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SC-CAMLR-1/BG.1
1982

# THE ECOLOGICAL PECULIARITIES, STOCKS AND ROLE OF E. SUPERBA IN THE TROPHIC STRUCTURE OF THE ANTARCTIC ECOSYSTEM


## Abstract

Soviet data on the abundance and geographical distribution of krill in the Southern Ocean are analytically reviewed. The location of heavy krill concentrations around Antarctica is discussed on the basis of the peculiarities of its biology and environmental conditions. Krill consumption by the major groups of predators is assessed taking into account the results of Soviet investigations as well as data published in other countries. An allowable catch of 25-30 million tons of krill is suggested on the basis of direct sampling in areas of krill concentration. Such annual catch of krill is considered safe for the status of stocks of krill and dependent consumers.


# LES PARTICULARITES ECOLOGIQUES, LES RESERVES ET LE ROLE DE E. SUPERBA DANS LA STRUCTURE TROPHIQUE DE L'ECOSYSTEME EN ANTARCTIQUE


## Résumé

Les données soviétiques sur l'abondance et la répartition géographique du krill dans l'océan Austral sont examinées de façon analytique. La position de fortes concentrations de krill aux environs de l'Antarctique fait l'objet d'une discussion fondée sur les particularités de sa biologie et les conditions du milieu. La consommation de krill par les principaux groupes de prédateurs est évaluée en tenant compte à la fois des résultats d'études soviétiques et de données publiées dans d'autres pays. Se basant sur un échantillonnage direct dans les régions de concentration de krill, il est suggéré d'autoriser une prise annuelle de krill de 25 à 30 millions de tonnes. Ce taux de prise n'affecterait pas, semble-t-il, l'état des réserves de krill et des consommateurs en dépendant.


# ЭКОЛОГИЧЕСКИЕ ОСОБЕННОСТИ, ЗАПАСЫ И РОЛЬ E. SUPERBA В ТРОФИЧЕСКОЙ СТРУКТУРЕ ЭКОСИСТЕМЫ АНТАРКТИКИ


## Резюме

Делается аналитический обзор советских данных по количеству и географическому распределению криля в Южном океане. Местонахождение больших концентраций криля в Антарктике обсуждается на основе его биологических особенностей и условий окружающей среды. Оценки потребления криля основными группами хищников делаются с учетом как результатов советских исследований, так и данных, опубликованных в других странах. На основе результатов взятия проб непосредственно в районах крупных концентраций криля предлагается установить уровень разрешенного вылова криля в 25-30 миллионов тонн. Делается вывод о том, что такой уровень ежегодного вылова криля не опасен для современного состояния запасов криля и питающихся им видов.

PECULIARIDADES ECOLOGICAS, EXISTENCIAS Y FUNCION DE E. SUPERBA EN LA ESTRUCTURA TROFICA DEL ECOSISTEMA ANTARTICO

Resumen

Se estudian analíticamente los datos de la Unión Soviética sobre la abundancia y distribución geográfica del krill en el Océano Austral. Se detabe sobre la ubicación de las grandes concentraciones de krill alrededor de la Antártida, basándose en las peculiaridades de sus condiciones biológicas y ambientales. Se evalúa el consumo de krill por los principales grupos de depredadores, tomando en consideración los resultados de las investigaciones de la Unión Soviética, así como los datos publicados en otros países. Se sugiere que una captura de 25 a 30 millones de toneladas de krill es aceptable, basándose en el muestreo directo realizado en las áreas de concentración de krill. Se considera que dicha captura anual no constituye un peligro para el estado de las existencias de krill y los consumidores dependientes.

## * INTRODUCTION

In recent years possibilities of exploitation of the resources of Antarctic krill (Euphausia superba) or more correctly, estimation of the scale of their utilization for man's needs has been discussed with a rising activity in the world literature and meetings of various international organisations, such as SCAR, FAO and the Consultative Meeting of the Antarctic Treaty.

All participants in the discussion are of a unanimous opinion on the principles of sustaining an equilibrium in the biological structure of communities of organisms in the Southern Ocean in which krill, as food, plays a significant role. The conclusions of scientists on an extremely high abundance of krill, one of the largest representatives of plankton Crustacea, are also compatible.

As a result of the discussion held by scientists of many countries in scientific literature and FAO publications as to the size of a possible annual catch of krill in the Southern Ocean the conclusions are varied and inconsistent, sometimes unfounded values ranging from 2000 million tons to 10-5 million tons are suggested. It seems that the inconsistency of opinions has originated from a different kind of approach to the assessment of the production, biomass and thus the catch size, from some overestimation or underestimation of the role of krill in the trophic communities and unjustified extrapolation of some or other quantitative data or information on oceanographic and biological parameters referred to certain areas to the whole Southern Ocean.

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* Presented at the First Meeting of the Scientific Committee in 1982.

An attempt has been made to analyse results of Soviet investigations on space and quantitative distribution of krill in the Southern Ocean in association with the main peculiarities of their biology, environmental conditions in their habitat and formation of heavy concentrations, as well as to consider literature data available together with our material collected on the extent of consumption of krill by principal consumers. Proceeding from the analysis it is shown what level of allowable catch may be accepted today, which would not affect adversely the stocks of krill and principal groups of Antarctic organisms feeding on krill.

## I. CHARACTERISTICS OF THE OCEANOGRAPHIC STRUCTURE, BIOPRODUCTIVE PROCESSES AND A DISTRIBUTION PATTERN OF PLANKTON IN THE SOUTHERN OCEAN

The main peculiarities of the oceanographic and biological structure of the Southern Ocean is the latitude zonality developed due to a distinct climatic difference between its northern and southern parts as well as a permanent influence of the Antarctic Circumpolar current (ACC), the most powerful circulation system in the World Ocean. Flowing round the Antarctic continent from west to east, it extends to more than 19,000 km and its width is 2,000 km. The ACC is a remarkably stationary flow in time and well developed vertically. Even at the depth of 3,000 m, its direction almost coincides with that of the surface flow and its velocity makes up 75%, on the average, of the surface flow velocity (Maximov, 1962; Neyman, 1961).

### Water dynamics

Owing to the meridional circulation, the frontal zones of the Antarctic convergence (AC) and Antarctic divergence (AD) are formed between 40°S and 67°S within the ACC. The subtropical and Antarctic surface waters are intensively mixed in the AC and being transformed into warm deep water move to the south. The cool surface water sinks to the depth of over 1,000 m and at the same time extends to the north (Neyman, 1966). The AC encircles the continent and serves as a natural northern boundary of the Southern Ocean and also as a boundary of various climatic areas in the Atlantic, Pacific and Indian Ocean.

The frontal AC is asymmetrically exposed. It extends as far to the north as beyond 50°S in the Atlantic sector of the Antarctic which is known for the lowest heat content, and reaches out 60°S in the relatively warm Pacific sector (Maximov, 1961; Ivanov, 1961; Kort, 1963).

The total area of the Southern Ocean lying to the south of the AC up to the Antarctic continental slope and marginal seas is occupied with waters of a uniform vertical structure : Antarctic surface (winter and summer modifications), deep warm and Antarctic bottom water masses (Deacon, 1937; Makarov, 1956; Maslennikov, 1969). Some local modifications of water masses are formed in the Antarctic inshore zone, marginal seas and bays. They are often characterized with the lack of a warm deep layer (upwelling is observed in some localities of the inshore zone of the continent, e.g. in the Lazarev Sea, Riiser-Larsen Sea and off the west part of the Sodruzhestvo Cape within the continental shelf (Klepikov, 1958; Ledenev, 1963) and a very low temperature in the whole column of water from the surface to the bottom (Klepikov, 1958; Korotkevich, Ledenev, 1962). In some marginal seas (Weddell, Bellingshausen, Ross, Mawson, Riiser-Larsen, Lazarev, Sodruzhestvo, Cosmonauts) and bays (Prydz, Lützow - Holm and Mackenzie) some local cyclonic gyres (Fig.1) are formed under the influence of atmospheric circulation, and upwelling occurs in the centres of the gyres (AD). The southern extremity of each gyre represents an inshore Antarctic current which is not strictly circumpolar. A discontinuous pattern is indigenous to the AD (Treshnikov, 1964). Powerful cyclonic circulations in the marginal seas and bays are responsible for the meridional exchange of waters between the coastal and central areas of the World Ocean. The zone separating the coastal waters of the high-latitudinal modification and ACC in the Pacific sector and the most part of the Indian sector is associated with the continental slope and lies primarily along 64-67°S. Of significance is the position of the Weddell Sea and adjacent Lazarev, Riiser-Larsen and Cosmonauts Seas where the separation zone does not concur with the continental slope.

The Weddell Sea juts far out into the continent and is protected by the Antarctic Peninsula from the west and the South Antille ridge from the north, and is, therefore, well dynamically isolated from the influence of the ACC. Owing to this, the water from the Weddell Sea extends widely to the north and northeast, and the zone separating the water masses from the ACC lies in the south and southeast parts of the Scotia Sea. The zone was ascertained during the first explorations made by VNIRO in the Antarctic and known as Secondary Frontal Zone (SFZ) (Bogdanov et al., 1969; Maslennikov, 1969; Maslennikov et al., 1971). It is oriented from the southwest to northeast in parallel to the Scotia Arc due to the prevailing transport of waters and its pattern is of a meandering character (Fig.2). The stable meridional transport of waters of a high-latitude origin from the Weddell Sea is observed up to 53-54°S. Due to the deviation of the main flow of the ACC to the north in the Atlantic sector and compensative movement of waters of the Weddell Sea the zone separating the coastal waters of the Lazarev, Riiser-Larsen and Cosmonauts Seas lies also to the north of the continental shelf over lower depths along 60-61°S. The investigations made in the Bellingshausen Sea and off the Antarctic Peninsula in the Pacific show that the zone separating the shelf water of the high-latitude modification and ACC is characterized with a high horizontal gradient of the deep maximum temperature, maximum horizontal gradient in the distribution of silicon, Si/P and other indices. The presence of the separation zone is responsible for the formation of a belt of weak unstable currents with gyres and eddies to the south of the zone. This phenomenon is noted alongside with the existence of a coastal Antarctic counter-current (Maslennikov, personal communication, 1977).

A complicated and peculiar pattern of water dynamics results from impediments encountered on the way of the zonal transport of the ACC off islands, archipelagoes, over banks and seamounts. The peculiarity of the water dynamics over insular shelves and seamounts is a high intensity of circulation processes in the area. As a result of the deviation of the ACC flow off islands, over banks and seamounts situated in the open ocean some close local circulation systems as well as secondary small gyres are formed over the outer edge of the shelf. The highest intensity of eddying is noted on the lee or "shade' side in relation to the prevailing wind and current (Elizarov, 1969; Maslennikov, 1969).

According to Uda's theory (Uda and Ishino, 1958) the position of gyres and their stability are dependent, to a considerable extent, upon the configuration and size of islands or banks. When the horizontal flow of the current interacts with the shelf water of an oval island the most intensive gyre is induced on its lee side. If the configuration of islands is close to a rectangular or triangle gyres arise both on the lee side and off their extremities. When the horizontal flow passes over a submerged bank circulation is induced over the bank itself and secondary eddies emerge in the slope area. The most stable and powerful circulation processes are induced in the areas of large islands and seamounts, e.g. the South Georgia, Crozet, Kerguelen, Heard Islands and Ob and Lena Banks which lie in the open part of the Southern Ocean in the zone affected by the ACC where the presence of stable eddies of cyclonic and anticyclonic types is ascertained (Maslennikov et al., 1971; Maslennikov, 1974; Bryantsev et al., personal communication). The relative stability of induced eddies is sustained by peculiarities of the bottom relief of the insular shelves. Of smaller islands and banks where the intensity of circular processes is rather high it is necessary to mention Scott, Peter I, Balleny Islands and Shpies, Banzare and Heracles banks (the South Pacific elevation).

The complicated dynamics of waters characterized by the presence of cyclonic gyres and eddies of different signs in the inshore waters of the Antarctic Peninsula (the South Shetland and Palmer Archipelagoes) is governed by common regularities of the meriodional circulation and formation of a separation zone similar to the SFZ due to the interaction of the ACC with the water of the high-latitude modification of the Weddell and Bellingshausen Seas (Maslennikov, in print).

## Ice conditions

The ice regime in the area lying from the south of the AC to the Antarctic continent is developed in the following way. In winter the drifting ice makes a belt round the continent. The belt area estimated on the basis of the latest information supplied by satellites is 18.9 million $km^2$. The ice edge reaches 60°S in the Atlantic and Indian sectors of the

Antarctic and 65°S in the Pacific sector in winter. The most southern position of the ice edge is recorded in February-March (not further than 50 miles from the mainland coast). In most eastern areas he ice edge reaches the mainland and it is only in some localities that stationary solid ice is sustained, e.g. in the west Weddell Sea, Bellingshausen Sea and off Balleny Islands (Buynitsky, 1973).

Due to a small heat content the Antarctic shelf water is free from ice for a very short period of time, one or two months. Thus, the whole area of about 20 million sq.km south of 60°S is covered with ice in winter.

As the total area of the Southern Ocean lying south of the AC (from 50°S) is about 46 million sq.km only a little more than half of it (about 27 million sq.km)is free from ice all the year round. However, it is ascertained that no pack ice is formed in the Antarctic, the bulk of the drift ice consists of one-year ice (Rybnikov, 1954), i.e. ice thaws and most of the area of shelf waters sets free of ice every year.

The main regularities of latitudinal changes in the oceanographic structure of the Southern Ocean are displayed in the pattern of the dynamics of bioproductive processes, in the specific composition of plankton, and marine organisms, in the pattern of their space and quantitative distribution in the area from the AC to the Antarctic shelf zone. In other words, the latitudinal zonality of the biological structure of the Southern Ocean is in accordance with the oceanographic structure zonality.

### Chemical basis of bioproductivity, phytoplankton and primary production

The latitudinal distribution pattern of biogenic salts in the Southern Ocean is correlated with the position of frontal zones and areas known for strong cyclonic circulations formed in the marginal seas and bays. The content of biogenic salts increases south of the frontal zone of the AC. The maximum concentrations of silicate and phosphates are found in the close vicinity of the continent (Volkovinsky, 1971). The longitudinal distribution of the biogenic substances is rather uniform and subject to regular fluctuations due to infringements of the zonal transport of the ACC off sub-Antarctic and Antarctic islands and seamounts where the content of biogenic substances and phosphates in particular increases. The reasons of such a high content of silicate and phosphates in the high latitudes of the Antarctic are as follows : intensive upwelling in the AD, melted continental ice, very incomplete utilization of biogenic substances by phytoplankton during the short vegetation season (Volkovinsky, 1971; Kozlova, 1962).

The regularities of fluctuations in the quantitative distribution of phytoplankton in the Antarctic are noted by Hart (1942). He believes that they are associated with light and ice conditions which are the most important factors for the development of plankton Algae.

The division of the Southern Ocean into three latitudinal biogeographical areas suggested by Hart is still timely nowadays since it is only boundaries of the following areas that have been outlined more accurately in recent investigation of the Antarctic plankton :

1. A Northern area confined with the AC and up to 330 miles south of the AC is usually free of ice ;

2. An Intermediate area extending to the Polar Circle is free of ice in summar and autumn ;

3. A Southern area including all seas south of the Polar Circle is covered with ice for the most part of the year.

Besides, Hart distinguished some specific areas, e.g. off the South Georgia and balleny Islands, Scotia Sea (to 62°S), waters north of the Ross Sea, Bransfield Strait and off the Palmer Archipelago. It is natural that because of the lack of regular observations at that time Hart failed to view the quantitative pattern of the development of phytoplankton in the whole Southern Ocean and specified areas. However, he has drawn a very important conclusion that the difference in the light and ice conditions resulted in latitudinal variations in the dates of maximum development of phytoplankton and duration of the vegetation period in the area from the AC to the coastal zone. The pigment content (maximum development of phytoplankton) increases in the Northern and Intermediate areas twice, in spring and autumn, whereas in the Southern area there is only one peak in the summer maximum period. Despite the fact that the vegetation season is actually long in the north as compared to the Southern area the period of maximum concentration of pigment is rather short in the Southern Ocean as a whole (Fig.6). The South Georgia area with two peaks in the vegetation season and a tenfold amount of pigment is remarkably distinguished on the background of the values of pigment concentrations in the range of 500-2300 units of Chlorophyll "a" presented by Hart. The yield of phytoplankton in the Scotia Sea is more than twice that in the Northern area (Hart, 1942).

As a result of the recent investigations of phytoplankton, primary production, sediments and suspended matter in the Southern Ocean, Hart's conclusions have been developed and specified (Volkovonsky, 1969, 1971, 1974; Zernova, 1966, 1970; Arzhanova, 1974; Maximova, 1977; Kozlova, 1962, 1964, 1970; El-Sayed, 1967, 1970; Licitsyn, 1966 and others). It is ascertained that the distribution pattern of diatoms which are predominant in the phytoplankton composition in the Southern Ocean is strictly zonal and the northern boundary of their distribution is outlined by the AC. The dates of the beginning of blooming in the latitudinal direction vary by 2-3 months and the vegetation season is shortened from three months to one month in the high-latitude zone as compared to the north area.

The maximum yield of phytoplankton is found near the edge of drift ice, in the AD in summer and reaches more than $10^5$ cells/l in the 0-100 m layer, which is in accordance with the values of primary production registered south of 65°S, i.e. 200-340 mg C/$m^3$/day (Volkovinsky, 1974) and 0.15 g C $m^2$ - 5.26 g C/$m^2$/day (El-Sayed, 1970). The maximum content of diatoms in the suspension is also observed in the continental shelf zone. The number of diatoms in the vegetation season ranges from 0.5 million to 1 billion cells/$m^3$ in different zones, that is, it is fluctuated by 2000 times (Kozlova, 1970). However, examining the remains of diatom delivered for a year (although they are very abundant in the coastal zone) the annual mean maximum occurs much more northerly than the summer maximum and biased towards the AC which may be explained by a shorter vegetation period in the southern part of the Ocean where the area is covered by thick ice for the most part of the year.

Thus, the annual dynamics of bioproductive processes in the Southern Ocean is extremely uniform due to latitudinal zonality of the oceanographic structure. The pattern of bioproductive processes of the Northern area (within the AC) is similar to that of the boreal region of the World Ocean while the Southern area (within AD) and secondary frontal zones north of the AD) is known for distinctly expressed seasons of formation of the chemical basis of bioproductivity and primary production.

Zooplankton

The investigations of the quantitative distribution and annual cycle of the development of the Antarctic herbivorous copepod plankton show that there is a two-month gap between the onset of the maximum abundance of phyto- and zooplankton. The prolonged delay between the onset of intensive vegetation in Algae and time of their maximum consumption provides evidence that the production cycle on this trophic level is poorly balanced (Voronina, 1971).

The total stock of mesoplankton in the 1000-0 m layer (Copepoda constitutes 72.8% of the total Antarctic stock) start declining from northward to southward (Foxton, 1956; Voronina, 1966, 1971). The maximum yield of zooplankton is found in the AC and up to 200-300 miles southward of it. The yield of zooplankton starts decreasing toward the continent, though it again increases somewhat in the frontal zone of the AD (Fig.7). By that, the water over the southern edge of the AC is characterized with high concentrations of zooplankton not only in the period of summer maximum but all the year round, and by intensive quantitative development of plankton in the water column to the depth of 500 m or lower. The highest concentrations of zooplankton in the coastal water occur in the surface productive 0-100 m layer and are sustained during the summer maximum of development. These phenomena and a high biomass of copepod zooplankton in the northern part of the ocean are associated with a constant transport of plankton from southward to northward owing to the meriodional circulation and accumulation of plankton in the AC. Based on the sinking velocity of water in the AC, it is estimated that the daily increase in the plankton biomass reaches 3% of the total size in the upper 500-m layer (Voronina, 1968). The regularity of latitudinal variations in the yield of zooplankton in the Southern Ocean in summer is observed in all its sectors (Fig.8). The mean values of the biomass of copepod zooplankton in the 100-0 m layer of the Atlantic Pacific and Indian Ocean are very close and equal to 73.9, 74.6 and 72.5 mg/m$^3$, respectively (Voronina, Naumov, 1968). The highest biomass (100 mg/m$^3$) is observed everywhere in the AC and its southern edge (Fig.9). In summer some individual localities rich in zooplankton where the biomass reaches 400-600 mg/m$^3$ occur near local gyres off sub-Antarctic and Antarctic islands (e.g. South Georgia, Krozet, Kerguelen, Heard, Balleny) and banks (e.g. Ob, Lena etc.) (Bogdanov, 1967; Vinogradov, Naumov, 1961; Kanaeva, 1969; Pervushin, Naumov, 1970).

It is noted that an extremely abundant biomass of large-sized form of carnivorous zooplankton, e.g. Parathemisto gaudichaudi, Salpae, Ctenophora etc. occurs in most areas discussed. In particular, the role of Parathemisto gaudichaudi is very important in the biological structure off South Georgia, Krozet, Kerguelen and over Ob and Lena banks where the number of specimens amounts to hundreds of milligrams per 1 cu.m. in plankton catches. In some seasons the pre-trawl catches of the species were as high as several kilograms.

The total high level of the quantitative development of zooplankton within the AC frontal zone is circumpolar. It is illustrated with a higher content of nitrates in the 100-150m layer in some areas of the Southern Ocean which are an indicator of the decay of a large amount of organic matter (Fig.10).

A relative decline in the total stock of copepod zooplankton observed from northward to southward in the Southern Ocean is associated with a rapid increase in the biomass of macroplankton represented by some species of the order Euphausiacea.

Abundant euphausids from 5 species (Euphausia superba Dana, E. frigidae Hansen, E. crystallorophias Holt et Tattersall, E. tricantha Holt et Tattersall and Thysanoessa macrura Sars) have circumpolar habitats in the Southern Ocean. Besides, E. vallentini Stebbing, a notal species, penetrates to the northern part of the Southern Ocean and occurs frequently within the AC from the Drake Passage to 30°W (Mackintosh, 1934; Hardy and Gunther, 1935; our data 1974-1978).

The distribution and life history of this important group of Antarctic macroplankton were studied by many workers and their conclusions are taken into account in the paper presented (Fraser, 1936; Johr, 1936; Bargmann, 1945; Mackintosh, 1937, 1972, 1973; Marr, 1962; Baker, 1959; Ozawa 1967; Ruud, 1932; Nemoto and Nasu, 1958; Sasaki, 1965; Rusted, 1930, 1934; Makarov, Naumov, Shevtsov, 1970; Lomakina, 1964; Makarov, 1971, 1972, 1976; Makarov, Shevtsov, 1971; Shevtsov, Makarov, 1969; Dolzhenkov, 1973, Shevtsov, 1973; Pavlov, 1976 and others). The data from the abovementioned contributions are added with new information obtained during the Soviet fishery investigations in the Southern Ocean in 1964-1978 which have not yet been fully published.

All the Antarctic euphausids are large-sized specimens measuring from 25 to 62 mm including T. macrura (up to 29 mm), E. crystallorophias (up to 33 mm), E. triacantha (up to 40 mm) and the largest-sized E. superba (up to 60-62 mm).

Antarctic euphausids are very abundant and all species are more or less capable of forming concentrations, therefore the term "Antarctic krill" is equally appropriate for all of them.

The distribution of euphausids in the Southern Ocean and their quantitative distribution are characterized with a markedly expressed latitudinal zonality (Fig.11).

E. crystallorophias, an exceptionally cold-stenothermic species, occurs frequently in mass in the inshore water of the continental shelf, never leaving the AD, and its life span proceeds in the high-latitude modification water (Fig.12). Here its habitat coincides with that of E. superba and it is likely that the coincidence is limited to the AD, since the development of such a relatively eurythermal species occurs in the warm deep layer (Fraser, 1936) which is, as mentioned above, practically not found in the shelf water column. There are indications that E. superba is substituted by abundant by abundant E. crystallorophias in the neritic zone of the Southern Ocean (Mackintosh, 1973). E. superba occurs frequently in mass in the AD and northward of it, but it is actually not found in the AC (Fig.13). Scarce E. frigida inhabits the area between the AD and AC.

Among all the Antarctic euphausids E. triacantha is most widely distributed. It penetrates far to the notal area, up to 450 miles north of the AC, and occurs in the south up to the AD (Fig.14). The habitat of the species coincides with those of E. superba and E. frigida in the greater part of the area south of the AC. However, E. triacantha is distributed at a lower depth, up to 500-750 m. Most adult specimens (up to 60%) are concentrated on the southern edge of the AC throughout the year (Baker, 1959). The concentration of adult specimens of the species in the zone very rich in copepod plankton is in full agreement with the feeding habits of this typically carnivorous species (Pavlov, 1976). In summer, shoals of E. triacantha are formed in the east Scotia Sea. The hauls made with a krill trawl on board R/V SUND at the depth of lower than 250 m at 56°S and 35°W according to echo sounding recording in December 1977 - January 1978 resulted in a catch of over 100 kg per 1.5 hour of trawling.

As to the frequency of occurrence in the area south of the AC and extending to the continental shelf water, T. macrura ranks second after E. superba (Fig.15). Heavy concentrations are observed in the AD over a vast area of the Pacific sector of the Antarctic, between 100° and 150°W (Nemoto and Nasu, 1958). Concentrations of T. macrura were traced by the echo sounder on board R/V Akademik Knipovich in the 0-50 m layer off Peter I Island in January 1978. The catch was about 150 kg per half an hour of trawling.

The life history, distribution pattern and concentration of Antarctic euphausids have not been comprehensively studied, except for E. superba. It is only known that all of them feed on phytoplankton with the exception of E. triacantha, inhabit the surface layer, make more or less substantial vertical migrations ; their life span is shorter, sizes smaller and their populations are less abundant than that of E. superba.

However, thanks to the latitudinal continuity of the habitats of the Antarctic euphausids in the Southern Ocean beginning with high-latitudinal E. crystallorophias and ending with notal E. vallentini, their evident abundance and hence accessibility for consumption, all the species (not only E. superba) are nutrient food for many groups of vertebrates.

## The main ecological and biological features, regularities of concentration of E. superba

As is mentioned, all species of Antarctic euphausids including E. superba are distributed over a circumpolar area. However, if all of them are rather evenly distributed in the area between the AC and AD (except for E. crystallorophias), the habitat of E. superba is distinctly asymmetrical. The most extensive northward distribution is found to be in the Atlantic sector, then the habitat starts narrowing gradually down southward in the Indian Ocean and in the Pacific sector in particular, except for the Antarctic Peninsula coast. The asymmetry of the habitat is caused by regularities of the meridional transport of water of the high latitude modification which is permanently inhabited by E. superba. The northern boundary of the mass distribution of E. superba in the Southern Ocean seems to lie in close vicinity to the separation zone between waters of the high-latitude modification and ACC. The boundary in the Pacific sector and along the most Indian Ocean sector coincides actually with the continental slope of the marginal seas (64-67°S). The northern boundary of the habitat in the west Indian Ocean sector (Lazarev, Riiser-Larsen, Cosmonauts Seas) and in the Atlantic sector lies in accordance with the position of the separation zone between 60-61°S and 53-54°S due to an extensive stretch of water from the Weddell Sea from northward to northeastward.

As is ascertained, the main habitat (the population reserve) of E. superba is the waters of the West drift, i.e. in the East Wind Drift (Mackintosh, 1937, 1972; Marr, 1962). According to the terminology accepted in the Soviet Antarctic Atlas (1969), the Coastal Antarctic current or East Wind Drift is not strictly circumpolar since it represents a southern circumference of quasi-stationary cyclonic circulations of several marginal seas and bays on account of which the west transport of water is induced in some localities of the coastal area (Fig.5). Therefore, the life history of krill is directly associated with local cyclonic circulations of shelf seas and bays, the basis of their habitat.

The life history of E. superba is, on the whole, similar to those of other euphausids, and at the same time it is very specific due to the association of E. superba with waters of the high-latitudinal modification.

In the course of spawning, non-floating eggs are liberated in the surface layer over the shelf or continental slope in summer. The fecundity of E. superba is much higher than that of other euphausids and amounts to 8000 eggs. Some fluctuations in the fecundity are known to occur in regard to environmental conditions in different years (Fig.16). Larvae are hatched at a low depth and developed in the warm intermediate layer. Having reached stage Caliptopis I, they drift with the warm water to the surface and start feeding from the environment, making diurnal vertical migrations the range of which is shortened with growth. The larval development of most specimens is completed in autumn. In the next spring this year class occurs as juveniles 20-25 mm long. In the second year of life (spring-summer) the juveniles feed intensively on phytoplankton, their growth rate is high and they reach 25-40 mm in length. Krill attain sexual maturity in the third summer, when they are about 50 mm in length. In fact, the size of krill from the same year class varies in relation to their habitat, environmental conditions and annual variability. After spawning specimens of older age are gradually eliminated from the population. However, recent investigations conducted in the Atlantic and Pacific Antarctic have revealed that far from all first-time spawners die. Regeneration of gonads is found in spent, and in the following spring one can see two groups of adult specimens of different size which are ready for spawning (Makarov, 1976; Dolzhenkov, 1973). The survival rate of adult specimens varies no doubt, by years. According to Soviet data, the most favourable conditions for survival of krill are observed in the years when the spawning starts and ends earlier in the season, therefore specimens are able to feed longer on phytoplankton whose vegetation season is still going on.

On the average, each year class is believed to live for 2.5 - 3 years and each population consists of three main groups corresponding to three generations : larvae, juveniles and adults. According to Soviet long-term observations on the distribution of krill on the spawning grounds, they start descending to adepth of lower than 250 m in late summer or early autumn with regard to annual environmental conditions when the feeding season is over due to the decline in the yield of phytoplankton. The descent of most specimens may be considered as a gradual transition to the autumn-winter distribution or a seasonal vertical migration and a subsequent drift to higher latitudes. Owing to this fact, the stability of the habitat of the population of E. superba is sustained (Mackintosh, 1937).

The isolation of closed cyclonic circulations and discontinuity of the Antarctic Coastal current could not help affecting the pattern of space and quantitative distribution of krill in the Antarctic ring of coastal waters. The comparison of the diagram of surface currents (Fig.1) with the map showing the distribution and relative abundnce of krill (E. superba) has indicated a certain relationship among the distribution of this passive migrant, position and scale of cyclonic circulations (Fig.13). The highest frequency of occurrence of krill is observed in cyclonic circulation areas in the Weddell, Bellingshausen, Amundsen, Ross, Durville, Mawson, Sodruzhestvo, Lazarev, Riiser-Larsen, Cosmonauts Seas and Prydz Bay. They occur far less frequently in the rest inshore area where no circulations are found. The data on the distribution of heavy concentrations of krill E. superba in the Southern Ocean in spring and summer obtained in the course of long-term investigations carried out by All-Union Research Institute of Marine Fisheries and Oceanography (VNIRO) in 1964-1978, Asov-Black Sea Research Institute of Marine Fisheries and Oceanography

(AzCherNIRO) and Pacific Research Institute of Marine Fisheries and Oceanography (TINRO) in 1970-1978, support the evidence of this regularity (Fig.28).

The concept of stability in the existence of plankton in the close circulation systems was suggested a long time ago (Damas, 1905; Hesse, 1924). The concept was developed on the population-biological basis by Beklemishev (1969) in his investigations on the structure and functioning of plankton biocoenoses of the World Ocean.

The analysis of the distribution of several hundreds of zooplankton species reveals that the degree of isolation and independence is determined on the basis of the morphological and functional structure of the population. In oceanic plankton species "independent" populations capable of self-reproduction and self-maintenance of their habitat without the arrival of any specimens from outside inhabit primary water masses (it means genesis of water masses) with closed circulation systems. "Dependent" populations bound with secondary water masses or various modifications of water masses are capable of reproduction, but they fail to survive for an indefinitely long time without newcomers from outside. However, the degree of their dependence upon self-reproductive population of the same species may vary. Based on this concept the notion of "Subpopulations" possessing a more or less considerable extent of independence and isolation is introduced. And finally, there are "pseudopopulations" inhabiting localities with rapid transformation of waters or on edges of the habitat of the species and where specimens fail to complete their life cycle for some or other reason.

Under condition of a large-scale deformation field (Defant, 1961) a functional complex is formed which includes an independent population together with dependent subpopulations and pseudopopulations, the distribution of which is regularly designed in accordance with certain elements of the hydrodynamical system.

The stock separation, from the point of view of the morphological and functional structure, is a very significant or frequently a decisive factor for the assessment of the total stock (or the total biomass) of marine species. It is particularly important for the assessment of the stock of E. superba which inhabits a vast circumpolar area. Actually the regularities of abundance and dynamics of krill populations are formed on the basis of peculiarities of the morphological and functional structure of certain parts of the total habitat.

The Soviet investigations made in 1964-1978 show that heavy concentrations of krill are regularly formed in the spring-summer season and in part in autumn and associated with the reproduction and feeding habits of krill. The time of appearance of concentrations and how long they stay in certain areas of the Atlantic, Pacific and Indian Ocean sectors differ in accordance with general regularities of ice conditions in the Antarctic, i.e. with the position of ice edge which governs the start and duration of the vegetation period. Of great importance is the annual variability of hydrometeorologic conditions in each particular area where concentrations occur in some or other sector.

In the Atlantic sector krill are concentrated in the spawning season in November-December and specimens stay together till April-May, whereas the aggregation in the Pacific and Indian Ocean sectors occurs not earlier than in late December. After the spawning and feeding seasons are over, they are dispersed in March-mid-April. However, the peak of spawning in all the areas is observed in January-February. The spawning, with regard to annual fluctuations in the hydrometeorological conditions, last, on the average, one month in the Pacific and Indian Ocean sectors and 2.5 months in the Atlantic, and specimens stay in shoals in the spawning and feeding seasons for 3 and 5 months, respectively. Most specimens are concentrated within the zone of separation or interaction of waters from the marginal seas of the high-latitude modification and ACC. In most seas of the Pacific and Indian Ocean sectors (Bellingshausen, Amundsen, Ross, Durville, Mawson, Sodruzhestvo Seas and Prydz Bay) concentrations of krill occur in the northern periphery of closed cyclonic systems. They are also distributed near the separation zone between the ACC and coastal cool waters off the Antarctic Peninsula (from the Adelaide Island to Palmer Archipelago) and in the Drake Passage (along South Shetland Islands). The general regularity of distribution is also retained in the Atlantic sector, though the water dynamics is more complicated there and the separation zone between the ACC and Weddell Sea is at a considerable distance northwards from the close cyclonic system formed in the Weddell Sea. Thus, if in the Pacific Indian Ocean heavy concentrations of krill are formed in the greater part of the inshore zone in the close vicinity of the AD, such concentrations in the Atlantic sector are found far northward from the upwelling of the Weddell Sea water, as far as in the Scotia Sea ; but they are also associated somehow or other in all areas with the separation zone between waters of various modifications.

The analysis of the vertical circulation of water in areas where concentrations of krill occur gives evidence of general regularities of the mechanism forming heavy concentrations in the area where krill are distributed in abundance. Heavy concentrations are formed in localities where water sinks, adjacent to places of upwelling. The important condition for concentration is that localities where water sinks should be confined with peculiar "walls" which may be either of a dynamic character (in the open sea) or of an orographic character (in the shelf and continental slope areas). The velocity of the horizontal flow in this case is not so important for concentrations of krill (Fig. 17, 18, 19).

The dynamic mechanism of krill concentrations ascertained is very important for understanding the distribution and sustained retention of krill within the boundary of a certain cyclonic system. It might seem that krill having been concentrated on the periphery of a closed cyclonic system, i.e. on the left from the horizontal flow of the current, should be carried outside the system since the transversal circulation in it is directed from the centre. But nothing happens due to the fact that it is just that type of vertical circulation where "walls" are of a dynamic nature, that is they are induced in the zone separating the ACC and high-latitude modification water.

The isolation of cyclonic circulations formed in the marginal seas and bays in the northern periphery of which krill concentrations are regularly formed pre-determines the existence of an independent population in most of them, if not in each. Therefore the opinion that there are only five or six populations of E. superba in the Southern Ocean (two of them in the Indian Ocean and three in the Pacific) seems to be, to a considerable extent, too simplified (Mackintosh, 1973).

The long-term observations on the distribution and biology of krill in concentrations in the Pacific and Indian Ocean Sectors give evidence of the existence of individual populations of E. superba in the Ross, Bellingshausen Sea, presumably in the Durville Sea, in the Sodruzhestvo Sea together with Prydz Bay and in the Cosmonauts Sea. The composition of concentrations is noted to remain unchanged from year to year. The concentrations are represented by three generations : larvae, juveniles and adults. The annual spawning takes place regularly in the same areas. In view of the fact that the northern boundary of krill concentrations lies in these areas rather close to the AD, different generations are spatially drawn together, especially adults and adolescents.

Concentrations of adult specimens and spawning are annually observed in the band between 64° and 74°S, 160°E and 145°W in January-February. Most spawning and pre-spawning specimens are found somewhat northward from the Balleny and Scott Islands as well as in the central part of the Sea (64°-68°S). In some years, juveniles occur among mature specimens on the main spawning grounds. In the southern part (68°-70°S) the number of juveniles, as a rule, increases in the catches, and south of 70°S juveniles prevail over adult specimens (Fig. 20 a, b). Larvae at stages Caliptopis and Furcilia are found in the surface layer of the southern part of their habitat in upwelling localities in late summer.

A similar pattern of the distribution and composition of krill concentrations is observed in the Bellingshausen Sea (Fig. 21). Mature specimens are concentrated in the band between 66°S and 68°S, gradually extending to the north in the east part of the sea off the Antarctic Peninsula.

Concentrations of krill in the Sodruzhestvo Sea and adjacent Prydz Bay is very likely to belong to a single population, the structure of which is similar to those from the Pacific sector. However, the distribution pattern is more distinctly displayed here, although some size groups are partly mixed in the concentrations. The intensive spawning takes place in the northern part of their habitat in February, where most adult specimens are concentrated (60°-64°S). The coastal waters south of 64°S are chiefly inhabited by juveniles including specimens at earliest stages of development. In the Cosmonauts Sea, the habitat is wider and adult specimens are distributed far northward beyond 61°S, and the evidence is supported by data on the distribution of size groups in concentrations in the east part of the sea (Fig. 22).

In general, the analysis of long-term data obtained in the spawning season on the distribution, size-age frequency of occurrence, sex composition, feeding habits, growth and maturity rate of krill inhabiting closed cyclonic circulatory systems in the Pacific and Indian Ocean sectors, demonstrates homogeneity of the morphologic and functional structure of isolated populations. Populations of E. superba inhabiting the Ross, Bellingshausen, Sodruzhestvo Seas with Prydz Bay and presumably the Cosmonauts Sea may be referred to as independent populations.

Although many areas of cyclonic circulatory systems in the Antarctic ring where concentrations of krill are annually observed in the spawning and feeding seasons, are evidently isolated, it is still premature to conclude that each circulatory system is inhabited by an independent population. At present, the problem of a possible exchange among separate populations in the northern part of the habitat of E. superba at the expense of the drift with the ACC (the southern periphery) has not yet been solved. Moreover, elements of the morphological and functional structure of the populations have not yet been recognized in all cyclonic circulatory systems where krill concentrations are found. Nevertheless, it is hardly probable that krill are carried outside circulatory systems, and thus no exchange between populations seems to take place in the inshore areas of the Pacific sector and most marginal seas of the Indian ocean sector where the northern boundary of the mass distribution of E. superba occupies the southernmost position close to the ice edge.

There are ample possibilities of exchange among populations in the Atlantic sector and west Indian Ocean sector owing to the drift of krill from the Bellingshausen Sea from the southern periphery of the ACC through the Drake Passage, with Weddell Sea current to the north to the Scotia Sea and northeast to the Lazarev, Riiser-Larsen and Cosmonauts Seas. Due to the lack of data, it is difficult to pass judgement on the extent of interaction among the ACC, Weddell Sea and shelf seas of the west Indian Ocean sector or on the impact inflicted on the morphological structure of the populations inhabiting this area. It is only evident that the interaction of waters from various modifications results in a wider habitat and distribution to the north of krill concentrations in the Lazarev, Riiser-Larsen and Cosmonauts Seas than in other regions of the Indian Ocean sector.

Peculiar conditions of habitance are observed in the Atlantic sector. The main habitat of krill, as in the other sectors of the Antarctic, is a closed quasi-stationary cyclonic circulatory system formed in the marginal Weddell Sea. However, if in most areas of the inshore water krill are concentrated in the close neighbourhood of the AD, the concentrations in the Atlantic sector are found far northward of the upwelling of the Weddell Sea. It is very likely that this phenomenon served as a starting point for recognition of the Weddell Sea population and "East wind drift" population (Marr, 1962), i.e. two independent populations of a single genesis.

The study of the size-age frequency of occurrence and biological state of krill in concentrations formed in the spawning and feeding seasons in the Atlantic sector as well as tracing of possible routes of drifting krill has actually indicated only one self-supporting independent population of E. superba, i.e. the Weddell Sea population. The formation of krill concentrations is observed within areas where the Weddell Sea water is penetrated northward and northeastward in the zone of interaction with the ACC, which is in accordance with the geostrophic circulation pattern in the area (Fig.23). Here the krill concentrations are distributed in the following areas :

(1) The Secondary frontal zone in the south Scotia Sea separating the water of the high-latitude modification of the Weddell Sea and ACC.

(2) Some localities in circulatory systems formed over the chain of South Antille seamounts and islands.

(3) The area extending to the northwest, north and northeast of South Georgia.

(4) Areas adjacent to the Antarctic Peninsula waters of some islands from the South Shetland Archipelago and east Bransfield Strait.

The distribution pattern of krill concentrations in the areas involved may vary from year to year in relation to weakening or strengthening of the Weddell Sea flow. The position of the Secondary Frontal Zone (SFZ) in the Scotia Sea is ascertained to be subject to regular annual variations associated with climatic fluctuations (Fig.2). Besides, long-term fluctuations in the SFZ are also known. So in the 1920s-1930s the development of climatic processes displayed a cool trend in the off-land air layer and surface water layer in the Atlantic ; the 1960s-1970s may be characterized, on the whole, as a "warm epoch" on the background of which some anomalously cool years are seen (Maslennikov, 1979). However, regardless of a different scale of extension of the Weddell Sea water with which variations in the position of the frontal zone are associated, the principal regularities of the distribution and concentration of krill as well as the mechanism forming heavy concentrations, remain unchanged.

The reproduction of the Weddell Sea populations of E. superba is annually observed in the SFZ in the south Scotia Sea, the meandering character of which contributes to accumulation and retention of krill for a long period of time (Fig.24). In spring and summer concentrations represented mainly by adult specimens in the pairing and spawning season are distributed here. By that, the formation of concentrations of mature specimens in the SFZ is observed long in advance of the beginning of blooming of phytoplankton (November-December) in some years.

Owing to a considerable extension of the SFZ from the southwest to northeast (from the South Shetland Islands to 35°-30°W) and therefore different environmental conditions for krill on the spawning grounds (a bias in the latitudinal course of "phenological spring") the spawning extends greatly and lasts up to 2.5 - 3 months. The reproduction cycle is observed to be sometimes up to one month late from westward to eastward (Fig.25). This regularly observed over many years may be undoubtedly one of the main reasons why the size structure of the Weddell Sea population is so complex. Substantial differences in the time of spawning on a vast spawning area in the meriodional direction produce variations in the growth rate of larvae.

It is also possible that the variations in the size composition of the population are due to a probable existence of some other spawning grounds of E. superba beside the SFZ which were discussed by Marr, namely in the Bransfield Strait and off Graham Land (Marr, 1962). No spawning in these areas was observed during the Soviet investigations, but if spawning of E. superba does occur here this fact, taking a direct dynamic connection of water of the areas involved with the Weddell Sea into account, should be considered as evidence of the expansion of the habitat of the Weddell Sea population and its high abundance, but not as evidence in favour of the existence of one more independent population. But if the assumption is made that some population does exist in the Bransfield Strait, since plenty of larve sometimes occur in this area and older groups of adolescents are concentrated here, it should be classified as a subpopulation dependent on the Weddell Sea population. However, it is very likely that concentrations formed here in some years are associated with the drift of the young from the Weddell Sea, the main part of the habitat of the population of E. superba. In view of this, it is necessary to note that the general regularity inherent to all the populations of E. superba in the Southern Ocean that mature and immature specimens live separately, is most conspicuously displayed in the habitat of the Weddell Sea population (Makarov, 1973).

Mature specimens are separately concentrated in places of stable meanders of the SFZ up to the end of the spawning season. The young are mainly distributed south and southeast of the spawning grounds (Fig.26). By autumn the habitats of mature and juvenile krill are gradually transgressed. The juveniles distributed over a vast area south and southeast of the SFZ are rather abundant, and in some localities characterized with concentrating forms of the horizontal circulation, some concentrations of krill which are sometimes very stable are formed. It is noted that it is only adolescents from older age groups (the second year of life) that make concentrations. No concentrations of larvae or young at early stages of development were found anywhere in the Southern Ocean over many years of observations. As a rule, younger juveniles form only surface patches. The regularity ascertained is very significant on a biological basis. The dispersed distribution of larvae and early juveniles guarantees the species a better chance for survival at early stages of ontogenesis on account of favourable feeding conditions within a restricted vegetation period and better escape from predators.

In accordance with the nature of the geostrophic circulation, some adults and a lot of young specimens drift to the northeast, reaching South Georgia Island. By that, the composition of mature specimens which reach these latitudes earlier than juveniles is mixed, since their drift to the northeast occurs, in the main, with ACC north of the SFZ. Adult specimens from the Weddell Sea population occur less frequently here as their distribution is restricted with the frontal zone, while the frequency of occurrence of specimens originating from the Bellingshausen Sea is very high. Judging from a rapid change in the size composition of adult specimens in the intersection of the frontal zone from south to north, the south outlying waters of the ACC are inhabited by krill from the Bellingshausen Sea population, in part drifted through the Drake Passage to the Scotia Sea. They, in fact, are scarce and cannot form independent concentrations (Makarov, 1977). A partial mixing of specimens from the Bellingshausen and Weddell Seas occurs off the South Shetland Islands and it becomes more pronounced in the meandering area of the SFZ. Due to this fact, areas adjacent to the South Shetland Islands (with the exception of Mordvinov and Shishkov Islands, where krill from the Weddell Sea are concentrated) are believed to be a peculiar transitional region between the populations from the Bellingshausen and Weddell Seas, since heavy concentrations of mature specimens formed here have a mixed composition.

Mature specimens appear irregularly off South Georgia Island and their abundance is incomparable with that of juveniles brought into the area from the main circulation zone of the Weddell Sea. This fact provides evidence that if mature specimens of some genesis drifted to the northeast with the ACC, their number is very insignificant.

Owing to the advection of water from the Weddell Sea to the shelf zone of South Georgia (Fig.27) and emergence of local closed circulation systems of a cyclonic character, heavy concentrations of krill represented mostly by juveniles from the Weddell Sea population are formed. They occur in the shelf water in early summer (January-February) and are sustained for a long time, sometimes to winter (June-July). However, krill are gradually brought out towards the northwest, beyond the island, to foreign for them waters of the ACC.

In some years no concentrations of juveniles were observed here, e.g. 1969 and 1978. Due to a large-scale variability in the horizontal circulation, when only one flow of a northwestern direction is virtually active over the shelf and insular slope, and there is no advection of the water from the Weddell Sea towards the shelf, krill drift with the current northward, eluding South Georgia Island, and are again in conditions foreign to them. Somehow or other, the drift of krill to lower latitudes outside their habitat corresponds to expatriation from the Weddell Sea population, and the South Georgia water is believed to be an expatriation area. By that, under certain conditions krill may not enter the island water of if they do, they are unable to complete their life cycle under these conditions ; therefore the South Georgia shelf is suggested to be characterized as a sterile expatriation area (Makarov, 1973, 1974). In any case, the area is not important for the reproduction of the Weddell Sea population, since the limited opportunities for reproduction of krill do not compensate for the natural mortality rate. It is believed that the regular loss suffered by the population due to expatriation of a certain number of juveniles is replenished at the expense of very favourable reproduction and feeding conditions of the majority of krill in the South Scotia Sea.

Thus in view of the morphological and functional structure, the Weddell Sea population of E. superba belongs to complex populations in contrast to simple populations from most other marginal seas, although all of them inhabit closed quasi-stationary circulatory systems.

On the background of general regularities in accordance with which the life cycle of E. superba proceeds and is closely genetically associated with the high-latitude modification water restricting their distribution and especially the distribution of heavy concentrations, there are differences governing peculiarities of the abundance and population dynamics in each closed circulatory system. The differences are firstly observed in feeding and reproduction conditions, and hence in the growth rate and extent of a possible drift of krill outside the habitat of this or another independent population inhabiting the closed circulatory system.

The analysis made indicates how advantageous are the feeding and reproduction conditions of the Weddell Sea population of E. superba as compared to those of most marginal seas, thanks to the fact that reproduction and feeding occur beyond cyclonic systems over the vast highly-productive Scotia Sea area which is free of ice for a long time. The main stages of the life cycle of E. superba from other marginal seas proceed within closed cyclonic systems where the opportunity of feeding and spawning are limited due to climatic and ice conditions. However, even there it is possible to recognise some individual populations whose spawning grounds extend rather far in the meriodional direction, e.g. the Ross Sea. It is observed that the warm deep layer extends far south to the shelf waters in the Lazarev, Risser-Larsen and west Sodruzhestvo Seas, which seems to create favourable conditions for the development of larvae. Apart from that, there are opportunities for a more extensive distribution of E. superba to the north in these seas. At the same time it should be noted that the possibility of a wider distribution of krill in certain areas may be displayed not only as a factor contributing to a better growth, feeding and reproduction rates, but as a factor affecting adversely the entire population. For example, it is well illustrated by the expatriation of a certain number of juveniles from the Weddell Sea population and the existence of the sterile expatriation area. Besides, the distribution of krill concentrations more or less northward increases the extent of accessibility of krill to some groups of consumers, especially in areas where there are many islands and seamounts.

It is very unlikely that any substantial number of specimens is brought out from simple populations inhabiting closed cyclonic systems as their distribution is northerly restricted, to a great extent, by zones separating the waters of the high-latitude modification and ACC. However, the existence of such a phenomenon may be assumed and its influence on some independent populations should be taken into consideration, e.g. in the transitional area between the populations from the Bellingshausen and Weddell Seas.

All the abovementioned supports, in our point of view, a conclusive evidence that the realistic assessment of the stock and dynamics of the population of E. superba in the Southern ocean can be made only on the basis of the morphological and functional structure of individual independent populations inhabiting closed quasi-stationary circulatory systems of Antarctic marginal seas and bays instead of extrapolating the biological and quantitative parameters of a certain locality over the entire area of the Southern Ocean.

## II. ASSESSMENT OF THE ABUNDANCE OF E. SUPERBA IN HEAVY CONCENTRATION OCCURRED IN CERTAIN AREAS OF THE ATLANTIC, PACIFIC AND INDIAN OCEAN SECTORS OF THE ANTARCTIC

The problem of the assessment of the size of krill biomass in the Southern Ocean has aroused interest of workers in relation to the feeding habits of whales long in advance of Soviet fishery investigations in the Antarctic as a result of which a potential possibility of exploitation of this resource was determined.

The first attempt at assessing the Antarctic krill biomass was made in 1958 and it was based on the data on the consumption of krill by baleen whales. Proceeding from the mean annual consumption rate (not more than 20% of the krill stock) of the stock of whales amounting to 500,000 individuals, and the daily consumption rate of blue whale equal to 3.0 t, it was estimated that the total abundance of krill makes up 1.4 billion tons (Ottestad, 1956; Pequegnat, 1958). Using this approach the total stock of Antarctic krill was estimated to be 0.8-0.9 billion tons (McQuillan, 1962).

Proceeding from the summary size of primary production, the mean annual production of total Antarctic zooplankton is estimated to 1.5-1.0 billion t which yields the estimate of the annual krill production of 750-500 million tons (Gulland, 1970; Hempel, 1970; Grand quoting Nasu, 1975). By that, it is accepted that krill constitutes about 50% of the total Antarctic zooplankton (Vinogradov and Naumov, 1958). There are indications that the total biomass of Antarctic zooplankton represented mostly by Euphausiacea reaches 5 billion tons (Klumov, 1963).

Based on the data obtained in the echo-sounding survey of krill concentrations in the Antarctic Indian Ocean, the total stock is estimated to be equal to 6 billion tons (Nemoto, 1974; Doi and Nemoto quoting Nasu, 1975).

Information available on the attempts at assessing the total biomass of Antarctic krill is actually exhausted by the abovementioned data. In fact, the information on the amount of krill which man can withdraw without affecting the stock and main consumers in the Southern Ocean, is more apprehensible.

Table 1 illustrates principal data obtained by some authors in relation to the assessment of the stock (biomass) of Antarctic krill and possibilities of exploiting their resources. It is far from a complete list of data available in the literature on the size of the permissible catch of krill from the total stock.

Considering the data available in literature and tabulated here, one can pay attention to the fact that they are very scarce and, on the whole, the inconsistency of opinions on the total stock of krill in the Southern Ocean is emphasised. It is very likely that none of the values suggested is sufficiently realistic in view of the imperfection of the indirect methods applied and a prejudiced approach to the solution of this very complicated and many-sided problem. It does not seem accidental that many workers do not think it necessary to give their opinion, i.e. to give a definite estimate of the stock to be comprehensively substantiated.

The matter is very likely to be explained by the fact that any attempt to assess and substantiate the size of the total biomass and production of krill on the basis of a turnover of substances, energy and their distribution between living and non-living parts of the ecosystem of the Southern Ocean would meet failure in view of the present level of knowledge. The evidence of the conclusion is Everson's investigation. Although he considers many sides of mass biological processes occurring in the Southern Ocean, he has yet been unable to come to a definite conclusion on the stock size and production of krill (Everson, 1977). The value of 5 million tons selected at random, stands clearly out as the lowest figure on the background of estimates suggested by most investigators which are actually of the same order (except for the unjustified enornously overestimated value of 2000 million t). The similarity of estimates lying within a rather close range of 50-150 million tons seems to be explained by the fact that most workers proceed from the assumption of a potential opportunity of fishing at the expense of a certain reduction in the consumption of krill by whales, i.e. at the expense of "surplus of krill".

It should be noted that the data obtained by Soviet workers in the first years of investigations, which characterise the distribution of krill concentrations over a wide area and a high density of specimens in concentrations (Moiseev, 1970; Makarov et al., 1970; Stasenko, 1965; Dolzhenkov, 1970, 1973; Ivanov, 1970; Shevtsov and Makarov, 1969; Makarov and Shevtsov, 1971, etc.) at first aroused some suspicion. At present, a sufficient amount of data has been obtained supporting the results of our investigations (Nemoto and Nasu, 1975; Nemoto, 1974; Fisher, 1974; Sahrhage, 1975; Kock and Neudecker, 1977 and others).

Thus, the high abundance of E. superba forming enormous krill concentrations and tangibility of their commercial exploitation is not disputed now and only some concern is discussed as to a possibility of affecting the stock of E. superba and the ecosystem of the Southern Ocean (Gulland, 1970; Mackintosh, 1970; Knox, 1970; Laws, 1977; Everson, 1977, 1978). The essence of most workers' opinion is the need, as soon as possible, to determine and accept such a size of catches which would secure managerial approach to exploitation of the krill stock without violating the equilibrium in the trophic structure of communities of Antarctic marine organisms. It is impossible not to agree with the conclusion. It is this principle that was the basis for the estimate of the size of a possible catch suggested by Soviet workers in 1973 proceeding from the preliminary results of investigations of the quantitative distribution of krill in the Scotia Sea and adjacent waters (Lubimova et al.,) ; moreover, we overestimated the role of E. superba in the trophic structure of the Southern ocean in the first years of explorations (Permitin, 1970; Permitin et al., 1972; Naumov and Permitin, 1973). On the basis of the assessment of one-time presence of krill in some localities where heavy concentrations occur in the Scotia Sea, Prydz Bay and off the Balleny Islands as well as on the data of trawling surveys made in 1965-1975, the minimum limit of the annual catch is estimated to be 15 million t (Bogdanov and Lubimova, 1978).

The analysis of actual data collected over a number of years on the space and quantitative distribution of krill in the Atlantic, Pacific and Indian Ocean sectors of the Antarctic makes it possible to assess the biomass of krill of older age groups (adolescent and adult specimens) over a vast area of the Southen Ocean where heavy concentrations were found. The quantitative survey of krill of older age groups has become possible with the use of a mid-water trawl equipped with a chafer with a mesh size of 5.0 - 6.5 mm which secures the escape of larvae and early juveniles. As far back as in the first years of exploration, it was ascertained that krill form extremely dense concentrations in mid-water recorded by hydro-acoustic devices. The biomass of krill in such concentrations is 2.3 - 4.5 kg/m$^3$ or more and trawl catches amount to 15-20 t per hour of trawling.

The highest density is found in the upper 0-100 m layer. The vertical range of the distribution pattern, density of concentrations and the depth of the layer vary in relation to the area where krill are concentrated in the course of the spring-summer season of a given year and time of the day. Some annual variability of the characteristics involved is observed too in these areas.

It was also ascertained that the distribution pattern of heavy concentrations is not uniform over the area inhabited and due to this fact the maximum parameters of the density and maximum size of trawl catches cannot be extrapolated to adjacent ares of the habitat. As was shown in Section I, the distribution of dense shoals in the area where krill are concentrated depends on the peculiarities of vertical circulation of water, i.e. on the presence or absence of concentrating forms of the circulation and their stability.

Knowing the regularities of the distribution of krill in the seas of the Atlantic, Pacific and Indian Ocean sectors in the reproduction and feeding season when heavy concentrations are formed, conditions favourable for forming dense concentrations and their vertical distribution, we used the method of direct sampling in certain localities. This simple method of stock assessment is well known to Soviet and foreign specialists (Baranov, 1971; Zasosov, 1970; Allen, 1966 and others) and it is not necessary to describe it in detail. It is quite evident, however, that the result obtained does not represent the size of the stock in some or other region, but is a value which indicates very reliably the quantity of krill of older generations in concentrations of krill of marketable size (35-60 mm) at a certain time in this area.

The direct sampling of krill was made for the first time in 1965 and 1967 by workers of VNIRO on some localities of the area inhabited by heavy concentrations in the SFZ of the Scotia Sea and in the shelf water of the South Georgia Islands (Shevtsov, 1973). In the following years the VNIRO continued and extended the investigations on the quantitative distribution of krill in some localities in the Bellingshausen Sea, off the Antarctic Peninsula, South Shetland Islands and in the Bransfield Strait. Similar investigations were made by specialists of the Pacific Research Institute of Marine Fisheries and Oceanography an Azov-Black Sea Research Institute of Marine Fisheries and Oceanography off Balleny and Scott Islands, in the north Durville Sea, Prydz Bay and in the east Sodruzhestvo Sea in 1973-1978 (Fig.28).

In each season (usually in January or February, and rarely in March) a one-time trawling survey was made with a mid-water trawl and the distribution of concentrations was continuously controlled with hydroacoustic devices. The survey usually lasted 10-20 days with regard to the area surveyed. The hauls were made 10 miles or a maximum of 30 miles apart in the area investigated.

The catch per haul per unit of time (usually 30-minute hauls were made) was converted into the biomass ($g/m^3$), the volume of filtered water being taken into account.

By that, the tlater was calculated by multiplying the distance fished with the trawl (in meters) at a certain speed (in knots) by the area of the opening of the trawl in the belly, just before the chafer of the codend, i.e. in that place where krill cannot escape through meshes and are caught by the trawl. The calculations were made using the well-known formula, but instead of the area fished ($m^2$) the volume of water filtered ($m^3$) was used.

$$N = \frac{A \cdot n}{a_v} \cdot \frac{I}{q}$$ (According to Zasosov, 1970)

where in this case

N - the weight of krill concentrated in the area at one time (million t) ;

A - the total volume of water in which concentrations are distributed ;

$A = S \cdot H$, where

S - the area occupied by concentrations ;

H - the vertical distribution of concentrations ;

n - catch per haul (empty hauls are also taken into account) ;

$a_v$ - the volume of water filtered per haul ;

$a_v$ = g.p, where g - the opening of the trawl, p - distance covered, with the trawl per haul ;

$\frac{I}{q}$ - catchability coefficient (accepted as 1 in this case i.e. it is assumed that all specimens concentrating in the layer covered by the trawl are caught).

Having assumed that the catchability coefficient is equal to 1 the final result of the calculations is beforehand known to be substantially lowered, but such a coefficient for krill trawl has not yet been estimated.

The results of estimation made on the basis of one-time trawl surveys are shown in Table 2.

The result of estimation of krill in concentrations and in the entire areas does not seem to represent even provisionally the size of the fishing stock. No doubt, the actual size is much bigger. Firstly, the estimation covers only that amount of krill which is concentrated in a certain locality for a short period of time equal to the duration of a haul, but krill are concentrated throughout the summer season owing to the drift of currents. Secondly, surface patches of krill staying in the 0-5 m layer are not taken into account since they are not recorded by hydroacoustic devices because the layer is higher than the submerged parts of the sound transducer of the echo sounder. Besides, this layer cannot be fished by mid-water trawls due to technical reasons. And thirdly, the area surveyed is very insignificant as compared to the whole region inhabited by krill concentrations. Presently, the area occupied by concentrations is measured by far not in all regions inhabited by populations of E. superba where heavy concentrations occur in the spring-summer season. At the same time, in those regions where investigations are carried out for a number of years, such areas are preliminarily determined and it is possible to have an idea on the ratio between the total and surveyed areas. For example, krill concentrations are distributed over the area of 500,000 $km^2$ only in the SFZ and adjacent South Shetland areas, 400,000 $km^2$ in the north Ross Sea, over 350,000 $km^2$ in the Sodruzhestvo Sea with Prydz Bay.

It is concluded that the estimated total abundance in krill concentrations at one time in certain areas of the Atlantic, Pacific and Indian Ocean sectors of the Antarctic equal to 47-53 million t is only a small portion of the fishing stock of krill.

In order to ascertain the permissible annual exploitation rate, it is believed reasonable that the method of assessing natural mortality rate worked out with regard to the life span of fish with a different structure of the population should be applied (Tyurin, 1962, 1974). Based on the principle of the method the annual exploitation rate is permitted to be over 40% of the spawning population of early maturing fish with a short life span (from 2 to 10 years) and a high reproduction rate where recruitment prevails over the residual part (e.g. anchovy, small-sized herring). Some data indicate that the exploitation rate may reach 50-70% (Marty, 1971). This method is successfully applied to the management of the demersal-pelagic shrimp (Palaemon adspersus) from lagoons of the Black Sea which are characterised by a short life span, a high natural mortality rate and a fishing mortality rate amounting up to 60%.

In view of a high reproduction ability of E. superba, their short life span and extremely high natural mortality rate, the permissible catch may be not less than 50% of the fishing stock.

Proceeding from our estimate representing only a small portion of the fishing stock of krill, the minimum annual catch, which would be safe for the population on the whole, may be permitted to be 25-30 million t. No doubt, the results of further investigations of the quantitative distribution of krill in marginal seas, in the habitats of individual populations of E. superba would allow us to increase the value in the near years to come.

## III. ON THE ROLE OF ANTARCTIC KRILL IN THE FEEDING HABITS OF PRINCIPAL CONSUMERS

The problem which concerns many workers nowadays is how the fishery for krill will affect the ecosystem of the Southern Ocean and it is directly associated with the problem of how much the kill of most baleen whales (Mystacoceti) has affected the ecosystem in the Antarctic.

On the basis of the up-to-date knowledge the problems are very unlikely to be solved in relation to the entire Antarctic ecosystem. For this purpose, it is necessary to consider such problems as how the turnover of substances in quantitative indices of the transport of energy between living and non-living nature occurred in the Antarctic ecosystem in the past ; what kind of quantitative alterations in the process have occurred now due to a drastic decline in the abundance of whales and what kind of changes may occur as a result of the withdrawal by man of a certain part of the krill population. At the same time, the determination of changes may be attempted by considering trophic interrelations inside the complex communities of marine organisms in the Southern Ocean, i.e. the tropic structure of the Antarctic ecosystem. In the first place, it is necessary to assess how the krill production is divided among their main consumers.

At present, some groups of animals representing direct consumers of krill in the Antarctic have already been determined and some reliable data on the consumption rate of the groups collected.

Krill are chiefly and directly consumed by baleen whales, pinnipeds, fish and birds. Some workers make an assumption that cephalopods may also belong to the consumers ; the actual data, however, indicate that they have no direct trophic contacts with krill.

The principal consumers were always believed to be whales and the amount of krill taken by other groups of animals was much less than that taken by whales (Pequegnat, 1958; McQuillan, 1962).

The data available in literature on the consumption rate of whales in the period prior to the decline in their stock indicate huge values, e.g. 120-250 million t (Mackintosh, 1970; Zenkovich, 1970; Doi, 1973; Quotation from Nemoto and Nasu, 1975; Laws, 1977; Ohmura quoting Everson, 1977 and others).

Among numerous conclusions, the most reliable estimate seems to be 190 million t suggested by Laws since he has analysed the zonal distribution of all species of whales in the Southern Ocean and determined the extent of accessibility of krill for each species (Laws, 1977; Table 3 here). According to Laws, the Minke whales, the permanent resident of the Antarctic, the smallest of all species of whales, consumed and are still consuming about 20 million t of Euphausiacea, of which E. superba makes up 60-70% owing to the fact that the species feed on E. crystallorophias in the neritic zone.

The largest quantity of E. superba (over 150 million t) was consumed by fin and blue whales having migrated regularly to the feeding areas of the Antarctic and about 17 million t were fed by sei and humpback whales. By that, it is ascertained that as a result of the seasonal migration of the species to the natal and subtropical waters after the feeding season is over up to 41.7% of energy accumulated in the form of fat in the Antarctic were annually brought outside the Southern Ocean (Laws, 1977). In conversion to krill consumed by whales in the Antarctic the annual loss of the krill biomass in the Southern Ocean was 60-70 million t (Fig.29, 30).

Due to the drastic decline in the abundance of baleen whales, the consumption of krill has been reduced from 190 million t to 43 million t, which corresponds to the surplus of the biomass amounting to 147 million t. The loss of energy in the Antarctic ecosystem on the account of whales migrating outside the Southern Ocean converted to krill consumed has been reduced from 60-70 million t to 9.7 million of their biomass. Thus, along with the apparent "surplus" of krill, a substantial part of the krill biomass (over 60 million t) which was annually lost from the Antarctic ecosystem has been released from the pressure of whales which, naturally, could not help reflecting on the availability of food for whales themselves and the other main groups of consumers. The evidence is supported by indirect data on changes in the reproduction cycle of certain species. It is found that the pregnancy rate of fin, sei and blue whales increased from 25% in 1946-1947 to 50-60% in the early 1960s (Lockyer, 1962, 1974; Gambell, 1973; Laws, 1977). At the same time these species have started attaining sexual maturity earlier, e.g. in fin whale by 6 years (from 10 to 4 years) and in sei whale by 5 years (from 11-12 to 6-7 years). The similar pattern is observed in crabeater seals, which attain maturity at the age of 2.5 years now instead of at the age of 5 years as it was registered earlier (Gambell, 1973; Laws, 1977).

Some changes are noted in the space distribution of sei whales which appear in more southern areas and earlier than in the past (Gambell, 1968).

The changes in the reproduction and distribution patterns of some species feeding on krill may be characterised as phenomena reflecting a more intensive reproduction rate and in part a certain extension of their habitat (in sei whale) owing to better feeding conditions. The regularity is common for all species of animals and displayed as a feature adopted in the process of historic development, as an adaptive response of the species to changes in the availability of food (Naumov, Nikolsky, 1962; Nikolsky, 1965).

Owing to the specific climatic conditions and markedly expressed zonality in the oceanographic and biological structure of the Southern Ocean, the decline in the abundance of main consumers and a tremendous amount of underutilized food available do not induce an equilibrium process, i.e. there is no complete replacement of whales by some other group of consumers. Any immigration of new groups of animals to the Antarctic in such a short historical period of time is hampered due to the existence of the AC being simultaneously a climatic, oceanographic and biological barrier. Here it is worth recollecting the relation of the Antarctic biogeography with climatic changes on the historical basis (Bakker, 1970).

The replacement of whales in the complex communities in the World Ocean could occur, provided the abundance of one or several groups of consumers possessing similar morpho-ecological adaptability which would allow them to use krill production as intensively as whales did, increased greatly. However, no noticeable increase even in the abundance of species closely related to whales in this respect has occurred. So the abundance of Minke whale and crabeater seal feeding on krill all the year round has remained on the same level (Laws, 1977). A present substantial increase in the abundance of southern fur seal in relation to the 1930s (Payne, 1977) which consume krill in an insignificant quantity should be interpreted as a recovery of the stock in the period when the fishery for them is under depression. Proceeding from an increasing trend observed in the abundance of some species of penguin (Sladen, 1964; Laws, 1977) some rise in the total abundance of birds and, probably, krill-eating fish can be assumed when their food is easily available. However, these changes do not seem to be of an "outburst" character, otherwise they would have been noticed by workers conducting investigations in the Antarctic for many years.

In view of this, it is worth remembering one of the biological laws saying that populations sustain their abundance on a more or less fluctuating level, but it never increases infinitely or decreases to zero despite considerable changes in the environmental conditions (Shefer, 1957).

No doubt the abundance of each population of the species from either groups of consumers inhabiting permanently or migrating to the Antarctic waters in the feeding season is sustained on a certain optimum level using the rich food resources (krill) with a varying degree of intensity in accordance with their morphoecological adaptation and accessibility of food.

The fact that pinnipeds, birds and fish consume krill has been known for a long time ; as far back as 1925-1939, the British Discovery Committee made expeditions and first observations on the feeding habits of these groups of animals were noted by well-known investigators (Murphy, 1928; Matthews, 1929; Bertram, 1940; Mackintosh, 1937, 1950; Emison, 1968;

Norman, 1937, 1938; Nybelin, 1951; Olsen, 1955; Pequegnat, 1958; McQuillan, 1962 and many others in later years). However, any assessment of krill consumption had not been actually made till the beginning of the 1970s. It happened that the first quantitative data on the feeding habits and abundance of populations of species from the main groups of consumers were obtained after the comprehensive analysis of the material on the distribution, population dynamics and feeding habits of certain species of Antarctic whales had been made. Due to the lack of data on the consumption of krill by pinnipeds, birds and fish in the period prior to the beginning of the decline in the consumption rate of whales when they used 190 million tons of krill, some authors are inclined to believe that the feeding rate of the other groups was less intensive at that time. This present rise in the consumption and emergence of "new" migrants, e.g. southern poutassou in the Scotia Sea, are somehow or other associated with the "surplus" of krill equal to 147 million t (Mackintosh, 1965; Everson, 1977, 1978). If one can agree, to some extent, with some rise in the consumption of krill by the said groups of consumers (of course, within the same range of values) it is impossible to explain the emergence of poutassou for such a short historical period of time. In view of this fact, it should be noted that no similar migration to the high productive (krill) zone has been historically formed in the Pacific population of southern poutassou inhabiting the Campbell and Bounty areas (Shust, 1978).

The available quantitative estimates of krill consumption by individual species and groups of consumers are actually not fully comprehensive, and in a number of cases are subject to discussion. However, for the time being it is possible to make a tentative estimate of the annual consumption of krill by the main groups of consumers although it is known beforehand that the final result will be overestimated.

The most comprehensive data available are referred to pinnipeds from the Southern Ocean which were analysed and summarised by Laws (Laws, 1977; Table 4 here). They indicate that the largest amount of krill (E. superba and E. crystallorophias) is consumed by crabeater seal (about 63 million t) while about 1 million t falls to the rest of the pinnipeds.

As to the group of Antarctic birds (Sphenisciformes, Procellariiformes and Anseriformes), one should use still unpublished and less comprehensive data obtained by J. Croxall and P. Prince (quotation by Everson, 1977) in the study of the Antarctic aviafauna off South Georgia (Table 5).

Thus, the total consumption of krill by penguins, albatrosses and petrels is estimated to amount to 20 million t. It should be noted that the estimate is based on the data obtained in the area which is not typical for the whole Antarctic, especially for the high-latitude zone. The shelf waters off South Georgia are known for an extremely high level of bio-productivity as compared to the remaining areas of insular shelves or moreover, the continental shelf (see Section I).

The specific composition of the Antarctic ichthyofauna is much more variegated than that of other animals, particularly of pinnipeds and birds.

The specific composition comprises over 200 species of fish inhabiting the open ocean, waters of insular shelves and seamounts, the high-latitude zone of the continental shelf and slope. If the overwhelming majority of pinnipeds and birds feed, to some or other extent, on krill, only a few species of fish due to differences in their morphological adaptation features managed to assimilate themselves to the highly productive Antarctic epipelagic zone.

The Antarctic ichthyofauna is represented by three different ecological groups (Andriyashev, 1962, 1964) :

Bathypelagic fish (families Myctophidae, Paralepididae and Bathylagidae) from the biocenosis inhabiting the open waters within the AC and its southern edge.

Bottom and off-bottom fish (families Nototheniidae, Chaenichthyidae, Harpagiferidae, Bathydraconidae, Muraenolepidae, Rayidae, Bothydae) including about 120 species inhabiting the shelf and slope waters of islands, seamounts and the Antarctic continent.

Bathyal fish (families Macruridae, Moridae, Liparidae, Zoarcidae) inhabiting abyssal depths of the Southern Ocean.

Each group is characterised by specific morphoecological and biological features formed in the course of phylogenesis as well as by peculiarities of the space and vertical distribution in the Southern Ocean. In view of these peculiarities, not all the ecologic groups are capable of using rich food resources represented by Antarctic krill (E. superba). In particular, krill are inaccessible for bathyal fish inhabiting deep-sea layers (lower than 700-800 m) and little-accessible for bathypelagic species.

As it is ascertained in recent years the main habitat, spawning and feeding grounds of the bathypelagic species of fish is in the water of the southern edge of the AC (Lubimova et al., 1973; Bogdanov, Lubimova, 1978; Efremenko, 1972, 1978 in print). The distribution of abundant bathypelagic fish (Electrona, Gymnoscopelus, Notolepis, Bathylagus sp.) at the depth of up to 500 m or even lower is in agreement with the vertical distribution and high biomass of food zooplankton, mainly Copepoda, their food. Besides, a high biomass of small-sized euphausids (as compared to E. superba) is recorded in the southern edge of the AC (see Section I).

As a rule, mass bathypelagic species are dispersed in mid-water throughout the year. In summer and in part in autumn (November-May) concentrations of adult specimens of some species of the family Myctophidae (E. antarctica, G. nicholsi, G. braueri) are formed in the 50-300 m layer in some localities south of the AC, between 55°S and 58°S (Bogdanov, Lubimova, 1978; Lubimova, 1979). Only large-sized specimens of Gymnoscopelus and Electrona sp. 12-15 sm in size feed on krill ; the frequency of occurrence of krill in their stomach content is 23% (Permitin, 1970). On the whole, the role of krill in the feeding ration of bathypelagic species is insignificant because they inhabit the deep sea layer throughout the year, their habitat does not coincide with that of krill, they are dispersely distributed and their size is small in most cases.

The main consumers of krill in summer and autumn are a number of species of bottom and off-bottom fish. Their habitat is in the shelf waters of islands and seamounts. Besides, some high-latitudinal species inhabiting permanently the water of the continental shelf may also feed on krill all the year round.

All these species belong to endemic families Nototheniidae and Chaenichthyidae and differ from all other species of the group of bottom and off-bottom fish by a high degree of adaptation to use food resources of krill primarily on account of the pelagic way of feeding. (Permitin, 1970, 1977; Lubimova et al., 1971; Lubimova et al., 1973; Shust, Silyanova, 1971; Shust, 1978, 1979 and others). These are N. rossii marmorata, N. squamifrons atlantica, N. larseni, Pleuragramma antarcticum and white-blooded Champsocephalus gunnari; Chionodraco hamatus, Pagetopsis macropterus, Neopagetopsis ionah (DeWitt, 1970; Abe and Suzuki, 1978; Bogdanov, Lubimova, 1978; Lubimova, 1979 and others). Krill sometimes occur in the stomach content of shelf typically bottom fish, but as we have recently ascertained they occur only off South Georgia in autumn, when some specimens of krill descend to the off-bottom layer probably in the course of dying.

The feeding rate of fish and predominantly of plankton-eaters in the water of insular shelves is the highest in summer and in part in autumn when the stomach content amount to 10-15% of body weight per day (Kanaeva et al., 1969; Kozlov, 1972). Alongside krill, they feed on other macroplankton species, e.g. Beroe, Salpae, Paratemisto gaudichaudii (Permitin, Tariverdieva, 1972; Naumov, Permitin, 1973). The role of these species increases in spring due to the absence of krill. It is ascertained that the composition of food of fish with a pelagic feeding habits comprises 25-30% of krill per annum in the shelf water (estimated by the consumption rate of N. rossii marmorata). The daily ration of N. rossii marmorata estimated by the feeding on E. superba exclusively throughout the year is 1.07% (Tariverdieva, 1972) which corresponds to the amount of krill consumed equal to the product of body weight x 3. The annual ration of other species of fish consuming krill is accepted also as body weight x 3 although the linear growth rate and weight increment of these species is much lower than those of N. rossii marmorata (Olsen, 1954, 1955; Shust and Pinskaya, 1978).

Proceeding from the mean fish productivity of insular shelves equal to 1.5 t/km$^2$ (Everson, 1970, 1977), total area of insular shelves and seamounts in the Southern Ocean averaging 300,000-350,000 km$^2$ the annual fish production and total biomass (stock) will be 450,000-500,000 t and 1.8-2.2 million t (400,000-500,000 t x 4), respectively. Thus, the consumption of krill by bottom and off-bottom fish from the shelf water of Antarctic islands (except for Kerguelen and Crozet where no krill occur) will be 5.4-6.6 million t with regard to the estimated annual ration of body weight x 3.

Fish productivity of the continental shelf water is certainly much lower than that of the insular shelf water. Assuming that the mean fish production of the continental and insular shelf water is equal to 1.5 t/km$^2$, it is possible to make a preliminary estimate that the total biomass of bottom and off-bottom fish on the area of 2-2.2 million km$^2$ will be 12-13.2 million t. As is known, E. crystallorophias plays a significant role in the feeding ration of plankton-eaters inhabiting the water of the continental shelf (DeWitt, 1970; DeWitt and Hopkins, 1977). Assuming the equal rate of consumption of E. crystallophorias and E. superba by high-latitudinal species of fish, the amount of krill consumed will be 50% of the total (39 million t), i.e. 18-19.8 million t. The general estimates for groups of bottom and off-bottom fish with pelagic feeding habits inhabiting the shelf water of the Antarctic continent and islands are shown in Table 6.

Beside bottom and off-bottom fish from the shelf areas of the Southern Ocean, the estimate is offered for Micromesistius australis, a notal species making feeding migrations to the Scotia Sea (Merett, 1963; Mikheev, 1965; Shubnikov et al., 1969; Shust, 1978). During the summer season lasting 2 or 3 months, poutassou make heavy concentrations in the SFZ in the feeding season of krill. The catch of poutassou reach 10 t per hour of trawling (Basalaev and Petukhov, 1969).

The size of the total biomass of southern poutassou in the Falkland-Patagonian area estimated by us is a little more than 1 million t and it is very close to those suggested by FAO (1974) and Everson (Everson, 1978). Only adult specimens of poutassou (the mean length and weight is 48-5 cm and 0.8-1.0 kg, respectively) make feeding migrations to the Scotia Sea, their abundance makes up 1/3 of the total stock, i.e. 300,000-350,000 t. The consumption of krill by poutassou in the Antarctic waters in the feeding season ranges from 0.9 to 1.5 million t. Therefore the total amount of krill consumed by fish in the Southern Ocean is estimated to be about 28 million t.

Some workers believe that krill may play a significant role in the feeding of Cephalopoda. The amount of krill fed by squid is tentatively estimated to be 80-100 million t (Everson, 1977). However, the consideration of the specific composition of squid occurring in the Antarctic, the space and vertical pattern of their distribution as well as some indirect data on their abundance southwards of the AC has not supported the preliminary estimate.

First of all, it should be noted that the abundance of squid is unlikely to be as high as it might seem at first sight. The accumulation of rostra of squid in the bottom sediments is an indirect characteristic, but it indicates reliably their quantitative distribution in the World Ocean. No rostra were found in the bottom sediments of the World Ocean southward of the AC (Belyaev, 1962; Fig.31). This fact may be explained by the absence of heavy concentrations of squid. In this respect, it should be added that no substantial by-catch of squid has been taken in mid-trawl catches during our long-term observations in the Antarctic. The declining trend in the frequency of occurrence of schools of squid southward of the AC is also observed in the analysis of data on food habits of sperm whales which, as is known, feed on relatively large-sized squid staying in schools. The main food species of sperm whales seem to be the most abundant, Onychoteuthis banksii and Moroteuthis ingens (Clarke, 1966; Klumov, 1959, 1963, 1971; Zuev and Nesis, 1971).

Of endemic Antarctic squids Mesonyrhoetuthis hamiltoni occurs most frequently in the stomach content of sperm whales, whereas 3-4 other species are found as individuals (Yukhov, 1971; Klumov and Yukhov, 1975).

A total of 8 endemic species are recorded in the Antarctic water of 18 occurring in the South hemisphere (Klumov, 1971). Therefore the habitat of most species of squid in the Southern Ocean does not coincide with that of E. superba. It is not insignificant that krill, as food, are not accessible for most species of squid in the Antarctic due to their different vertical distribution patterns. All squids found in the stomach content of sperm whales and specimens of many species caught in the Antarctic water are referred to by scientists as deep-sea or bathypelagic forms inhabiting the depths ranging from 300-400 to 2800 m (Clarke, 1966; Voss, 1956, 1967; Dell, 1959; Filippova 1969, 1971; Klumov, 1959, 1971 and others). The dissection of stomachs of squid in mass swallowed by sperm whales has indicated that the principal food species of deep-sea squid (the mantle up to 100 cm long) are bathypelagic fish and less frequently squid (Klumov and Yukhov, 1975; Yukhov, 1979). In view of this fact, the assumption can be made that alongside the existence of the main food chain in the Southern Ocean (phytoplankton - krill - baleen whales and other consumers), there is one more chain also very important for the Antarctic trophic dynamics : phytoplankton-zooplankton-bathypelagic fish-Cephalopoda -sperm whale and other consumers. The existence of the second chain is referred to in literature (Dell, 1952, 1959; Knox, 1970).

Of all known species of Cephalopoda, only 2-3 endemic species occurred in the 50-100 m layer : one specimen of B. riisei (family Brachitenthidae), one unidentified specimen and a new species Kondacovia longimana recently described by Filippova (Filippova, 1969, 1971; Clarke, 1966). All of them are rather small-sized squids : the mantles are 3.35-26 cm long. Although nothing is known of their food habits because no data are available, the assumption can be made that they feed, to a certain extent, on krill as their space and vertical distribution coincides with that of E. superba.

It is very likely that baleen whales, pinnipeds (except for sea elephant) and birds feed on these small-sized squids as the latter are distributed in the surface layer (50-100 m). Because of the lack of data it is difficult to conclude where the feeding grounds of sea elephant, the biggest seal, lie. It may be assumed that they are somewhere closer to the AC judging by their more northern distribution in the Southern Ocean as compared to other species of pinnipeds (Fig.32).

The consumption of squids by pinnipeds (crabeater, Ross and Weddell seals) amounts to 2.4 million t, by baleen whales (fin, blue and Minke whales) to 0.4 million t (Laws, 1977) and by birds (penguin etc.) to 8 million t (Croxall and Prince quoted by Everson, 1977) ; therefore the total amount of squid used by the abovementioned consumers reaches 10.8 million t estimated on the basis of the maximum rate of consumption. Further, using the simple method of estimation suggested by Everson (1977) it is possible to assume that the total amount of food consumed by squid is 108 million t including 50-54 million of krill (E. superba).

Thus, the total estimate obtained on the consumption of krill by all major groups of consumers (except for baleen whales) amounts to 166 million t.

If one neglected for a moment the main biological laws of the abundance of animal populations and assumed that the abundance of the populations of these groups of consumers increased twice after the kill of whales thanks to a great increase in the food available, the estimate of the up-to-date consumption (166 million t) should represent double the amount of krill consumed in comparison with the past. Even in case the assumed two-fold increase in the consumption of krill occurred at the expense of the surplus of krill equal to 147 million t, a substantial part of krill production equal to 64 million t has remained unused now.

It is concluded that the permissible catch size of 25-30 million t estimated on the data obtained by the method of direct sampling in krill concentrations is the minimum annual exploitation rate quite safe not only for the stock of E. superba, but also for all major consumers.

It appears that the withdrawal of up to 60 million t would be safe as much for the stock of krill and conservation of the optimum level of food resources for major consumers since the annual loss of energy brought by baleen whales outside the Southern Ocean was estimated to be 50-60 million t of krill production.

No doubt, further investigations in the Southern Ocean will make it possible to analyse more accurately the quantitative distribution of E. superba in the habitats of individual populations, to determine regularities of the abundance of populations and the size of fishing stock as well as to specify the quantitative trophic relations between krill and their individual consumers.

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**Table 1.** Data on assessment of the stock and possible withdrawal of krill in the Southern Ocean

| Author, year | Assessment of stock (biomass) in million tons | Possible withdrawal in million tons | Basis for assessment |
|---|---|---|---|
| 1 | 2 | 3 | 4 |
| Pequegnat, 1958 | 1400 | - | Annual consumption of krill |
| McQuillan, 1962 | 800-953 | - | " " |
| Gulland, 1970 | 750 | * | Estimate of mean annual production of Antarctic zooplankton on the basis |
| Hempel, 1970 | 750 | 10 | of the summary size of primary production |
| Grand quoting Nasu, 1975 | 500 | - | " " |
| Nemoto, 1974 | 6000 | 2000 | Data on krill concentration obtained in hydroacoustic surveys |
| Doi and Nemoto quoting Nasu, 1975 | 6000 | 50-160 | " " |
| Mackintosh, 1970 | - | 100-150 | At the expense of reduction in the consumption of krill by |
| Moiseev, 1970 | - | 100 | baleen whales ("surplus of krill") |
| Lubimova, Naumov, Lagunov, 1973 | - | 25-50 | Preliminary results of invest. on the quantitative distribution of krill in the Antarctic Atlantic |
| Naumov, 1978 ** | production 1700-1800 biomass 2100-2900 | - | Preliminary theoretical counting of krill consumption |

| 1 | 2 | 3 | 4 |
|---|---|---|---|
| Sahrhage quoting Nasu, 1975 | 200 | 50-100 | Estimate on consumption of krill and "surplus" |
| El-Sayed, 1976 | - | 100 | " " |
| Chenard et al., 1976 | - | 50-100 | " " |
| Everson, 1977 | - | 5 | No basis |
| Anonym. (FAO), 1975 | - | 150 | Interpretation of data available on the assessment of possible catches |
| Anonym., 1974 | - | 100 | " " |
| Anonym., 1975 | - | 100 | " " |
| Bodganov and Lubimova, 1978 | - | Not less than 15 | Estimate of one-time abundance of krill concentrated in some areas in the Scotia Sea, Prydz Bay and off Balleny Islands in 1965-1975 |

* In the discussion on possible withdrawal of krill by man (Antarctic Ecology, v.1, London and N.Y., 1970, pp.224-225), J. Gulland estimates the potential annual catch in the amount of 200 million t.

** "Rybnoe khosaistvo", N° 11, 1978, (In Russian).

**Table 2.** Estimate of krill concentrated in some localities of the Southern Ocean at one time

| Area | Year | Area of trawl survey (km2) | Density ($g/m^3$) | Depth of layer (m) | Amount of krill (million t) |
|---|---|---|---|---|---|
| 1 | 2 | 3 | 4 | 5 | 6 |
| 1. SFZ of Scotia Sea | 1965-1978 | 175 | 1.0-2.7<br>1.5 | 40-60<br>50 | 7.0-28.4<br>13.1 |
| 2. South Georgia | 1965-1976 | 16 | 1.1-3.2<br>2.1 | 50-70<br>55 | 0.9-3.6<br>1.9 |
| 3. Northwest Weddell Sea | 1978 | 20 | 1.2 | 40 | 0.9 |
| 4. Bransfield Strait, E. | 1978 | 21 | 3.0 | 30 | 1.9 |
| 5. Shetland Is. Palmer | 1976-1978 | 130 | 2.0-2.5<br>2.2 | 35-50<br>45 | 9.1-16.3<br>12.9 |
| 6. Peter I Is. | 1976 | 10 | 2.1 | 50 | 1.0 |
| 7. Northward and northwest of Scott Is. | 1973-1977 | 12 | 0.9-1.1<br>1.0 | 35-45<br>40 | 0.4-0.6<br>0.5 |
| 8. Off Balleny Is. | 1974-1977 | 25 | 1.0-1.1<br>1.0 | 35-50<br>45 | 0.9-1.4<br>1.1 |
| 9. North Durville Sea | 1976-1977 | 5 | 1.4 | 50 | 0.4 |
| 10. East Sodruzhestvo Sea | 1976-1977 | 60 | 0.9-1.3<br>1.1 | 40-60<br>50 | 2.2-4.7<br>3.4 |
| 11. Prydz Bay | 1976-1977 | 35 | 2.3 | 40-70<br>55 | 3.2-5.6<br>4.4 |
| TOTAL : | | 509000 | 1.8-2.2 | 50 | 46.5-53.4 |

**Table 3.** Crude estimates of large whale populations, biomass and food consumption in the Antarctic and of their biomass loss outside the Antarctic

| Species | Stock (thousands) | Mean weight t | Mean Antarctic Biomass $10^3$t | Food consumption in Antarctic ($10^3$t) | | | Biomass loss outside Antarctic ($10^3$t) | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Krill | Squid | Fish | Metabolic | Mortality | Total | % of Mean Antarctic Biomass |
| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
| | | | | **Initial Stocks** | | | | | | |
| Baleen Whales | | | | | | | | | | |
| Fin | 400 | 50 | 20000 | 81480 | 840 | 1680 | 8000 | 530 | 8530 | |
| Blue | 200 | 88 | 17600 | 71702 | 740 | 1478 | 7040 | 580 | 7620 | |
| Sei | 75 | 18.5 | 1387 | 5651 | 58 | 116 | 555 | 67 | 622 | |
| Humpback | 100 | 27 | 2700 | 11000 | 113 | 227 | 1080 | 124 | 1204 | |
| Minke | 200 | 7 | 1400 | 19827 | 204 | 409 | - | - | - | |
| Total | 975 | - | 43087 | 189660 | 1955 | 3910 | 16675 | 1301 | 17976 | 41.7 |
| Sperm Whale | 85 | 30 | 2550 | - | 10200 | 500 | 510 | 102 | 612 | 24.0 |
| | | | | | **Present Stocks** | | | | | |
| Baleen Whales | | | | | | | | | | |
| Fin | 84 | 48 | 4032 | 16426 | 169 | 339 | 1612 | 109 | 1721 | |
| Blue | 10 | 83 | 830 | 3381 | 35 | 70 | 332 | 27 | 359 | |
| Sei | 40.5 | 17.5 | 709 | 2888 | 30 | 60 | 284 | 33 | 317 | |
| Humpback | 3 | 26.5 | 79 | 322 | 3 | 7 | 32 | 4 | 37 | |
| Minke | 200 | 7 | 1400 | 19827 | 204 | 409 | - | - | - | |
| Total | 337.5 | - | 7050 | 42844 | 441 | 885 | 2260 | 173 | 2434 | 34.5 |
| Sperm Whale | 43 | 27 | 1161 | - | 4632 | 244 | 232 | 31 | 263 | 23.0 |

**Table 4.** Crude estimates of Antarctic seal populations, biomass and food consumption

| Species | Stock (thousands) | Mean Weight kg | Population Biomass $10^3$t | Annual Food Consumption ($10^3$t) Total | Krill | Squid | Fish |
|---|---|---|---|---|---|---|---|
| elephant | 600 | 500 | 300 | 6000 | - | 4500* | 1500* |
| leopard | 220 | 272 | 60 | 1403 | 519 | 112 | 182 |
| Weddell | 730 | 246 | 180 | 4211 | - | 463 | 2232 |
| crabeater | 14858 | 193 | 2868 | 67245 | 63210 | 1345 | 2017 |
| Ross | 220 | 173 | 38 | 892 | 80 | 571 | 196 |
| fur | 200 | 50 | 15 | 351 | 117 | 117 | 117 |
| TOTAL | 16828 | - | 3456 | 80102 | 63926 | 7108 | 6244 |

* According to Laws, the ratio between main food species is tentatively shown. When elephant seals stay on land they do not feed. The quantitative composition of their of food in sea water has not yet been ascertained.

**Table 5.** Standing stock and food consumption by Antarctic birds (from data supplied by J. Croxall)

| | Penguins | Other Species | Total |
|---|---|---|---|
| Standing Stock (ton x $10^3$) | 487 | 48 | 535 |
| Total Food Consumption (M ton) | 20 - 27.5 | 6 - 8.5 | 26 - 36 * |

* Of these :

krill : 14.7 - 20.3
squid : 5.9 - 7.9
fish : 5.7 - 7.8

**Table 6.** Total stock and consumption of krill by Antarctic species of fish

| Areas and Species of Fish | Area of Habitat ($.000\ km^2$) | Mean* Fish Production (.000 t/yr) | Total Stock (biomass) (.000 t) | Consumption of Krill (million t) |
|---|---|---|---|---|
| Shelf water of islands *Nototheniidae* and white-blooded *N. rossii marmorata*, *Ch. gunnari* etc. | 300-350 | 450-550 | 1800-2200 | 5.4-6.6 |
| Shelf water of the continental high-latitudinal *Nototheniidae* and white-blooded *Pleurogramma antarcticum*, *Neopagetopsis ionah* etc. | 2000-2200 | 3000-3300 | 12000-13200 | 18.0-19.8 |
| South Scotia Sea (SFZ) *Micromesistius australis* | (220-250) | 300-350 | 300-350 | 0.9-1.5 |
| TOTAL | 2300-2550 or with habitat of southern poutassou 2520-2800 | 3750-4200 | 14100-15750 | 24.3-27.9 |

* Mean fish productivity is accepted to be equal to 1.5 $t/km^2$ for all areas (Everson, 1970, 1977).

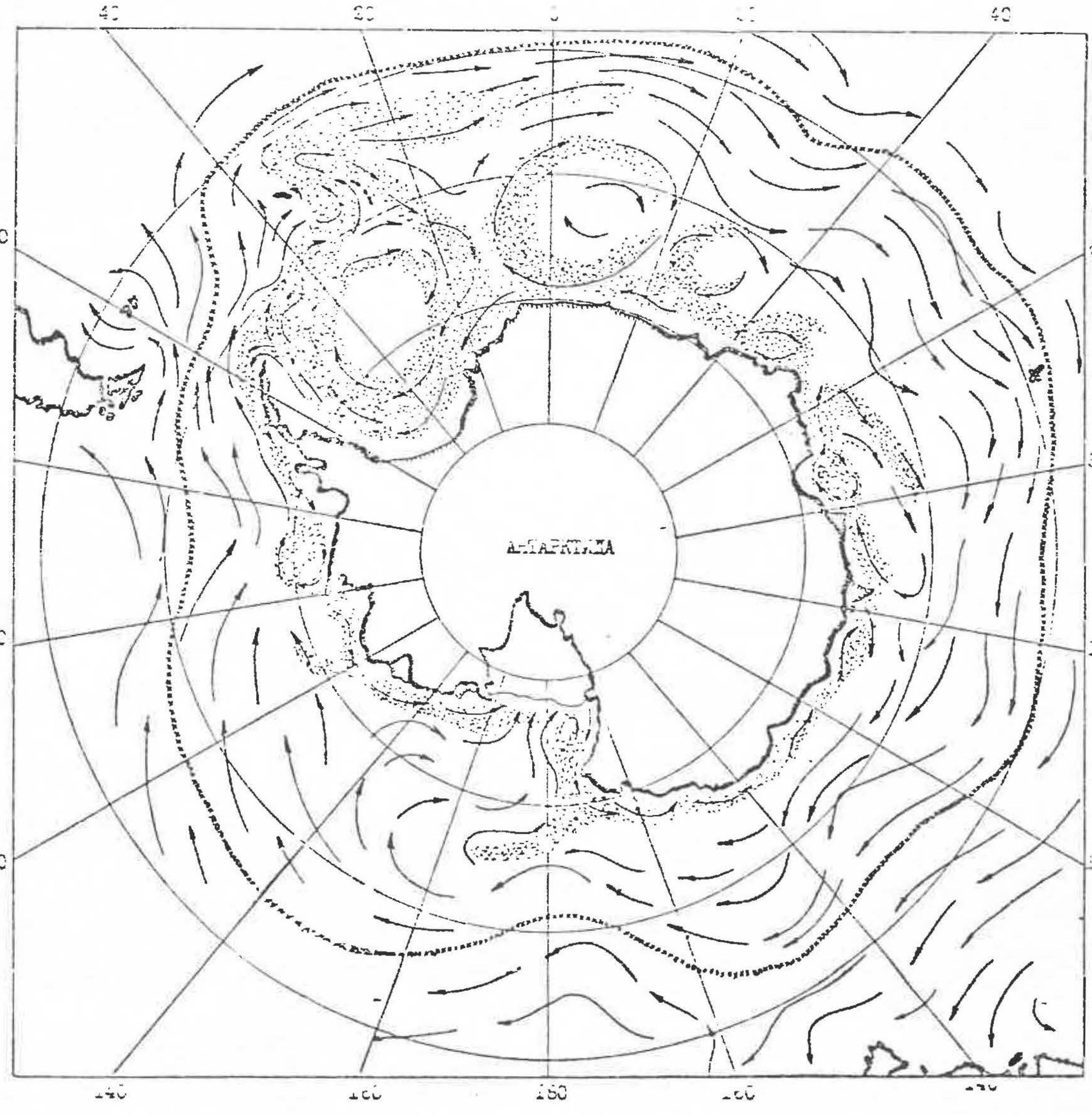


Fig.1 Diagram of the circulation of surface water in the Southern Ocean (compiled by Maslennikov after Treshnikov, 1964, Klepikov, 1962 and others).

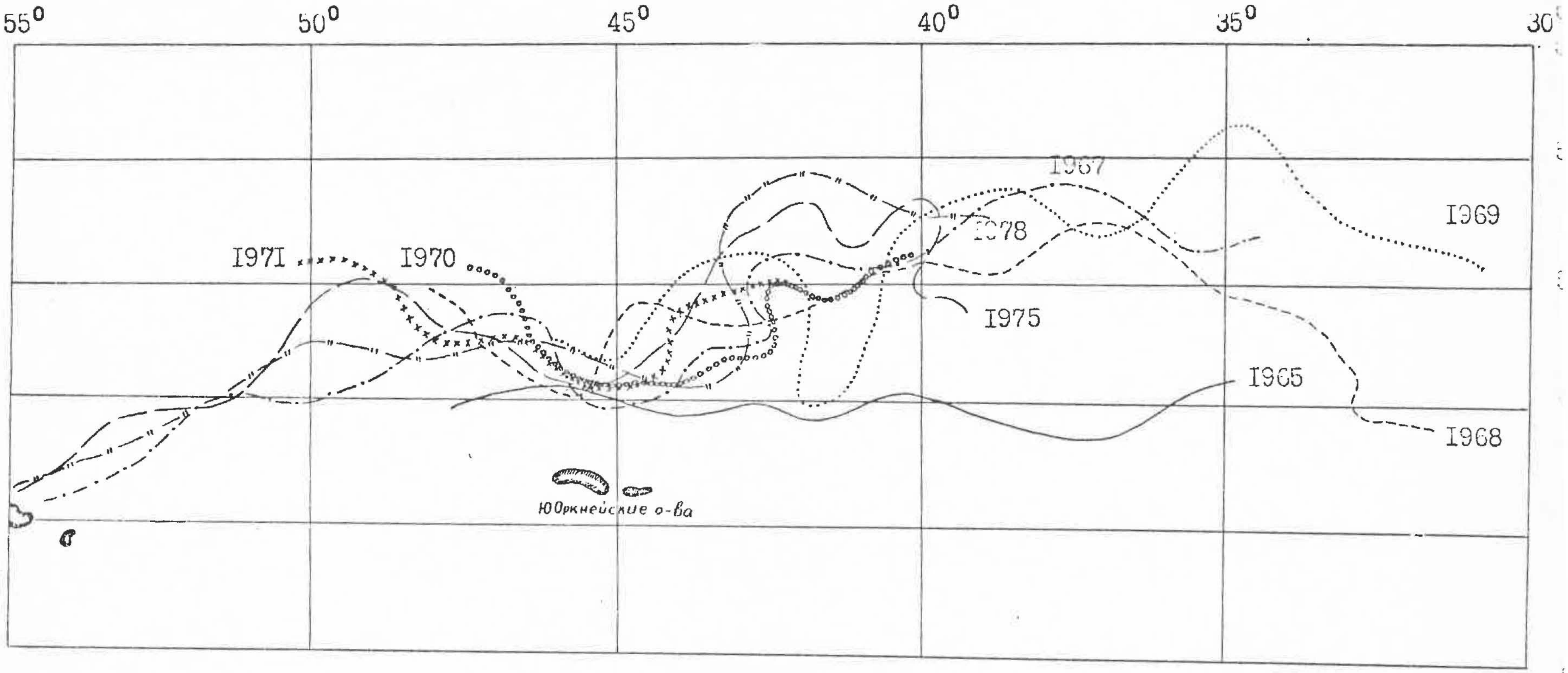


Fig.2 The position of the Secondary frontal zone (SFZ) in the Scotia Sea by years.

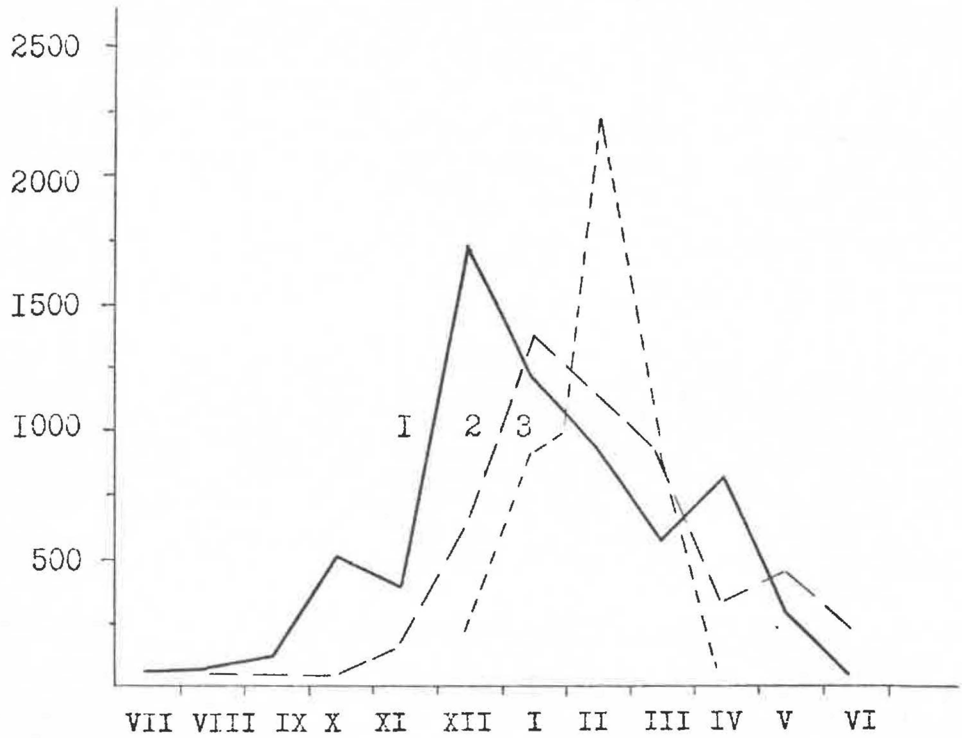


Fig.6 Seasonal changes in the content of vegetation pigments in the upper 0-50 m layer in three latitudinal zones of the Southern Ocean (after Hart, 1942) : 1. northern; 2. intermediate and 3. southern.

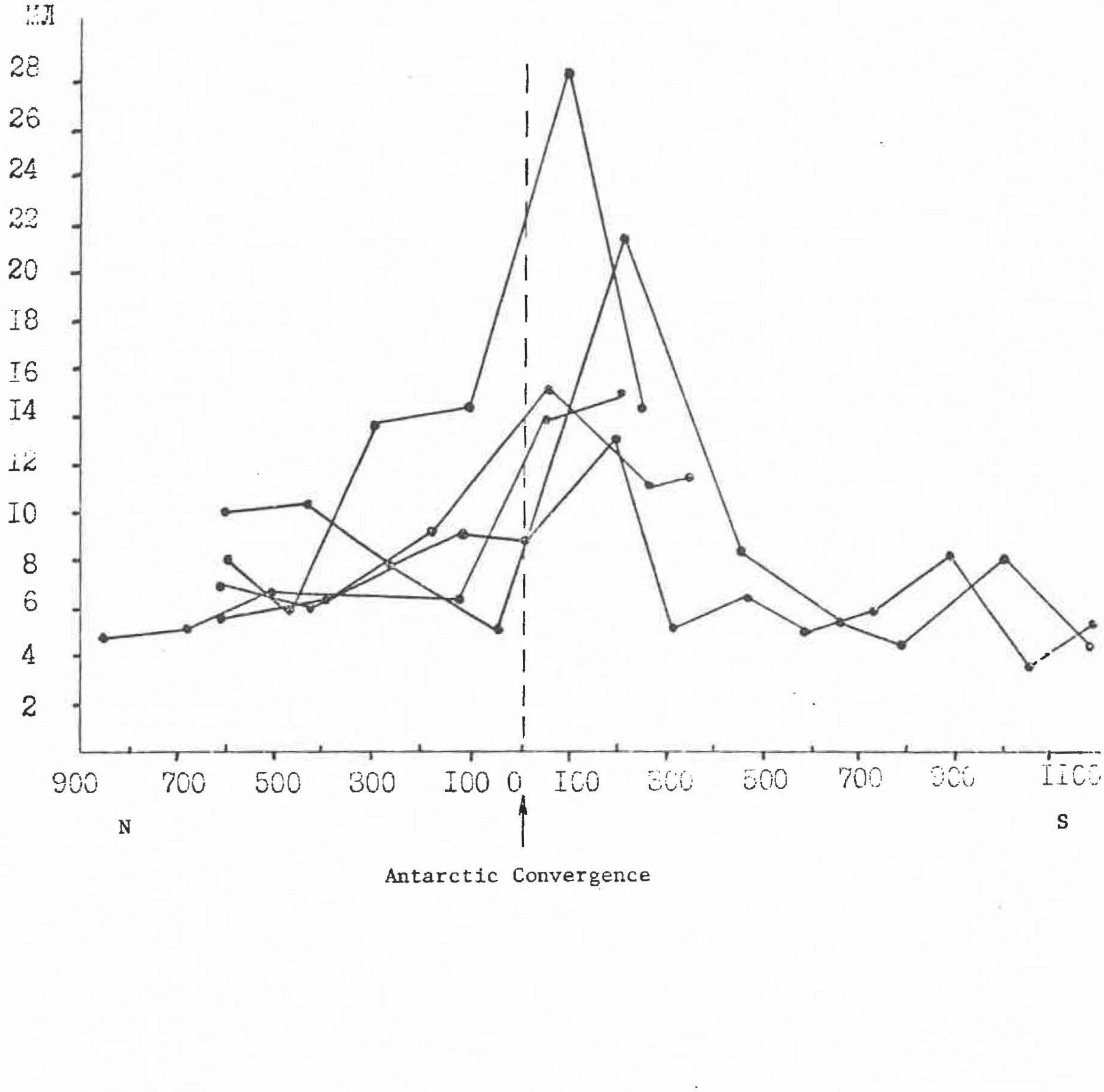


Fig.7 The distribution of zooplankton (ml) in the 1000-0 m layer (after Foxton, 1956).

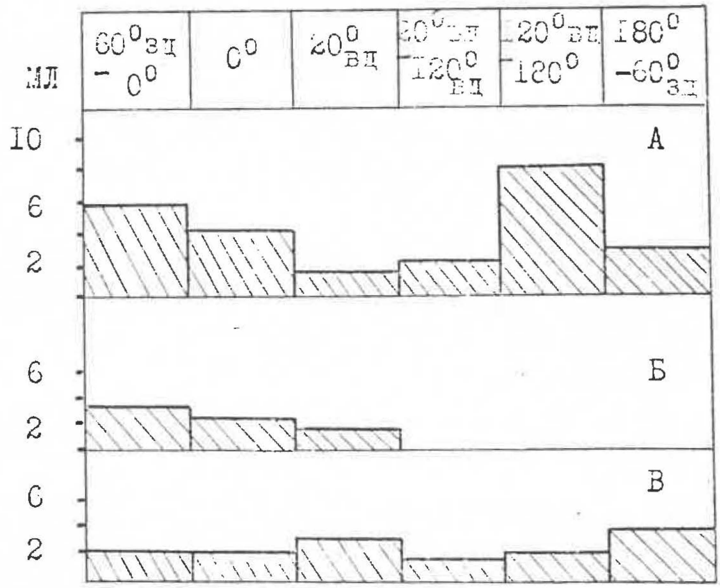


Fig.8 The mean summary volume of zooplankton (ml) in the 100-0 m layer A- in the Antarctic Coastal current (West Wind Drift); B- in the Weddell Sea current; C- in the Antarctic circumpolar current (East Wind Drift), (after Foxton, 1956).

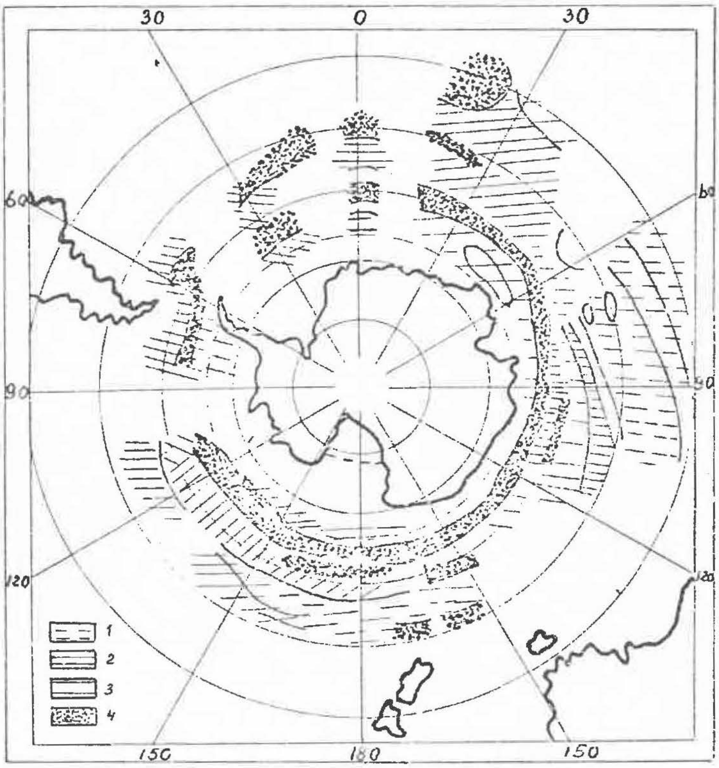


Fig.9 The distribution of the zooplankton biomass in the 100-0 m layer of the Southern Ocean (after Voronina and Naumov, 1968) 1-10 mg/m³; 2-10-49. 9 mg/m³; 3-59-99 9 mg/m³; 4-100 mg/m³.

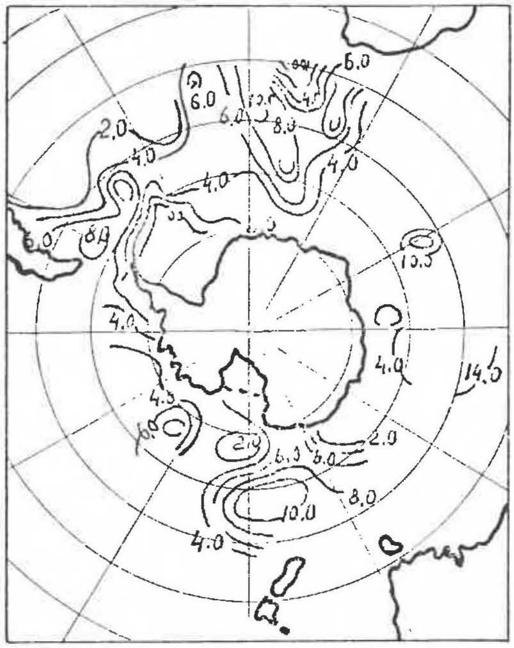


Fig.10 The distribution of nitrates (mg/at/m²) in the 100-150 m layer (after Volkovinsky, 1971).

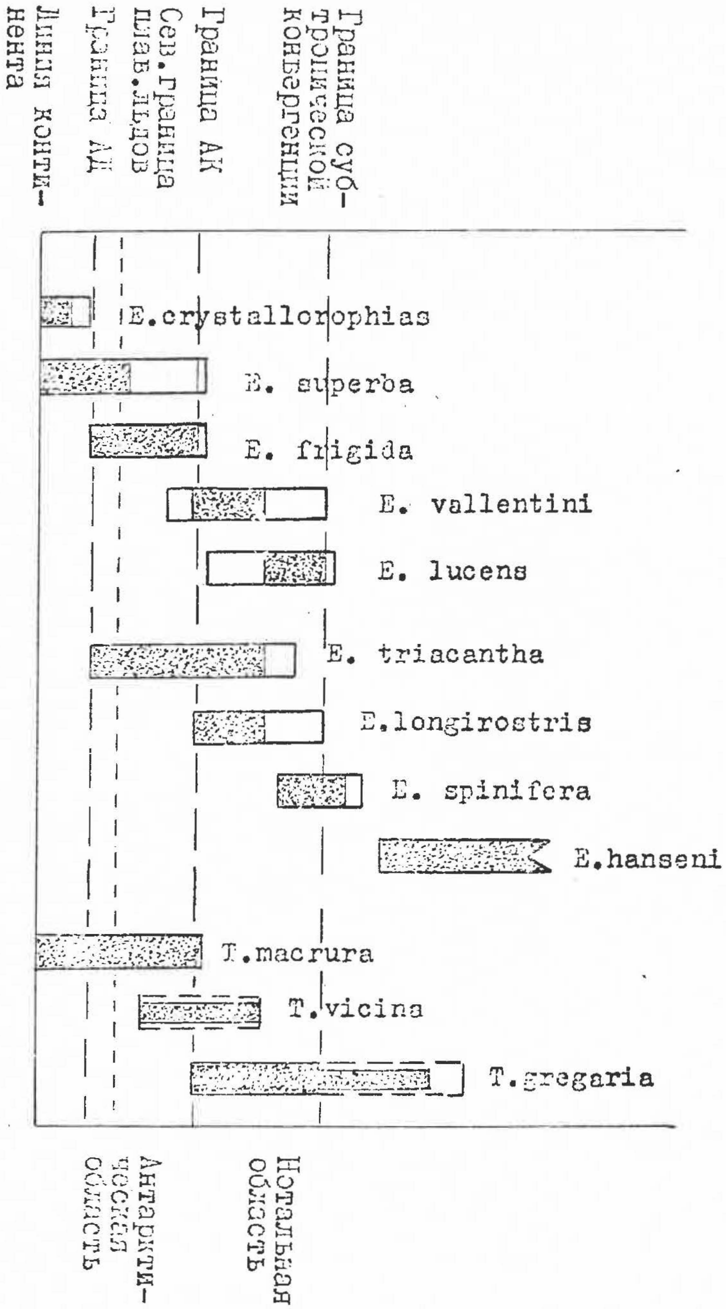


Fig.11 The latitudinal distribution of genus Euphausia and genus Thysanoessa in the Southern Ocean (after John, 1936; Lomakina, 1964).

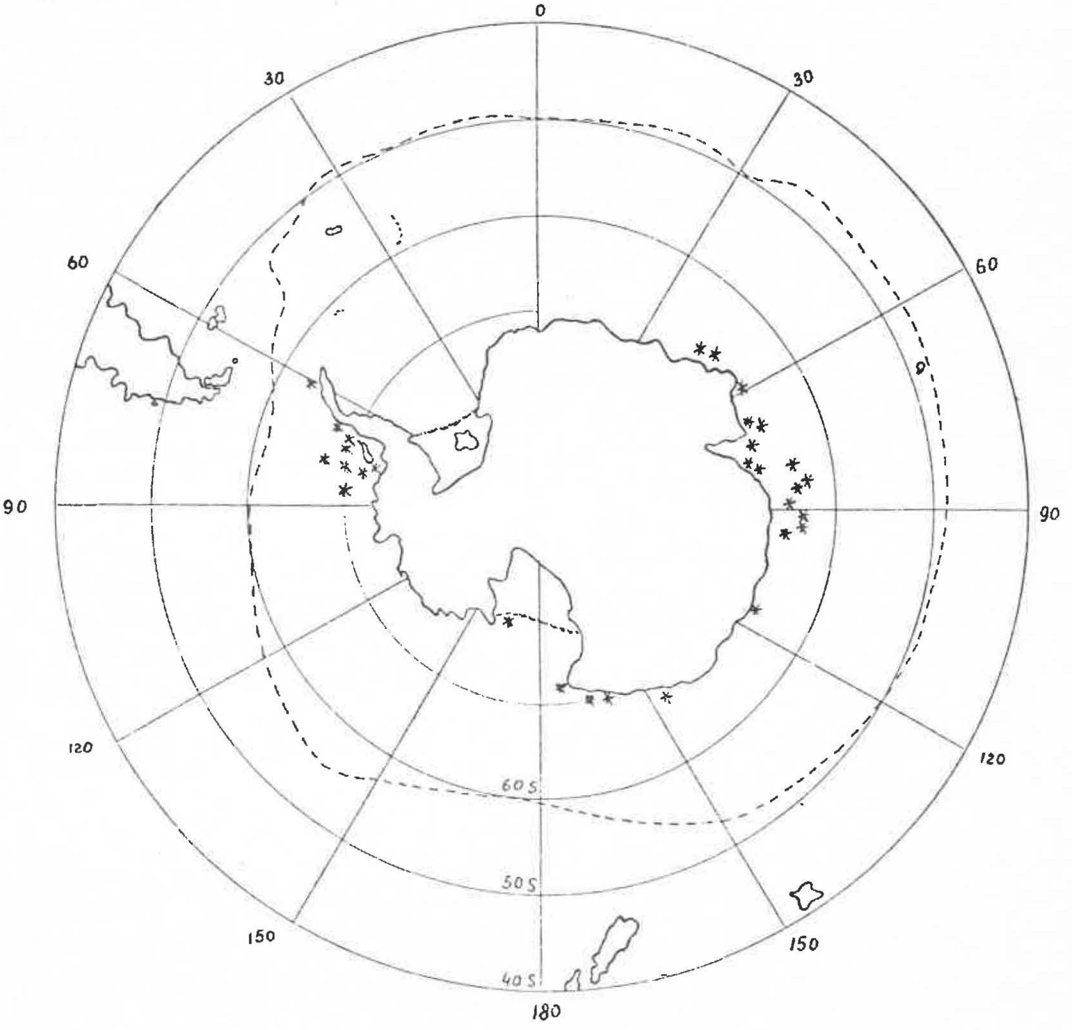


Fig.12 The distribution of E. crystallorophias
(after Lomakina, 1964).

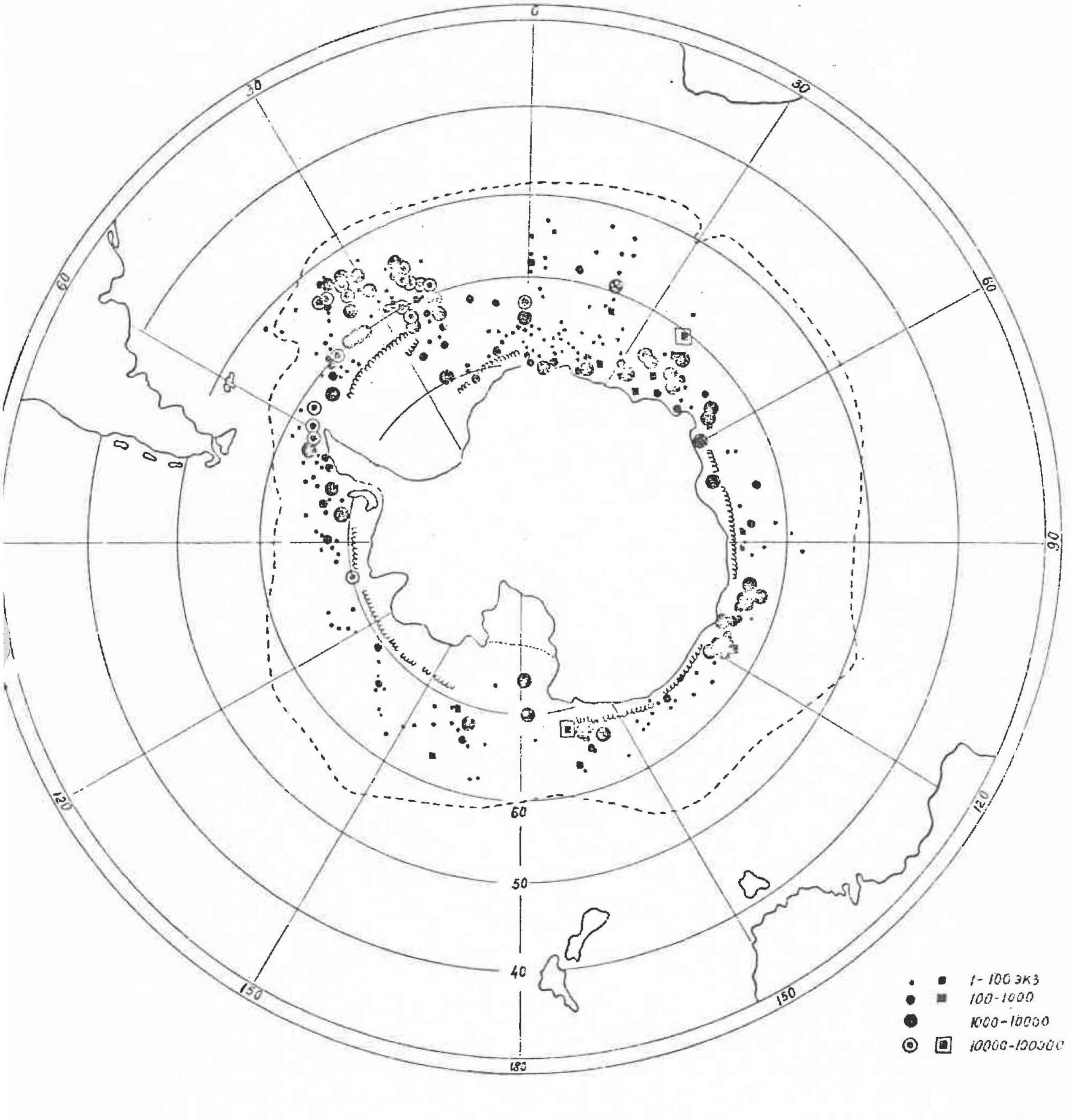


Fig.13 The distribution and relative abundance of E.superba (after Marr, 1962; Lomakina, 1964).

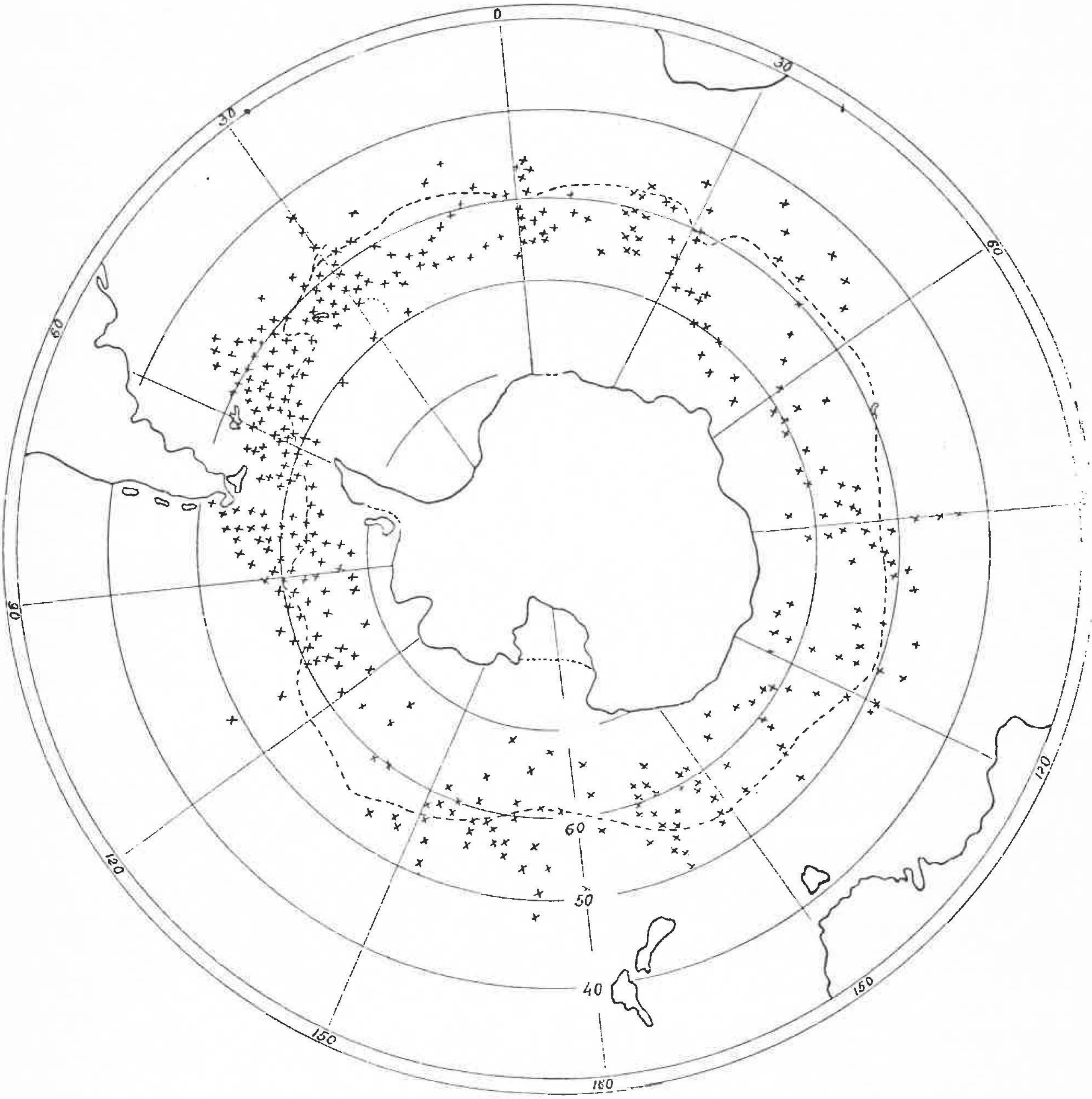


Fig.14 The distribution if E. triacantha (after Lomakina, 1964).

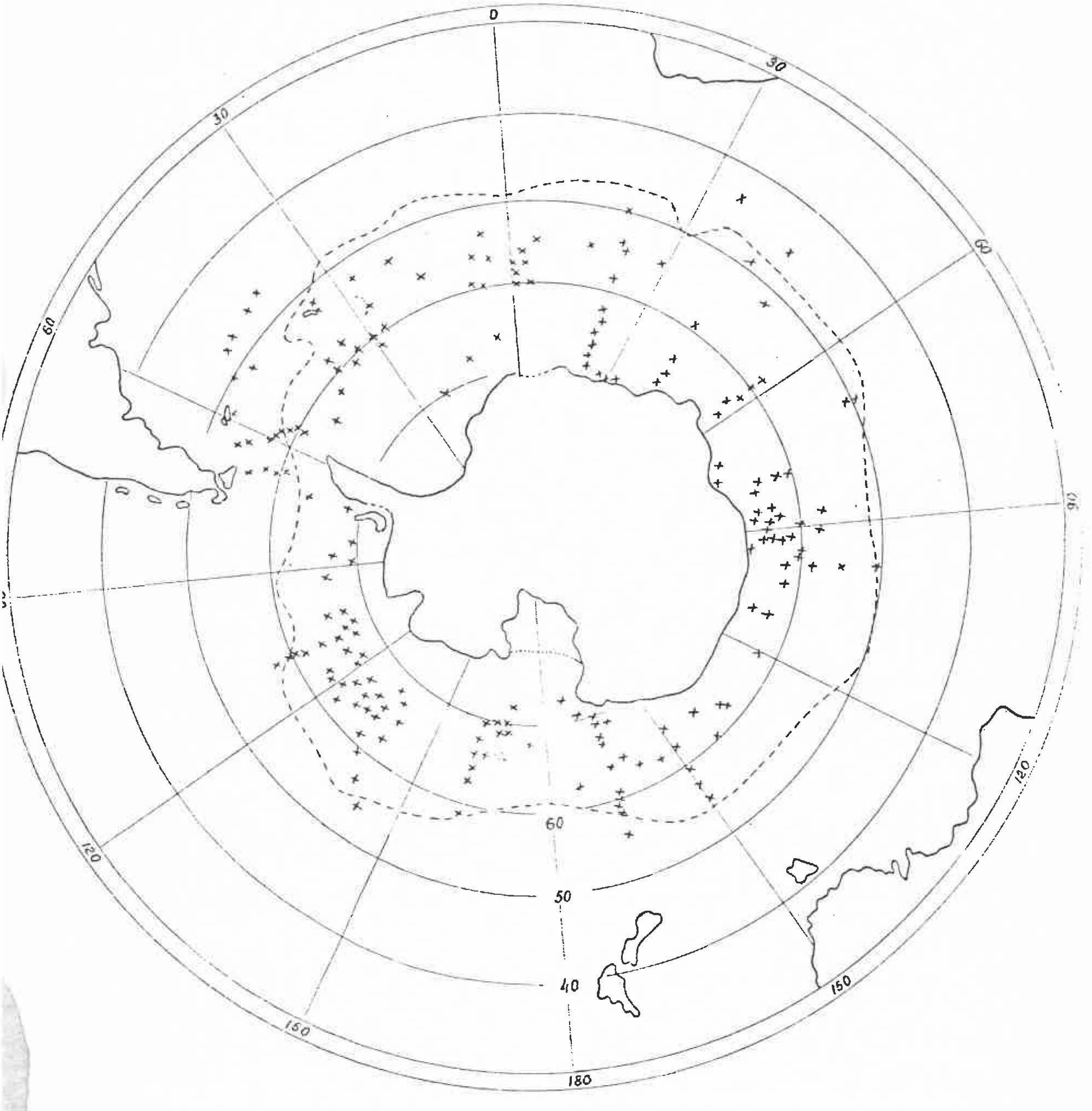


Fig.15 The distribution of Th. macrura
(after Lomakina, 1964).

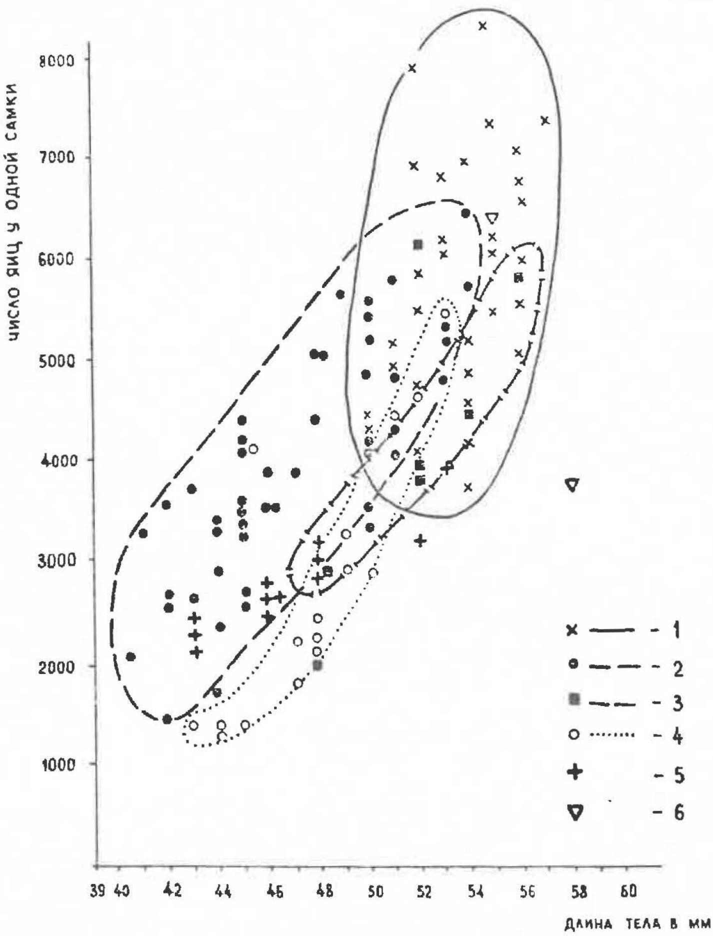


Fig.16 The fecundity of E. superba by areas in different years (after Makarov, 1971) 1 - off South Georgia, 1969; 2 - the southern Scotia Sea, 1967; 3 - the southern Scotia Sea, 1969; 4 - the southern Scotia Sea, 1968; 5 - off Balleny Islands (Naumov, 1962); 6 - off South Georgia, 1965.

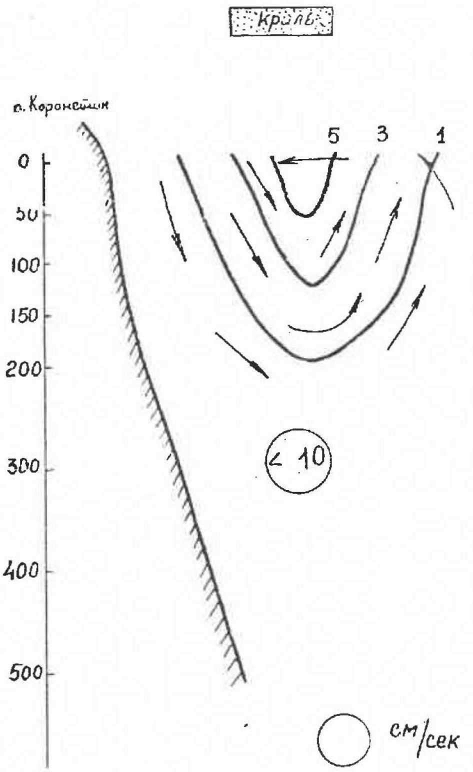


Fig.17 Forming of krill concentrations in relation to specific features of the vertical circulation of water off islands (after Elizarov, 1971).

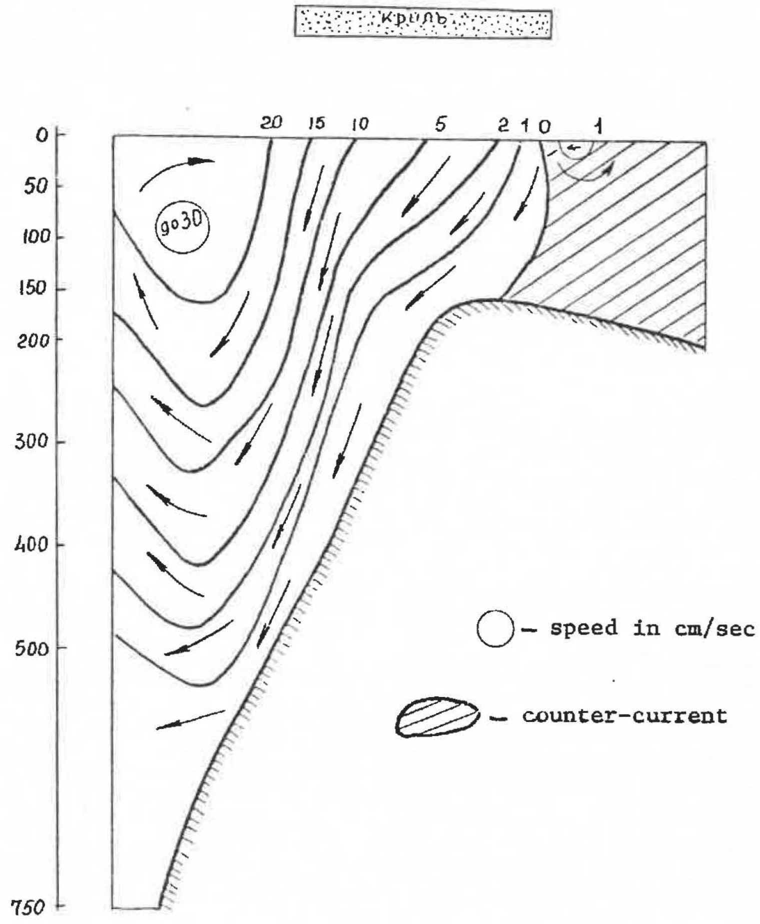


Fig.18 Forming of krill concentrations in relation to specific features of the vertical circulation of water over seamounts (after Elizarov, 1971).

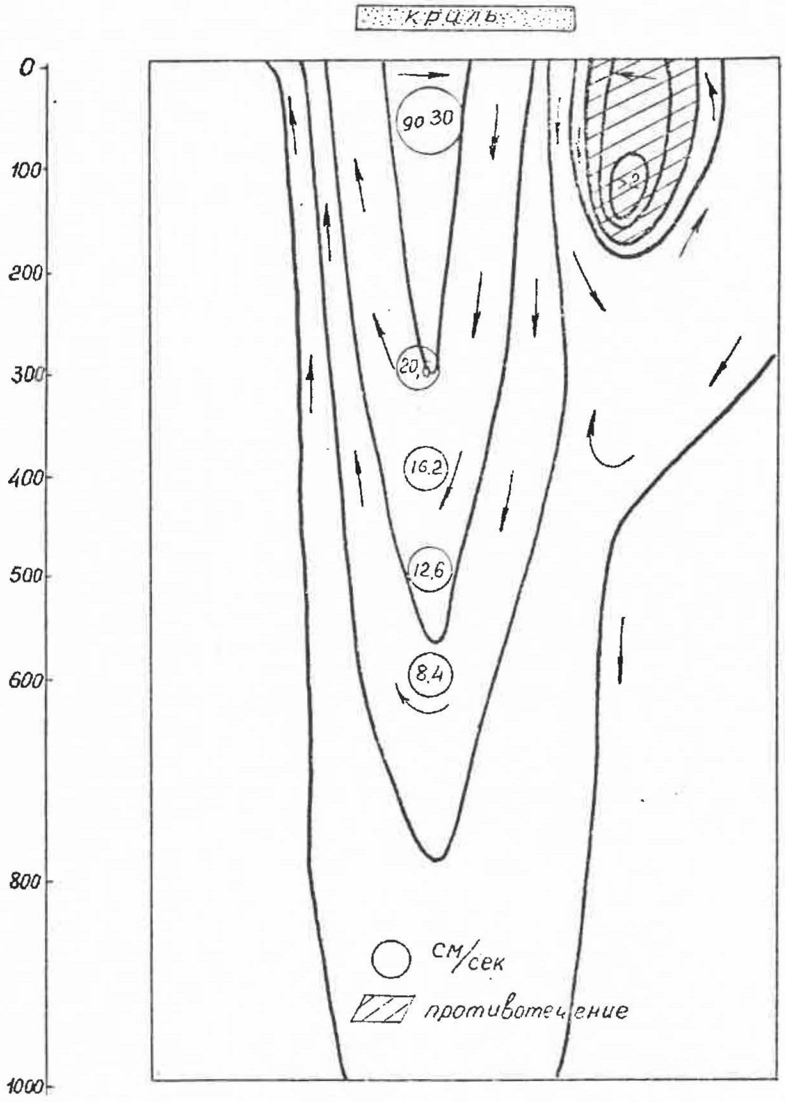


Fig.19 Forming of krill concentrations in relation to specific features of the vertical circulation of water in the open sea (after Elizarov, 1971).

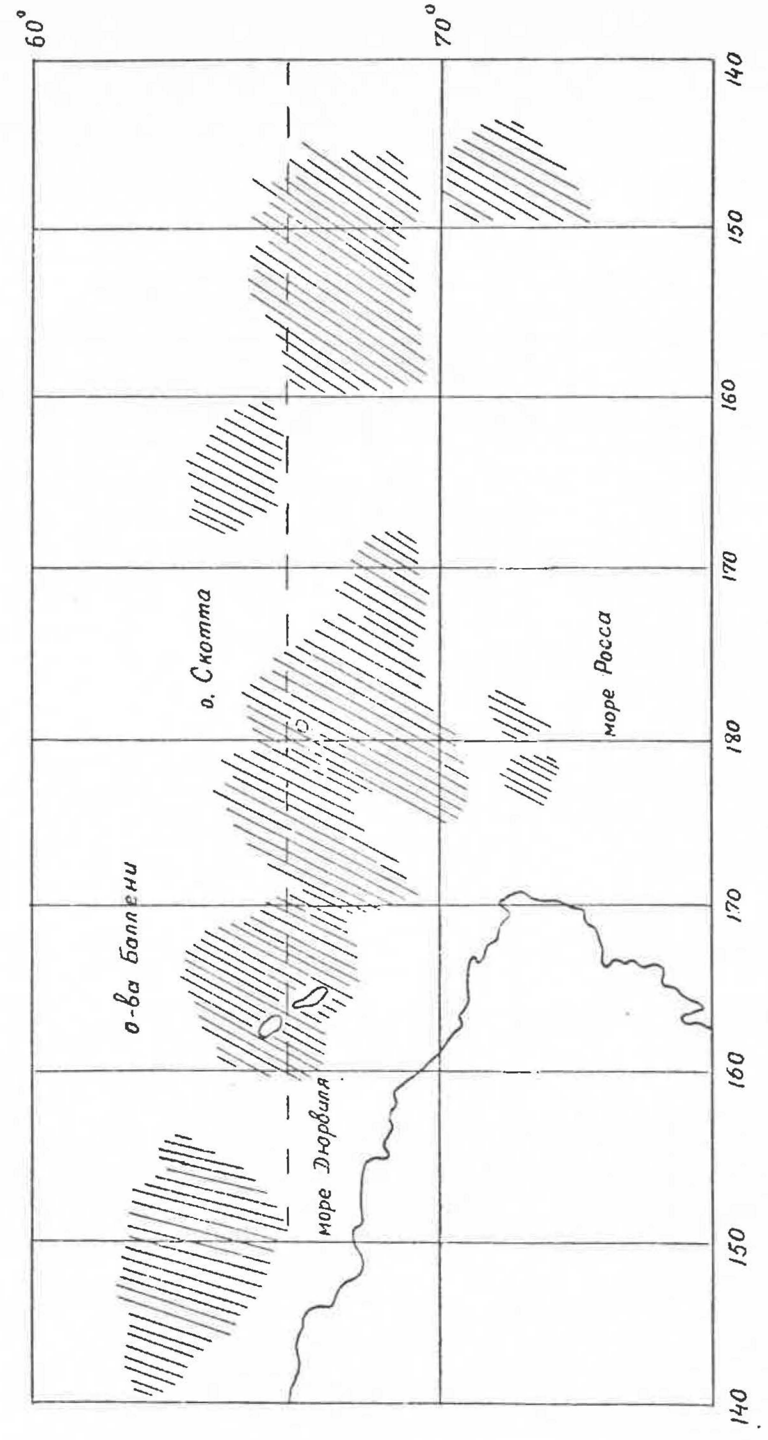


Fig.20-a The distribution of concentrations of E. superba in latitudinal zones of Balleny Islands and northern Ross Sea by years (data of TINRO).

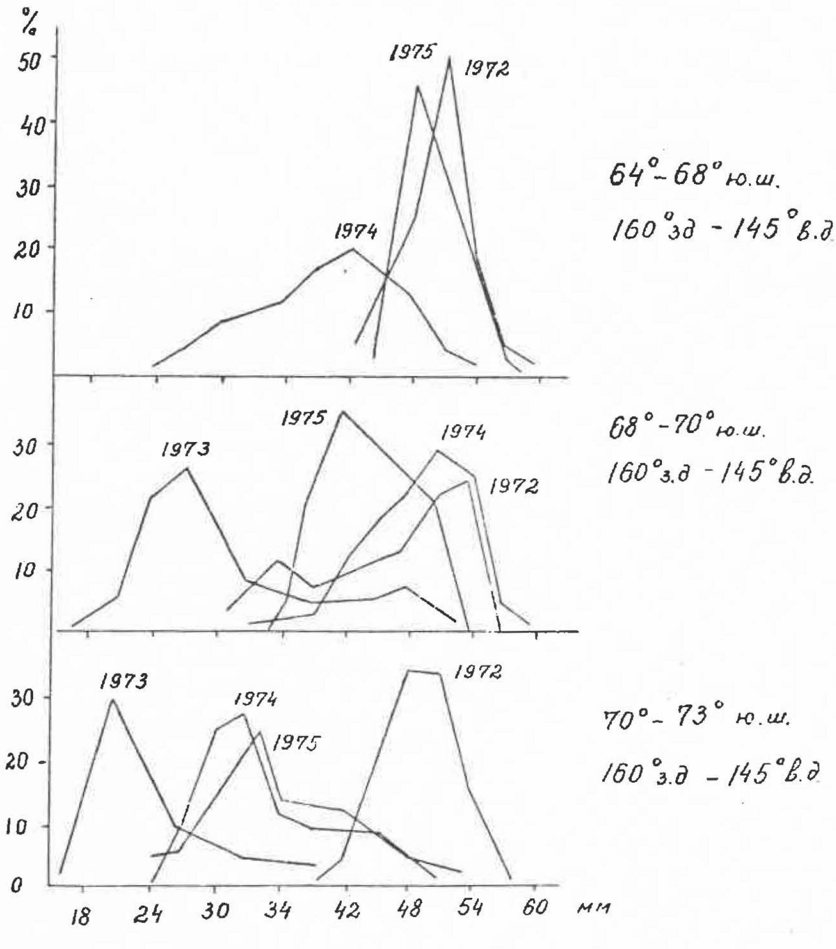


Fig.20-b Size composition of E. superba in latitudinal zones of the Balleny Islands and northern Ross Sea by years (data of TINRO).

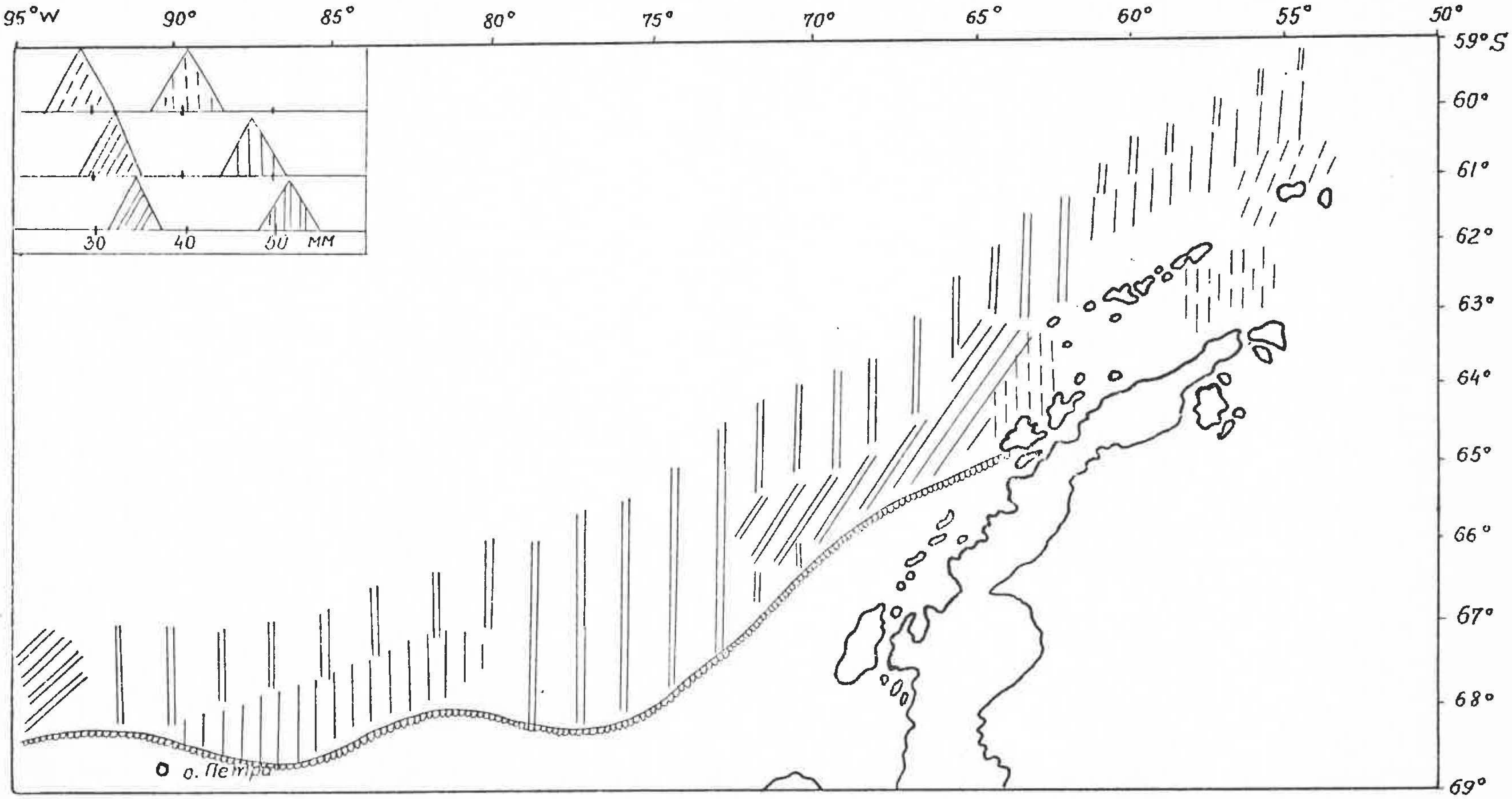


Fig.21 The distribution of various size groups of E. superba in the Bellingshausen Sea (the authors' data, 1976-1978).

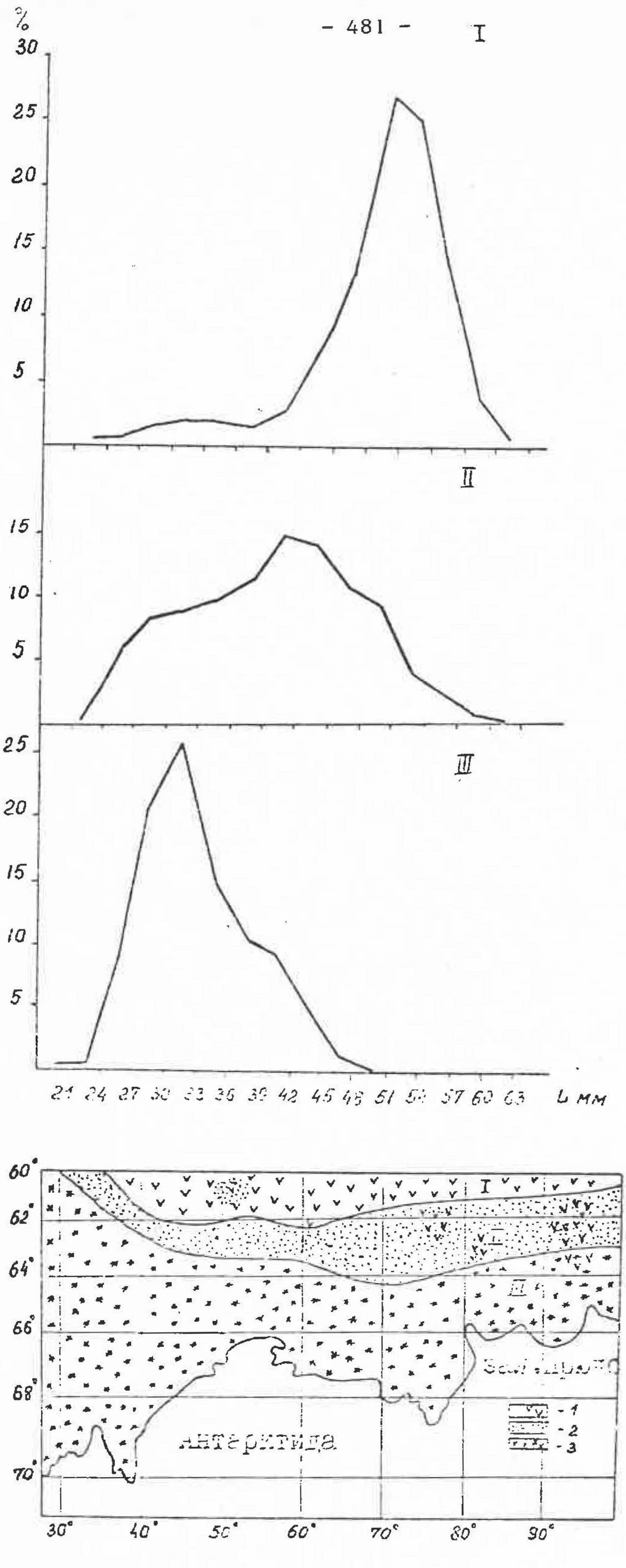


Fig.22 The distribution of various size groups of E. superba in latitudinal zones of the Prydz Bay, Sodruzhestvo Sea and eastern Cosmonauts Sea (data of the Azov-Black Sea Research Institute of Marine Fisheries, 1973-1978).

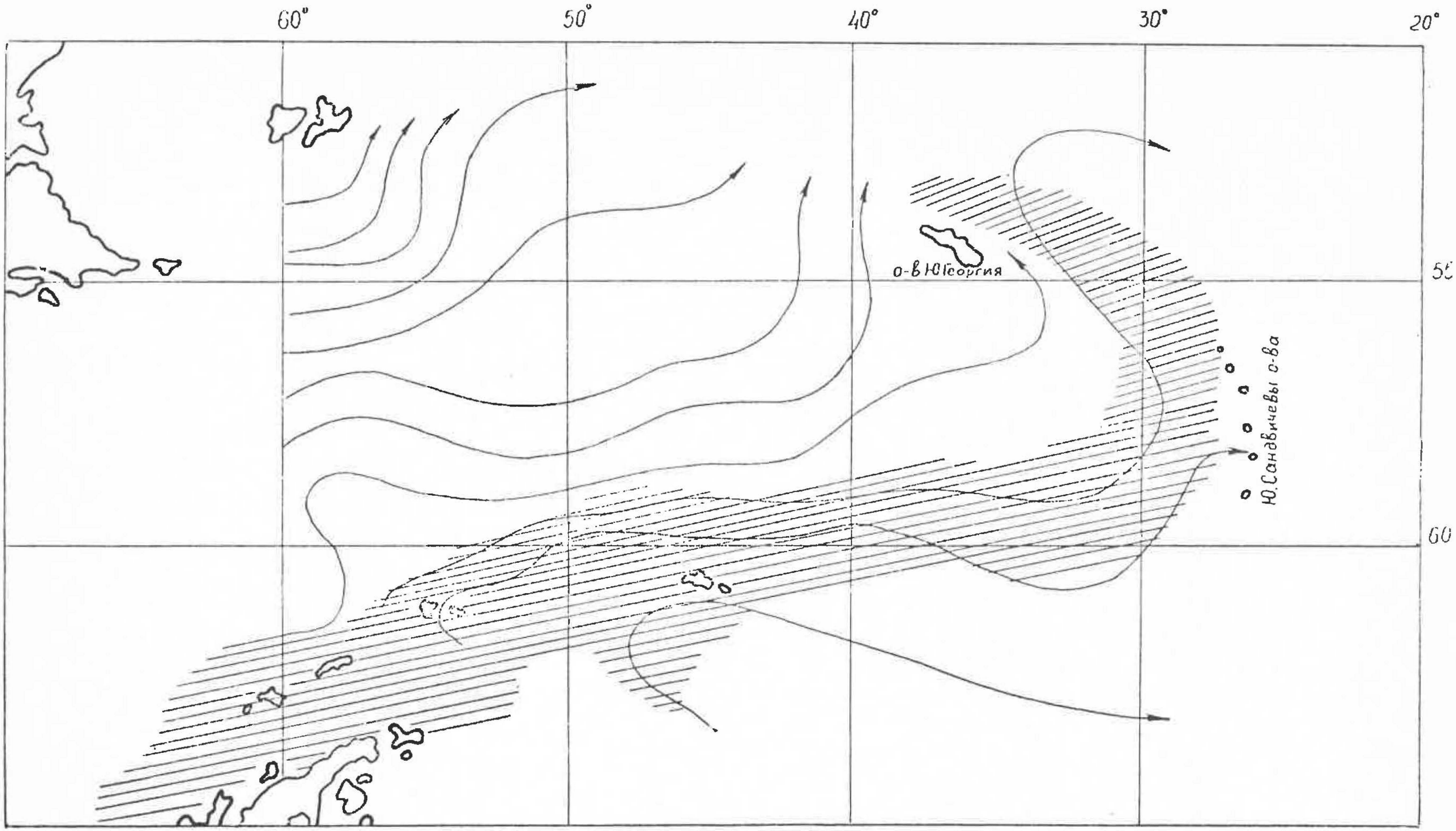


Fig.23 The extension of the Weddell Sea water in the Antarctic Atlantic in relation to the geostrophic circulation pattern.

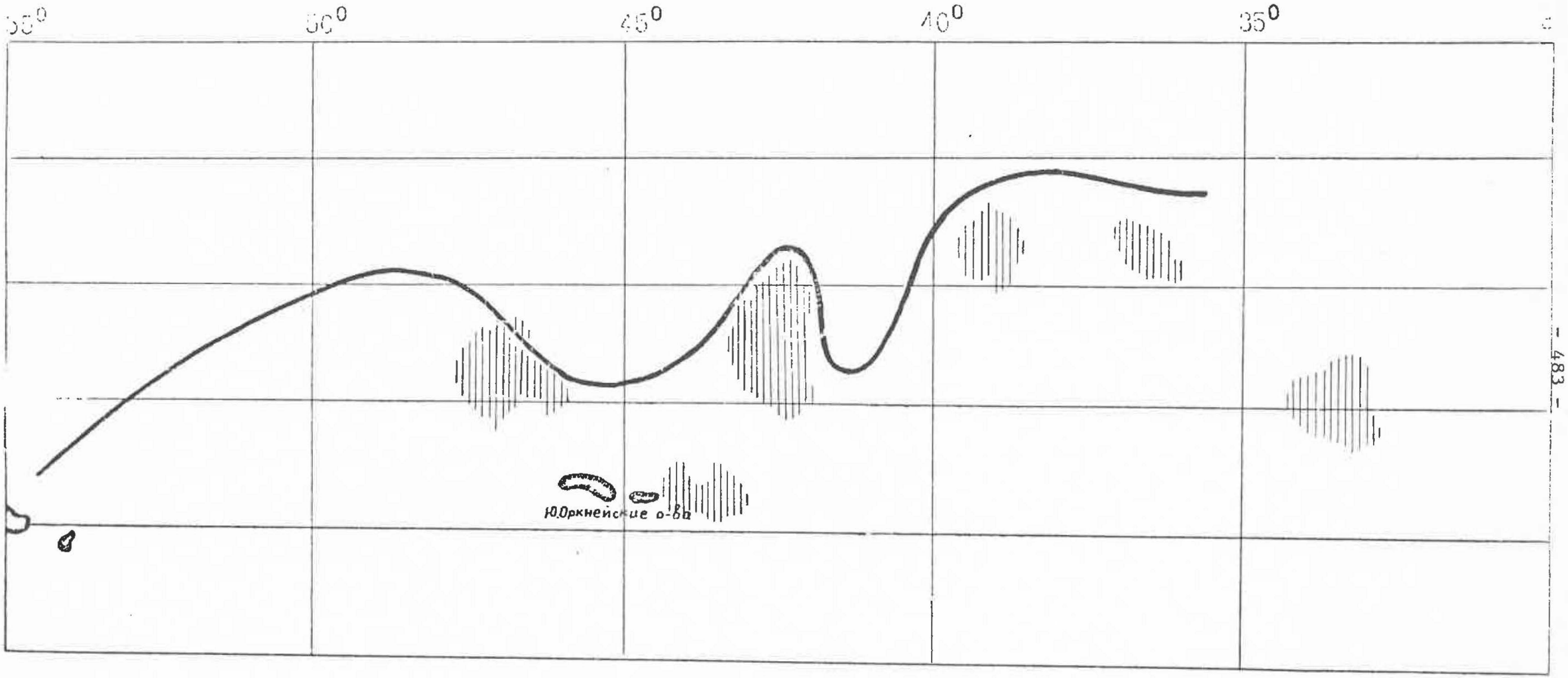


Fig.24 Distribution of dense stable concentrations of *E. superba* in meanders of the SFZ
- dense stable concentrations of krill
- average long-term position of the SFZ

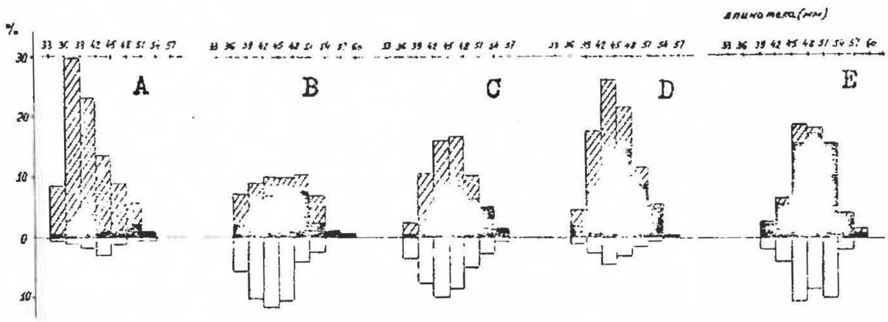


Fig.25 Spawning stages of E. superba in various areas of the Scotia Sea from westwards to eastwards

- females prior to spawning
- mature females
- spent

A - South Shetland Is., B, C - water of the SFZ northwestwards of South Orkneys, D-E - water of the SFZ northeastwards of South Orkneys.

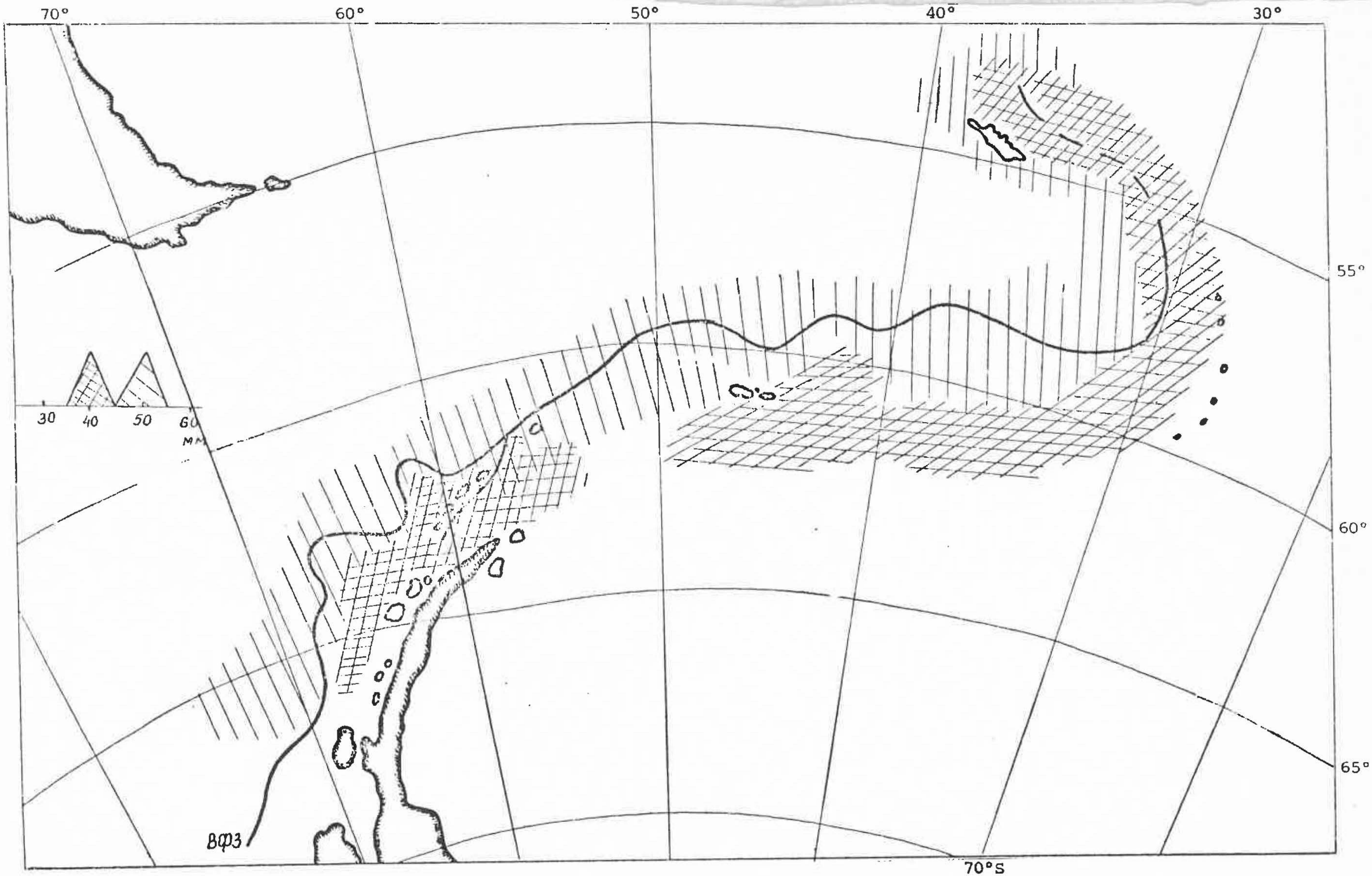


Fig.26 The distribution of various size groups of E. superba in the Antarctic Atlantic in relation to the SFZ

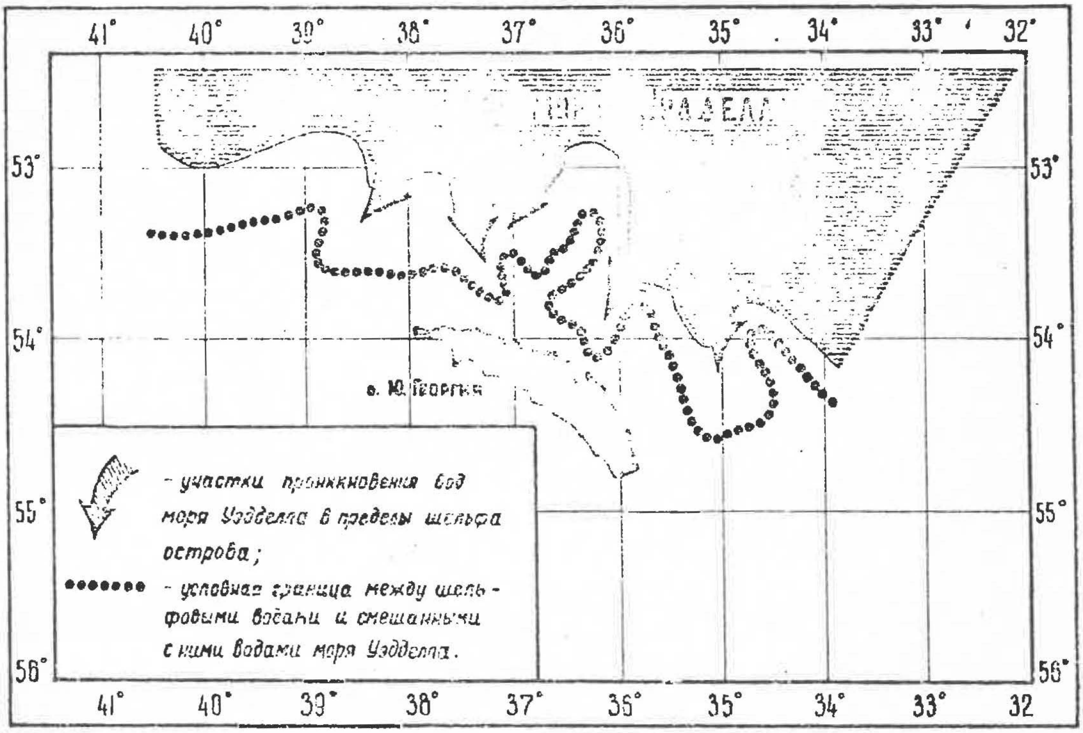


Fig.27 Penetration of the Weddell Sea water into the shelf water of the South Georgia Is. and the position of the interaction zone between the shelf water and transformed Weddell Sea water

- localities of penetration of Weddell Sea water into the shelf water
- a conditional boundary between the shelf water and mixed water of the Weddell Sea and shelf

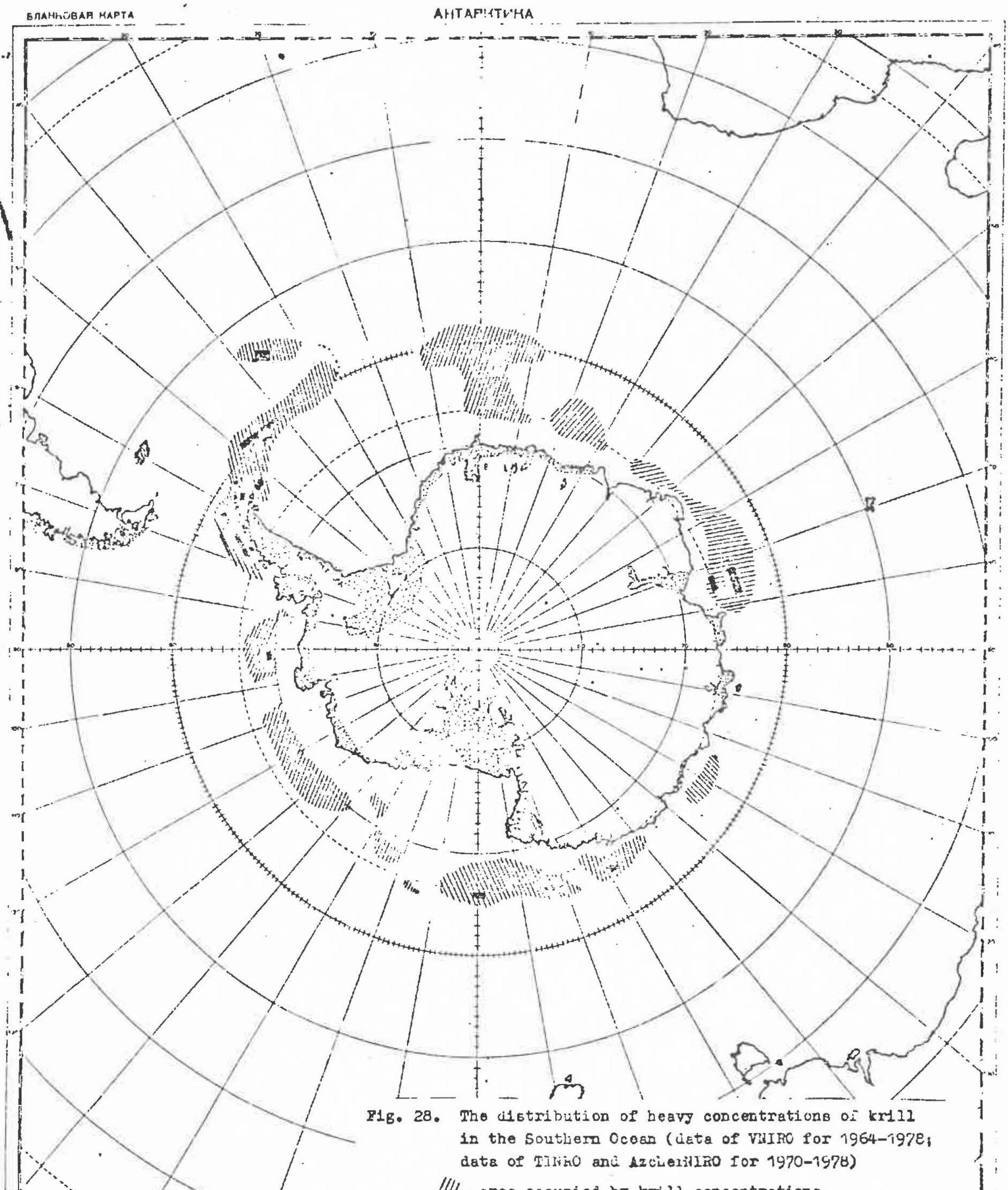


Fig. 28. The distribution of heavy concentrations of krill in the Southern Ocean (data of VNIRO for 1964–1978; data of TINRO and AzcherNIRO for 1970–1978)

////- area occupied by krill concentrations

▬ - places where trawl samples were taken

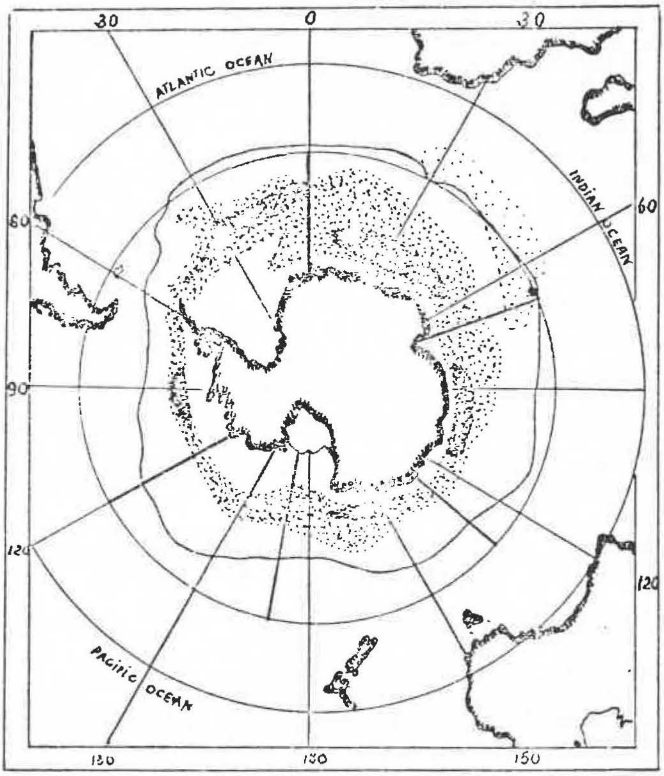


Fig.29 The habitat of baleen whales (Mystacoceti) in the Southern Ocean (after Mackintosh, 1965)

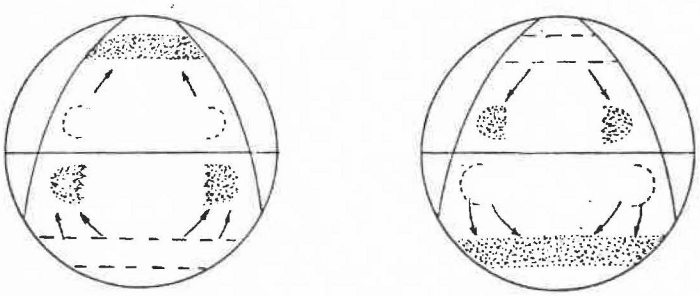

Fig.30 Pattern of seasonal migrations of baleen whales (Mystacoceti) (after Mackintosh, 1966)

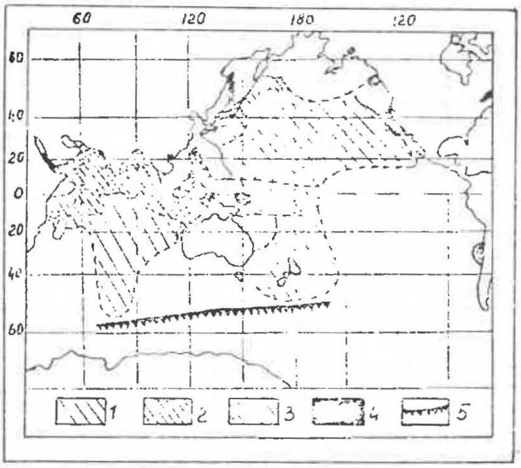


Fig.31 Quantitative distribution of rostra of squids in bottom sediments of the Pacific and Indian Ocean (pieces/m²) (after Belyaev, 1962).

1 - up to 100
2 - 100 - 1000
3 - 1000 - 10000
4 - over 10000
5 - a northern boundary of the area where no rostra occurred in sediments of the Antarctic

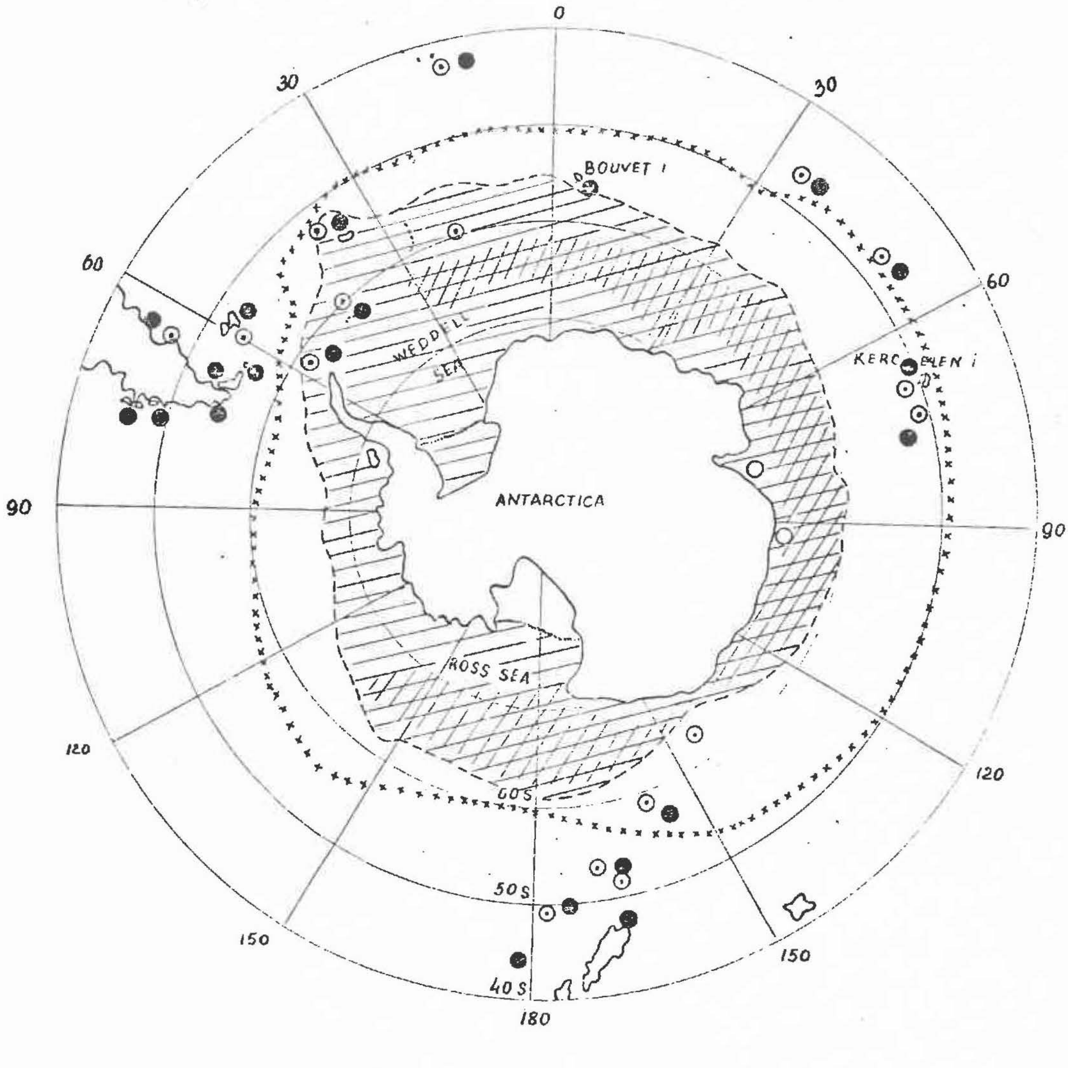


Fig.32 The distribution of pinnipeds in the Southern Ocean (data of Antarctic Atlas, 1966, 1969);

- sea elephant
- southern fur seal
- crabeater seal

Table 1 - Data on assessment of the stock and possible withdrawal of krill in the Southern Ocean.

Table 2 - Estimate of krill concentrated in some localities of the Southern Ocean at one time.

Table 3 - Crude estimates of large whale populations, biomass and food consumption in the Antarctic and of their biomass loss outside the Antarctic.

Table 4 - Crude estimates of Antarctic seal populations, biomass and food consumption.

Table 5 - Standing stock and food consumption by Antarctic birds (from data supplied by J. Croxall).

Table 6 - Total stock and consumption of krill by Antarctic species of fish.

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Fig. 19 - Forming of krill concentrations in relation to specific features of the vertical circulation of water in the open sea (after Elizarov, 1971).

Fig. 20-a - The distribution of concentrations of E. superba in latitudinal zones of Balleny Islands and northern Ross Sea by years (data of TINRO).

Fig. 20-b - Size composition of E. superba in latitudinal zones of the Balleny Islands and northern Ross Sea by years (data of TINRO).

Fig. 21 - The distribution of various size groups of E. superba in the Bellingshausen Sea (the authors' data, 1976-1978).

Fig. 22 - The distribution of various size groups of E. superba in latitudinal zones of the Prydz Bay, Sodruzhestvo Sea and eastern Cosmonauts Sea (data of the Azov-Black Sea Research Institute of Marine Fisheries, 1973-1978).

Fig. 23 - The extension of the Weddell Sea water in the Antarctic Atlantic in relation to the geostrophic circulation pattern.

Fig. 24 - Distribution of dense stable concentrations of E. superba in meanders of the SFZ

- dense stable concentrations of krill
- average long-term position of the SFZ

Fig. 25 - Spawning stages of E. superba in various areas of the Scotia Sea from westwards to eastwards

- females prior to spawning
- mature females

- spent

A - South Shetland Is., B, C - water of the SFZ northwestwards of South Orkneys, D-E - water of the SFZ northeastwards of South Orkneys.

Fig. 26 - The distribution of various size groups of E. superba in the Antarctic Atlantic in relation to the SFZ.

Fig. 27 - Penetration of the Weddell Sea water into the shelf water of the South Georgia Is. and the position of the interaction zone between the shelf water and transformed Weddell Sea water.

- localities of penetration of Weddell Sea water into the shelf water

••••• - a conditional boundary between the shelf water and mixed water of the Weddell Sea and shelf

Fig. 28 - The distribution of heavy concentrations of krill in the Southern Ocean (data of VNIRO for 1964-1978; data of TINRO and AzcherNIRO for 1970-1978)

//// - area occupied by krill concentration

- places where trawl samples were taken

Fig. 29 - The habitat of baleen whales (Mystacoceti) in the Southern Ocean (after Mackintosh, 1965).

Fig. 30 - Pattern of seasonal migrations of baleen whales (Mystacoceti) (after Mackintosh, 1966).

Fig. 31 - Quantitative distribution of rostra of squids in bottom sediments of the Pacific and Indian Ocean (pieces/m²) (after Belyaev, 1962).

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2 - 100 - 1000
3 - 1000 - 10000
4 - over 10000
5 - a northern boundary of the area where no rostra occurred in sediments of the Antarctic

Fig. 32 - The distribution of pinnipeds in the Southern Ocean (data of Antarctic Atlas, 1966, 1969);

- sea elephant

- southern fur seal

- crabeater seal

Tableau 1. Données sur l'évaluation du stock et sur le retrait éventuel de krill dans l'océan Austral

Tableau 2. Estimation de la concentration de krill dans quelques régions de l'océan Austral à un moment donné

Tableau 3. Estimations sommaires des populations, de la biomasse et de la consommation alimentaire des grandes baleines en Antarctique, et de la chute de leur biomasse en dehors de l'Antarctique

Tableau 4. Estimations sommaires des populations, de la biomasse et de la consommation alimentaire des phoques de l'Antarctique

Tableau 5. Réserves existantes et consommation alimentaire chez les oiseaux de l'Antarctique (selon les données fournies par J. Croxall)

Tableau 6. Stock total et consommation de krill chez les espèces de poissons de l'Antarctique

Figure 1. Diagramme de la circulation de l'eau de surface dans l'océan Austral (préparé par Maslennikov d'après Treshnikov, 1964, Klepikov, 1962 et d'autres)

Figure 2. Position de la zone frontale secondaire (SFZ) par années dans la Mer du Scotia

Figure 6. Changements saisonniers relatifs à la teneur en pigments de végétation dans la couche supérieure de 0-50m dans trois zones latitudinales de l'océan Austral (d'après Hart, 1942): 1. septentrionale; 2. intermédiaire et 3. australe

Figure 7 Répartition de zooplancton (ml) dans la couche 1000-0m (d'après Foxton, 1956)

Figure 8. Volume sommaire moyen de zooplancton (ml) dans la couche 100-0m. A - dans le courant côtier antarctique (courant de dérive des vents d'ouest); B - dans le courant de la Mer de Weddell; C - courant circumpolaire antarctique (courant de dérive des vents d'est) (d'après Foxton, 1956)

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1. au large de la Géorgie du Sud, 1969;
2. le sud de la Mer du Scotia, 1967;
3. le sud de la Mer du Scotia, 1969;
4. le sud de la Mer du Scotia, 1968;
5. au large des Iles Balleny (Naumov, 1962);
6. au large de la Géorgie du Sud, 1965.

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Figure 20-b. Composition de E. superba par tailles dans les zones latitudinales des Iles Balleny et du Nord de la Mer de Ross pour différentes années (données TINRO)

Figure 21. Répartition de groupes de E. superba de différentes tailles dans la mer de Bellingshausen (données des auteurs, 1976-1978)

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Figure 24. Répartition des concentrations denses et stables de *E. superba* dans les méandres de la zone frontale secondaire (SFZ)

- concentrations denses et stables de krill
- position moyenne à long terme de la zone frontale secondaire (SFZ)

Figure 25. Stades reproductifs de *E. superba* dans différentes régions de la Mer du Scotia de l'ouest à l'est

- femelles avant le frai
- femelles matures
- femelles après le frai

A Iles Shetland du Sud
B,C eau de la zone frontale secondaire (SFZ) au nord-ouest des iles Orcades du Sud
D,E eau de la zone frontale secondaire (SFZ) au nord-est des Iles Orcades du Sud

Figure 26. Répartition des groupes de *E. superba* de différentes tailles dans l'Atlantique Antarctique par rapport à la zone frontale secondaire (SFZ)

Figure 27. Pénétration de l'eau de la mer de Weddell dans l'eau de plateau de l'île de la Géorgie du Sud, et position de la zone d'interaction entre l'eau de plateau et l'eau transformée de la mer de Weddell

- lieux de pénétration de l'eau de la mer de Weddell dans l'eau de plateau
- limite conditionnelle entre l'eau de plateau et l'eau mixte de la mer de Weddell et du plateau

Figure 28. Répartition des fortes concentrations de krill dans l'océan Austral (données VNIRO pour 1964-1978; données TINRO et AzcherNIRO pour 1970-1978)

- région occupée par les concentrations de krill
- lieux d'échantillonnage par chaluts

Figure 29. Habitat des baleines mysticètes (Mystacoceti) dans l'océan Austral (d'après Mackintosh, 1965)

Figure 30. Mouvement des migrations saisonnières des baleines mysticètes (Mystacoceti) (d'après Macintosh, 1966)

Figure 31. Répartition quantitative des rostres de calmars dans les sédiments de fond de l'océan Pacifique et de l'océan Indien (unités/$m^2$) (d'après Belyaev, 1962)

1 - jusqu'à 100
2 - 100-1000
3 - 1000-10000
4 - supérieur à 10000
5 - limite nord de la région où les rostres sont absents des sédiments de l'Antarctique

Figure 32. Répartition des pinnipèdes dans l'océan Austral (données de l'Atlas de l'Antarctique, 1966, 1969)

⊙ éléphant de mer
● phoques à fourrure du sud (Arctocephalus sp.)
# phoque crabier

Таблица 1. Данные по оценке запаса и возможного сокращения количества криля в Южном океане.

Таблица 2. Оценка скоплений криля некоторых районов Южного океана в определенное время.

Таблица 3. Приблизительные оценки крупных популяций китов, их биомассы и объема потребляемой пищи в Антарктике и потери их биомассы вне Антарктики.

Таблица 4. Приблизительные оценки популяций тюленей Антарктики, их биомассы и объема потребляемой пищи.

Таблица 5. Постоянный запас антарктических птиц и объем потребляемой ими пищи (по данным, представленным Дж. Кроксаллом).

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Рис. 16. Плодовитость E. superba в различные годы по районам (по Макарову, 1971 г.): 1 - в районе Южной Георгии, 1969 г.; 2 - в южной части моря Скотия 1967 г.; 3 - в южной части моря Скотия, 1969 г.; 4 - в южной части моря Скотия, 1968 г.; 5 - в районе островов Баллени (Наумов, 1962 г.); 6 - в районе Южной Георгии, 1965 г.

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Рис. 20-b. Размерный состав E. superba по широтным зонам в районе островов Баллени и северной части моря Росса по годам (данные ТИНРО).

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Рис. 23. Распространение вод моря Уэдделла в атлантическом секторе Антарктики в связи с геострофической циркуляцией.

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- плотные постоянные концентрации криля;
- приблизительное долгосрочное положение ВФЗ.

Рис. 25. Стадии нереста E. superba в различных районах моря Скотия с запада на восток:

- самки до нереста;
- взрослые самки;
- отнерестившиеся;

A - Южные Шетландские острова, B, C - воды ВФЗ к северо-западу от Южных Оркнейских о-вов, D-E - воды ВФЗ к северо-востоку от Южных Оркнейских о-вов.

Рис. 26. Распределение различных размерных групп E. superba в атлантической части Антарктики по отношению к ВФЗ.

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- участки проникновения вод моря Уэдделла в пределы шельфа;

••••• - условная граница между шельфовыми водами и смешанными с ними водами моря Уэдделла.

Рис. 28. Распределение крупных концентраций криля в Южном океане (по данным ВНИРО на 1964 - 1978 гг.; ТИНРО и АзчерНИРО на 1970 - 1978 гг.):
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▬ - места взятия образцов тралом.

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1 - до 100;
2 - 100-1000;
3 - 1000-10000;
4 - более 10000;
5 - северная граница района, в котором клювы отсутствовали в донных осадочных слоях Антарктики.

Рис. 32. Распределение ластоногих в Южном океане (по данным "Атласа Антарктики", 1966 г., 1969 г.):
⦿ - морской слон;
● - антарктический морской котик;
# - тюлень-крабоед.

Cuadro 1 - Datos sobre la evaluación de la existencia y posible retirada del krill del Océano Austral

Cuadro 2 - Estimación del krill concentrado en algunos lugares del Océano Austral en un tiempo dado

Cuadro 3 - Estimaciones aproximadas de las poblaciones, biomasa y consumo de alimento de las grandes ballenas en el Océano Antártico y de su pérdida de biomasa fuera del Océano Antártico

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Ilustración 1 - Diagrama de la circulación del agua de la superficie en el Océano Austral (recopilado por Maslennikov según Treshnikov, 1964, Klepikov, 1962 y otros).

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- densas concentraciones estables de krill

- posición promedio a largo plazo de la SFZ

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- hembras antes del desove

- hembras que han llegado a la madurez

- consumido

A - Islas Shetland del Sur, B, C - agua de la SFZ al noroeste de las Orcadas del Sur, D-E - agua de la SFZ al noreste de las Orcadas del Sur.

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- ubicación de la penetración del agua del Mar Weddell en el agua de la plataforma

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Ilustración 28 - Distribución de grandes concentraciones de krill en el Océano Austral (datos correspondientes a 1964-1978 obtenidos de VNIRO; datos correspondientes a 1970-1978 obtenidos de TINRO y AzcherNIRO).

- área ocupada por concentraciones de krill

- lugares de donde se obtuvieron muestras con red arrastrera

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Ilustración 30 - Modelo de migraciones estacionales de las ballenas Mysticetas (Mystacoceti) (según Mackintosh, 1966).

Ilustración 31 - Distribución cuantitativa de rostra de calamares en sedimentos profundos de los Océanos Pacífico e Indico (piezas/$m^2$) (según Belyaev, 1962).

1 - hasta 100
2 - 100 - 1000
3 - 1000 - 10000
4 - más de 10000
5 - límite norte del área donde no se encontró rostra en sedimentos del Océano Antártico

Ilustración 32 - Distribución de pinnípedos en el Océano Austral (datos del Atlas Antártico, 1966, 1969);

⊙ - elefante marino

● - foca peletera Austral

# - foca cangrejera