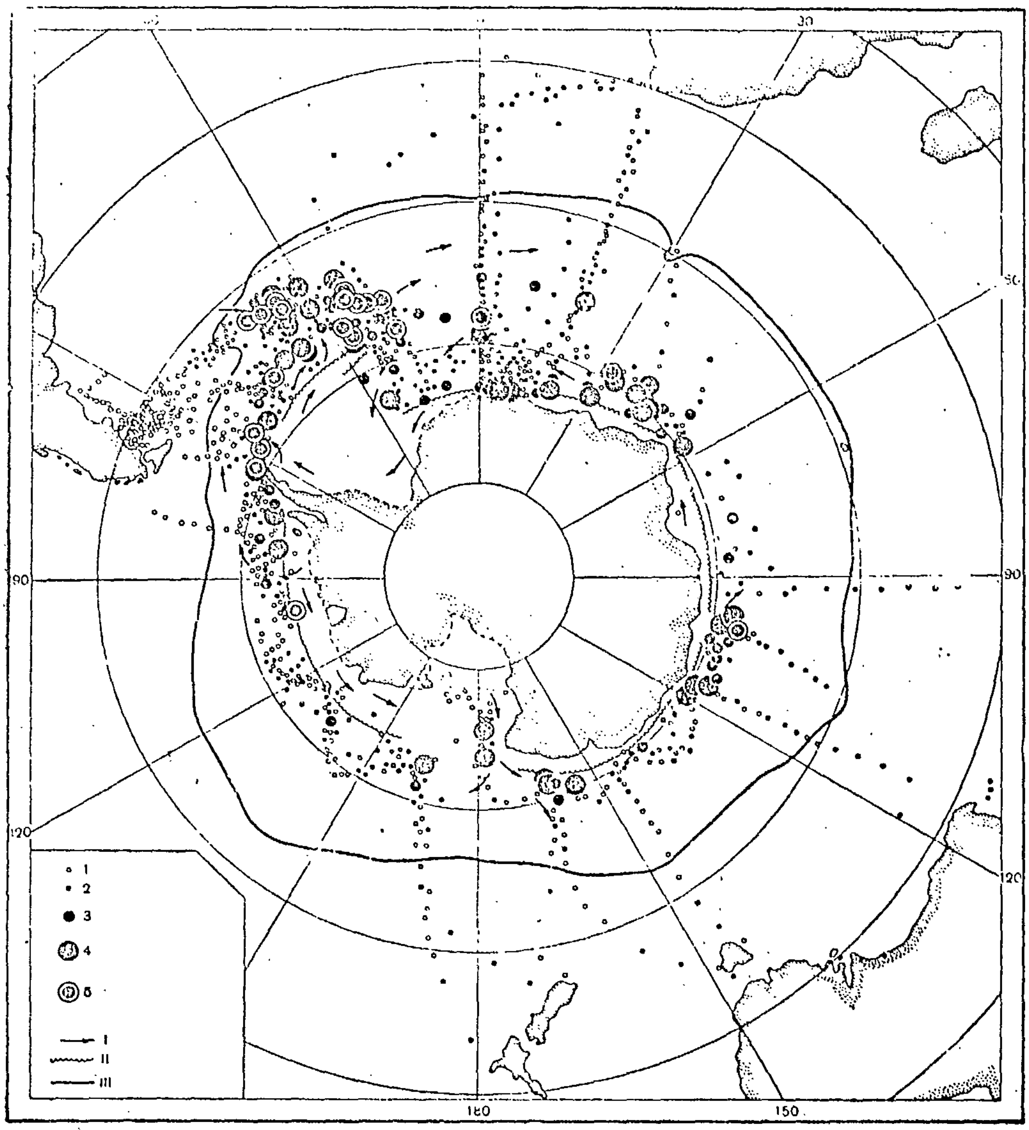

Рис. 10. Распределение Euphausia superba более 20 *мм* длиной, в январе — марте. Показано количество экземпляров на один лов планктонной сеткой диаметром 1 *м*

1 — 0; *2* — 100 экз; *3* — 100—1000 экз. *4* — 1000—10 000 тыс. экз.; *5* — 10 тыс. — 100 тыс. экз. *I* — течения; *II* — среднее положение границы паковых льдов для февраля; *III* — линия антарктической конвергенции. (По Марру, 1956)

<u>Fig. 10.</u> Distribution of <u>Euphausia superba</u> (more than 20 mm long) in January - March. Figures indicate the number of specimens per catch using planktonic net, 1 m in diameter.

1- 0; 2- 100 specimens; 3- 100-1,000 specimens; 4- 1,000-10,000 specimens; 5- 10,000 - 100,000 specimens. I- currents; II- average boundary position of pack ice for February; III- line of Antarctic convergence. (After Marr, 1956.

Thus, at present, we may name ten species of crustaceans as the prey for all the Antarctic herds of the blue whales; seven species of these belong to the Euphausia group, one species of cephalopod mollusks of the group of squids, and five species of fish; all in all, sixteen species belonging to three classes. However, only a few of the mentioned animals may be regarded as basic source of food. First of all, it is E. superba; to a lesser degree, it is T. macrura, E. vallentini, and E. crystallophias,-all being Euphausia species. The remaining animals are not as important as the ones just mentioned. Consequently, the blue whales which in the summer inhabit the Antarctic Ocean and the waters adjacent to it are capable of selecting their food; the latter, as will be shown below, being traced also in other whales and in other regions of the World Ocean. [126]

A very important question is how to establish the reasons for the formation of the aggregations of food plankton, in particular, E. superba.

Back in 1951, while investigating the distribution of the whales and their feeding grounds in the waters around the Kuriles (north-west of the Pacific Ocean), we established that the basic accumulations of food plankton visited by the whales are located in the regions where there is a rise of water from below and, consequently, the enrichment of the surface layers in biogenic elements (Klumov, 1952). Later, during the expeditions of 1955 and 1956 (Klumov, 1956, 1957), we were able to confirm this hypothesis and- and this is important- to record the constant accumulation of zooplankton in the waters around the Kuriles in one and the same places where the water rose from below, and where the shifts in space were insignificant in individual years, due to changes in hydrometeorological conditions[1].

Somewhat later, Uda, a Japanese scientist, quite independently, came to the same conclusion (1954). He pointed out that "the boundaries between the rise of cold abyssal waters, cyclonic eddies and warm water which form cyclonic tongues of cold and warm currents, correspond to the centers of the regions with the most favourable conditions for whaling. This is possible in a zone rich in food for whales, i.e. euphausids, copepods, squids, sardines, anchovy, etc., which aggregate near the boundary of water masses, i.e. the convergence of currents"[2].

1. The rise of the water from below is due to various reasons: geostrophic phenomena, the divergence of currents which is connected with the activities of atmospheric cyclones, the relief of the bottom which causes the local vertical circulation of water. All these are also present in the waters around the Kuriles.

2. This seems to be erroneous: the rise of water from below and the enrichment of the surface water in biogenic elements causing an accumulation of prey for whales take place in the divergence zones, and not in the convergence zones, where the opposite phenomenon is observed.

M. Uda points out that "... the principles of the formation of regions for whaling in the Antarctic Ocean... may be similar to those found in the waters around Japan...".

Uda and Nasu (1956) continued the study of the problem pertaining to the effect of fronts and cyclones on the accumulation of plankton in some regions of the north-west of the Pacific Ocean and the relations of these accumulations to the distribution of whales. In their work, the authors have come to the conclusion that "... the main regions of whaling are located at the fronts of cold and mixed water bodies... with abundant plankton..." and that the catches of the whales increase "... during the days following the passing of cyclones...".

K. Nasu published in 1957 yet another work on the same subject, on the region of the Bering Sea and the waters around the Aleutians. He states that "...favourable conditions for whaling originate in the waters adjacent to the convergence line as the line which divides the currents (apparently, the divergence.-S.K.), where plankton is abundant". He further states: "Large accumulation... of zooplankton... is due to the rise of the abyssal waters loaded with large amounts of nutritive salts".

Thus, the regularity we stated (Klumov, 1952) [127] was confirmed by both the data of our expeditions (Klumov, 1956, 1957) and the work of the Japanese scientists (Uda, 1954; Uda and Nasu, 1956; Nasu, 1957). Now we may state with confidence that the basic causes for the formation of the feeding grounds of whales, accumulation of their food plankton in strictly definite places, their relative constancy in regard to the terms and places of development and formation, as well as the relation with the whales in the northern part of the Pacific Ocean, and, apparently, in other regions of the World Ocean are the hydrometeorological conditions, i.e. the water temperature, frontal lines, divergences of currents, rise of abyssal waters, atmospheric cyclones, etc. The biological factors, too, should be added to the aforesaid abiotic ones, i.e. the enrichment of the surface waters in biogenic elements and nutritive salts causes a spectacular development (blooming) of the diatoms, which serve as the basic food for the planktonic crustaceans, the accumulations of which, in turn, attract "their" consumers: squids, fish, marine birds, and whalebone whales. All these processes and phenomena are interrelated in time and space. They were formed into one system during the development of the environment and the animals which inhabited it. It seems that there is a whole series of chiefly biological aspects, which were not mentioned above, which form part of this complicated and quite diversified complex of factors which influenced the formation of the accumulations of zooplankton, their density, places and terms of formation, etc. For instance, the intensity of the propagation of individual species, which varies greatly annually, the consumption, which also may vary considerably both in regard to terms and amounts (even within one and the same season, not to mention the comparative consumption during various years), and a number of other factors which complicate even more and hamper the clarification of all the varied aspects of the mentioned phenomenon as a whole.

In 1961, K.V. Beklemishev wrote an article on this same problem. He proposed a hypothesis which explains the formation of the aggregations of E. superba in the surface waters of the Antarctic divergence by the rising of a warm intermediate layer as a result of the action of atmospheric cyclones. When this layer is raised, the euphausiids in it, according to the author, are brought up to the surface.

We believe that the reasons for the accumulations of the euphausiids are not as simple. In reality, this process is much more complex than a purely mechanical lifting of such active and rapidly moving forms as E. superba. K.V. Beklemishev (1961) considers that during the period of rapid growth (hence also intensive feeding), the furcilias, or older stages of this crustacean, brought up to the surface layers of water, find themselves in extremely unfavourable conditions for feeding, because, according to Beklemishev (1961, p. 124), "... the atmospheric cyclone rises the waters that form a 'polynia'* in the diatom "blooming" and facilitates the rise of the euphausiids in the middle of the polynia... (underlining is ours. -S.K.). The diameter of such a polynia, according to Beklemishev, "... may be of the magnitude of 500 km...". Consequently, the crustaceans which are carried to the surface in the middle of such a polynia are in advance confined to a rapid death from starvation, as they would need much time to get to the margin of the polynia, where they would find food and be able to satisfy their vital needs.

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* Russian term; it is used to indicate a space of open water in the midst of ice. Translator.

We may speak about it with confidence, as Ponomareva's data (1963) indicate that the euphausiids, once joined in large aggregations, always feed intensively on the diatoms. They switch to feeding on the animals (Copepoda) only when [128] they are spread and do not find abundant plankton. This also is substantiated by Naumov's data (1962), who during the Third Arctic Expedition aboard the "Ob'" in 1958 collected in the zone of the Antarctic divergence a great many samples of the euphausiids (of these, about 300 specimens of E. superba were examined). The stomachs of these euphausiids were studied in the Institute of Oceanology by V. Zernova. It was found that E. superba which forms the aggregations in the surface zone feed very intensively (it could not be otherwise!) and that, on the whole, they feed primarily on the diatoms, and only to some degree on the tintinoids.

Consequently, there can be no question about any 'polynia' in the diatomic "blooming" (Beklemishev, 1961), as this contradicts the reality. We do not doubt that the transportation of the euphausiids to a zone in which food is absent at a radius of 250 km, during the period of their rapid growth and feeding, is biologically inexpedient, and, in regard to the existence of the species, even harmful. And if it is so, a similar phenomenon cannot exist in nature.

On the whole, this problem seems to have been studied inadequately. Constant accumulations of food plankton in the same places and approximately during the same times, the interrelation between these accumulations and feeding on them by the whales and other animals do not speak of incidental coincidences but of a long evolutionary process which has led to the adaptation of the organisms to the seasonal phenomena of their environment. Academician I.P. Pavlov spoke about it (1938, p. 652): the nervous processes "... cause a more advanced adaptation of the animal's organism to its surrounding conditions, or, in other terms, a complete equilibrium of the organism, as a system, to the external medium, i.e. they provide the existence of the organism". And further: "As a system, the organism of an animal exists in the nature which surrounds it only because of a ceasless equilibrium of this system with the external environment..." (p. 710). This "equilibrium" consists of numerous factors, of numerous, most diverse elements, small and minute details of both the external medium and the internal impulses of the organism. The clarification of all these details and the determination of the causes for the development of the noted regularity have yet to be discovered.

In the North Atlantic (see Table 6), we have seven species of crustaceans and two species of mollusks which serve as food for the blue whales. Among the crustaceans, three species belong to the euphausiids, two to the amphipods, one species to the copepods, and one to the mysids. Both mollusks belong to the gastropods inhabiting a layer of water and sometimes forming large aggregations.

The main prey for the blue whales in the North Atlantic is justly considered <u>Thysanoessa inermis</u>, followed in importance by Meganyctiphanes norvegica. Other animals are not as important; they are found in the stomachs of the blue whales of the North Atlantic only seldom and then in small numbers. We do not find in literature any information regarding the feeding of the blue whales in the North Atlantic on schools of fish and squids. It is quite probable that the fish and squids are not at all the prey for the blue whales of the mentioned region. However, it also is possible that, in exceptional cases, when there are no euphausiids, the blue whales might from time to time feed on fish, such as caplin or herring, and squids (Illex illecebrosus, for instance).which form large aggregations. The lack of [129] these animals in our lists (see Table 6) may be explained simply by the incomplete knowledge of the feeding of these whales in the mentioned regions.

When we analyse the data we collected, we may state that the blue whales of the Northern Atlantic also are capable of selecting food as they do in the Antarctic Ocean. The basic source of food for the blue whales here are, undoubtedly, the euphausiids.

The general list of the food objects of the blue whales inhabiting the northern half of the Pacific Ocean includes fifteen species of animals, i.e. only one species less than for the Antarctic Ocean. Nine out of fifteen species belong to the crustaceans (six of these belong to the euphausiids); three species belong to mollusks: two to brachiopods,which also are among the prey for the whales of the North Atlantic, and one species belongs to cephalopod mollusks (pelagic squid which sometimes forms enormous rapid-moving schools). The remaining three species of prey belong to the fish: two of these are of a school type, pelagic, while the third species is sand ell, leading a benthonic way of life, and which also forms large aggregations. Not all of these animals are as important to the feeding of the whales. The main food, as already noted for the two preceeding regions, consists of the euphausiids, the most important being Euphausia pacifica, Nematoscelis difficilis, Thysanoessa inermis, T. longipes, and, in some regions, also T. raschii. All the other animals listed in Table 6, which were discovered by various scientists in the stomachs of the blue whales, are captured by these whales very seldom, either accidentally, while feeding on the euphausiids, or due to necessity, when no usual food is found.

As may be seen, the capacity of the blue whales to select the euphausiids may be traced quite distinctly also in the northern half of the Pacific Ocean. Our data coincide with the findings of Japanese scientists. T. Nemoto (1957) points out in his work on the feeding of the whales in the northern part of the Pacific Ocean (primarily the whales captured in the waters around the Aleutians) that among the 426 stomachs of the blue whales he examined, 228 were empty, 196 contained only the euphausiids, and 2 contained both the euphausiids and the Calanus spp. T. Nemoto did not discover any other food in the stomachs of the blue whales.

On August 28, 1955, a large (17.8 m long) (Pacific) right whale was captured in the Sea of Okhotsk, in the area adjacent to Paramushiro Island, in the area of the fourth Kurile strait; in its stomach, only Calanus plumchrus (Klumov, 1962) was discovered. On the same day, and in the same geographical location, but a few hours later, another whaling vessel captured a blue whale; its stomach contained a clot of food consisting of Euphausia pacifica exclusively. It may be maintained that this whale fed at a depth of more than 50 m and did not rise to the upper layers of water where Calanus spp. were abundant, as may be judged from the stomach of the whale captured in that area. This blue whale, while rising to the surface for breathing and diving, went on two occasions through accumulations of the Calanus sp., without touching it. This, undoubtedly, indicates why these crustaceans were not found in its stomach. This fact once more confirms that the blue whales can select the euphausiids and that they are not rivals either of right whales or sei whales, as will be seen later.

During June and July, 1957, according to the oral report of N.N. Martynov, the Commander of the Second Far East Whaling Flotilla, the blue whales were present constantly in the waters around the Kuriles, on the Pacific Ocean side, in one and the same strictly delimited region, at the traverse of Rasshua and Shiashkotan islands. The whaling vessels of the aforesaid flotilla captured more than forty blue whales in that area during a very short period of time. When their stomachs were examined, /130/

it was found that they contained a "large 'kapshak'"[*], i.e. the euphausiids. End of July - beginning August[1], the blue whales were no longer seen in the mentioned area.

Proceeding from Martynov's report, it may be assumed that the constant stay (for about two months) of the blue whales in the waters of the Kuriles, at the traverse of Rasshua and Shiashkotan islands was connected with the abundant accumulation of the euphausiids there (most probably, E. pacifica), which served as prey for them. After the euphausiids descended to a considerable depth, or after the aggregations were eaten up, the blue whales disappeared from that area. No other whales, except the blue whales, were observed there constantly for the period of time referred to.

These data confirm once more that the euphausiids should be regarded as the chief source of food for the blue whales and that the feeding grounds of these whales are located in the places of large accumulations of these crustaceans. It is doubtful that sardine and caplin, and especially sand eel, might be the prey for the blue whales, and hence it is doubtful that they might play any essential role in the feeding of these whales.

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* The term "kapshak" is transliterated from the original. Translator.

1. Last groups of blue whales were seen as follows: August 1st- three groups of two whales in each; August 3rd- three groups, two whales in each, one group consisted of four, and another still, of five whales. After August 3rd, the blue whales were not seen (the observations were carried on).

It is probable that the aforesaid may also be applied in regard to the squids.

In summing up the aforesaid about the feeding of the blue whales in the World Ocean, we come to the following conclusions: in the Antarctic waters, the local herds of blue whales prey on 16 species of various animals, the basic of which are four species of the euphausiids. In the northern half of the Pacific Ocean, the local herds of blue whales feed on 15 species of animals, the chief ones being three species of the euphausiids. For the North Atlantic, regarding the feeding of the blue whales which have been studied least, two local herds of these whales feed on nine animals, the main being only two species of the euphausiids. All the other animals listed in Table 6 do not play any significant role in the feeding of the blue whales and are secondary, and some are accidental.

The change in the feeding region of whales, even within one province, may cause the change in the series of the prey or the rearrangement of their importance, as was seen in the blue whales of the Antarctic Ocean (for instance, the blue whales of the Kergeulen herd feed mainly on _E. vallentini_, while the herds with the feeding grounds located in sectors I and VI of the Antarctic feed, along with _E. superba_, also on _T. macrura_). Similar phenomenon was noted in two herds of sperm whales inhabiting the northern and the southern waters of the Kuriles (Klumov, 1959).

In 1936, while comparing the feeding of the beluga (Delphinapterus leucas. Translator) from various regions which are characterized by various hydrological conditions, specific climate, peculiar fauna, etc., we introduced the term "biological analogues of feeding" (Klumov, 1936). These analogues are forms which replace one another in the feeding of one and the same species in various regions of the World Ocean. They must /131/ have approximately the same ecological "profile".

As biological analogues for the whalebone whales are such marine animals which, firstly, form concentrations abundant enough (Klumov, 1961) so that these whales might take within a short period of time large numbers of these small animals. Secondly, these animals should inhabit the same horizons (in regard to depth) which usually serve as the feeding grounds for these whales. Thirdly, they should meet the selective capacities of the whalebone whales (of each species individually). Fourthly, their behaviour and accumulations should provide the whalebone whales with some clues as to their presence (they produce some sounds or noises which are due to their movement).

Table 7

BIOLOGICAL ANALOGUES OF THE FEEDING OF BLUE WHALES IN MAIN WHALING AREAS OF THE WORLD OCEAN (I- most important; II- secondary)

Antarctic	North Atlantic	Northern half of the Pacific Ocean		
		south- & middle Kurile waters	north-Kurile, Commander & Kamchatka waters	east-Aleutian waters
		I		
Euphausia superba	Thysanoessa inermis	Euphausia pacifica	Euphausia pacifica	Thysanoessa inermis
Thysanoessa macrura	Meganyctiphanes norvegica	Thysanoessa inermis	Thysanoessa inermis	Thysanoessa longipes
Euphausia vallentini*				
		II		
Euphausia crystallorophias	Thysanoessa longicaudata	Thysanoessa longipes	Thysanoessa longipes	Thysanoessa spinifera
Parathemisto gaudichaudi	Themisto libellula	Thysanoessa raschii	Calanus plumchrus	
		Calanus plumchrus		

* This species is the most important prey only to the blue whales of the Kergeulen herd [Ichikhara, 1961].

In spite of the insufficient data, we, nevertheless, have attempted to compile a table of the biological analogues of the feeding of the blue whales, in accordance with the basic whaling regions of the World Ocean (Table 7).

The data in this table reveal clearly that the blue whales, discovered everywhere in the World Ocean, have a rather quite small number of prey and during their evolution, they adapted themselves to feeding on the euphausiids.

HELMINTHOFAUNA

It seems most probable that the composition of the helminthofauna of these whales depends to some degree upon the composition and the number of the prey, i.e. upon the specific weight of this prey used as food for them. Hence it may be quite appropriate to study, before drawing general conclusions, the data at hand pertaining to the helminths of the blue whales in the Antarctic, the North Atlantic, and the northern half of the Pacific Ocean.

In order to be able to judge the composition of the helminthofauna of the blue whales inhabiting various regions of the World Ocean, and also in order to compare the helminthofaunas of these whales among themselves, we should have detailed and complete data.

For the northern half of the Pacific Ocean, we have series of helminths of the blue whales of the Asiatic population produced by our expedition (Skr'abin, 1959) (20 whales captured in the north-west of the ocean were studied). We do not have any data on the helminthofauna of the American population of the blue whales. Even in the latest report on the endoparasites of marine mammals published by Margolis (1954) and supplemented by Margolis and Pike's article (1955), the data on the helminths of the blue whales are lacking completely. We are unable to find a single work on this subject in the extensive bibliography supplied by the above authors.

Some twenty works, written primarily at the turn of the past and the beginning of this century, treat of the helminthofauna of the cetaceans of the North Atlantic, including that of the blue whales. Although these works are based on the review of a relatively small volume of the material, they allow us, nevertheless, to visualize a picture about the helminthofauna of the blue whales of this vast area, although not to the degree of minuteness we desire.

The helminthofauna of the blue whales of the Antarctic here seems to be studied best, as the number of their catches reached (1920 - 1940) some 15 - 30 thousand animals during one whaling season (see Table 4 and Table 5). During those twenty years, the biology of the blue whales, and also their helminthofauna, were studied quite intensively. Episodic collections of the helminths of the cetaceans have been continued in the Antarctic by both the Soviet and foreign scientists. However, sad as it is, the said collections were gathered, and still are being collected, chiefly in order to study the classification, and not to clarify the zoogeographical peculiarities of the distribution of the helminths and their hosts. Only this may explain the present "break" of the helminths from their hosts, and chiefly their break from the place where they have been collected (Baylis, 1932; Margolis, 1954, etc.). Even in the latest report on the helminths of the sea mammals of the World Ocean (compiled by Delamure), comparative material is given only for the large zoogeographical regions of the globe, while the descriptions of each individual species of helminths as presented in the classification lack data from which one might conclude who was their host and when their discovery was made. In the future, while collecting helminths, no matter where, one should accurately note the coordinates of the catches of whales containing a certain helminthofauna and the number of the species of the endoparasites. The place of the collection should also be considered when treating and describing the endoparasites, as we now know for sure (Klumov, 1952, 1955, 1957, 1959, etc.; Ichikhara, 1961; Coldwell, 1955; Jonsgard, 1955; Fudzino, 1960, etc.) that on large areas of the World Ocean we always deal with a heterogeneous population of whales; this population is divided into local, and sometimes even microlocal herds, which originated because of individual peculiarities of the animals, i.e. their biological diversity (Klumov, 1955) or the difference in their capacities (Guryanova, 1957). Each of these herds occupies "its" secluded winter and summer grounds.

S.L. Delamure (1955, p. 483) lists in his report on the blue whale (as a species inhabiting the World Ocean) 11 species of helminths, i.e.: Ogmogaster antarcticus, O. plicatus, Tetrabothrius affinis, Priapocephalus grandis, Anisakis simplex, Terranova decipiens, Crassicauda crassicauda, Bolbosoma balaena, B. brevicolle, B. turbinella, B. hamiltoni. [133]

Among the mentioned endoparasites, there is not a single endemic characteristic of only this whale.

The list quoted above may be supplemented by the following helminths which were recently discovered in the blue whales.

1. Tetrabothrius wilsoni. Markowski (1955) identified and described it anew. According to the latter, this species was assigned to T. affinis without sufficient evidence. His conclusions and the differences of T. wilsoni described are quite convincing and deserve some considerations. We regard this species as one existing parallel with T. affinis.

2. Tetrabothrius schaeferi. Markowski (1955) described a new species of the trematode of the named genus, which was discovered in a blue whale captured in the Antarctic. The distribution of this species, according to the author, encompasses the Antarctic Ocean and the waters around St. George Island.

3. Crassicauda tortilis- a new species, which was described by A.S. Skr'abin (1959), a member of our expedition. It was discovered in two blue whales of a Pacific herd of the Asiatic population, captured in the waters near the northern Kuriles in 1955.

4. Diplogonoporus balaenoptera. Markowski (1955) noted for the first time this cestode as a parasite of the blue whale captured in the waters adjacent to South Georgia (Antarctic Ocean).

5. Bolbosoma nipponicum. It was discovered for the first time in the blue whales of a Pacific herd of the Asiatic population by A.S. Skr'abin, a member of our expedition (1959). The whales were captured in 1955 near the southern Kurile Islands.

6. Bolbosoma paramuschiri- a new species, described by A.S. Skr'abin (1959). It was discovered in 17 blue whales (out of 18 examined) of a Pacific herd of the Asiatic population. The whales were captured north of the Kuriles in 1955.

7. Anisakis sp. larva- larval stages of the nematodes of the genus Anisakis, which cannot be identified as to species. They were discovered in the blue whales of a Pacific herd of the Asiatic population, captured in 1955 north of the Kuriles, by A.S. Skr'abin (1959).

Thus, the list of the helminths of the blue whales has recently increased considerably and contains 18 species. Moreover, we have included in this list one more nematode, which cannot be assigned to the endoparasites. This is Odontobius ceti, which is a commensal and which was discovered by the scientists in a gluey slime on baleen plates of whalebone whales. It should be noted that A.S. Skr'abin (1959) had examined the slime he took from the baleen plates in five blue whales captured in the north of the Kurile waters of the Pacific Ocean. He discovered for the first time, in all five whales, the aforesaid nematode "... in great numbers...".

We have included the commensal nematode Odontobius ceti in the general list of the endoparasites of the blue whales, disrupting in this way, to some degree, the principle of its compilation, as the new species represents, from our viewpoint, great interest to the clarification of the ontogenetic relation of the blue whales inhabiting various regions of the World Ocean.

If we compare the helminthofauna of the blue whales inhabiting the Antarctic Ocean with that of the blue whales of the North Atlantic, we find that both share five common helminths (two nematodes and three acanthocephals). The blue whales of the Antarctic herds have one endemic form (Tetrabothrius schaeferi), which, for the time being, has not yet been discovered in other whalebone whales and the toothed whales of the Antarctic, as well as in other regions of the World Ocean. No endemic forms of helminths were discovered in the blue whales of the North Atlantic.

Table 8

HELMINTHOFAUNA OF THE BLUE WHALES INHABITING

THE BASIC WHALING REGIONS OF THE WORLD OCEAN

Arctic & adjacent regions	North Atlantic	North of Pacific Ocean
Ogmogaster antarcticus	Ogmogaster plicatus	
Tetrabothrius affinis		Tetrabothrius affinis
Tetrabothrius wilsoni		
Tetrabothrius schaeferi		
Priapocephalus grandis		Priapocephalus grandis
Diplogonoporus balaenopterae		
Anisakis simplex	Anisakis simplex	Anisakis sp. larva
Terranova decipiens		
Crassicauda crassicauda	Crassicauda crassicauda	Crassicauda tortilis
Bolbosoma balaenae	Bolbosoma balaenae	Bolbosoma nipponicum
Bolbosoma brevicolle	Bolbosoma brevicolle	Bolbosoma paramuschiri
Bolbosoma turbinella	Bolbosoma turbinella	
Bolbosoma hamiltoni		
Odontobius ceti		Odontobius ceti

Note. The data on the helminths of the blue whales inhabiting the Antarctic and adjacent regions are according to the works of Delamure (1955); Baylis (1929, 1932); Freund (1932); Markowski (1955), etc. The data on the North Atlantic are taken from Delamure (1955); Freund (1932), and others; on the northern half of the Pacific Ocean, on the whole from the collections of our expedition (Skr'abin, 1958, 1959, etc.), the data of Margolis (1954), and Margolis and Pike (1955), and other sources.

When we compare the helminthofaunas of the blue whales of the Antarctic waters and the northern half of the Pacific Ocean, we note that they share only two common species of helminths and one nematode (commensal), which lives on the baleen plates. The blue whales of the Pacific herd of the Asiatic population have two endemic forms of helminths, which have not been discovered in other whales inhabiting both the Pacific Ocean and other regions of the World Ocean. This is nematode Crassicauda tortilis and acanthocephal Bolbosoma paramuschiri. If we compare the helminthofaunas of the blue whales of the North Atlantic and the northern half of the Pacific Ocean, we do not find a single common endoparasite. The last aspect, which should be borne in mind while examining the data summed up in Table 8, is the complete lack of the information on the helminths of the blue whales, the representatives of the America population of the Pacific Ocean.

What conclusions should, then, be drawn from the above comparisons? First of all, there is a conclusion about the relatively closer, and probably older (or, at any rate, more prolonged in time) link between the blue whales of the North Atlantic and the blue whales inhabiting the Antarctic Ocean. This is substantiated by five common species of helminths, out of six discovered in the blue whales of the North Atlantic which belong to three divisions and three families.

Species	Family	Division
Anisakis simplex	Anisakidae	Ascaridida
Crassicauda crassicauda	Crassicaudidae	Spirurida
Bolbosoma balaenae		
Bolbosoma brevicolle	Polymorphidae	Palaeacanthocephala
Bolbosoma turbinella		

The blue whales of the North Atlantic and the Antarctic Oceans have one more endoparasite, represented by one genus but various species: Ogmogaster antarcticus and O. plicatus. However, according to Skr'abin (oral report), these species are, if not identical, then, at any rate, very closely interrelated and difficult to distinguish from one another[1]. It is most probable that a comparison of these two trematodes on large series will lead to the fact that O. antarcticus will be reduced to the synonym of O. plicatus. Consequently, it may be considered that all six species of the helminths so far discovered in the blue whales of the North Atlantic are common with the helminths discovered in the blue whales of the Antarctic Ocean.

1. It is possible that the beginning of the divergence of the classification characters of these trematodes is quite recent, and the distinguishing characters have not yet reached the required degree of differentiation. Most probably, however, we are dealing here with individual variability.

2. It is also possible that the list of the endoparasites of the blue whales in the North Atlantic will be enlarged considerably, if their helminthofauna is studied rather more thoroughly, as the investigations which were carried out before (primarily at the turn of the past century) were inadequate. In particular, a hypothesis may be proposed that such helminths as Tetrabothrius affinis, which was discovered in the blue whales of the Antarctic (undoubtedly "brought in" by them from the Atlantic) and in sei whales inhabiting the North Atlantic, or Diplogonoporus balaenopterae, which also had been discovered in the blue whales in the Antarctic Ocean and in sei whales and fin whales in the North Atlantic, and a number of other helminths have not yet been discovered in the blue whales inhabiting the North Atlantic. Should this hypothesis prove to be correct, then the presence of the above-named endoparasites in the blue whales of the North Atlantic would strengthen even more the hypothesis concerning the penetration of the blue whales from the North Atlantic into the Antarctic. It seems that this really was the way they spread.

The blue whales of the Antarctic Ocean have also endemic forms of helminths (Tetrabothrius schaeferi) and the parasites which, although occurring in other whales of the Antarctic, differentiate the Antarctic whales from the blue whales of the North Atlantic (Tetrabothrius wilsoni, Terranova decipiens, Bolbosoma hamiltoni, etc.)[1]

1. We do not touch upon the morphological differences of the blue whales inhabiting the North Atlantic and the Antarctic Oceans.

and undoubtedly bears witness to their modern, at any rate, isolation from one another. [136]

The second conclusion which may be drawn from a comparison of the helminthofaunas of the blue whales located in various regions of the World Ocean is the presence of a lesser link between the blue whales of the Antarctic Ocean and the blue whales inhabiting the northern half of the Pacific Ocean. Here we discover only two common endoparasites which belong to one family and one division: Tetrabothrius affinis and Priapocephalus grandis (Tetrabothriidae, Cyclophyllidea).

Of course, the helminthofauna of the North-Pacific blue whales, and especially that of the American population, has not yet been studied adequately. However, the endemic forms specific of only the whales of the Asiatic population of the northern half of the Pacific Ocean (Crassicauda tortilis, Bolbosoma paramuschiri; Skr'abin, 1959) point to its weaker relation to the helminthofauna of the Antarctic whales and its more pronounced originality. However, we should not deny the relation which took place between the Antarctic and Pacific blue whales, proceeding not only from the two discovered endoparasites mentioned above. This relation is also substantiated by the presence of one more mutually common nematode-commensal Odontobius ceti, discovered in the whalebone whales of the Antarctic for the first time by Russel de Vauzeme in 1834, later investigated in the same place by Baylis (1923; after Delamure, 1955, p. 335) and for the first time discovered in the blue whales inhabiting the north-west of the Pacific Ocean by A.S. Skr'abin. It seems that formerly the scientists did not pay any attention to the study of the baleen plates and did not look for these nematodes in the whalebone whales inhabiting the Pacific, and, perhaps, even the Atlantic oceans.

We may conclude from the aforesaid that along with the relation, weak as it may have been which once existed between the blue whales of the Antarctic Ocean and the blue whales of the northern half of the Pacific Ocean, there are noted in the helminthofaunas differences which bear witness to their quite remote isolation.

Finally, the third conclusion which follows from the comparison of the helminthofaunas of the blue whales of the North Atlantic and the northern half of the Pacific Ocean is the complete lack of former and contemporaneous links between them. The blue whales of the above-named regions, in spite of the presence of common genera, do not have even one single species of helminths in common. This indicates a very remote isolation of the populations of the blue whales described and the lack of any contacts between them.

Thus, having analyzed all the data on the comparison of the helminthofaunas of the blue whales inhabiting various regions of the World Ocean, we may state the following hypothesis.

Many scientists are inclined to think that the centre of origin of the whales, including the rorquals, was located somewhere in the area of the modern North Atlantic. Proceeding from the paleontological data available and modern geological evidences, this hypothesis seems to be the most plausible. If we accept the idea that the North Atlantic is the cradle of the origin of the blue whales, we may trace the following route of their distribution. The blue whales of the North Atlantic, having been pressed south during the period of glaciation, penetrated into the North Atlantic, and from there further south, into the Antarctic Ocean, where they occupied the waters around the Antarctic Continent. From the Pacific sector of the Antarctic Ocean, they went up north and penetrated [137] into the northern half of the Pacific Ocean, having formed there an individual population, which soon had lost any links with the population of the blue whales of the southern hemisphere. As a result of the above-said spread, there came into being a population of blue whales in the North Atlantic, which presently has been divided into two local herds, North-American and European. The population of the blue whales in the southern hemisphere, separated into a number of local herds, the boundaries of the areas occupied not being accurately established, and two populations in the North--Pacific Ocean- Asiatic and American, of which the former has also been divided into two local herds (Fig. 11).

It is most probable that the greatest exchange existed in due time between the populations of the blue whales inhabiting the North Atlantic and the Antarctic Oceans. A rather weaker and short-lived exchange did exist between the blue whales of the South Pacific and the North Pacific seas; and there was no communication of any kind via the Arctic Ocean between the blue whales of the North Atlantic and the North Pacific oceans.

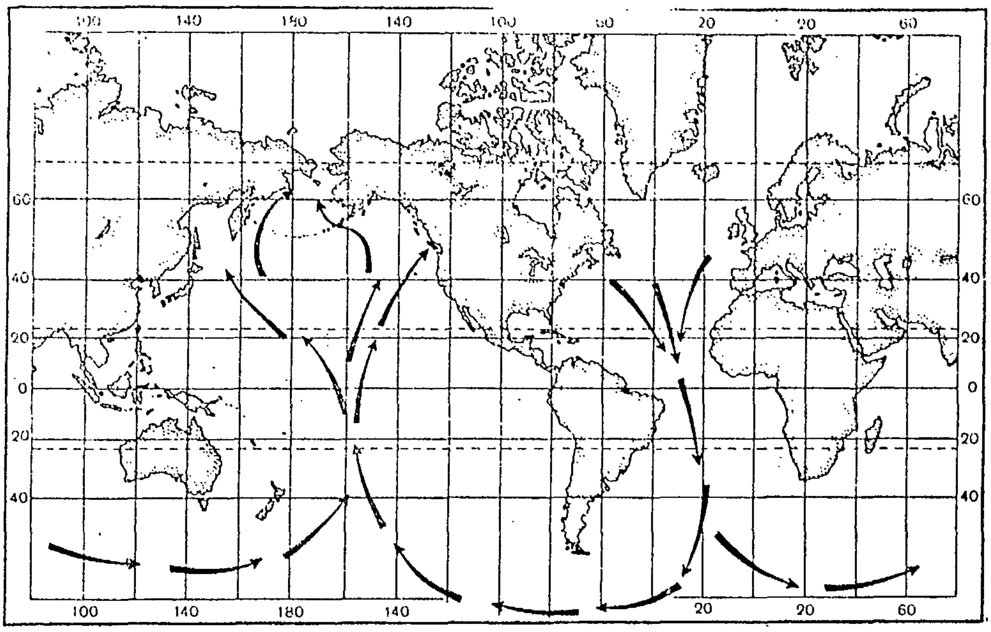

Рис. 11. Пути проникновения синих китов в Южный Ледовитый океан и в северную половину Тихого океана. Схема составлена на основании сравнения гельминтофаун синих китов из разных областей Мирового океана (ориг.)

Fig. 11. The route of the blue whales along which they penetrated into the Antarctic Ocean and the northern half of the Pacific Ocean. The scheme compiled on the strength of the comparative study of the helminthofaunas of the blue whales inhabiting various regions of the World Ocean (orig.).

At present, the exchange of individual blue whales in individual populations does not at all take place, and all the populations mentioned above are separate, isolated. The contacts mentioned above ceased to exist a long time ago. This may be substantiated by the presence of endemic species in the series of the helminths discovered in the blue whales of the Antarctic and the North Pacific.

While studying the lists of helminths of the blue whales inhabiting the three regions of the World Ocean, our attention is drawn by the large number of endoparasites discovered in the blue whales of the Antarctic herds as compared with others. At first sight, this causes contradictory ideas. On the one hand, it seems that it should be so, as the largest number of helminths corresponds also to the greatest number of prey (Table 9).

Table 9 [138]

Comparative Number of Species of Endoparasites and of Prey for the Blue Whales Inhabiting Various Regions of the World Ocean

	Antarctic whales	North-Atlantic whales	North-Pacific whales
Number of species of helminths	13	6	6
Number of animals of prey	16	9	15

On the other hand, however, we know that the food of the blue whales of the Antarctic herds is very monotonous, as E. superba plays the most important role in feeding local and individual whales. All the other animals serving as prey for the whales (see Table 6) are, on the whole, not as important (this holds true, on the whole, for the Antarctic waters).

The data of our expedition, and Nemoto's published data (1959) on the blue whales of the northern half of the Pacific Ocean, indicate that the food of these animals is more varied, as may be seen from Table 7. The stomachs of the blue whales captured in various regions of the Pacific Ocean may be filled with one of the following species: E. pacifica, T. inermis, T. longipes, and sometimes T. raschii, and even Nematoscelis difficilis. It might seem then that it was here that the dependence expressed above should be manifested completely, i.e. the more varied the food, the greater number of species of helminths should be discovered in a given species of whales. However, our data (see Table 9) do not seem to substantiate this statement, and the number of the helminths discovered in the whales of the North Pacific and the North Atlantic oceans is twice as little as it is in the whales of the Antarctic Ocean. We interpret this phenomenon as follows.

First of all, the knowledge of the helminthofaunas of the blue whales of the Antarctic, North-Atlantic and North-Pacific waters varies. We know best the helminthofaunas of the blue whales of the Antarctic Ocean, hence the more complete list of helminths typical of these whales. The helminthofauna of the North-Atlantic blue whales has been studied less, and less still is the helminthofauna of the whales inhabiting the northern half of the Pacific Ocean. The data on the helminthofauna of the North-Pacific blue whales is the result of a study of only twenty specimens (Skr'abin, 1959) of a local Pacific herd of the Asiatic population (Klumov, 1959). In passing, we would like to note that the infestation of the blue whales of the mentioned local herd was relatively weak. Twenty whales were examined; of these, one did not have any helminths; eight whales contained one endoparasite in each; five whales had two helminths in each; five had three in each; and one whale had five species of endoparasites.[1]

Secondly, the large list of helminths and the animals serving as prey for the blue whales inhabiting in the summer the Antarctic Ocean may be explained, in our opinion, also by the circumstance that here we are dealing with two combined data obtained as a result of the study of several local herds (at least four or five, perhaps even six) [139] occupying various regions of the Antarctic Ocean and possessing their specific features. The biological variability in regard to the quality of these herds (Klumov, 1955) also plays a very important role, especially when food is selected; this, no doubt, also affects the helminthofauna. Thus, if it were possible for us to separate this list (see Table 8) and assign the individual species of helminths in accordance with individual local herds, and also to do the same thing in regard to the list of the animals which serve as prey for the whales (see Table 6), then the common

1. Calculated from the journal of helminthological discoveries by A.S. Skr'abin. S.K. Klumov.

composition of the helminthofauna of each local herd of blue whales would be small, as the series of prey for the blue whales of the mentioned herds would, undoubtedly, change both in regard to the quality and to the number of species. The reason for this relatively large number of helminths and the prey for the blue whales of the Antarctic Ocean is that it is impossible to make such a division. Ichikhara's interesting data (1961) on the local Kergeulen herd of blue whales whose food was only one species, i.e. Euphausia vallentini, as quoted above, substantiate this statement. The specificity of these whales, no doubt, could not but influence both the composition of their helminthofauna and the degree of their infestation. Unfortunately, T. Ichikhara did not pay any attention to this part of the question and while studying the whales of the Kergeulen herd, he did not do a detailed study of their helminths.

Thus, the hypothesis stated above pertaining to direct dependence of the number of prey and the number of species of the endoparasites, we believe, is not contrary to the data present on the blue whales of the Antarctic Ocean.

If we compare the material on the helminthofauna of and the prey for the whales of various regions, and especially of close, adjacent areas, we should always establish the affiliation of the whales to a certain local herd and determine accurately the boundaries of their habitation.

COMPETITION FOR FOOD

In one of our works (Klumov, 1958), we have already noted that the whalebone whales have numerous rivals which feed on the zooplankton, i.e. pelagic fish, marine birds, sephalopod mollusks, and other animals, not to mention the presence of the competition for food among the whalebone whales themselves. During the years when the plankton is scarce, it is consumed quite rapidly, and the competition in regard to food becomes even more pronounced. The scientists have never paid enough attention to the rivals of the whales and the role they play in eating up the food plankton. The observations made by the members of our expedition reveal that for the northern half of the Pacific Ocean this is a very essential factor, which affects quite strongly the distribution of the whales, their movements and behaviour, especially during the years when the plankton is not abundant.

The rivals in regard to the food of the blue whales of the Antarctic Ocean are, first of all, all other whalebone whales, i.e. fin whale, sei whale, humpbach whale, lesser rorqual, and, although not numerous, the right whale. Moreover, this list should also be supplemented by some seals, i.e. crab-eating seal, Weddel seal, to a lesser extent Ross seal, all the marine birds and some species of penguins, which, on the whole, also feed on Euphausia superba.

However, in spite of the abundance in regard to the species and the number of the feeders on the euphausiids in the Antarctic Ocean, the general productivity of the Antarctic Ocean is such that an enormous amount of the zooplankton annually remains unused. This is why it cannot be considered that there is an eager competition between the species mentioned above in regard to food. [140]

The main rivals of the blue whales in the North Atlantic may be fin whale, sei whale, and lesser rorqual; herring, caplin, cod, coalfish, ocean perch, and mackerel; murre (Kaftanovsky, 1951; Storer, 1952), and some others. Because of the extremely active whaling, the number of the whalebone whales in the North Atlantic has reached such a low level that there can hardly be any mentioning of a lack of the food plankton for the whales and any rivalry between them and other animals feeding on the same animals.

The most complete list of prey [? competitors] for the blue whales is that for the northern half of the Pacific Ocean. Of the whalebone whales these are, first of all, fin whale, to a lesser extent sei whale, humpback whale, and lesser rorqual, and less still grey whale. Of the seals we may mention Phoca hispida ochotensis, which during a certain period of the year feeds almost exclusively on the euphausiids, mainly Thysanoessa raschii. Of the pelagic fishes, the main rivals are herring and the salmonids (except keta) during their life in the sea (Mednikov, 1961; Ponomareva, 1963), walleye pollock, sardine, mackerel, and some others. The main rivals on the part of cephalopod mollusks are pelagic squids Ommatostrephes sloanei-pacificus and Loligo opalescens. A study of the content of the stomachs of the birds (I.N. Sukhanova and Klumov) has revealed that slender-billed shearwater and sooty shearwater, Laysan albatross and black-footed albatross, fulmar, and, to a lesser degree, murre (see also Storer, 1952), and some other species, too, feed primarily on the euphausiids.

We believe that the competition for the zooplankton as food among the animals inhabiting the northern half of the Pacific Ocean is not intense. It becomes keen only during the years when the plankton is not developing sufficiently enough (the "lean years").

In connection with the aforesaid, it is of interest to note that there is a division of the feeding zones in the water (along the vertical) and the prey between the blue whales, on the one hand, and the right whales and sei whales, on the other. This division may be traced everywhere in the World Ocean where the areas of the three above--named whale species overlap.

The right whales feed only on the Calanus spp. which accumulate in surface waters, up to 15 - 20 m deep. The sei whales, also preferring the Calanoida to any other prey, migrate in search of food and feed primarily in the surface layer, hence they resemble the right whales very much and are their rivals. The blue whales, while "avoiding" the competition with the right whales and sei whales, and so also with other marine animals feeding on the Calanoida which feed in the upper zone of the pelagic zone, "submerged" deeper during their evolution, adapted themselves to the search of food in the water below the level 50 m deep, and turned to the feeding on the euphausiids. In this zone, the competition for food for the blue whales has considerably diminished, as of all the whalebone whales, this zone is penetrated chiefly by the fin whale, which screens the entire surface of the pelagic zone to a depth of more than 100 m and is a polyphagian to a greater extent than all the other whalebone whales. As regards the humpback whale, at least under conditions of the northern half of the Pacific Ocean, it cannot be regarded as a serious competitor of the blue whale as it feeds primarily on fish, only seldom descends to a depth of more than 50 m, and feeds on the zooplankton only when it does not find its choice prey in abundance. The aforesaid is presented in Fig. 12 [☆]. /141/

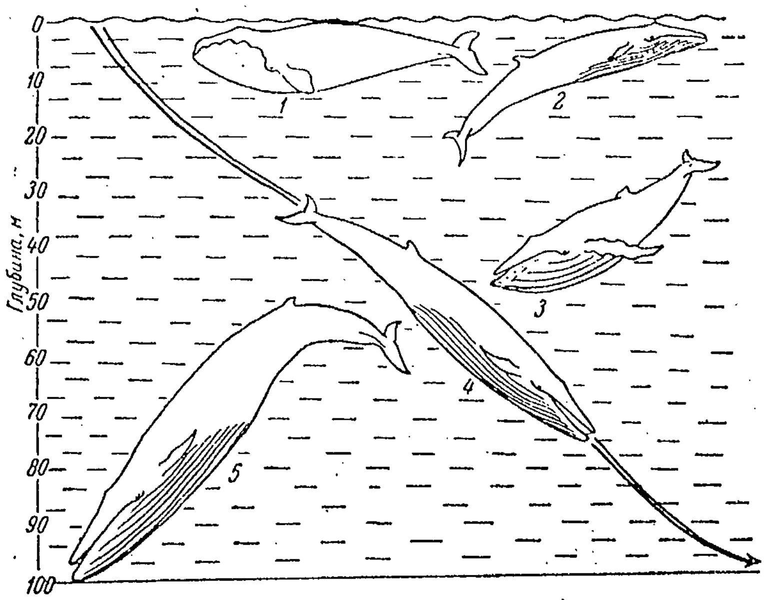

Рис. 12. Схема распределения зон питания усатых китов в толще воды (по вертикали).

1 — японский кит; 2 — сейвал; 3 — горбатый кит; 4 — финвал; 5 — синий кит (ориг.)

Fig. 12. Feeding of the whalebone whales (vertically).

1- Pacific right whale; 2- sei whale; 3- humpback whale; 4- fin whale; 5- blue whale (Orig.)

☆ This scheme does not include the grey whale the zone of feeding of which is presented separately.

QUANTITATIVE CHARACTERISTICS OF FEEDING

In literature, there are scarcely any quantitative indices pertaining to the feeding of the blue whales. Salnikov (1956) points out that he used to discover simultaneously up to 1,000 - 1,200 kg of euphausiids in the stomachs of individual blue whales of the Antarctic Ocean. These data coincide well with those of Collet (1889) on the blue whales of the North Atlantic. Collet writes that on one occasion, a blue whale was captured in the stomach of which 1,200 l of Thysanoessa inermis was discovered. This seems to be the limitation of the filling of the whale's stomach, which fact was recorded by the scientists.

As regards the quantitative characteristic of the feeding of the blue whales of the northern half of the Pacific Ocean, the number of the stomachs studied by the members of our expedition were so small, so that we do not have any representative data on this problem. This kind of data was also missed by the Japanese scientists who in their studies, judging from the works published, left the problem of the feeding of the whalebone whales untouched.

Nevertheless, it should be pointed out that the maximum filling of the stomachs in all whalebone whales is rare. The whales of the Antarctic waters present an exception in this regard. As a rule, the actual filling of the whale's stomach is much less than the stomach can hold, and it does not exceed 50% of the stomach's volume. [142]
In most cases, however, the filling is even less than 50%.

Our calculations indicate (Klumov, 1961) that during the feeding period, the whalebone whales require about 30 - 40 g per kilogram of live weight. Proceeding from the above indices, the 24-hour-long requirement of food for the blue whale of average size and weight (23.5 - 24.5m, 60 - 70 t) is 2 - 2.5 t. The whale can obtain this amount of food only under the following two conditions: if it possesses a perfect apparatus needed in search and discovery of food or if the biomass of the zooplankton is abundant enough. We already noted (Klumov, 1956b, 1959, 1961) that the cetaceans, while in search of food in the ocean, make use of the sound- (or echo-) location. This enables them to explore large areas within a relatively short period of time (they move fast). This capacity has been developed in the whales as a result of their evolution.

The second condition is the sufficient density of the tiny organisms. We have calculated (Klumov, 1956, 1959, 1961) that the biomass of the zooplankton must be more than 2000 mg/sq.m. Only under such condition can the whales use it efficiently and filter the amount which they require during a 24-hour-long period of time. This kind of biomass is quite often found in nature in boreal and sub-arctic waters, in particular, in the northern half of the Pacific Ocean. It must be noted that there are few reliable data on the accumulation of the euphausiids, which are very active and move rapidly, and cannot be captured using our planktonic nets, especially at a depth more than 50 m. It is most probable that these accumulations reach much higher indices than we assume on the strength of our catches using planktonic nets. At any rate, this hypothesis may be substantiated by the catches of the euphausiids using the Isaacs-Kidd midwater trawl (during a short period of time several kilograms of these animals were caught).

CONCLUSION

1. The blue whales of all the areas of the World Ocean so far discussed possess a well-pronounced selective capacity in regard to their food; they have a rather narrow food range and are stenophagous animals specialized in feeding on the euphausiids. Depending on the region (and even microregion) of their habitation, only the species composition of the euphausiids changes, while the biology of these euphausiids remains everywhere almost the same. The feeding of the blue whales on these crustaceans is due to their mass aggregations. The list of the main objects of food- the biological analogues of the blue whales (see Table 7) which replace one another in various regions of the World Ocean substantiates the statement expressed above. All other food objects- crustaceans of other groups (except the euphausiids), mollusks, fish, etc. are secondary or accidental, and do not play an important role in the feeding of the blue whales.

It is only natural that the stenophagous animals, including the blue whales, have a low index in regard to their food plasticity (the latter term was introduced by A.A. Shorygin in 1952). The blue whales change to another food only when forced. Actual material indicates that this is observed in nature only during the years when due to various reasons the normal (average) hydrological conditions of a certain area is disrupted, [143] causing a sharp drop in the number of the euphausiids.

2. Specialization of the blue whales in regard to the feeding on the euphausiids determines their distribution in time and space in accordance with the distribution of places and terms of the accumulation of these crustaceans within the feeding grounds of each individual local herd. This is why it is so important to know the time, place, and boundaries where the feeding grounds of whales are being built. These data are of an extreme significance to man, as they reduce the wasteful voyages of whaling vessels in search of whales.

3. The accumulation of zooplankton, in particular, that of the euphausiids, is observed year in year out for one and the same regions and sections. This happens approximately during the same terms, with some minor changes in space and fluctuations in time. However, the variability of the "density" (biomass) of these accumulations in individual years may be considerable: during some years the number of the euphausiids may be larger than in others[1];

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1. Nemoto (1957) singles out for the northern part of the Pacific Ocean years with abundant biomass of the euphausiids (for instance, 1954, 1956) calling them the years of "krill", and those with abundant biomass of Calanoida, the years of "Calanus" (for instance, 1953). However, he does not explain the reasons for the fluctuations of the number of the above-named crustaceans.

this is determined by the complex of various biotic and abiotic factors. These annual fluctuations of the biomass of zooplankton affect essentially also the distribution, the movement, and behavior of both the individual specimens and the entire herd of the blue whales. This is why it is very important to know ahead the conditions under which the zooplankton in each region accumulates.

4. The reasons for the permanent places in which the zooplankton is formed, in particular, the euphausiids, in the areas of the divergence of water bodies varying in their respective characteristic, have been stated above. In spring, in these areas phytoplankton develops. In its turn, this determines also the development of the zooplankton the accumulations of which depend from year to year upon the local arrangement of the zooplankters which form winter reserves for individual populations of this micro- and even macroregion. These wintering local schools of individual Calanus spp. or of the euphausiids descend in fall to corresponding depths (these are specific for every individual species) and rise in spring to the surface in order to feed and to propagate. The biological state of these groups, their number, capacity and readiness to propagate, conditions for feeding of adults before spawning, feeding conditions which are formed before the larvae appear, and a number of other factors of both the physiological state of the organisms and those of the external medium determine the quantitative development of a certain species. This regularity was

noticed well by V.G. Bogorov (1939), who wrote as follows: "The unity of the environment and of the internal biological state of organisms causes a transfer from one biocoenosis into another. This coincidence of the biological state (readiness) and of the corresponding internal conditions is not accidental, but a result of an evolutionary process which has led to the adaptation of the organism to the seasonal changes of the environment".

5. During the evolution of the marine fauna, not only the whalebone whales, but also many other groups of animals (squids, fish, marine birds, etc.) developed [144]
apparatus for feeding on the zooplankton (including the euphausiids). Natural division of the "zones of feeding" in the water (along the vertical) took place. It seems most likely that the cetaceans (their ancestors, to be more precise) at first developed adaptive organs for feeding only in the surface water (the right whales), and only gradually adaptive apparatus which enabled the whales to descend to deeper and deeper depths (rorquals). In order to avoid the competition in surface waters, the blue whales, apparently, gradually adjusted, first of all, to the feeding at greater depth than the right whales, sei whales, marine birds, a number of pelagic fish and other animals feeding in surface waters, and, secondly, to the feeding on a rather "coarser" food, on faster moving and larger animals than the calanids, the euphausiids, to be more precise, the accumulations of which they found at a depth below 50 m. The evolutionary course of the cetaceans, in particular, the blue whales, was determined, we believe, chiefly by the

conditions of the feeding in the water medium, as all the main properties of the adaptation of these animals, and especially of the whalebone whales, are trophic adaptations.

6. In the boreal, antiboreal and subantarctic waters of the World Ocean, the presence of a great number of the zooplankton, in particular, the euphausiids, which is far from being used up by marine animals, especially during the years of its mass development, allows us to consider that increased competition may start only in the whalebone whales of the northern half of the Pacific Ocean when the prey they feed on does not develop sufficiently enough. Enormous masses of zooplankton, estimated to weigh billions of tons, annually remain unused. The populations of the whalebone whales in the North Atlantic are so small that here, too, as also in the Antarctic waters, the source of their food is more than sufficient.

7. The quantitative aspect of the feeding of the blue whales is presented in literature rather inadequately, and our own data are not indicative and insufficient. The data at hand allow us to speak of a possibility that a blue whale may swallow up to 1,000 - 1,2000 kg of zooplankton at one time. This seems to be the limit of the amount of food for this animal. However, this amount of food is rarely found in the stomach of a blue whale (except for that of the Antarctic). Investigations indicate that 40 - 50% of the stomachs are empty, and those containing food are filled 20 - 50%.

Estimations (Klumov, 1961) allow us to assume that a blue whale, average in size (24 m) and weight (60 - 70 t) requires t - 2.5 of food per 24-hour period.

8. Food interrelations of the blue whales are schematically presented in Fig. 8 for the northern hemisphere and in Fig. 9, for the southern. These schemes also show the degree of resemblance of food objects of the whalebone whales. As already stated, the food relations of the whalebone whales have to be studied more, by presenting in detail the feeding of the prey itself.

9. The study of the helminths in the whales and a comparison of their helminthofaunas and objects of food from various regions of the World Ocean is a question extremely important both theoretically and practically. Our insufficient knowledge of the helminths prevents us, for the time being, from making final generalizations; however, some preliminary considerations regarding the links of individual populations of blue whales, the centre of their origin, and routes of their distribution may be stated.

As regards the resemblances, and also the differences in the helminthofaunas of the blue whales, representatives [145] of individual populations, a rather closer contact is established between the blue whales of the North Atlantic and those of the Antarctic. Weaker ties existed between the Antarctic and the North Atlantic blue whales, and were lacking completely between the blue whales of the North Atlantic and the North Pacific. It seems that direct contacts between the populations of these whales had been interrupted a long time ago and do not exist at present.

The formation of the helminthofaunas of the whales in various regions of the World Ocean is, no doubt, connected with their feeding. This is why these problems should be studied together. On the other hand, the feeding of the whales should be studied parallel to and simultaneously with a thorough study of the helminthofauna of each individual specimen. The most important problem is the most detailed determination of the place where each studied specimen comes from, in order to be able later to determine its belonging to a particular local herd, and also to determine the number of the endoparasites by species for each individual whale.

10. The data at hand indicate that the blue whales from various regions of the World Ocean have not been studied to the same extent. We may note that there is a direct link between the development of whaling (number of animals taken) and the degree to which the blue whales have been studied. Where the catches of these animals were more numerous, they were studied better (the waters of the Antarctic Ocean); where the fishing of whales was not as developed, the knowledge of them was not as advanced (North Atlantic). This circumstance prevented us from presenting comparisons of equal worth. Hence the conclusions drawn in this work are to some degree preliminary.

FIN WHALES

Feeding

The biology of the fin whale, and also its feeding, have been studied more thoroughly than the biology of all the other whalebone whales. This is explained by the fact that recently this species ranks number one in the whaling industry in the World Ocean, and particularly in the waters of the Antarctic (Table 10). In the northern half of the Pacific Ocean, where the sperm whale ranks first as an object of fishing, the fin whale occupies the second place. However, among the whalebone whales of this region of the World Ocean, it, too, takes the first place. A similar picture is also observed in the North Atlantic; there, among large whalebone whales (excluding rorqual), the fin whale is fished for most. However, as the fishing for the fin whales is distributed unevenly in individual regions of the World Ocean, its feeding has been studied to various degree, depending on the region. The feeding of the fin whales inhabiting the northern half of the Pacific Ocean is known better than that of the southern hemisphere.

Table 11 contains all the known data on the feeding of the fin whales of the Antarctic Ocean, North Atlantic, and the northern half of the Pacific Ocean. If we examine these data individually for each of the regions mentioned, we may come to the following conclusion.

Euphausia superba is the chief source of food for the fin whales inhabiting the Antarctic waters and also for the whalebone whales. *Thysanoessa macrura* was discovered in the stomachs of the fin whales in a considerably smaller amount. However, Nemoto (1959) points out that where this euphausia was dominant -140 to 80° w.long. and 40 to 60° e.long., it also was predominant in the stomachs of the fin whales, although *E. superba* was also present in a small number. Besides the above-named euphausiids, of some importance as food for the fin whales of the Antarctic herds is also *E. crystallorophias*. In the area of the waters washing the islands of St. Georgia, the fin whales had in their stomachs Grimothea and Parathemisto gaudichaudi. The latter was sometimes more important as food for these whales, as it was quite frequently discovered that the stomachs of the fin whales were filled exclusively with this amphipod. The fin whales captured near the shores of South Africa contained in their stomachs euphausiids typical of these species, i.e.: E. lucens, E. recurva, and also some fishes (Scomber sp. and representatives of the Clupeidae).

[146]

Fin Whales Caught in Main Fishing Regions of the World Ocean During

Table 10

Таблица 10

Добыча финвалов в основных промысловых районах Мирового океана в 1949—1961 гг. (голов) (animals)

Год Year	Южное полушарие Southern Hemisphere: в Антарктике и водах Южной Георгии Antarctic & South Georgia	Южное полушарие Southern Hemisphere: в водах Южной Африки, Южной Америки, Австралии South Afr. S. America & Australia	Северное полушарие Northern Hemisphere: в Северной Атлантике и Арктике North Atl. & Arctic	Северное полушарие Northern Hemisphere: в северной половине Тихого океана North of Pacific Ocean	Всего Total
1949	19 124	871	1237	441	21 709
1950	20 060	878	1475	489	22 902
1951	19 456	1347	1336	680	22 819
1952	22 527	1147	727	1159	25 605
1953	22 867	879	614	1221	25 581
1954	27 659	979	530	2167	31 335
1955	28 624	843	586	2132	32 185
1956	27 958	818	481	2239	31 496
1957	27 754	961	673	2225	31 613
1958	27 473	1017	406	2602	31 498
1959	27 128	1015	372	2407	30 922
1960	27 575	1014*	289*	2055**	30 933
1961	28 761	839	304	1866	31 790

* Нет данных о добыче одной китобойной компании Чили; известно, что в 1960 г. было взято 169 усатых китов, без определения вида.

** В Испании было добыто 75 усатых китов; сколько из них финвалов — неизвестно. Эти киты в таблице не учтены. Таблица составлена по данным, опубликованным в «Norsk Hvalfangst tidende» за 1951—1961 гг. и в «Internationale Whaling Statistics», V. 30—39.

* The data of one whaling company in Chile is lacking; it is known that 169 whalebone whales were captured (the species were not identified).

** 75 whalebone whales were captured in Spain; how many of those were fin whales, we do not know. These whales are excluded from this table, which was compiled on the strength of the data published in "Norsk Hvalfangst tidende" for 1951 - 1961, and in "Internationale Whaling Statistics", V. 30 - 39.

Some cases of the presence of the representatives of cephalopod mollusks (Cephalopoda - Decapoda) in the stomachs of the Antarctic fin whales were noted in literature. These were, most probably, Onychoteuthis banksii. As was shown by L. Korabelnikov (1957) in the eleventh voyage of the whaling flotilla "Slava", the mentioned squid is the main food object of the sperm whales in the Antarctic waters; other authors indicate that it is an accidental component in the feeding of the blue whales in this region. Hence we may conclude that O. banksii is not rare in the waters of the Antarctic and the Sub-Antarctic, that it might be considered as accidental prey for fin whales.

We know that pelagic fish are practically absent in the Antarctic; at any rate, they do not form mass schools. This is why we may maintain with certainty that individual specimens of fish discovered in the stomachs of the fin whales were captured by them either accidentally, mainly while feeding on zooplankton, and they do not play any (at any rate, any essential) role as their source of food. Numerous scientists note unanimously that the number of fish in the stomachs of the fin whales are never significant and, usually, do not exceed some ten specimens. The list of fish discovered in the stomachs of the whales under investigation inhabiting the Antarctic Ocean in summer may be of more interest to ichthyologists interested in the fauna or to zoogeographers. For instance, Abe (1957), noted Japanese ichthyologist, has described a new genus and a species of fish Xenocyttus nemotoi, which for the first time was discovered (one specimen) in the stomach of a fin whale. A.P. Andriyashev (1960) described also

[147]

Composite Data on the Food Objects of Fin whale (Balaenoptera physalus) in Main Whaling Regions of the World Ocean

Table 11

Таблица 11

Сводные данные по кормовым животным финвала (Balaenoptera physalus) в главных промысловых районах Мирового океана

Antarctic & adjacent waters / Антарктика и прилегающие к ней воды	North Atlantic / Северная Атлантика	Northern Half of the Pacific Ocean / Северная половина Тихого океана	
Crustacea	**Crustacea**	**Crustacea**	**Cyclostomata**
Grimothea (post-larvae Munida gregaria)	Calanus finmarchicus	Calanus plumchrus	Eptatretus burgeri (-Bdellostoma)
Parathemisto gaudichaudi	Mysis oculata	Calanus cristatus	**Pisces**
Euphausia superba	Meganyctiphanes norvegica	Metridia ochotensis	Clupea harengus pallasi
E. crystallorophias	Thysanoessa inermis	Mysis oculata	Sardinops sagax melanosticta
E. lucens	Th. raschii	Gnathophausia gigas	Engraulis japonicus
E. recurva	Th. longicaudata	Themisto sp.	Clupanodon punctatus
Thysanoessa macrura		Euphausia pacifica	Oncorhynchus keta
Nyctiphanes africanus		Nematoscelis difficilis	Hypomesus olidus
Cephalopoda	**Cephalopoda**	Thysanoessa inermis	Mallotus villosus socialis
Decapoda, gen. sp. (Onychoteuthis banksii?)	Illex illecebrosus	Th. longipes	Exocoetidae, gen. sp.
Pisces	**Pisces**	Th. raschii	Cololabis saira
Clupeidae, gen. sp.	Clupea h. harengus	Th. spinifera	Gadus morhua macrocephalus
Paralepis coregonoides	Mallotus v. villosus	Eualus gaimardi belcheri	Boreogadus saida
Notolepis coatsi	Scomber scombrus	Pandalus sp.	Theragra chalcogramma
Myctophum sp.	Odontogadus m. merlangus	**Cephalopoda**	Eleginus gracilis
Harpodontidae, gen. sp.	Micromesistius poutassou	Ommatostrephes sloanei-pacificus	Podonema longipes
Electrona antarctica	Boreogadus saida	Loligo opalescens	Ammodytes h. hexapterus
Xenocyttus nemotoi	Ammodytes hexapterus marinus	Gonatus fabricii	Pneumatophorus japonicus
Notothenia sp.		Watasenia scintillans	Sebastodes glaucus
Cryodraco pappenheimi			S. polyspinis
Scomber sp.			Pleurogrammus azonus
Neopagetopsis ionah			P. monopterygius

a similar case of one poorly preserved specimen of fish, discovered in the stomach of a whalebone whale captured in the Antarctic waters near the Balleny Islands in 1947. This helped to identify a genus and species from the family of the pike family (Neopagetopsis ionah Nybelin). Although this whale was not identified to the species and was simply marked as a "whalebone whale", one may assume that it was a fin whale, as this species was the one which was caught in the Antarctic after the war more than any other species of whalebone whales. Another specimen of this fish was caught only ten years later, in 1957, by the Second Soviet Sea Expedition aboard the "Ob'" (Andriyashev, 1960). /148/

Of interest are also the data obtained by L.V. Korabelnikov in the eleventh voyage of the whaling flotilla "Slava" in 1956/57. He discovered in the stomachs of fin whales four species of fish which earlier were not noted by scientists; we assign these fishes (Cryodraco pappenheimi, Electrona antarctica, Notothenia sp., and Notolepis coatsi) for the first time to the list of prey for these whales.

Fish like Scomber sp. and the representatives of the Clupeidae have been discovered in the stomachs of the fin whales in sub-Antarctic waters and even antiboreal waters of the shores of South Africa, where the effect of warm waters is felt. In this region, the species named above, which live in schools, definitely form part of the food ration of the fin whale.

Thus, the Antarctic herd of fin whales feed on twenty-one species of animals belonging to three different classes (i.e. crustaceans, mollusks, and fish): eight species of crustaceans (of which six species belong to the euphausiids, one to the amphipods, one to the decapods), two species of cephalopod mollusks of the group of squids, and eleven species of fish. In spite of the seeming abundance of the source of food of the fin whales of the Antarctic herds, it should be considered, nevertheless, that the main food of these whales is Euphausia superba, and the food of the local herds inhabiting the area of the first and sixth Antarctic sectors, in addition to E. superba, also Thysanoessa macrura. In individual places, E. crystallorophophias might be of some significance. Moreover, E. lucens and E. recurva play some role in the feeding of these whales in the waters around the coasts of South Africa. Nevertheless, other representatives of the zooplankton, cephalopod mollusks, and pelagic fishes are of a secondary importance or are captured accidentally (such as Notolepis coatsi, Xenocyttus nemotoi, Cryodraco pappenheimi, etc.).

Further studies of the feeding of the fin whales in the southern hemisphere will undoubtedly increase considerably the list of the food objects, and new animals will be included. At present, we do not have data on the feeding of these whales inhabiting both the Pacific and the Atlantic waters of South America, the coasts of Australia, and some other regions. We also lack the data on the feeding of the fin whales of the Antarctic herds during the late fall and the early spring seasons, during their migration to the wintering grounds, toward the north, and especially to the feeding grounds, to the south. It is most probable that the feeding being similar (zooplankton, mass forms of pelagic fishes and cephalopod mollusks, etc.), the food of the fin whales in the waters mentioned above has specific under normal conditions; they number about fifty million individual birds. Murphy (1936) has estimated that in the area where there were about ten million birds, the entire population consumed three million tons of fish (feeding mainly on anchovy (Engraulis ringens). In the area of the current divergence, the anchovy mentioned above, sardine, and herring aggregate in great masses. It may be assumed with certainty that in these waters, fin whales, too, feed, perhaps, not only on the zooplankton (although this is not excluded), but more on the above named fishes. Although we lack the actual data on the feeding of the fin whales in this vast area of the Pacific, we, nevertheless, are entitled to make this statement. All the data on the feeding of the fin whales, and especially of the local herds of the Asian population which inhabit the north-west of the Pacific Ocean, confirm that the degree of their plasticity in regard to food allows them to turn easily from one mass object to another.

Consequently, it cannot be considered that the feeding of the fin whales inhabiting the whaling regions of the southern hemisphere has been studied completely, as much is to be done in this regard.

As far as the quantity of the food intake of the fin whales of the Antarctic herds is concerned, it, too, has been studied inadequately. We have only one reliable report by N.Ye. Salnikov (1953), who weighed the content of the stomachs of several fin whales (22 m). He points out that in fin whales with the most filled stomachs there were some 800 - 900 kg of the euphausiids, among which there were usually found some three to four small fishes of the Sudidae family.

The filling of the stomachs of the fin whales, similar to that of the blue whales, is in most of the cases considerably less than the stomach can hold. Salnikov considers that the miximum volume of the stomachs in the Antarctic fin whales prevents them from taking more than 800 - - 900 kg at one feeding.

The main source of food of the fin whales in the North Atlantic are the euphausiids- Meganyctiphanes norvegica, Thysanoessa inermis, and Th. raschii, and of the Copepoda, Calanus finmarchicus. However, when we compare the feeding of the fin whales of the North Atlantic and the Antarctic herds, we may note that while the fish do not play any significant role in the feeding of the fin whales (since there are no mass aggregations of fish in the upper pelagic zone) in the Antarctic waters, the stomachs of the fin whales of the North Atlantic, and also of the northern half of the Pacific Ocean, are quite frequently filled with fish only. Thus, the fish forming large aggregations- such as herring (Clupea h. harengus) and caplin (Mallotus v. villosus)- serve as food for the fin whales.

During the past decades the fishing of fin whales in the North Atlantic was insignificant. Annually, only a few hundred animals are captured (see Table 10). We do not know of the latest works which would present, if even in passing, the feeding of the whalebone whales (except lesser rorqual) in this area, and even more so the works /150/ which would treat of nothing else but this problem, and also the study of the helminthofauna of these whales. This was why we sent Dr. A. Jonsgard a request asking him to answer a number of questions. The excerpts from his letter of

February 16th, 1962 are given below. We would like to express our gratitude to Dr. Jonsgard for his data.

"I have studied your questions and would like to inform you that we have examined primarily the fin whales captured by Norwegian whaling coastal stations. We also obtained some material on the sei whales; however, these data were insufficient. The study of the helminths was not included in our work; we dealt only with the animals which serve as prey to the whales.

"As far as the food of the North Atlantic fin whales is concerned, I can provide you with some information on the content discovered in their stomachs, although my article on this problem is not ready yet for publication. The main source of food are the crustaceans.

"There are three species of these: Meganyctiphanes norvegica, Thysanoessa inermis, and Calanus finmarchicus; the first of these three is the main source of food of the fin whales near the coasts of Norway.

"As far as fish are concerned, the following were discovered: herring, caplin, mackerel, a gadid fish, and whiting. Caplin was discovered in the fin whales captured only near the coast of Norway. In some cases, we noted a mixture of food, i.e. fish and crustaceans. It was noted that 21.6% of the whales studied had empty stomachs. And this percentage proportion (empty and filled stomachs. S.K.) remained almost uniform for different places. In my article on this problem (which I intend to finish in one year), the feeding of the fin whales will be discussed in detail".

Thus, new investigations confirm the old data on the food composition of the fin whales; they also introduce some supplements, which were considered when the general list (see Table 13, middle column) was compiled.

It may be assumed that the list of the food objects of the North Atlantic fin whales is almost complete. Nevertheless, it may be much enlarged, if new data on the feeding of the fin whales in the waters around the shores of Spain, Iceland, New Foundland, and North America should be discovered.

As noted in Jonsgard's letter, the main forms of the fin whales' feeding, judging from recent investigations, should be regarded: Meganyctiphanes norvegica, Thysanoessa inermis, and Calanus finmarchicus; herring and caplin, which is in accord with the old data. Jonsgard stresses that caplin was discovered in the stomachs of the fin whales which were captured only near the shores of Norway. This indicates that the change in the composition of the food, as noted above, occurs when the region, or even the microregion of feeding is changed, which, in its turn, depends upon the conditions of the habitat which facilitates the formation of aggregations of certain animals or, on the contrary, hindering their aggregation and, perhaps, their life under given conditions.

The distribution of the feeding grounds of the fin whales of the North Atlantic during the summer (feeding) period is connected with the distribution of the main food objects mentioned above.

Nobody yet has studied the quantitative aspect of the feeding of the North Atlantic fin whales or their activity during a 24-hour period, or other problems which are connected with feeding; hence it is impossible /151/ to make any generalizations in this regard[1].

In accordance with our calculations (Klumov, 1961), a large whalebone whale requires some 35 - 40 g per one kilogram of its live weight during a 24-hour period. Considering the average weight of the North Atlantic fin whale (in analogy to that of the North Pacific) as being about 30 tons, the food required for a 24-hour period does not exceed 1.2 tons. However, this figure should be confirmed by weighing or determining the volume of food found in the stomachs of the captured fin whales.

Thanks to the work of Japanese scientists (Mizue, 1951; Nishimoto, Tozawa and Kawakami, 1952; Nakai, 1954; Nemoto, 1957, 1959; and Nishiwaki, 1959) and the investigations of our expeditions (1951 - 1956), the feeding of the whales, including that of the fin whales of the northern half of the Pacific Ocean, has been studied quite thoroughly during the past decade, and it is doubtful whether the list

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1. Nothing has been mentioned in literature about the volume of food found in the stomachs of the fin whales of the North Atlantic herds. True, A.G. Tomilin (1957) points out that up to 800 specimens of cod were discovered in the stomach of one fin whale taken in the waters of the North Atlantic. What was the weight and size, or the total weight of the alimentary bolus, we do not know, as the author does not say anything about it.

of the food objects of these whales might be expanded. As regards the feeding of the fin whales of Pacific local herds, they note (see Table 13, right column) fourteen species of crustaceans, compared to eight species in the southern hemisphere and six in the North Atlantic, four species of cephalopod mollusks, against two (or one) in the Antarctic waters, and one in the North Atlantic, and twenty-two species of fish, compared with eleven species in the Antarctic and seven in the waters of the North Atlantic. So the following correlation is obtained: the number of food objects of the fin whales in the northern half of the Pacific Ocean is twice as large as it is in the waters of the Antarctic and three times as large as it is in the North Atlantic. This may be explained, partly, by a better knowledge of the feeding of the fin whales in the Pacific Ocean, and also by the greater variety and richness of the Pacific marine fauna.

The identification of the leading food objects of the fin whales of the northern half of the Pacific Ocean presents some difficulties because of the vast extent of the region, stretching from the subtropic province to the Arctic, and because of the changes in the nature of the fauna. The composition of the prey for the whales changes also in regard to individual regions (and even microregions) of this vast extent of the World Ocean, and in regard to seasons, individual years, and it depends upon the development and concentrations of certain prey in a certain feeding grounds of the fin whales. During the years when the zooplankton is quite abundant in the waters abundant in the waters of the North Atlantic, the fin whales feed to the same extent on both the euphausiids and the calanoids, depending upon the accumulation they discover. During such times, there are neither fish nor squids present in their stomachs. However, if large aggregations of the zooplankton are lacking, then the fin whales easily turn to another source of food. This marked plasticity of these whales in regard to their feeding hampers the identification of their main source of food, as presented in the large list, in Table 13.

The stomachs of some of the fin whales captured in the waters near the Kuriles sometimes were filled exclusively with squids alone (Ommatostrephens sloanei.-pacificus). In a number of cases, these squids were quite fresh, almost untouched by the digestive juices, i.e. they were captured quite recently and simultaneously. If the whales did not discover aggregations of squids, but there were concentrations of pelagic fishes (herring, anchovy, sardine, walleye pollock, and in the north- arctic cod, etc.) in the area of their "feeding ground", then the stomachs of the fin whales were filled with these fish. Similar observations were repeatedly quoted by a number of scientists, for instance, B.A. Zenkovich (1952), and by us. In May, 1956, while on the expedition, we observed a large number of fin whales feeding on huge schools of spawning herring in the Sea of Okhotsk, near the shores of West Kamchatka, in the area of Ozernaya. A similar picture was also observed by N.N. Martynov in this area in 1958 and 1959.

If herring is absent within the boundaries of the feeding areas of local herds of the fin whales inhabiting the northern half of the Pacific Ocean, but there are large schools of Pacific saury, as we repeatedly noticed during our first expedition (1951), the fin whales willingly feed on this fish, capturing it sometimes in great amounts. There were cases recorded when the Pacific saury discovered in the stomachs of the fin whales by the workers of our expedition weighed up to 80 and 130 kg. On one occasion, a fin whale, captured on August 13th, 1953, had in its stomach five thousand individual specimens of this fish weighing about five hundred kilograms (Betesheva, 1955).

Striking in the materials of the expedition is the presence of bathypelagic fish as Podonema longipes in the stomachs of the fin whales, numbering 140, 760, and 1,059 specimens, respectively. In the latter case, this fish weighed almost four hundred kilograms. Except for Podonema longipes, no other food was discovered in the stomachs of the three fin whales captured.

The fact alone that the fin whales feed on Podonema longipes reveals that this bathypelagic fish rises from the abyss to the surface (probably, in the night), at any rate, to the upper layer of 100 - 150 m, where it falls prey to the fin whales. We know that the fin whales, while in search of food, usually do not submerge to a depth below 150 - 1?0 m. In addition, the presence of some 400 kg of this fish in the stomachs of fin whales makes us believe that this fish swims in schools. This allows us to recommend that the organizations involved in fishing should clarify the question whether or not it is possible to fish it on a large scale.

We also should mention one more fish which is eaten in large quantities by the fin whales. N.N. Martynov, in charge of the Second Whaling Flotilla in the Far East repeatedly observed (oral report) during the main part of a run of pink salmon that the fin whales fed on it in the north of the Kurile waters, in the area of Paramushiro Island, and, while personally present during the opening of the stomachs of the captured fin whales at the Whaling Combine "Podgorny" (Paramushiro Island), he witnessed the presence of pink salmon in the stomachs of these whales. On July 19, 1951, we opened a humpbach whale. Its stomach, too, contained pink salmon.

Thus, the composition of the food of the fin whales depends upon the presence of mass aggregations of prey in a given region of the sea. Whenever there is no lack of food, we always find a monotonous composition of food objects in the stomachs of the fin whales. If it is the zooplankton, then as a rule, we discover the animals of one species, same size, and the same stage of development. The same may be said also in regard to squids and fishes the size of which is always similar; that means that the whale captures one school or its part.

However, if there is lack of food, when strong aggregations of zooplankton, fish, or other animals running in schools are lacking in the feeding grounds of the fin whales, then the content of their stomachs is most diverse. In such times then, while examining the stomachs, we discover simultaneously a small amount of zooplankton (we [153] might discover various species of the euphausiids and calanids), and individual squids belonging to various species, and also individual specimens of fish. This kind of food allows us to say with certainty that the food reserves are insufficient, that mass forms of prey and their aggregations during the time the whales are captured are lacking. The abovesaid is substantiated by our investigations conducted in the north-west of the Pacific Ocean in 1951 - 1956.

Thus, we have established that when the zooplankton is scanty in the northern half of the Pacific Ocean, the fin whales easily turn to feeding on another prey; when aggregations of the animals they live on are wanting, they feed on the most diverse food objects simultaneously. This allows us to speak of the fin whales as typical euryphagous animals among the cetaceans, which fact distinguishes them completely from both the blue and the (Pacific) whales. This is why we cannot agree with Nemoto's (1957) idea that the fin whales, like the blue whales, possess a well developed capacity to pick the euphausiids, preferring them to all the other food objects.

The fin whales have a very wide food range. While hunting in the surface pelagic zone, they may successfully feed on the aggregations of the Calanus spp., as do the right whales or sei whales. While submerging to a depth more than 50 m, they also feed on the zone where the euphausiids are aggregated in large masses on which they feed, thus being rivals of the blue whales. After having discovered large aggregations of small fish, the fin whale fills its stomach with them and in this way is a rival to the humpback whale and the lesser rorqual (under conditions of the northern half of the Pacific Ocean; when the mentioned prey is lacking, while encountering pelagic squid (Ommatostrephens sloanei-pacificus), which sometimes forms large schools, the fin whale swallows it by the thousand. Consequently, if some of prey in nature multiplies to multitudes in aggregations, then the fin whale easily turns to feeding on this prey, and the presence of aggregations of prey in sea is immediately revealed in the content of it as found in the stomach of a fin whale.

Proceeding from the aforesaid, it is clear that it is not so easy to determine the main animals which serve as preferred food for the fin whale. Hence it is much more difficult to establish the links between the distribution of the fin whale and the distribution of its feeding grounds, as compared to the same task in regard to other whales. We might state that wherever there are large aggregations of animals, whether the calanids or the euphausiids, there one should look for the fin whales. There is also a regularity noted, which is not always substantiated. If there are simultaneous aggregations of the zooplankton, fish, and cephalopod mollusks, the fin whales prefer the zooplankton, to the same degree the euphausiids and the Calanus spp., then the fish, and only then the cephalopod mollusks.

The euryphagy of the fin whales is also substantiated by the quantitative analysis of the contents of their stomachs.

In 1951, we examined the filling of the stomachs of the fin whales captured in the waters of the Kuriles. In accordance with the notes in the field journals[1] as recorded by the observers of the expedition, the following amount of the plankton (in kg) was discovered in the stomachs of [154] the fin whales:

Thysanoessa longipes, and some *T. raschii* ...	365
Thysanoessa raschii	290
-"- -"-	205
-"- -"-	130
Euphausiids (no further specifications)	130
-"- -"- -"-	80
Thysanoessa raschii	70
-"- -"-	60
-"- -"-	52
Calanoida (no further specification)	43

The stomach of one fin whale contained euphausiids and squids (390 kg); the stomach of another, euphausiids, calanids, and squids (72 kg). In the same year, and the same regions, fin whales were captured which contained in their stomachs only the pelagic squids: one stomach contained about 600 kg of them (2,800 specimens); another, about 300 kg (1,300 specimens); third, about 100 kg (450 specimens). Along with plankton and squids, some whales fed also on fish. The stomach of one fin whale contained 157 kg of walleye pollock; another, 120 kg of

1. These records were treated and published by Ye. Betesheva in 1954.

anchovy; third, remains of some kind of fish which were not identified (104 kg).

In the years that followed, the members of the expedition supplemented the list, which was compiled as a result of the investigations conducted in 1951, with some other prey; however, no principally new data, especially in regard to the quantitative aspect of the feeding, were discovered.

The observations by the expeditions during those years reveal that the maximum amount of food discovered in the stomach of one fin whale did not exceed 500.- 600 kg, if the alimentary bolus consisted of squids, 400 - 500 kg of fish, and 350 - 400 kg of zooplankton. The least amount discovered was then when various types of food were present in the stomach. The more diversified food discovered in the stomach, the smaller its amount; this indicates the lack of aggregations of mass forms of animals in the sea and a general lack of food.

Thus, the stomachs of not only the fin whales, but also of all cetaceans in the north-west of the Pacific Ocean are filled completely only in individual cases. Some specialists on whaling and scientists have proposed a hypothesis that the presence of incompletely filled stomachs of whales is frequently due to the regurgitation of the food on the part of the whales when the latter are killed. If this is true to some extent in regard to the toothed whales, in particular, the sperm whales, which indeed regurgitates partly, and sometimes even completely, its food when wounded, this is not quite so in regard to the whalebone whales, as the regurgitation of food by these is quite rare. We personally never had a chance to observe it. While aboard whaling vessels, during actual killing, we frequently noticed that even in the cases when the whalebone whale was killed immediately, from the first shot, or even after a second or third, no food particles were seen in the water. Nevertheless, when the stomachs of thus killed whales were examined, it was found that the amount of food was never to the limit, and in the fin whales captured in the north-west of the Pacific Ocean, it never reached 700 - 800 kg.

Estimations reveal that the need for food for a 24-hour period on the part of the North Pacific fin whales of average size (18 - 19 m) and weight (35 t) is approximately 1 - 1.5 t (Klumov, 1961). These data, however, should be verified and substantiated by actual material.

Changes in the composition of the food of the fin whales in the northern half of the Pacific Ocean by geographical zones are, on the whole, quite easy to trace. However, the actual material is not identical for all zones and all species of prey; for some geographical regions, these data are lacking completely. /155/

Let us trace the change in prey for the fin whales of the Asiatic population, proceeding from the north to the south, from the Chuckchee Sea to the Yellow Sea, prey such as fish in regard to which we have the most complete material. These data are summed up in Table 12. In the column "Food object", the fish are arranged in accordance with the role they play in the feeding of the fin whales.

Table 12

COMPARATIVE DATA ON THE FEEDING OF FIN WHALES OF THE ASIATIC POPULATION ON THE FISH IN VARIOUS GEOGRAPHICAL ZONES OF THE WESTERN HALF OF THE PACIFIC OCEAN

Region of feeding	Prey
Chuckchee Sea	Arctic cod
Bering Strait, Lavrentiya Gulf, Mechigmenskaya Bay, Provideniya Bay	Arctic cod; to some degree, navaga
Anadyr Bay, waters of Bering Sea, near Navarin Cape	Caplin; to lesser extent, herring
Olyutorsky Gulf	Herring; to lesser extent, caplin
Central part of the shallow zone of Bering Sea (along drop-off)	Walleye pollock
Waters near the Commander Islands	Caplin, walleye pollock; to lesser extent cod and, singly, yellowfish (Pleurogrammus monopterygius)
Waters near the Aleutian Islands (west and centre)	Ditto
Waters near Kamchatka and Northern Kuriles	Herring, walleye pollock, gorbusha (very seldom), individual specimens of Pacific saury
Sea of Okhotsk	Herring, gorbusha, sand eel, cod
Waters of Central Kuriles	Pacific saury, walleye pollock, podonema
Waters of South Kuriles	Pacific saury, anchovy, walleye pollock, podonema
Waters of Northern Japan (near Hokkaido Islands)	Pacific saury, anchovy, yellowfish (Pleurogrammus azonus)
Waters adjacent to Honshu Island	Pacific saury, sardine, mackerel
Yellow Sea	Clupanodon punctatus, Eptatretus burgeri
North of Sea of Japan	Flying fish (Exocoetidae)

In the Chuckchee Sea and Bering Strait, there is only one pelagic fish, Arctic cod, which during some years aggregates in extremely large schools. The fin whales passing into the Chuckchee Sea for a short feeding (not every year), feed on this fish. According to the data (Tomilin, 1957), the fin whales there feed not only on Arctic cod, but also on the euphausiids (Thysanoessa raschii). In Lavrentiya Bay and in Mechigmenskaya Bay, besides feeding on Arctic cod, which here diminishes in number, the fin whales feed also on navaga. However, since navaga is a benthic species, and it is rather difficult to be taken by the fin whales, its number in the stomachs of these whales is insignificant. Navaga as prey for the fin whale is found in small numbers in Anadyr Bay; its role there, however, is even less important, hence it has not been included in Table 12 for the mentioned region. In the southern part of Anadyr Bay, and also in the waters around Navarin Cape, the fin whales, according to Nemoto (1959), feed quite intensively on caplin and, to a lesser extent, on herring, which here numbers less /156/ than, say, in Olyutorsky Gulf, where caplin retreats leaving the first place to herring. In the central part of the northern half of the Bering Sea, at the boundary of shallow water, at the continental slope, the fin whales feed intensively on walleye pollock (Nemoto, 1959), which, apparently, forms here large aggregations.

In the west and the central parts of the waters near the Commander Islands and the Aleutians, fish is not as significant as prey for the fin whales, as was noted for the northern waters of the Chuckchee and Bering seas, as this zone is rich in zooplankton. Among the food objects of the fin whale here, we notice caplin, to lesser extent walleye pollock; cod is found in their stomachs less frequently, while yellowfish occurs singly.

In the waters near Kamchatka (Pacific) and Northern Kuriles (Pacific and Sea-of-Okhotsk), large schools of spawning herring are observed during individual years. During such years, the stomachs of the fin whales are filled with nothing else but this fish. Besides herring, the fin whales feed on walleye pollock, gorbusha, and, for the first time, individual specimens of Pacific saury. In the Sea of Okhotsk (in the waters to the east), the stomachs of the fin whales contain herring, gorbusha, sand eel, which here forms extremely large schools, for instance, near Atlasov Island, and, to some extent, cod.

In the waters of the Central and South Kuriles (Pacific), we quite often encounter Pacific saury, which here replaces herring; walleye pollock still plays some role; there appear anew fishes which form large schools, such as anchovy, which inhabits the upper pelagic zone and forms here, although not every year, large schools, and podonema, a bathypelagic fish. It seems that the fin whales take the latter fish at night, when it rises to the surface waters. Around Hokkaido Island, the fin whales feed, if compared with the fin whales inhabiting the Southern Kuriles, on only one more species, i.e. yellowfish. Otherwise, the feeding of the whales here is identical. In the Pacific waters of Honshu Island, of the fish which serves as prey to the fin whales, which were typical of the regions further north, only Pacific saury is preserved; there appear new, warm-water species, such as sardine and mackerel.

In the Yellow Sea, during their wintering, the fin whales do not eat much. Among the prey for the fin whales of this basin, Nemoto (1959) mentiones "spotted herring" (Clupanodon punctatus) and, of the cyclostomous animals, Eptatretus burgeri.

In the East-China Sea, flying fish, not identified to the species, is recorded as an incidental component of fin whale's prey. It should be noted that the feeding of the fin whales in the Yellow and East-China seas has been studied inadequately, which may be explained by the fact that fishing for these whales here is insignificant.

If we examine all the fishes listed in Table 12, we may state that most of them- Arctic cod, caplin, herring, gorbusha, walleye pollock, Pacific saury, anchovy, sardine, mackerel, sand eel, and, apparently. ponodema- are the fishes which form aggregations, stay in schools, and hence are an easy prey for fin whales. Even such fishes as navaga and yellow-fish (Pleurogrammus azonus) form aggregations, if even not for a long period of time (in number, however, they are as abundant as other fish forming large schools).

The data in Table 12 confirm, first of all, the /157/ change in the composition of food of the fin whales by geographical zones; secondly, they point to a distinct euryphagy of the fin whale; thirdly, their capacity to feed only on prey forming large aggregations, regardless whether or not these are planktonic which serve as prey to such stenophagous animals as right and blue whales, cephalopod mollusks and fish, which serve as prey for the whales, such as, say, fin whale, sei whale, humpback whale, and lesser rorqual.

The behaviour of the whales depends considerably upon the presence in the sea, within the feeding grounds, of aggregations of food organisms. Observations pertaining to the distribution and change in quantity of the food plankton by years in the north-west of the Pacific Ocean (1951 - 1956), as well as the observations pertaining to the feeding and satiation of whalebone whales during the same years, have allowed us to draw the following conclusions.

We noticed a relative abundance of the zooplankton in the waters near the Kuriles during 1950, 1951, and 1953. Insignificant development of the zooplankton was observed during 1952, 1954, 1955, and 1956. The development of the zooplankton during these years was not identical: it was greater during 1952 and 1956 and not as pronounced during 1954, and especially 1955.

During the years when the food plankton was not abundant, the stomachs of the whales (fin and sei whales) were more often empty or just slightly filled with food, and usually not as filled as during the years of abundant plankton (Table 13).

Table 13

FILLING OF THE STOMACHS OF FIN AND SEI WHALES DURING THE YEARS OF ABUNDANT DEVELOPMENT OF PLANKTON AND DURING INSUFFICIENT FOOD RESERVES

Stomach	1951 (abundant plankton)		1955 (scanty plankton	
	No. of stomachs	%	No. of stomachs	%
Empty	-	-	21	25.3
Very little food	21	38.8	33	39.8
Average amount of food	10	18.5	22	26.5
Abundant food	23	42.7	7 ☆	8.4
Total:	54	100.0	83	100.0

Table 14

NUMBER OF ENCOUNTERS WITH WHALES DURING THE YEARS OF ABUNDANT AND SCANTY PLANKTON

Month	1950 (abundant plankton)	1955 (scanty plankton)
June	18	86
July	74	325
August	121	262
September ..	41	297
Total:	254	970

☆ The stomachs of the fin and sei whales contained much food in 1955, were filled with fish and squids. Almost no plankton was recorded.

During the years when the zooplankton was scarce, the whales were restless, were constantly on the move, swiftly moved from one place to another within their feeding grounds in search of food. Since the amount of the food plankton in the sea was small, the whales were forced to strain the water quite rigorously and in larger quantities than during the years of plenty. Even on usual, constant places where plankton accumulated, the whales ate up their prey rather swiftly, and hence had to move from one place to another. The more and swifter they moved, the more frequently they encountered the whaling vessels, which may be confirmed by direct observations in the sea. Hence one may get the impression that during the times when the plankton is scarce, the number of the whalebone whales appears to be greater. On the other hand, when the plankton is abundant and the whales find their food everywhere, they stay in smaller herds in their large areas, are calmer, do not move from one place to another in search of food, and there is no need for them to strain large volumes of water during a 24-hour period. Hence they are not seen by the whaling vessels as frequently. It appears then as if their number were smaller, although actually their number remains more or less constant, at any rate, almost constant, if compared with the preceding year. The decrease in the number of the encounters with the whaling vessels during the years of plenty of the zooplankton is substantiated by the data of twelve whaling vessels conducted in the north-west of the Pacific Ocean (Table 14).

The number of the whales seen by the whaling vessels in 1950 in the waters near the Kuriles (Table 14) indicate that the number of whales seen was about four times less than seen in 1955. However, in 1950, 71% of the whales met were killed, while in 1955, only 42%, i.e. in 1950, two whales out of every three met were killed, while in 1955, only two whales out of five encountered. This may be explained by the rather more calm behavior of the satiated whales in 1950 and their rather agitated state in 1955 when they were hungry. In 1955, the number of whales (fin and sei whales) during the whaling season was considerably greater in 1955, as well as during other years which are characterized by a rather scanty development of the food plankton.

Thus, there is a reverse relationship between the catches of the whalebone whales and the amount of the food plankton: the more abundant plankton in the sea, the less whalebone whales killed, and vice versa. This fact allows us, once more, to stress the practical significance and necessity of a most minute study of the problems pertaining to the feeding of the cetaceans, not to mention the theortical role.

HELMINTHOFAUNA

The broad food spectre of the fin whales, high degree of their plasticity in regard to the food, increased (in our opinion) vitality, quite high density, action and speed of movements, overlapping of the areas in regard to the wintering and feeding grounds with other populations of whales of the same species, constant contact with other species of whales- all this indicates a tremendous influence upon the nature of their helminthofauna.

As already mentioned about the blue whales, we do not have detailed, complete data, in order to be able to judge about the composition of the helminthofauna of the fin whales inhabiting various regions of the World Ocean, and also the data in order to compare the helminthofauna of these whales among themselves.

Our expedition has collections of helminths for the whales of the northern half of the Pacific Ocean. A.S. Skr'abin (1959) has studied the helminthofauna of 107 fin whales of the Kamchatka-Commander-Islands herd of Asiatic populations (Klumov, 1959). Small, but quite [159] interesting data on the helminthofauna of American populations have been published by Canadian scientists, Margolis (1954) and Margolis and Pike (1955). Nothing has been published on the helminthofauna of the fin whales of the North Atlantic; almost all works were written at the end of the past and the beginning of the present centuries. The helminthofauna of the fin whales of Antarctic herds has been studied in detail. Here, too, however, additional research in regard to individual geographical regions is needed, considering the distribution of singled out groups of fin whales in the Antarctic Ocean; this is a must in order to be able to determine the boundaries of the habitation of local herds.

In Delamure's report (1955, p. 483) on the fin whale, as a species inhabiting the World Ocean, the following fifteen species of helminths are listed: Lecithodesmus goliath, Ogmogaster antarcticus, Ogmogaster plicatus, Priapocephalus grandis, Priapocephalus minor, Tetrabothrius affinis, Tetrabothrius ruudi, Diplogonoporus balaenopterae, Crassicauda boopis, Crassicauda crassicauda, Bolbosoma balaenae, Bolbosoma brevicolle, Bolbosoma hamiltoni, Bolbosoma nipponicum, and Bolbosoma turbinella.

From the works written by Baylis (1932), Margolis (1954), Freund (1932), and also from Delamure's report, and from some other works, it is impossible to understand in which regions of the World Ocean a certain endoparasite has been discovered in a fin whale (or some other marine animal). In order to be able to solve this problem and to separate the list of the helminths of the fin whale if even in three provinces (North Atlantic, Antarctic Ocean, and the northern half of Pacific Ocean), a tremendous job had to be made. Nevertheless, we do doubt the authen- /160/ ticity and accuracy of the data on the presence of certain helminths in the fin whales. Whenever there was even the slightest doubt (Table 15), a question mark (in bracket, with our initials) was put.

Since the time which has elapsed from the time Delamure's report was published, the list of the helminths of the fin whales has been supplemented with the following species:

1. Anisakis pacificus, a new species; it has been described by A.S. Skr'abin (1959), a member of our expedition. It was discovered in a sperm whale, killer whale, lesser rorqual, and in a fin whale of a Commander-Islands-Kamchatka herd of the Asian population, which was captured in the summer of 1955 in the area of the northern Kuriles.

2. Crassicauda pacifica- a new species, described by Margolis and Pike (1955). They discovered it in a fin whale of an American population captured near the shores of British Columbia (North America).

3. Phyllobothrium delphini- discovered for the first time by Margolis and Pike (1955) in the Pacific Ocean in fin whales of American population, captured near the shores of British Columbia. The authors note that nobody before had discovered this helminth in the whalebone whales inhabiting the northern half of the Pacific Ocean, although it is not rare in toothed whales (sperm whale, etc.).

Table 15 *

HELMINTHOFAUNA OF FIN WHALES INHABITING BASIC WHALING REGIONS OF THE WORLD OCEAN

Antarctic and adjacent waters	Northern Atlantic	Northern half of Pacific Ocean: Asiatic population of fin whales	Northern half of Pacific Ocean: American population of fin
	Lecithodesmus goliath	Lecithodesmus goliath	Lecithodesmus goliath
	Ogmogaster plicatus	Ogmogaster plicatus	Ogmogaster plicatus
Ogmogaster antarcticus		Ogmogaster antarcticus	
Tetrabothrius ruudi	Tetrabothrius ruudi	Tetrabothrius ruudi	
Tetrabothrius affinis	Tetrabothrius affinis (? C. K)		
		Tetrabothrius sp.	
Priapocephalus grandis		Priapocephalus minor	
Diplogonoporus balaenopterae	Diplogonoporus balaenopterae (? C. K.)	Diplogonoporus balaenopterae	
			Phyllobothrium delphini
		Anisakis sp. larva	Anisakis sp larva
		Anisakis pacificus	
Contracaecum sp.		Contracaecum sp.	
Crassicauda crassicauda	Crassicauda crassicauda		
	Crassicauda boopis	Crassicauda boopis	
			Crassicauda pacifica
Bolbosoma brevicolle	Bolbosoma brevicolle		
		Bolbosoma sp.	
Bolbosoma hamiltoni			
	Bolbosoma turbinella	Bolbosoma turbinella	
	Bolbosoma balaenae		
Odontobius ceti		Odontobius ceti	

* Compiled from a number of sources listed in Footenote to Table 8.

Having considered these supplements, the total number of the helminths registered in fin whale (as a species) form at present eighteen species of endoparasites and one nematode-commensal, i.e. Odontibus ceti. As already seen in the preceeding chapter, exactly the same number of helminths has been registered also for the blue whale. However, the number of prey and the number of the endoparasites by the regions inhabited by the abovenamed whales are not evenly distributed (Table 16).

Table 16

NUMBER OF FOOD OBJECTS AND OF ENDOPARASITES IN FIN WHALES AND BLUE WHALES AND THEIR DISTRIBUTION BY THE REGIONS OF THE WORLD OCEAN

Species	Antarctic		North Atlantic		Northern part of Pacific Ocea	
	prey	species of helminths	prey	species of helminths	prey	species of helminths
Blue whale	16	13	9	6	15	6
Fin whale	21	9	14	10	40	15

The figures shown in Table 16, we believe, reveal, first of all, the insufficient knowledge of the helminthofauna of the fin whales of the Antarctic Ocean and North Atlantic and a somewhat better knowledge (although incomplete) of the helminthofauna of the fin whales of the northern half of the Pacific Ocean. Secondly, these data indicate a rather more diverse variety of prey for the fin whales inhabiting the northern half of the Pacific Ocean. These two statements are, apparently, true especially in regard to the fin whales of the Antarctic Ocean. When we compare the data on the blue whales and the fin whales of the region mentioned above, we notice that although the number of prey for the latter is increased by five species (from 16 to 21), nevertheless, the number of their endoparasites decreases in the same figure (the same figures here is a mere coincidence). The lists of helminths in the fin whales of Antarctic herds lack such Acanthocephala as Bolbosoma turbinella, although the latter has been known to exist in the Antarctic blue whales and a number of other mammals and it has also been discovered in the fin whales of the North Atlantic and the northern half of the Pacific Ocean. The same holds true also in regard to Bolbosoma balaenae and some other [161] helminths which, in our opinion, had not yet been registered in the Antarctic fin whales merely because of the insufficient knowledge of their helminthofauna.

While analyzing the data on the helminthofauna of the fin whales in three regions of the World Ocean, as shown in Table 15, we notice that for the fin whales of the North Atlantic, there are recorded ten species of helminths; out of this number, three species, Ogmogaster plicatus (antarcticus), Tetrabothrius ruudi, and Diplogonoporus balaenopterae, are widely distributed and are found in the fin whales of the Antarctic and Pacific oceans[1].

As stated above, A.S. Skr'abin proposed a hypothesis that Ogmogaster antarcticus is a synonym of O. plicatus. This same view is also shared by Margolis and Pike (1955). In order to solve this question completely, we should compare the two mentioned species using larger series. However, having considered the view expressed by the helminthologists, it seems that it would not be a great error

1. Here and from now on, only the northern half of the Pacific Ocean is meant.

now, with some reservations, to regard both these species as one form.

It should also be pointed out that *Tetrabothrius ruudi* could be considered as an endemic of the fin whales, and, as yet, has not been discovered in any other marine or terrestrial mammals, excepting the Pacific whales of the Asiatic population[1].

Seven other species of helminths in the fin whales of the North Atlantic Ocean are distributed as follows: three species (*Tetrabothrius affinis*, *C. crassicauda*, and *Bolbosoma brevicolle*) are common with the helminths found in the fin whales of the Antarctic; three species (*Lecithodesmus goliath*, *Crassicauda boopis*, and *Bolbosoma turbinella*), with the helminths found in the fin whales of the Pacific Ocean; and one species (*Bolbosoma balaenae*) has not yet been discovered in the fin whales of the Antarctic and Pacific oceans, although it was discovered in the blue whales of Antarctic herds and in those of the North Atlantic Ocean. Thus, there is a definite link between the fin whales of the three mentioned regions of the World Ocean. It follows from this that the helminthofauna of the fin whales of the North Atlantic Ocean is not a unique feature common to them alone. Some components of this fauna -six species- had spread into the Antarctic Ocean, others -also six species- penetrated into the Pacific Ocean.

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1. The presence of *Tetrabothrius ruudi* in the fin whales inhabiting all three regions of the World Ocean under investigation confirms their spread initially from one cradle.

While examining the helminthofauna of the Antarctic fin whales, we note that among the helminths, which are widely distributed in all three mentioned regions of the World Ocean, there are Contracoecum sp. and Odontobius ceti, a nematode-commensal, which point to a direct link between the fin whales of the Antarctic and the Pacific oceans, besides the North Atlantic Ocean.

A study of the helminthofauna of the fin whales of the northern half of the Pacific Ocean allows us to regard it as the most original and most distinctive. We find in the fin whales of the North Pacific Ocean such species as Priapocephalus minor, Phyllobothrium delphini, Anisakis pacificus, and Crassicauda pacifica which until now had not been discovered in the fin whales of other regions of the World Ocean, while such species as, for instance, Crassicauda pacifica is an endemic of the fin whale of the region mentioned above. The noted deviations of the helminthofauna of the fin whales of the Pacific Ocean from the helminthofaunas of the same whales from other regions substantiate its originality and, apparently, its long separation.

The aforesaid allows us to draw the following conclusion in regard to former and contemporatneous links between the fin whales distributed in the World Ocean.

It is most probable that the cradle of the fin whales (or of their close ancestors) and also of other whalebone whales was located in the North Atlantic. This same region was also the original area from which they spread. The fin whales, like also the blue whales, were forced, [162] due to glaciation, to move from the North Atlantic to the south. Once landed in the South Atlantic, they found their way later also to the Antarctic Ocean. Having spread in it and acquired some new species of helminths (*Contracaecum* sp. and also nematode-commensal *Odontobius ceti*), these whales penetrated into the northern half of the Pacific Ocean via the Pacific sector of the Antarctic Ocean (Fig. 13). We believe that this was the main route along which the fin whales spread from the place of their origin. Having accepted the aforesaid, however, it is impossible to understand and to explain the presence of the links between the helminthofaunas of the fin whales of the North Atlantic and the northern half of the Pacific Ocean, considering that they have common species of endoparasites, which are lacking in the fin whales of the Antarctic herds.

This circumstance allows us to assume that the whales penetrated from the Northern Atlantic, during the Middle Pleistocene (Mindel-Rissian interglacial period), during the time of one of marine transgressions, into the Pacific Ocean via the Arctic Ocean.[1] It was they who "transported" the helminths *Lecithodesmus goliath*, *Crassicauda boopis* which due to certain circumstances could not reach in due course the Antarctic Ocean[2].

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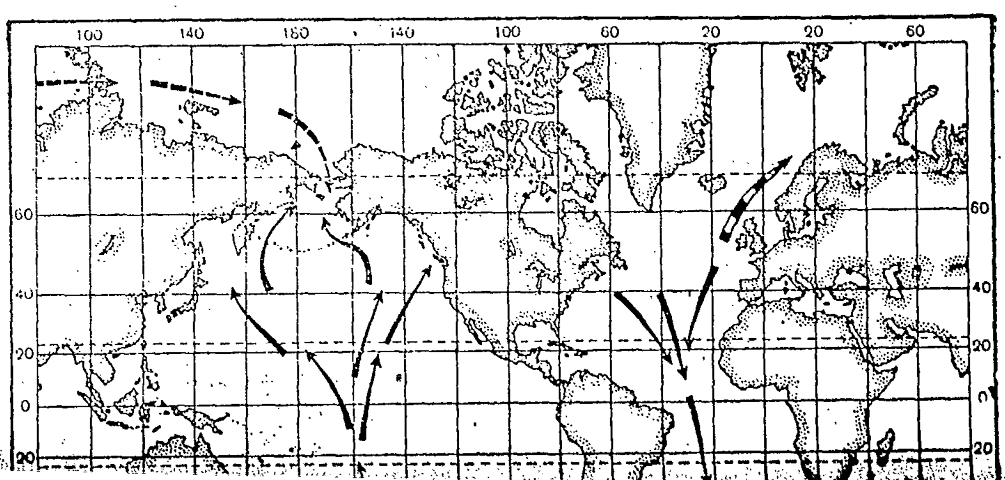
1. A.S. Skr'abin (1958) notes the presence of an exchange in the helminthofauna of the fin whales and the sei whales via the basin of the Arctic Ocean.

2. It is possible that during the first period of their spread, the fin whales did not have these endoparasites.

We believe, however, that contact between the populations of the fin whales of the North Atlantic and those of the Pacific Ocean was brief and relatively weak, at any rate, if compared with the contact that existed between the populations of the North Atlantic and the Antarctic Oceans. [163] It should be noted, however, that even at present, during the period of the maximum warming up in the Arctic, the fin whales, apparently, could have reached the Pacific Ocean in one summer, from the North Atlantic via the Arctic Ocean. This hypothesis may be offered on the strength of a recent arrival of a fin whale in the Yenisey River, where it came from the Kara Sea.



CONCLUSION

It should be noted that the fin whale is the greatest euryphagous animal among the whalebone whales. As will be shown later, even the humpback whale and the lesser rorqual do not match it in regard to the plasticity of food, although they, too, feed on both the plankton and fish. Nevertheless, they are limited to some extent (we shall call this limitation, conventionally, "geographical specialization"). In certain regions, the humpback whale and the lesser rorqual prefer to feed on the zooplankton, in others, on fish. Neither of these species feeds on cephallopod mollusks. The fin whale, on the other hand, does not know of any food or geographical "specialization". It is the most active, most vital of all the whalebone whales. This is ~~namely~~ the reason why it consumes the largest amount of food.

The quantitative aspect of the feeding of the fin whale.-this is true also in regard to all other whales- cannot be accurately estimated. Nevertheless, we believe that the data presented above have some grounds and are not too far from the truth: an average size fin whale, under conditions of the northern half of the Pacific Ocean, requires 1 - 1.5 t of food every 24-hour period. The whales, like also other wild animals in nature, and especially predators, pass some days during which they cannot take the required volume of food; so that, on the whole, for the summer feeding season, this figure should be smaller. It is probable that it is one ton.

The conclusions to the chapters on the right and blue whales contained large material on the distribution of the fin whales and on the whalebone whales on the whole, including the distribution of their food objects. It can be added that while the right whales, in accordance with their distinct capacity to select prey, should be sought in the areas with large accumulations of the Calanoida, and the blue whales in the areas with mass aggregations of the euphausiids, the fin whales should be looked for in all those regions where there is a mass accumulation of the zooplankton (Calanoida or Euphausiacea), or large schools of small fish, or cephalopod mollusks-pelagic squids.

V.A. Arsentyev (1958) has written an excellent work on the regularity pertaining to the aggregations of whalebone whales and accumulations of their prey in the Antarctic waters. Using concrete examples, V.A. Arsenyev shows that in the Antarctic, there is a direct relationship, a well-expressed link between the distribution of feeding areas and aggregations of whalebone whales.

We would like to draw the attention of the zoologists to the necessity for further investigations of the helminthofaunas of the fin whales, in particular, and of the marine mammals of the World Ocean, in general. S.L. Delamure is right when he states that :"... not all commercial animals have attracted the attention of the helminthologists. For instance, the pinnipeds and the cetaceans, very valuable animals in regard to the helminthology, have been studied inadequately. The fact is that the branch of helminthology we have selected is lagging behind its other, rapidly developing branches. It is also intolerably behind the commercial study of the pinnipeds and cetaceans which have been studied in our country to such a great extent (Delamure, 1955, p. 9). [164]

The data on the helminthophauna of the fin whales of various populations at hand are quite insufficient in order to be able to solve a number of problems. They do, however, allow us to express some preliminary considerations about the presence of the past links and ways of distribution of these populations.

It is most probable that the fin whales, like also the blue whales, penetrated from the place of their origin (North Atlantic) into the Antarctic Ocean, and thence into the northern half of the Pacific Ocean. The presence of several species of helminths (typical only of the fin whales of the Northern Atlantic and lacking in the fin whales, and, on the whole, in all the whalebone whales of the Antarctic Ocean) in the fin whales of the North Pacific Ocean points to a direct link of the Atlantic and the Pacific oceans via the Arctic Ocean. It seems, however, that the exchange was weak and short-lived.

S E I W H A L E S[1]

Feeding

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1. This chapter does not single out or treat individually the sei whales proper and Bryde's whales, as, in practice, it was impossible to determine which data published in literature pertain to Bryde's whales and which to the sei whales proper. Until now, in all scientific works and in the world statistics of the whaling industry, these both whales are given as "sei whales".

Before the war, the fishing of sei whales (and also of Bryde's whales) in the World Ocean was insignificant. And it was only seldom that more than one thousand animals were caught during a season. The sei whales were taken in small numbers by coastal stations in Japan; several hundreds of animals were captured also in the Antarctic Ocean; two to three hundred animals, at the most, were killed at the coasts of Africa. Also one to two hundred sei whales were captured annually in the North Atlantic.

At the end of the forties and beginning of the fifties, the whalers of all countries, and especially those of Japan, turned their attention more and more to the sei whales, and the killing of these animals has been increased. In 1961, about eight thousand animals were killed (Table 17).

It seems that for sei whales, too, there is a certain dependence between the volume of the number of the animals taken and the degree to which various cetaceans have been studied. Because of small catches of sei whales in the World Ocean before the war, its study could not much advance. Only recently, there appeared works in which the biology of these animals is explained, and also individual works specially on the questions pertaining to its feeding. As far as the latter is concerned, the contributions of Soviet and Japanese scientists are great. The right column of the compound table of the prey for these whales (Table 18) is based on the data of the scientists mentioned above. The remaining columns of the table are compiled on the numerous literary sources listed in the supplement to Table on p. 187[*].

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[*] In the original. Translator.

The main food component of the sei whale (and also of all other whalebone whales in this region) is *Euphausia superba*, and in this regard the sei whale does not differ at all from its relatives. However, no species of the whalebone whales, inhabitants of the Antarctic waters, except sei whale, has Calanoida as its food. This is the only whale which under conditions of the Antarctic Ocean has preserved a stereotype of behaviour peculiar of it and did not abandon its preferred food, although the volume of the latter here is smaller than in the northern hemisphere and it is much more difficult to obtain it. In the northern waters, the sei whale feeds on Calanoida only [166]
in the surface layer, in which these crustaceans form aggreagations the biomass of which has high indices, while in the Antarctic Ocean it is forced to look for them in rather deeper horizons. The biomass of these accumulations is, as a rule, deeper than is the case in the north. Consequently, the nature of feeding of the sei whales changes in the Antarctic Ocean (as compared with that of the northern hemisphere), and also the nutritive value of the Calanoida which yield the first place to *Euphausia superba*.

However, as soon as the sei whale coming from the Antarctic finds itself north of the Antarctic convergence, it immediately turns to the feeding on its preferred food. In these places, its stomach is filled with *Calanus simillimus* and other Copepoda, as was established by A.G. Naumov, who has treated the samples taken from the stomachs of the sei whales collected by V.A. Zemsky.

Pelagic amphipod- *Parathemisto gaudichaudi*- which during large aggregations serves sometimes as the only prey for these whales, if even for a short period of time (Nemoto, 1959), is important as a food object of the sei whales in the waters of St. Georgia.

As regards the fish swimming in schools (Table 18, left-column)- anchovy, the Clupeida, Scombridae- they undoubtedly form part of sei whale's important food, but in the waters of the Antarctic Ocean more to the north: near the shores of South Africa, Australia, and other places. Sharks and especially marine birds discovered in the stomachs of sei whales (Olsen, 1913) are, of course, accidental victims.

Table 17

SEI WHALE CATCHES IN INDIVIDUAL REGIONS OF THE WORLD OCEAN

Year	Southern hemisphere		Northern hemisphere		Total
	Antarctic and South Georgia	South Africa, South America, Australia	Arctic and North Atlantic	Northern half of the Pacific Ocean	
1949	577	238	62	959	1836
1950	1284	536	29	622	2471
1951	886				3033
1952	530	1228	51	1314	3123
1953	621				2208
1954	1029				2491
1955	569	409	158	804	1940
1956	560	362	100	1054	2076
1957	1692	479	85	882	3138
1958	3309	714	101	1549	5673
1959	2421	1222	76	1820	5539
1960	4309	1431	44	1238	7022
1961	5102	1675	65	943	7785

Table 18

COMPOUND DATA ON PREY FOR SEI WHALE (BALAENOPTERA BOREALIS) FOR MAIN WHALING REGIONS OF THE WORLD OCEAN

Antarctic and waters adjacent to it	North Atlantic	Northern half of Pacific Ocean	
Crustaceans	Crustaceans	Crustaceans	Fishes
Calanoides acutus	Calanus finmarchicus	Calanus plumchrus	Sardinops sagax melanostic
Calanus simillimus			
Calanus propinquus	Temora longicornis	Calanus cristatus	Engraulis japonica
Drepanopus peetinatus			
Parathemisto gaudichaudi	Meganyctiphanes norvegica	Calanus glacialis	Engraulis mordax
Euphausia superba	Thysanoessa inermis	Calanus pacificus	Osmerus sp. (? Hypomesus)
Grimothea (post-larvae Munida gregaria)		Eucalanus elongatus	Mallotus villosus socialis
		Metridia ochotensis	Yarrella microcephala
Pisces		Metridia pacifica	Argyropelecus sp.
		Pleuroncodes planipes	Polyipnus sp.
Selachii gen. sp.		Euphausia pacifica	Myctophum asperum
Clupeidae gen. sp.		Euphausia similis	Cololabis saira
Engraulis australis		Thysanoessa inermis	Boreogadus saida
Scomber sp.		Thysanoessa longipes	Theragra chalcogramma
		Thysanoessa raschii	Trachurus japonicus
Aves		Thysanoessa gregaria	Trachurus declivis
			Ammodytes h. hexapterus
Spheniscus demersus		Cephalopoda	Pneumatophorus sp.
Morus capensis		Ommatostrephes sloanei pacificus	Sebastodes sp.
			Pleurogrammus monopterygius
		Loligo opalescens	Ranzania typus
		Watasenia scintillans	
		Gonatus fabricii	
		Octopus sp.	

As regards the feeding of the sei whale in the North Atlantic is concerned, the data are very scanty. As may be seen from Dr. Jonsgard's letter quoted above (p. 150*), his new observations, too, are quite insignificant and do not present anything spectacular. This may be explained by the extremely small catches of sei whale in that area of the World Ocean (see Table 17).

Among the food objects of the sei whale in the North Atlantic, we find two representatives of the group Calanoida and two of the group Euphausiacea. It seems, however, that the main food is Calanus finmarchicus, and the second place should be assigned to Meganyctiphanes norvegica.

There is no doubt that in the North Atlantic, where the main food reserves (zooplankton) of the sei whales is also subject both to seasonal fluctuations of the number and to the uneven quantitative development in individual years, the sei whales have a somewhat larger food spectre than is shown in Table 18. It is probable that the list of their prey, and especially during the years of insufficient development of the plankton, should include also other crustaceans, and, of course, the fish forming large schools, as is also seen in the Antarctic and the Pacific oceans, and, perhaps, even cephalopod mollusks forming schools (Illex illecebrosus, Loligo, sp., etc.). This is why it may be considered that the list of food objects of the sei whales in the North Atlantic (Table 18), compiled on the strength of the data found in literature, is not exhaustive, as the feeding of this whale has been studied inadequately. In the future, we shall know more about it.

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* In the original. Translator.

The list of the food objects of the North-Pacific sei whales whose feeding has been studied much better includes 38 species of prey, compared to eleven species for the Antarctic Ocean and four for the North Atlantic. Among the listed prey, fourteen species are crustaceans (of these, seven species belong to the group of Calanoida), five species of cephalopod mollusks (of these, four species are pelagic squids and one octopus), and nineteen species of fishes most of which stay in schools, forming sometimes mass aggregations. Of interest is the presence of a large number of typical bathypelagic fishes, such as Myctophum asperum, [167]
Argyropelecus sp., Polyipnus sp., Ranzania typus. Some of them were discovered in the stomachs of sei whales as individual specimens (Ranzania sp.), while others (Myctophum asperum) were discovered in large numbers. Since we know that the sei whale, while in search of food, does not submerge to a great depth and feeds primarily in the upper layer of 100 - 150 m, it should be considered that, firstly, all the named bathypelagic fishes rise at night to the surface; secondly, that Myctophum asperum stays in surface waters in schools, else the sei whale would not hunt these tiny fish; and, thirdly, the presence of the above-named fish in the stomachs of sei whales bears witness to the fact that this whale feeds at night.

Formation of schools of Myctophum asperum is also substantiated by the presence of several species of fish of the same family (Myctophidae) in the stomachs of the fur seal, as noted by Taylor, Fudjinaga and Wilke (1955), and also in the stomachs of striped dolphins and the dolphins of the genus Lissodelphis and in harbour porpoises, as has been established by Wilke, Taniwaki, and Kuroda (1953). The first of the mentioned authors note that during February - -June, in the waters of the northern part of Honshu Island and the eastern shores of Hokkaido Island, approximately from 38 to 44° n.lat., luminous pelagic fishes, along with squid Watasenia scintillas, form 68% of the entire food discovered in the stomachs of fur seals[1]. The authors of the second work (mentioned above) on dolphins and harbour porpoises note that the luminous fishes of the family Myctophidae form 70 - 77% of food for the named dolphins and harbour porpoises. These data obtained by the authors as a result of the analysis of the content of the stomachs of dolphins and harbour porpoises captured during March - May approximately in the same area where also the fur seals were taken (38 - 42° n. lat.).

In its food range, the sei whale of the northern half of the Pacific Ocean occupies the intermediate position between the right and the blue whales, on the one hand, and the fin whales, on the other; however, it tends to be closer to the latter. Yet, the sei whale cannot be called an euryphagous animal, although the number of animals of various groups forming part of the list of its prey is no smaller than in the fin whale. While often it is rather

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1. Taylor and others (1955) note that fur seals catch luminous fishes and small squids at night, when they rise to the surface.

difficult to establish the main food objects of the fin whale, the guide forms of feeding of the sei whale, on the other hand, are always, in all the regions of the World Ocean, a few species of fine planktonic animals. In the northern hemisphere, the main prey are the representatives of the Calanoida. If we were to evaluate the sei whale from this point, we might call it a "Calanus-eater". However, where no aggregations of Calanus sp. are present, the sei whale readily turns to feeding on other animals, although to a lesser degree. According to the data of our expeditions of 1951 - 1956, treated by Ye.I. Betesheva (1961), the analysis of 48 stomachs of sei whales filled with food revealed the following results:

Prey	No. of stomachs	%
Calanus sp.	14	29.3
Euphausiids	1	2.1
Calanus sp. & Euphausiids ...	1	2.1
Zooplankton (undetermined)...	2	4.2
Squids	21	43.3
Fish	9	19.0

All the sei whales were captured in the waters near the Kuriles (north-west of the Pacific Ocean).

T. Nemoto, Japanese scientist, has published (1957) quite interesting data on the analysis of the content of the stomachs of the sei whales taken in the waters near the Aleutian Islands. The food discovered in 132 stomachs was as follows:

Prey	No. of stomachs	%
Calanus sp.	107	81.3
Euphausiids	4	3.0
Calanus sp. and Euphausiids.....	4	3.0
Squids	12	9.0
Squids and fish	1	0.7
Fish	4	3.0

The data above reveal that, in spite of the quite wide range in regard to the sei whale's food (see also Table 18), there are serious reasons to regard this species as being capable of selecting a certain kind of food. At the same time we see, however, that 43% of the stomachs of the sei whales taken in the waters near the Kuriles were filled with squids and almost 20% were filled with fish. In the waters near the Aleutian Islands, the squids take the second place (after *Calanus* sp.) in the feeding of the sei whale, although the absolute number of the stomachs filled with squids and their correlation are small.

When we compare our data and the data of the Japanese scientists, we note that the number of the stomachs containing the euphausiids is quite small both in regard to the absolute role and to the comparison with the number of the stomachs filled with *Calanus* sp. In the waters near the Kuriles, the proportion of the stomachs containing *Calanus* sp. and the stomachs filled with the euphausiids only is 14 to 1. In the waters near the Aleutian Islands, 107 stomachs were filled with *Calanus* sp. and only four with the euphausiids. In regard to all the stomachs studied, these figures form in the first case 2.1%, in the second, 3.0%. These figures confirm beyond any doubt that the sei whale only seldom hunts the euphausiids and that it adapts itself much more readily to the surface water than to the water 50 m below. In this regard, it differs from the blue whale and the fin whale and is the strongest rival of the right whale. This rivalry and the lack of the Calanoida has led, it seems, to the broadening of its food range and forced it to feed also on other pelagic animals which were discovered in great masses in the surface water; these were, first of all, the squids and, secondly, the fish, although the latter play a much smaller role in the feeding of the sei whale than do the cephallopod mollusks. From this viewpoint, the name Balaenoptera musculus* given to the sei whales of the northern half of the Pacific Ocean is quite inappropriate, as the distribution of the sei whales during the summer period (their feeding migration) is considerably broader and only partly coincides (in the south) with the spread of Balaenoptera musculus*. In winter, the whales practically do not feed. It seems that this might be better applied to Bryde's whale.

A.A. Shorygin (1952), while introducing the term "feeding activity", explained this term as follows: "Under feeding activity we understand the capacity of the organism to preserve the composition of food which fits it best, its physiological state being what it is, in spite of the changes in the quantitative composition of the food

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* "Ivasevy kit", i.e. sei whale. Translator.

reserves and the action on the part of its rivals. It is evident that the greater the food activity... the lesser is the change in the food composition, and vice versa". A.A. Shorygin further writes that the more active is the animal, the more important becomes the feeding on its preferred food: "... the composition of its main and preferred food will coincide". [169]

When we evaluate the sei whales from this viewpoint, we should admit that these whales, in spite of their quite high degree of plasticity, are at the same time also quite active. The data quoted above which characterize the content of the stomachs reveal that the choice food of the sei whale around the Aleutian Islands is the Calanus sp., 80% (rounded). Consequently, we have here a complete coincidence of the main and the preferred (choice) food. A somewhat different picture seems to be in the waters near the Kuriles. Here, too, however, the number of the stomachs filled with Calanus sp. is quite high - 30% (rounded), leaving the first place to the stomachs filled with squids (43%). This correlation, however, not only disproves the intense food activity of the sei whale, but, on the contrary, confirms it. The thing is that the data quoted on the feeding of the sei whales in the waters near the Kuriles were taken on the whole for the years when the plankton was insufficiently abundant, when all the whalebone whales, including the sei whales, felt a lack of food (Klumov, 1958). But even during these years the number of the stomachs containing the choice food

(*Calanus* sp.) remained quite high, which indicates its high activity in regard to feeding.

We notice clearly that the sei whales display a high degree of activity in regard to their food and their selective capacity.

Nemoto and Nasu (1958) report that in some regions of the Antarctic Ocean, *Thysanoesa macrura* and not *Euphausia superba*, is the leading form of food. In such regions the first *Euphausia* is also predominant in the stomachs of the fin whales. In the sei whales, which in the Antarctic feed chiefly on *E. superba*, *T. macrura* was absent, and their stomachs were filled only with *E. superba* even in the regions where *T. macrura* was predominant in the sea. This is quite an important fact! That means that the sei whale "understands" its food, it does not feed on anything it meets, but it seeks actively and selects its choice food.

It seems that the aforesaid prevents us from regarding the sei whales, like also the fin whales, as euryphagous animals. However, we cannot regard the sei whales as stenophagous animals, either, as the food range of these whales is quite wide. We think that the sei whale occupies an intermediate position between the blue whales and the right whales, which are typical stenophagous animals, with a low degree of plasticity in regard to food and an extremely high activity in regard to food, and the fin whales which are characterized by a high degree of food plasticity and, perhaps, the lowest activity in regard to food, among all the whalebone whales. This is why the sei whales should be called moderate euryphagous animals with quite a distinct selective capacity and food activity, which at the same time possess a certain and quite wide range in regard to the plasticity of food. Table 19 illustrates the data on the biological analogues in regard to the feeding of the sei whales by various geographical zones, which confirm, to some extent, the expressed positions.

The distribution of the sei whales in each of the whaling regions is connected first of all with the places of aggregation of food objects preferred by them. As already stated, for the Antarctic, this is E. superba, for the North Atlantic, C. finmarchicus, and to a lesser extent M. norvegica.

The distribution of the sei whale in the waters of the North Pacific is connected with the aggregation of several species of the Calanoida (depending upon the season and the geographical region occupied by a certain local herd) and, secondly, with the distribution of the Pacific [170] pelagic squid (Ommatostrephes sloanei-pacificus). As regards these squids, their distribution in the north-west of the Pacific Ocean is confined, apparently, to 55° n.lat. (Akimushkin, 1958); in the southern zone of this vast region, this squid forms sometimes enormous schools. Once (summer, 1951), we were able to observe an aggregation in South-Kurile shallow waters when Pacific saury concentrated there (it was pursued by squids). Another huge school of squids was observed in the same year, at the end of August, by Ya.Ye. Markitanov, a worker of the Board of the Whaling Flotilla in the Far East. He notified us that at the traverse of Shikotan Island, some two hundred miles from the shore, for two hours and a half, a tanker on which he was aboard, passed across an enormous school of squids. Ahead, on the sides and at the back of the vessel, everywhere, there were seen squids which jumped up, several at a time. A. N. Pokrovsky, a scientific worker of the Sakhalin Branch of the TINRO, observed large schools of squids in September, 1955, in the Pacific Ocean, south-east of the Small Kurile Range at the time Pacific saury was fished. We have at hand numerous literature with similar observations, confirming the presence of large aggregations of squids. In the same regions, in the fall, the presence of sei whales is noticed.

The distribution of the Calanoida is much wider and it changes in accordance with biological seasons. For a number of regions, however, it remains constant from one year to another, and only insignificant shifts in time and space is noticed.

Nobody has studied yet the quantitative aspect of the feeding of the sei whales, and there are hardly any data on this subject. This is especially true in regard to the Antarctic and the North Atlantic. As regards the sei whales of the North Pacific, during our first expedition in 1951, organized specially to study the cetaceans in the Far East, our program included also a point in which the special attention of the members of the expedition was drawn to the necessity of a most thorough collection of the data on the quantitative characteristic of the filling of the stomach in all the whales studied. This was quite a difficult task for the investigator, as much time and effort is required. We conducted a number of quite interesting observations while studying the sei whales which were dressed on the coastal whaling stations situated on the Kuriles.

According to the records in field journals, the filling of the stomachs of the sei whales (in accordance with the increase in food) was as follows:

Plankton (Calanoida)	Squids	Fish (Pacific saury)
4	9	10.5
17	35	70.0
52	122	130.0
60	130	More
299	340	500.0
	360	
	370	
	530	
	620	

As a rule, the squids were counted. As a result of these calculations, the following series of figures were obtained: 1,740 specimens, 1,800, 1,850, 2,630, and 3,100 specimens. In numerous instances, the number of squids in the stomachs did not exceed several hundred. One stomach contained remains of Pacific saury (about 60 kg), and remains (semidigested) of squids (about 80 - 85 kg). There was not a single case where there was a mixed food, i.e. plankton and squids, or plankton and fish. During all the years of the expedition, only two sei whales were captured in which the stomachs were filled up completely:

Table 19

BIOLOGICAL ANALOGUES IN FEEDING OF SEI WHALES BY VARIOUS GEOGRAPHICAL REGIONS OF THE WORLD OCEAN

Antarctic	North Atlantic	East-China & Yellow seas	Northern half of the Pacific Ocean			
			Waters of North Japan	Waters around South Kuriles	Waters around North Kuriles	Waters around Aleutians
			I			
Euphausia superba Parathemisto gaudichuadi	Calanus finmarchicus Meganyctiphanes norvegica	Euphausia similis	Calanus plumchrus Calanus pacificus	Calanus plumchrus Calanus cristatus Calanus pacificus Ommatostrephes sloanei-pacificus	Calanus plumchrus Calanus cristatus Calanus pacificus	Calan plumch... Calanus cristatu... Calanus glaciali...
			II			
Calanus propinquus Calanoidas acutus	Thysanoessa inermis	Trachurus japonicus	Watasenia scintillans Thysanoessa gregaria Myctophum asperum	Cololabis saira Engraulis japonicus	Ommatostrephes sloanei-pacificus	Ommatos... phes sloanei -pacifi cus

on one occasion, when 3,100 Pacific pelagic squids (620 kg), counted by Ye.I. Ivanova, a scientific worker aboard the whale-dressing station "Kosatka", were discovered in a sei whale, and on another occasion, when more than 500 kg of Pacific saury were discovered in the stomach of a sei whale. In all other cases, the filling of the stomachs was considerably less than they could hold.

Once a sei whale was dressed; in its stomach, there were 3,100 squids. They all were fresh, untouched by the digestive juices. Even their typical fine pinkish pigmentation was preserved along the sides of the fringe, passing into a violet one at the back. This means that the squids were taken by the whale right before it was killed and simultaneously, i.e., probably from one school. The uniform size of the squids also suggests this assumption.

The observations conducted during the expedition reveal that the maximum volume of food discovered in the stomach of a sei whale at any one time did not exceed 620 kg, if the alimentary bolus consisted of squids [1]; 500 kg if it consisted of fish; 300 kg, if it consisted of zooplankton-the Calanoida.

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1. This is the largest amount of food taken even by the largest sei whale. On the average, however, the weight of the squids in the stomachs of sei whales varies between 300 - - 350 kg.

These figures reproduce almost completely the data which were obtained during the quantitative evaluation of the feeding of sei whales (see p. 154[☆]). The fin whales fill their stomachs most with squids, the alimentary bolus of which, according to our observations, never exceeded 600 kg. The filling of the stomachs of fin whales with fish -up to 500 kg- also resembles the filling of the stomachs of sei whales. As regards the plankton, we discovered that the fin whales had a somewhat larger amount of it than did the sei whales. This is natural, as the fin whales can strain much more food than the sei whales during the same period of time.

Having pointed out the similarities in regard to the quantitative characteristic of the feeding of fin whales and sei whales, we also must notice the differences. If 600 - 620 kg of the alimentary bolus are the limit for the sei whale and no more food can be taken, then the stomach of a fin whale allows it to take up to 800 kg of food, i.e. considerably more than has been discovered by the members of our expedition during field investigations.

A sei whale's need for food for a 24-hour period has been estimated only approximately, proceeding from the same calculations (Klumov, 1961) which were used in regard to other whalebone whales (see above). These data have shown that an average sei whale (13 - 15 m, weighing 15 - 20 t) requires about 600 - 800 kg of food in 24 hours. We also

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[☆]In the original. Translator.

should keep in mind the caloricity of the food which changes depending not only upon the species taken but also upon the fact in which place, and when this prey was taken, i.e. during which particular biological season. I.V. Kizevetter* (1954) has established that the caloricity of the zooplankton in the Far East (in particular, the Sea of Okhotsk) changes from south to north: the fat content in one and the same planktonic animals increases, i.e. the plankton in the north is "fatter", hence more nutritious than that found in the south. The general caloricity is higher, in spite of some drop in the volume of protein and carbohydrates. V.G. Bogorov (1960) has substantiated these data on the tropic zone of the Pacific Ocean: "Chemical investigations of plankton (fat, nitrogen and carbohydrates were determined) yielded some most interesting results on the change in the amount of fat in the planktonic organisms located in various latitudes. The content of fat changes readily depending upon various conditions. The content of fat is on a steady decrease while moving from subtropic zones to the equator. The least amount of fat in the plankton is found in that of the Equatorial Countercurrent**". Consequently, the caloricity of the tropic plankton is very low, especially if compared with the caloricity of the zooplankton in the north. This, apparently, explains that the whales move for foraging excursions into the cold zones of the oceans, where they [173]

*Transliterated from Russian. "Kiezewetter"? Translator.

** ? "Mezhpassatnoye protivotecheniye". Translator.

find more abundant and more nutritive food. While consuming smaller amounts of food, they obtain more nutrition within a shorter period of time.

If this hypothesis is correct, then it is possible that, first of all, the 24-hour need of the whales in food in the north is less than in the south, in warm waters. Secondly, in spite of long journeys of, say, fin whales, humpback and grey whales from their wintering grounds (the area of 20 - 30°n.lat.) to their foraging grounds (for instance, the Chuckchee Sea, 68 - 70° n.lat.), in spite also of very brief feeding season in high latitudes, these whales, nevertheless, "manage" to accumulate reserves required for their journey back and the wintering in southern latitudes, where they practically do not feed.

Unfortunately, we lack the necessary comparative biochemical data on the composition and the caloricity of all the species of food of all the whalebone whales from various geographical regions of the World Ocean. Such data would allow us to make exceptionally interesting and important comparisons and to understand many things pertaining to the biology of these whales. I.V. Kizevetter (1954, p. 108 - 109) notes quite appropriately that "... while describing the food resources of a water reservoir for the fish (or whales.-S.K.) feeding on the plankton, it is important to know, besides the data on the specific gravity of the content of the zooplankton in the water, also the true food value of this mass. Keeping this in mind, weight correlation of basic species of the biomass should be determined and calculations made using the differentiated (depending on the species, place and season) or averaged energy-producing coefficients. Using only such an evaluation, one may form distinct notions regarding both the volume and the actual food value of the planktonic mass" (underlining is ours.-S.K.).

If we had this kind of data, we might be able to determine the energy-producing balance of the whales, to find out the reasons why some prey is preferred to another, perhaps even to compile a seasonal "schedule" of the accumulation of food reserves for the feeding grounds of whales located in various geographical regions, to determine rather more accurately the rate and periods of growths of whales, etc. It is high time that our biochemists should start the investigation of the domain of the comparative biochemistry of marine organisms, and first of all that of the prey for fish and whales, as we stressed in our reports back in 1951, at the Institute of Oceanology and at the TINRO. This task is extremely important and timely. If we do not solve it completely, we shall never be able to clarify many questions of the biology of marine (and especially commercial) animals or to solve the main problem- the balance of the organic matter in the ocean.

HELMINTHOFAUNA

Despite the distinct selective capacity of the sei whale in regard to its food, the relatively large list and differences in the composition of prey by geographical zones affect, no doubt, also the composition of its helminthofauna. Table 20 contains all the data on the helminthofauna of the sei whales in various local herds inhabiting the three basic whaling regions of the World Ocean.

Table 20 ☆

HELMINTHOFAUNA OF THE SEI WHALES INHABITING

BASIC WHALING REGIONS OF THE WORLD OCEAN

Antarctic & adjacent waters	North Atlantic	Northern half of Pacific Ocean	
		Asiatic population of sei whales	American population of sei whale
	Lecithodesmus goliath	Lecithodesmus goliath	Lecithodesmus spinosus
	Ogmogaster plicatus	Ogmogaster plicatus	Ogmogaster plicatus
Diplogonoporus balaenopterae	Diplogonoporus balaenopterae	Diplogonoporus balaenopterae	
	Tetrabothrius affinis		
Tetrabothrius wilsoni			
Tetrabothrius arsenyevi			
Priapocephalus grandis			
	Priapocephalus minor		
		Diphyllobothrium sp. larva	
		Phyllobothrium sp. larva	
		Tetrarhynchidae gen. sp. larva	
		Anisakis sp. larva	
	Anisakis simplex		Anisakis simplex
		Anisakis pacificus	
	Crassicauda crassicauda		
Bolbosoma turbinella	Bolbosoma turbinella	Bolbosoma turbinella	Bolbosoma turbinella
	Bolbosoma balaenae		
		Bolbosoma nipponicum	
		Rhadinorhynchus tenax	

☆ Source given in the Footnote to Table 8.

As already mentioned in Delamure's report (1955) on the sei whale inhabiting the World Ocean, without any division into geographical regions, there are 13 species of the endoparasites, i.e.: Lecithodesmus goliath, Ogmogaster plicatus, Priapocephalus grandis, Priapocephalus minor, Tetrabothrius affinis, Tetrabothrius arsenyevi, Diplogonoporus balaenopterae, Diphyllobothrium sp., Crassicauda crassicauda, Bolbosoma balaenae, Bolbosoma balaenae, Bolbosoma brevicolle, Bolbosoma nipponicum, and Bolbosoma turbinella.

This list should also be supplemented with eight species of the endoparasites discovered in the sei whales by the scientists in various countries after the publication of Delamure's report.

1. Lecithodesmus spinosus. This trematode was described by Margolis and Pike (1955). It was discovered in two sei whales of the American population captured near Vancouver Island, close to British Columbia. This trematode was not discovered in the sei whales of the Asiatic population of the northern half of the Pacific Ocean or in any other whales. Thus, it is an endemic of the sei whales of the American population and an endemic of the Boreo-Pacific subregion.

2. Tetrabothrius wilsoni. As already mentioned (p. 133[☆]), Markovsky (1955) has identified and described anew this species, which, according to him, had been presented as a synonym of T. affinis. Markovsky discovered this cestode also in a blue whale (1955) in the Antarctic waters.

☆ In the original. Translator.

3. Phyllobthrium sp. This cestode was discovered by A.S. Skr'abin, a participant in our expedition in 1955, in a sei whale of the Asiatic population (captured in the waters of the Northern Kuriles).

4. Tetrarhynchidae gen.sp. larva were discovered in two sei whales of the Asiatic population (captured in waters of the Northern Kuriles by A.S. Skr'abin (1959).

5. Anisakis sp. larva. A.S. Skr'abin discovered larvae of this nematode (1959) in four sei whales of the Asiatic population (captured in waters of the Northern Kuriles). Formerly, nobody ever discovered the Anisakidae in the sei whales.

6. Anisakis simplex. Earlier this species was known as an endoparasite of the blue whale and the lesser rorqual inhabiting the Northern Atlantic; however, it was not recorded in the sei whales of the Boreo-Pacific subregion. Margolis and Pike (1955) discovered this nematode in the sei whales of the American population. It was not discovered in the Asiatic population of the northern half of the Pacific Ocean.

7. Anisakis pacificus. A.S. Skr'abin (1959) has described a new species of the nematode of the mentioned genus, which is characteristic of the sei whales, fin whales, and lesser rorquals of the Asiatic population of the northern half of the Pacific Ocean.

8. Rhadinorhynchus tenax. A.S. Skr'abin discovered and described (1959) a new type of an acanthocephalid in two sei whales of the Asiatic population; until then, it was not known to exist either in the sei whales or in other whales. It is known that this genus is also discovered in

a number of fish. A.S. Skr'abin (1959) considers the sei whales as the facultative hosts of this acanthocephalid.

Thus, the total number of the helminths discovered at present in the sei whale (as a species) is twenty-one. Their distribution among the sei whales inhabiting the main whaling zones of the World Ocean is shown in Table 20. The analysis of Table 20 is undoubtedly of interest to the establishment of former and present links between individual populations. First of all, we should note the best understanding (which still is insufficient) of the helminthofauna of the sei whales of the northern half of the Pacific Ocean on the whole, where 13 species of endoparasites have been recorded in the mentioned whales of the Asiatic and American populations[1].

The helminthofauna of the sei whales of the North Atlantic has been studied even less, and our knowledge of the helminthofauna of the sei whales of the Antarctic waters, where up to date only five species of endoparasites have been discovered, is quite poor.

While comparing the resemblances and the differences of the helminthofaunas of the sei whales from various regions of the World Ocean, we note, first of all, that two endopa-

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1. Delamure (1955) and Skr'abin (1959) stress the relative richness of the helminthofauna of the Boreo--Pacific subregion; this, undoubtedly, is a true fact, although the reasons for this phenomenon still remain obscure. It should be noted that the helminthofauna of the whales of the American population has been studied inadequately, so far.

rasites- Diplogonoporus balaenopterae and Bolbosoma turbinella- are found in all three regions of the World Ocean about which we are talking in this paper. It seems that these species, while possessing a broad range of biological plasticity, i.e. the eurytopic species which have a wide range of tolerance to various environmental factors, can hardly serve as guides when establishing the links which are of interest to us. In addition, it should be noted that D. balaenoptera was also discovered in the fin whales and in all three regions of the World Ocean we have been examining. As regards B. turbinella, it was discovered not only in the sei whales, but also in the right whales in the Antarctic, in blue whales in the Antarctic and North Atlantic, and in the fin whales [176]
in the North Atlantic and in the Pacific Ocean.

As far as the quantitative links between the helminthofaunas of the sei whales in individual regions are concerned, they are expressed in the following figures. The sei whales of the Antarctic are connected with the sei whales of the North Atlantic and the Pacific Ocean only by two widely distributed endoparasites named above (Diplogonoporus balaenopterae and Bolbosoma turbinella). The species Tetrabothrius arsenyevi is an endemic of Antarctic sei whales which are not discovered either in other whales or in another region; Tetrabothrius wilsoni is a species endemic for the whales of the Antarctic waters, confined within the boundaries of the Antarctic Ocean, which, within the boundaries of this ocean, occurs not only in sei whales, but also in blue whales; the third species, Priapocephalus grandis, was also discovered in other regions (in the northern half of the Pacific Ocean) and also in other whales (in right whales, blue and fin whales). In the sei whale, however, this endoparasite was discovered only in the Antarctic waters.

The helminthofauna of the sei whales in the North Atlantic, represented by nine species of endoparasites, reveals the following links: Here we have five species common to those of the Pacific Ocean, two of which are widely represented and are common to the three regions. The remaining three species are typical of the North Atlantic: Lecithodesmus goliath, Ogmogaster plicatus, and Anisakis simplex, which link the helminthofaunas of the sei whales of these two regions, which also are discovered in the fin whale. These three species of endoparasites penetrated, undoubtedly, from the Atlantic Ocean into the Pacific Ocean either along with the sei whales, in which they are now discovered, or with the fin whales (Lecithodesmus goliath and Ogmogaster plicatus), and then, already being in the waters of the Pacific Ocean, discovered for themselves yet another host, the sei whale. However, we also should point to the third endoparasite, i.e. Anisakis simplex which is not found in the fin whale in any of the regions of the World Ocean which, consequently, could not have penetrated from the North Atlantic into the Pacific Ocean along with the whale already mentioned. It seems that the fin whale, due to some physico-chemical and biological conditions, is sterile to the nematode mentioned above. This nematode is also not found in other whalebone whales in the northern half of the Pacific Ocean, while it is present.

in the blue whales and lesser rorquals in the Antarctic and the North Atlantic. Of interest is also another circumstance: A. simplex was discovered only in the sei whale of the American population and was not found in the sei whales of the Asiatic population.

Proceeding from the aforesaid, we may assume that the above nematode penetrated into the Pacific Ocean from the North Atlantic along with the sei whale. However, what was the route of its host? This question is presented in detail below.

Out of the number of the endoparasites discovered in the sei whales of the North Atlantic, Tetrabothrius affinis (in the Pacific Ocean, it was discovered only in the blue whale), Crassicauda crassicauda, and Bolbosoma balaenae did not penetrate into the Pacific Ocean, and also Priapocephalus minor which, although discovered in the Pacific Ocean only in the fin whales, not in the sei whales. Priapocephalus minor in the North Atlantic was discovered only in the sei whale, i.e. it is endemic of this particular region.

While examining the helminthofauna of the sei whales of the Pacific Ocean and dividing these whales into two populations- American and Asiatic- we noticed that there is a definite difference between these two populations. This difference is substantiated by the peculiar helminthofauna and even by the presence of endemic endoparasites (Lecithodesmus spinosus in the sei whales of the American population and Rhadinorhynchus tenax in the sei whales of the Asiatic population). In its turn, this speaks of the lack of contemporaneous contacts between the two populations [177] named and their separation a long time ago (Klumov, 1952, 1955, 1956, etc.) on the whole in regard to the American and the Asiatic populations of the cetaceans. This was substantiated by A.A. Skr'abin (1958, 1959) who compared the helminthofaunas of both.

When we compare the helminthofaunas of the sei whales inhabiting the Antarctic Ocean, North Atlantic, and the northern half of the Pacific Ocean, we discover that the least resemblance noticed in the composition of the helminthofaunas is found in the composition of the helminthofaunas between the population of the Antarctic sei whales and the populations of the sei whales in the North Atlantic and in the North Pacific. As already stated, they have only two common, widely distributed species, which cannot serve as reliable indices of the former links between the whales of these three regions. Nevertheless, other remaining endoparasites discovered in the sei whales in the North Atlantic and in the northern half of the Pacific Ocean, are not present in the Antarctic sei whales. Tetrabothrius affinis, Ogmogaster plicatus (antarcticus), Crassicauda crassicauda, Anisakis simplex, and Bolbosoma balaenae were discovered in the sei whales of the North Atlantic, but they are not found in the sei whales of the Antarctic herds. The Antarctic sei whales lack also the parasites which were discovered in the sei whales of the North Pacific, such as: Ogmogaster plicatus (antarcticus), Diphyllobothrium sp., Phyllobothrium delphini, Tetrarhynchidae gen.sp., Anisakis simplex, Bolbosoma nipponicum, etc.

These quite important circumstances should be especially stressed. The comparison of the helminthofaunas of the North Atlantic and the North Pacific sei whales has revealed that between them, there is a quite distinct link. These populations of the sei whales share a number of common endoparasites: Lecithodesmus goliath, Ogmogaster plicatus, and Anisakis simplex. All the species just enumerated originate definitely from the North Atlantic. For instance, Lecithodesmus goliath has not yet been discovered in the whalebone whales in the Antarctic Ocean, and Anisakis simplex was discovered in the Antarctic only in the blue whale and in the lesser rorqual.

Along with the similarities, there is also a marked difference in the helminthofaunas in all three regions: each of the populations of the sei whales has its endemic parasites (one-two species). In the sei whales of the North Atlantic we discover Priapocephalus minor; in the sei whales of the Antarctic, Tetrabothrius arsenyevi; and in the sei whales of the northern half of the Pacific Ocean, Lecithodesmus spinosus (American population) and Rhadinorhynchus tenax (Asian population). Besides the endoparasites mentioned above, the helminthofaunas of all the three populations of the sei whales have endoparasites endemic of only one region and not found in the sei whales of other regions (see Table 20). This also stresses the peculiarity of the helminthofaunas of the sei whales of these populations. The data presented substantiate without any doubt the long isolation of the sei whales of various populations and the lack of their contemporaneous contacts. This is also confirmed by the presence of local herds of sei whales within each population. These local herds adhere strictly to their feeding grounds (and, apparently, to their wintering grounds). Using tags, Japanese scientists have established that the sei whales, representing a Bonin herd, never pass beyond the boundaries of 40° n.lat. and do not mix with the herd of the sei whales which we call Pacific (the Japanese call them northern) which feeds on the grounds occupying the area from the South Kuriles to the Aleutian Range. This limitation in regard to the spread of local herds interferes with the mixing of the sei whales; this is namely the factor which explains the peculiarity of their helminthofauna.

Using the actual data as a basis, we may assume the following hypothesis regarding the paths of the distribution of the sei whales in the World Ocean and formation of individual populations, which we are witnessing at present.

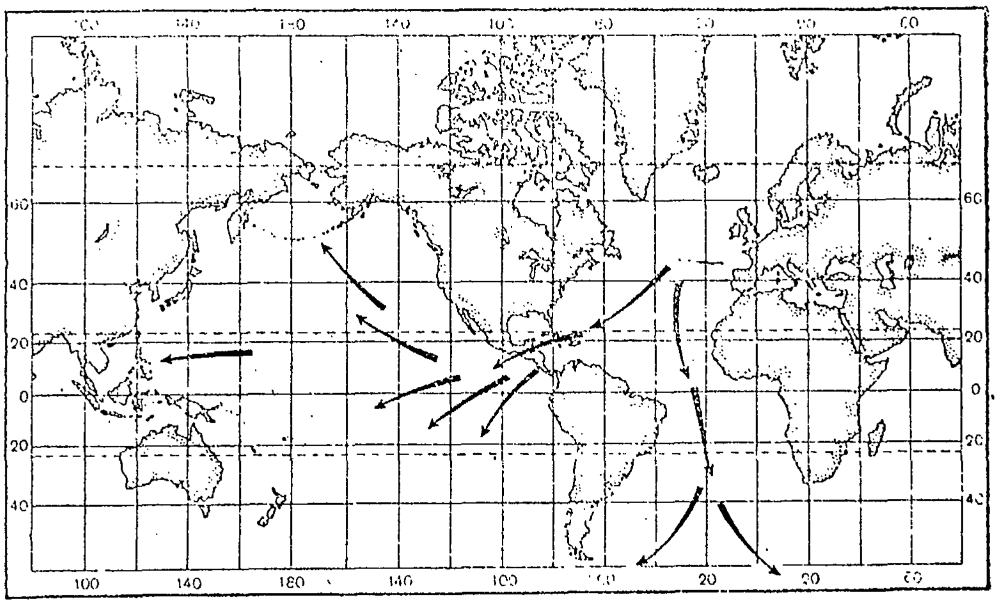

Рис. 14. Схема путей расселения сейвалов в Мировом океане из первичного центра возникновения — Северной Атлантики (ориг.)

Fig. 1

Fig. 14. Distribution of the sei whales in the World Ocean from their original centre- North Atlantic (orig.).

Having originated like other whalebone whales in the Atlantic Ocean and staying in the zone of warm waters in this ocean, the sei whales (or their ancestors), while preferring warm waters more than other whalebone whales (this is also observed at present), gradually expanded their range by moving and adapting themselves to less warm, moderately warm waters more abundant in prey. First of all, they mastered, it seems, the waters of the North and South Atlantic.

We know well that there were numerous breaks and subsequent links between the northern and southern American continents; at times these breaks lasted for long geological periods of time. South America, having lost the terrestrial link with North America, was separated from the latter for the entire Paleocene, Eocene, Oligocene, Miocene, and part of the Pliocene. During one of these breaks, probably at the end of Miocene, the sei whales penetrated from the warm zone of the Atlantic Ocean into the Pacific Ocean, where they gradually began to spread, occupying new areas. The penetration of the marine Atlantic fauna into the Pacific Ocean and that of the Pacific into the Atlantic Ocean via the mentioned break has been well known. The sei whales do not form any exception in this regard. On the contrary, we deal here with a number of analogies in regard to various groups of the animal kingdom (Fig. 14).

The penetration of the sei whales into the Antarctic waters took place, we believe, simultaneously with their spread into the Pacific Ocean or even later, perhaps already during the Pleistocene, when the cooling which took place forced these whales which prefer warm waters to move south. Later, due to the differences in seasons in the southern and the northern hemispheres, the contacts terminated first of all between the sei whales in the Antarctic and in the North Atlantic waters (it seems that there were no previous contacts between the sei whales of the Antarctic and the North Pacific). They developed different biorhythms which [179] prevented them from moving freely from one hemisphere into another.

Each population occupying a vast water area with different conditions in habitat underwent a process of differentiation. As a result of the adaptation to specific conditions of individual regions, and also to the biological differences of individual animals that found themselves in a large grouping, local herds emerged within the populations .

The analysis presented above allows us to regard the helminthofauna of the sei whales in the North Atlantic as initial. If it is compared with the helminthofauna of the sei whales of the Pacific and the Antarctic oceans, we come to only one conclusion in regard to the paths along which the spread and the subsequent isolation of the population of this whale took place. The facts on the sei whale at our disposal do not permit us to assume that the sei whale- the whalebone whale which loves warm water more than any other species of whales- penetrated from the Atlantic Ocean into the Pacific Ocean via the basin of the Arctic Ocean even during the interglacial period, the period of the maximum warming up of this basin, or via the Antarctic Ocean. The links about which we spoke above do not corroborate this hypothesis. On the contrary, the penetration of the sei whales from the Atlantic Ocean into the Pacific Ocean in the zone of warm water, via the break between the northern and the southern American continents, and later the penetration into the Antarctic Ocean directly via the South Atlantic and the subsequent formation of the populations and their isolation (cessation of contacts) are substantiated not only by the resemblance of their helminthofaunas, but also by their peculiarity and the presence of endemism. The latter bears witness to a prolonged isolation of the populations of the sei whales mentioned above.

It should be added that the monk seal of the pinnipeds is a good analogue to the sei whale. It is known to be the only thermophilic seal inhabiting warm waters (tropic and subtropic) of the globe. The scientists are unanimous in regard to the centre of its origin and distribution (Bötticher, 1934; Romer, 1939; Scheffer, 1958). The place of origin of these seals, like also of the sei whale, is believed to be the North Atlantic. As regards the spread of the monk seals, there are several hypotheses. Many scientists believe that it penetrated into the Pacific Ocean via the break between the southern and the northern American continents. King (1956) showed that anatomically the Mediterranean monk seal (Monachus monachus) differs more from Monachus tropicalis inhabiting the subtropic waters of the North Atlantic than Monachus tropicalis from Monachus schauinslandi. The latter two species have several features in common, in spite of the fact that they are separated by dry land (the Panama Isthmus), while the two first ones belong to one or the same initial population. It is not excluded that their older isolation (perhaps different conditions of the habitat) facilitated their isolation. This fact, remarkable in itself, does not make us hesitate to express the view that the Hawaiian monk seal (Monachus schauinslandi) penetrated into the Pacific Ocean via the only path, i.e. via the break between the two American continents as mentioned above. Following the current, it reached the Hawaiian islands and formed here a colony which at present counts somewhat more than one thoudand animals; sometime in the past, however, according to the data at hand, the monk seals were numerous there.

One more remarkable point should be stressed. The monk seals quite often are hosts to several species of cestodes of the family Diphyllobothriidae. Yet, this endoparasite was never discovered in any of the whalebone whales. And it was only in 1946 that sexually immature specimens of this helminth were discovered in a sei whale inhabiting the northern half of the Pacific Ocean and captured in the Commander Islands (Delamure, 1955). This fact also indicates the undeniable resemblance in regard to the paths along which the sei whales and monk seals spread. Both species- sei whales and monk seals- are thermophilous, both originated in and spread from the North Atlantic, both could have had (and, apparently, had) similar paths of spreading. Kellog (1922, cited after Scheffer, 1955) has shown that the monk seals could have had a very wide range of spread in the tropic seas during Miocene "... when there was a marine road connecting the Caribbean Sea with the Pacific". This remark of an erudite scientist confirms even more so the old links which undoubtedly took place in the sei whales and monk seals, which still have been preserved (both share their distribution and the endoparasites common to them). They allow us to assume that the penetration of these animals into the Pacific Ocean from the initial place of origin- the North Atlantic- went along the same paths.

LESSER RORQUALS

Feeding

The biology of the lesser rorquals has been studied rather poorly. This is due to the fact that, first of all, the lesser rorqual is taken in small numbers. It is hunted by the Norwegians in the Barents Sea and by the Japanese, in the waters surrounding the Japanese islands. In the USSR, during one year, less than ten animals are killed.

The Japanese fish for this whale from coastal whaling stations located chiefly on Hokkaido and Honshu islands. The annual catch reaches several hundred animals (on the average, about 300 - 350 whales).

Japanese scientists have gathered good material on the feeding of the lesser rorqual in the Pacific Ocean, the Sea of Japan and the Sea of Okhotsk, although they have not analyzed their studies in detail, as it would be desired (Omura and Sakiura, 1956).

Nobody hunts this species of whale in the Antarctic waters. Even in the latest works of G. Williamson and V.A. Arsenyev (1961) on the lesser rorquals in the Antarctic, there are no new data on the feeding of these whales.

Table 21 contains all the data as found in world literature on the feeding of the lesser rorquals in the Antarctic waters, in the North Atlantic, and in the northern half of the Pacific Ocean; also included in this table are the findings of our expeditions of 1951 - 1956. The data on the feeding of the lesser rorquals in the North Atlantic (the Sea of Barents) were taken from A. Jonsgard (1951) and some older literary sources.

Even a slight look at Table 21 reveals that the feeding of the lesser rorquals inhabiting the northern half of the Pacific Ocean has been studied better than it was in other regions of the World Ocean.

The first thing which should be noted is the preference of the lesser rorquals in regard to fish. In our waters, these whales are primarily ichthyophagous animals. The examination of their stomachs revealed the remains of fish. In the area near the Kuriles, from the most southern to the most northern islands, the leading prey was walleye pollock. This coincides with the data /181/ of the ichthyological investigations conducted by the Institute of Oceanology of the Academy of Sciences of the USSR (Gorbunova, 1954), which show that in the area of the arch of the Kuriles, there are large aggregations of the above-mentioned spawning fish. We examined the stomachs of lesser rorquals which were filled completely with the bones of the walleye pollock, its otoliths, and crystallized lenses. It was possible to establish that up to 200 - 300 specimens of this fish were found in one stomach.

Table 21

COMPOSITE TABLE OF PREY FOR LESSER RORQUALS (Balaenoptera acutorostrata) IN MAIN FISHING REGIONS OF THE WORLD OCEAN

Antarctic & adjacent regions	North Atlantic	Northern half of Pacific Ocean
Crustacea	Crustacea	Crustacea
Euphausia superba Euphausia crystallorophias	Calanus finmarchicus Meganyctiphanes norvegica Thysanoessa inermis	Calanus glacialis Calanus sp. Nephrops thomsonii Euphausia pacifica Thysanoessa inermis
		Cephalopoda
		Ommatostrephes sloanei pacificus
	Pisces	Pisces
	Clupea h. harengus Mallotus v. villosus Odontogadus m. merlangus Pollachius virens Gadus m. morhua (juv.) Boreogadus saida Scomber scombrus	Etrumeus micropus Clupea harengus pallasi Sardinops sagax melanosticta Engraulis japonicus Cololabis saira Gadus morhua macrocephalus Eleginus gracilis Boreogadus saida Theragra chalcogramma Ammodytes h. hexapterus Pneumatophorus japonicus Pleurogrammus azonus

A similar picture of the feeding of lesser rorquals on fry in the North Atlantic was observed by Jonsgard (1951). There, the following kinds of fish serve as the main prey for the lesser rorquals: caplin, herring, Arctic cod, young cod, etc. The zooplankton as food does not play a very important role.

Such a condition, however, is not observed everywhere. Omura and Sakiura, Japanese scientists (1956), note that in the water adjacent to the islands of Japan, the lesser rorquals feed for the most part on the "krill" (in brackets, they add "Copepoda"). Unfortunately, no further explanation is given. At the same time the identification to the species of the copepods discovered in the stomachs of the lesser rorquals would help us understand better their biology, and also the reasons for their seasonal locations.

The data of the Japanese scientists (Table 21) confirm also that the fish, too, play an important role in the feeding of the lesser rorquals, and especially in the southern part of the Sea of Okhotsk, near the shores of Hokkaido Island (44 stomachs were filled with krill, 38 stomachs with fish); near the Pacific shore of the same island (14 stomachs containing zooplankton, and 16 containing fish); near the Pacific coast of Honshu Island (10 stomachs filled with plankton, 28, with fish), etc. However, while examining these data in regard to individual years, Omura and Sakiura (1956) point out that such a picture of the distribution of the food in the stomachs in which the zooplankton is discovered increases, exceeding considerably the number of the stomachs containing fish.

It should be noted that in our waters, we never observed similar phenomena, and we never discovered in the stomachs of the lesser rorquals any other food than fish. If there was some zooplankton, it was secondary, not the main food.

It seems that here one ought to speak about some "geographical specialization" of individual local herds of lesser rorquals, which proceeds, of course, not only from the biological heterogeneity of the species (Klumov, 1955; Guryanova, 1957), but also from the presence in nature of food that is easiest to obtain. It seems that for the lesser rorqual of the north-west of the Pacific Ocean, in the Bering Sea, in the south of the Chuckchee Sea, there are conditions forcing this whale to compete with other species feeding on the plankton, that it is easier and simpler for this species to feed on fish. The whale's plasticity in regard to food, that developed during its biological progress due to the external conditions, including the competition, permits it to prey on fish. On the other hand, in the regions more to the south, the conditions of the internal medium are such that they do not prevent the lesser rorqual from feeding on the zooplankton. In all the regions where the lesser rorqual is found, this whale does not feed on cephallopod mollusks. True, our list (see Table 21) has a Pacific pelagic squid which was included in it on the strength of the discovery of the beaks of squids in the stomachs of these whales. Yet, they could have got into the whale's stomach indirectly, via the stomach of the walleye pollock. At any rate, we did not get a single squid intact from the stomach of a lesser rorqual.

The distribution of the lesser rorqual in the waters near the Kuriles depends only on the distribution of walleye pollock, and in the north (the Bering Sea) also on the distribution of navaga and Arctic cod. In the Gulf of Anadyr, Providence Bay, Lavrentiya Gulf, Mechigmen Bay, etc., according to the reports we obtained from the directors of the Plover and Mechigmen Whaling Stations, the lesser rorqual comes to the shore if either the Arctic cod or navaga are present there, and also in the Chuckchee Peninsula.

HELMINTHOFAUNA

The data on the helminthofauna of the lesser rorquals from individual regions of the World Ocean are quite inadequate. Their helminthofauna was not subject to special studies, hence tremendous research lies ahead.

We present only the composite Table 22, due to the lack of sufficient material.

Delamure in his report (1955) names nine species of helminths which are found in the lesser rorquals in the World Ocean; he does not present their distribution according to regions. These endoparasites are as follows: Fasciola skrjabini, Lecithodesmus goliath, Ogmogaster plicatus, Anisakis simplex, Terranova decipiens, Crassicauda, crassicauda, Bolbosoma balaenae, Bolbosoma nipponicum, and Bolbosoma brevicolle.

We can supplement this list with two species of endoparasites which were found by A.S. Skr'abin (1959) in lesser rorquals, that were captured near the northern

Kuriles. These are, first of all, the nematode _Anisakis pacificus_ of the North Pacific, which is endemic of the named region, and the larval stage of a cestode from the family Tetrahynchidae. [183]

It should be noted that Bailis considered (cited after Margolis and Pike, 1955) that Kreplin,* who discovered and published the data on the presence of the trematode _Ogmogaster plicatus_ in the lesser rorqual, committed an error in his identification by taking a sexually immature fin whale for the lesser rorqual. He stressed that nobody discovered this trematode in the lesser rorqual, either before or after Kreplin. This is why this trematode in Table 22 is followed by a question mark. Further investigations of the helminthofauna of the rorquals will allow us to solve this problem.

*Transliterated from Russian. Translator.

Table 22

HELMINTHOFAUNA OF THE LESSER RORQUALS INHABITING BASIC WHALING REGIONS OF THE WORLD OCEAN

Antarctic and adjacent waters	North Atlantic	Northern half of the Pacific Ocean
	Fasciola skrjabini	
	Lecithodesmus goliath	
	Ogmogaster plicatus (?C.K.)	
		Tetrarhynchidae gen. sp. larva
Anisakis simplex (?C.K.)	Anisakis simplex	Anisakis pacificus
Terranova decipiens	Terranova decipiens	
Crassicauda crassicauda	Crassicauda crassicauda	
	Bolbosoma balaenae	
Bolbosoma brevicolle	Bolbosoma brevicolle (C.K.?)	Bolbosoma nipponicum

In Table 22, we tried to place the helminths in accordance with the regions we are interested in. However, it was impossible to make this arrangement for all the endoparasites. Whenever there was any doubt, a question mark was used, followed by my initials.

Our knowledge of the feeding and the helminthofauna of the lesser rorquals is so inadequate that no generalizations can be made, except the conclusions which might be applied also to the lesser rorquals (they were given at the end of the chapters dealing with right, blue, and fin whales).

HUMPBACK WHALES

The humpback whales in the northern half of the Pacific Ocean, and particularly in its north-west, are not too important from the commercial viewpoint. They are killed in small numbers near the shores of America, particularly near the shores of California and in the Alaska Strait. Several tens of animals, and sometimes up to two-three hundred whales, are taken in the waters around the Riukiu Islands. The Soviet whalers operating in the Kuriles and Commander Islands are not interested in hunting this species. Nothing indicates that the humpback whales in these waters might be of some commercial value in the future. The reserves of this species in the northern half of the Pacific Ocean are so negligible that even if there were a decree prohibiting the killing of them, scores of years would pass before one might speak of them as commercially important animals.

The Soviet whaling fleets kill annually no more than ten humpback whales. A small herd of these whales has been preserved in the northern part of the Bering Sea and in the south of the Chuckchee Sea, to which place they migrate in summer. Since the mentioned regions are not exploited extensively, a small number of the humpback whales are taken by both the Soviet and the Japanese whalers along the migratory routes, when the humpback whales proceed from the south (their wintering place) to the north, or migrate back, southward, for wintering.

At the beginning of our century, the humpback whales in the Antarctic waters were one of the main species of commercial value, and they were killed by the thousands. At present, however, they are almost extinct, and the takes of the few remains, which have managed to survive, are regulated by restrictions and the season during which they may be killed. The humpback whales in the North Atlantic also are almost extinct, and during recent years their catches have not exceeded 4 - 7 animals annually.

Nevertheless, many books have been, and still are being written in which also their feeding is presented.

Table 23.

COMPOSITE TABLE OF THE PREY FOR THE HUMPBACK WHALES (*Megaptera nodosa*) IN MAIN WHALING REGIONS OF THE WORLD OCEAN

Antarctic and adjacent waters	North Atlantic	Northern half of the Pacific Ocean	
Crustacea	Crustacea	Crustacea	Pisces
Grimothea (post-larvae Munida gregaria) Euphausia superda Euphausia hemigibba Thysanoessa macrura Nyctiphanes australis Pseudeuphausia latifrons Pisces Clupeidae gen. sp. Clupea fimbriata	Calanus sp. Meganyctiphanes norvegica Thysanoessa inermis Mollusca Gastropoda Limacina helicina Cephalopoda Decapoda gen. sp. Illex illecebrosus Pisces Clupeidae gen. sp. Clupea h. harengus Mallotus v. villosus Osmerus eperlanus Boreogadus saida Aves Phalacrocorax sp.	Calanus cristatus Calanus plumchrus Calanus glacialis Mysis oculata Themisto sp. Euphausia pacifica Euphausia similis Thysanoessa inermis Th. longipes Th. raschii Th. spinifera Eualus gaimardi belcheri Nephrops thomsonii Pandalus goniurus Pleuroncodes planipes Cyclostomata Entosphenus tridentatus	Clupea harengus pallasi Sardinops sagax mela-nosticta Salmonidae gen. sp. Oncorhynchus gorbuscha Osmerus sp. Mallotus villosus socialis Cololabis saira Gadus morhua macrocephalus Eleginus gracilis Boreogadus saida Theragra chalcogramma Ammodytes h. hexapterus Sebastodes polyspinu Pleurogrammus monopterygius

We have summed up all the literary data at our disposal, as well as the scanty material obtained as a result of our expeditions in the northern half of the Pacific Ocean during 1951 - 1956, and compiled a list of the prey for the humpback whales for three regions of the World Ocean, similar to what has been done in regard to other whalebone whales (Table 23).

We believe that a study of the data presented in Table 23 reveals the resemblance in regard to the feeding of the humpback whales and other whalebone whales in the Antarctic, where Euphausia superba serves as the basis of its existence. The list of the prey for the humpback whales in the North Atlantic and in the northern half of the Pacific Ocean greatly resembles the list of the prey for the fin whale and the lesser rorqual. [185]

The statement about the lesser rorqual may be fully applied also to the humpback whale (as far as the geographic specialization is concerned). In the northern part of the Pacific Ocean, the humpback whale, like also the lesser rorqual, is, first of all, an ichthyophagous animal. It feeds in this region only to a slight extent on the zooplankton and it does not feed at all on the cephallopod mollusks. Like the lesser rorqual, it feeds in the waters around the Kuriles primarily on walleye pollock. We personally examined the stomachs of humpback whales filled with these fish (remains of bones, otoliths, and crystalline lenses). True, during the run of pink salmon, we also discovered this fish in the stomachs of humpback whales. Thus, the distribution of the humpback whales in the waters near the Kuriles, and also in the area.

of the Commander Islands and South Kamchatka is closely connected with the distribution of the aggregations of the spawning of walleye pollock.

The humpback whales in the Soviet waters - the Bering Sea and the Chuckchee Sea- are found where there are aggregations of Arctic cod, herring, and caplin.

As regards the helminthofauna of the humpback whales, the members of our expedition examined the stomach of only one whale and discovered only one endoparasite, i.e. Bolbosoma nipponicum, and in Delamure's report (1955), there are given only four species of endoparasites: Crassicauda crassicauda, Crassicauda boopis, Bolbosoma balaenae, and Bolbosoma turbinella. All the named helminths are quite widely distributed in the whalebone whales and are of no particular interest to us. It is evident that this is only a small "fragment" of the helminthofauna of the humpback whales that is now known. We may assume without any reservations that their helminthofauna should be much larger, and the fact that we do not know them yet bears witness to the fact that we do not pay attention to the extremely important branch of the helminthofauna, i.e. the study of the endoparasites of marine mammals.

GREY WHALES

As is generally known, the grey whales at present inhabit only the northern half of the Pacific Ocean, although fossil remains of them were also discovered in the North Atlantic (Van Deinse and Jung, 1937). According to a number of scientists (Dudley, 1725; J. Colenso, 1832; Van Deinse, 1931; Jung, 1936; etc.), the grey whales inhabited and were captured in the waters of the North Atlantic back in the

A.G. Tomilin (1957) wrote that until 1932, at which time the Soviet whaling flotilla "Aleut" began its operations in the north-west of the Pacific Ocean (before the publication of Zenkovich's work in 1934), there were scarcely any data on the feeding of the grey whales. Ch. Townsend (1885) and P. Andrews (1914), although they examined the stomachs of these whales captured in the waters of the south-east of Korea, i.e. on the wintering grounds of the Sea-of-Okhotsk-Korea herd (Vasilyev, 1891), they did not discover any food in them, except for the remains of algae and also some jelly-like mass and liquid. In particular, Townsend (1885) wrote the following about the feeding of the grey whales (cited after Zenkovich, 1934): "The people with whom I have spoken about the grey whales believe that these whales, while beyond the boundaries of their Arctic habitat (i.e. on their wintering grounds. S.K.), do not eat much. They are much leaner when they move to the north than when they move to the south... The whalers say that they do not know what constitutes the food of these species, and that they cannot find anything in the stomachs of these animals during their reproduction".

This is quite natural as the whaling for the grey whales took place on the whole on their wintering grounds, in particular, near the shores of Korea (this is found in Townsend's description). On the wintering grounds, as a rule, the grey whales do not feed on anything. This explains why the whalers did not find any food in the stomachs of these animals.

This fact is also substantiated by Ch. Scammon (1869) for the waters of South California. Scammon writes that the stomachs of the grey whales captured during the winter in the waters of South California contained either "... very little food or none at all... until now we have been unable to determine what they do feed on".

During our expedition (1951 - 1956; Klumov, 1959), no collections were made, as we did not capture a single species, although we had special permission to kill five animals for scientific purposes. Hence the list of the prey for the grey whales has been compiled exclusively on the strength of the material published by Soviet scientists and the scientists abroad (their names are given at the end of the present article, in the bibliography).

It should be stressed that almost all food objects, excepting a few, were extracted from the stomachs of the grey whales of the Chuckchee-Californian herd during the summer period.

We would also like to point to the distinct capacity of the grey whales to select some definite food objects- benthopelagic and benthic animals, primarily the amphipods, and hence their complete neglect of planktonic animals during feeding. The inclusion of such representatives of the zooplankton as Euphausia pacifica, Nephrops thomsonii, and Pleuroncodes planipes in the list of the prey may be explained by their discovery in the /187/ stomachs of the grey whales only on the wintering grounds- in the waters of South California and Mexico

(Howell and Huey, 1930; Matthews, 1932). Unfortunately, the number of the mentioned crustaceans in the stomachs of the grey whales remains unknown. Most probably it was single specimens. The following facts allow us to make such an assumption: the general regularity which we have established for the whalebone whales- as a rule, on the wintering grounds, the whalebone whales do not feed on anything, but live on the reserves they have accumulated during the summer feeding; the authors do not indicate the volume of the food discovered in the stomachs of the grey whales examined. Usually, if the stomachs are filled up,this fact cannot but be reported by the scientist, as it usually strikes him much (a great volume of one and the same food consisting of a multitude of crustaceans).

Prey for the Grey Whales (Eschrichtius gibbosus) in the Northern Half of the Pacific Ocean[1]

Polychaeta

Travisia forbesii

Crustacea

Calanus sp.
Mysis oculata
Euphausia pacifica
Isopoda gen. sp.
Lysianassidae gen. sp.
Anonyx nugax
Ampelisca macrocephala
Pontoporeia femorata
Atylus carinatus
Eusirus sp.
Gammaridae gen. sp.
Lembos arcticus
Nephrops thomsonii
Pleuroncodes planipes

Pisces

Clupea sp.

Aves

Phalacrocorax sp.

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1. The present list and Tables 1, 6, 11, 18, 21, and 23 have been compiled on the strength of the original material of the author, which were given to the Expedition of the Institute of Oceanology on the Study of the Cetaceans in the Far East, as well as on the strength of numerous literary sources of which only some are listed below:

Akimushkin (1958); Betesheva (1954, 1955, 1961), Betesheva and Akimushkin (1955), Zenkovich (1934, 1937), Klumov (1952, 1956, 1957, 1958, 1959, 1961, 1962), Korabelnikov (1957), Ponomareva (1948), Sal'nikov (1953), Smirnov (1935), Tomilin (1957), etc.

Andrews (1914), Abe (1953),Collet (1877, 1886, 1900), Freund (1932), Howell and Huey (1930), Ichichara (1961), Jonsgard (1951), Kellog (1928), Matthews (1932, 1937, 1938), Mizue (1951), Nakai (1954), Nemoto (1957, 1959), Nomoto and Nasu (1958), Nishimoto, Tosawa and Kawakami (1951), Nishiwaki (1959, 1960), Olsen (1913), Omura (1957, 1958), Omura and Sakiura (1956), Rice (1961), Schubert (1955), Scammon (1896).