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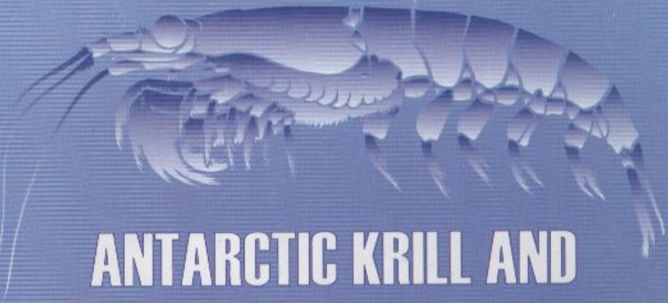
Ernest Z. SAMYSHEV



ANTARCTIC KRILL AND THE STRUCTURE OF PLANKTONIC COMMUNITY IN ITS DISTRIBUTION AREA

MOSCOW
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1991

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Data of long-term field and experimental studies conducted at a typical region of Antarctic underlie the analysis of major structural and functional characteristics of the Antarctic krill *Euphausia superba* Dana prevailing in Antarctic ecosystem and other planktonic community members in the area. A solid theoretical basis has been formed that allows to have an insight into economic prospects for the krill.

For hydrobiologists, ecologists.

Figs. 64, Tables 28, Refs. 297; 268 p.p.

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BRIEF SUMMARY

The array of major structural and functional characteristics of the Antarctic krill, *Euphausia superba* Dana, and other essential living components of the planktonic community are discussed based on the knowledge having been gained through the long-term surveys and experiments and the regional complex monitoring (1973-1986), conducted in a typical Antarctic area – the Sea of Commonwealth and the adjacent water areas. The resulted original biological data have brought answers to many crucial questions and fostered integrated approach to the entire Antarctic ecosystem. Basic concepts and conclusions made by other researchers are also discussed and commented; in particular, well-grounded explanation is given why of the two relevant hypotheses advanced by Marr only one is valid for handling functional structure of the krill area. The scale of interannual biomass and abundance variations is assessed and the underlying mechanism is discussed as linked with the events of krill explanation which, in their turn, are associated with the intensity of meridional water transfer depended on the solar activity and the complex seawater structure and circulation.

Along with the krill, other organisms constituting Antarctic planktonic community are described with emphasis on their taxonomic composition, abundance, general and special features of the development; balance estimates are given for the substance and energy fluxes in the ecosystem based on measurements made in the years of the Antarctic investigations. It was found that in the upper 100-200-m seawater layer only 25-30% and less of the primary production generated by phytoplankton is decomposed and assimilated by heterotrophs, the rest descends to the sea floor or is carried away with the currents to the north.

Chapter VI, absent in the Russian version of the book, is included on the English version in order to characterize trophic

structure of Antarctic zooplankton and to provide better understanding of production-destruction processes going in pelagial of the Southern Ocean.

The reported results and deductions provide solid theoretical basis for further study and the insight into krill fishing perspective.

The author's approach to study of Antarctic krill and Antarctic ecosystem as a whole was incorporated into the National Programme of Ukrainian Researches in Antarctic (1997-2001 and 2002-2010) and has been successfully used during Ukrainian Antarctic Expeditions to the Atlantic sector of Antarctic.

Translation of this book into English is on the initiative of Ukrainian Antarctic Centre and under the support of Alfred-Wegener Institute of Polar and Marine Research (AWI, Bremerhaven); the book was printed under the support of Ukrainian Automobile Centre (Kiev).

This book is addressed to experts, researchers and students whose interests and ambitions focus on the discussed topic.

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INTRODUCTION

Today, the growing commercial interest to the Antarctic krill *Euphausia superba* Dana is evident. Yet experts have not come to an agreement about the actual stock of and economic prospects for this small crustacean. The discord is due to technical difficulties related to very uneven distribution over as huge area as more than 20 000 000 km^2. Sensible and effective fishing of krill requires a theoretical concept which would be based on the knowledge of major biological parameters (total stock, concentration, distribution, functional structure of the population range, diet, production, metabolic expenditure) of the crustacean and the entire planktonic community in the distribution area. Combining population and ecosystem studies has both methodological and practical significance; in particular, it provides a diversity of variants of mutual verification of results for a wide range of research topics, and the possibility of predicting the aftereffects of krill fishing on the entire ecosystem. Inasmuch as the cited difficulties impede regular complex studies of krill over the entire water area, a reasonable alternative would be doing such studies at an extensive location of the Subantarctic near-continental seas treated as a part of the circle of krill distribution area. This would permit to exercise regular control (direct counting) over the chosen population segment with the totality of vital characteristics inherent to the population on the whole and to simultaneously investigate the structure of Antarctic planktonic community over the model area.

These ideas inspired research works reported in this book. In their turn, the studies allowed to attain the author's ambition to formulate theoretical grounds for assessing prospects of krill fishing. The Sea of Commonwealth was taken as the model; later it became an important region of commercial fishing of the krill which conformed to the typical standards and where the series of essential studies were made from 1972 to 1987.

The approach offered in this book is based on the recent methodology of ecosystem studies in pelagic zone of the World Ocean. Valuable information has been obtained from research cruises organized by M.E. Vinogradov, a corresponding member of the Russian Academy of Sciences (RAS)[1] from Moscow Institute of Oceanology RAS to the tropical Pacific (Functioning of pelagic communities in tropical waters of the Pacific Ocean, 1971) to the Peruvian shore (Ecosystems of the Peruvian pelagic zone, 1980), to the frontal zones of the Southern Pacific (Vinogradov and Fedorov, 1984). Employment of the recent approach to our investigations of the Antarctic community was the pioneer endeavour in the fisheries practice.

In writing this book, the author used the vast body of original biological data from field and experimental studies. The materials were collected in 12 research cruises mounted by the Azov-and-Black Seas Institute of Fisheries and Oceanography (AzCherNIRO) during 1977 – 1987 to the "ring" of krill distribution area. The location under study lies between 55 and 90° E and 58 and 60° S, bordering the shoreline in the south. These are the northern and the southern limits of the krill distribution range.

Each of the expeditions made a macroscale survey which embraced hydroacoustic krill scouting, target trawling of the detected aggregations, and oceanological studies at a standard station grid. In several cases the macroscale survey was repeated during vegetation season. At the stations seston components were collected, primary and bacterial production measured and standard oceanographic observations made. During the cruises krill ration and balance estimates were experimentally studied.

The investigations were carried out under the scientific supervision and with the active participation of the author of this book.

Acknowledgements. I am grateful to many helping hands who did their part of the work in field or at laboratory and thus contributed to this book. I give my sincere thanks to the South Fisheries Scouting Agency (Kerch, Ukraine), G.V. Voloshina from AtlantNIRO (Kaliningrad, Russia), A.I. Lushov, N.G.

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[1] formerly the Academy of Sciences of the USSR (Ac. Sci. USSR)

Petrova, E.L. Romanova-Sokolova, A.I. Gaidamak, N.I. Mironenko and E.V. Budnichenko from AzCherNIRO (Kerch, Ukraine) who took active part in collection and handling of the huge biological material. This monograph would be less convincing without earlier data (echosounding, krill trawling records, phyto- and zooplankton samples) obtained during five research cruises and fisheries expeditions launched by AzCherNIRO and the South Fisheries Scouting Agency to the Indian sector of the Antarctic (Southern) Ocean. Another valuable contribution were bacterioplankton samples and other seston components taken at the Atlantic sector of the Antarctic Ocean during two research cruises of AtlantNIRO in 1981 and 1984; results obtained from processing of the materials were kindly offered by V.A. Sushin and Yu. A. Shulyakovsky to the author.

BRIEF PHYSICO-GEOGRAPHICAL DESCRIPTION OF THE INVESTIGATED REGION

Materials gathered during the repeated expeditions under the auspices of the Azov-and Black Seas Institute of Fisheries and Oceanography (AzCherNIRO) and the South Fisheries Scouting Agency provide a realistic picture of the abiotic background in the Sea of Commonwealth and the adjacent waters as a biotope of ecosystem under the study.

Geological background. Analysis of the materials collected (Dubinets et al. 1983) shows that the sea floor relief (Fig. 1) in the region is determined by Antarctic continental slope and shelf, the eastern Afro-Antarctic Depression and the Southern Kerguelen Archipelago. The ice-free continental shelf has a very complicated structure. Its width is from 40 to 150 miles, being largest in the central part (Prudz Bay); the outward depth is 500-600 m, 350 m on the average; the bottom is a complex combination of transverse and longitudinal fissures, hollows and trenches due to moving ice.

The continental slope also has a complex relief with longitudinal and transverse underwater valleys to 500 m deep, ridges and elevations. Upper (1300-2000 m) part of the slope is smooth and steep (10° - 15°) while deeper part lying below 1300-2000 m with the slope angle about 2° are hill-like bottom elevations. The foot of the continent lies 3100-3500 m deep, below goes Afro-Antarctic Trench, its eastern extremity bordering the southern part of the Kerguelen Ridge.

Bottom substrates are very diverse. Boulders, gravel and sand prevail on the continental shelf, sand mixed with silt on the continental slope and clay mixed with silt in the depth.

Hydrological background. Earlier papers (Pomazanova et al. 1983; Ryabchikova 1983; Ryabchikova et al. 1979; Samyshev 1985) point, out that of two forms of atmospheric circulations - meridional and zonal - characteristic of the region, the former prevails during the vegetation season. Its seasonal recurrency averages 73%, usual duration is about 2 days though 15-17-day-long events are also known. Meridional atmospheric circulation intensifies air exchange between the subtropical and polar zones, cyclonic activity and adds to

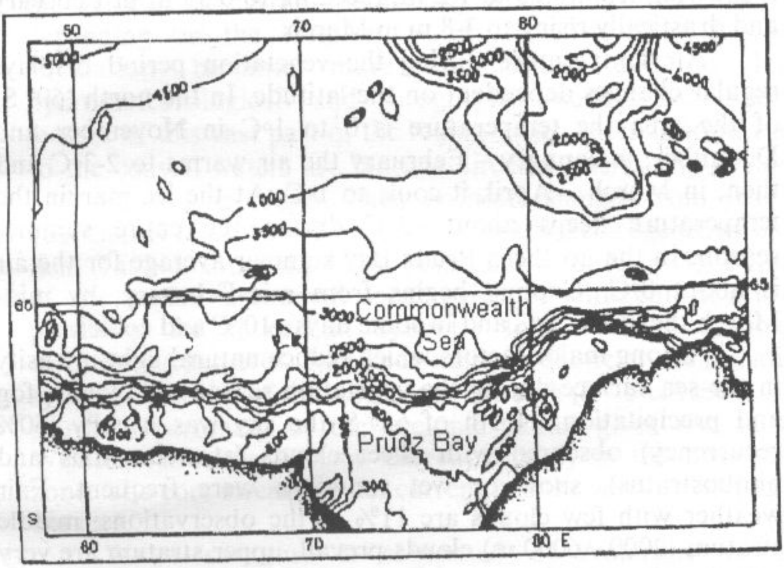

Fig. 1. The underwater landscape at the Sea of Commonwealth area (cited from Dubinets et al., 1983).

the frequency of events of the near-shore depression stabilization.

During austral summer (December - February) weak and moderate (0 to 10 m·sec^{-1}, wind force 3-5 by Beaufort notation) winds prevail. Wind force increases to 6 - 8 (11 to 25 m·sec^{-1}) in late autumn - early winter (March). In the coastal zone 10 miles in width the determinant wind is coastal south-eastern with the force 15 m·sec^{-1}. Its intensity is especially high during the month preceding and that coming next after the summer season; in summertime the wind force has a distinct daily rhythm with a minimum post meridiem. 150-200 miles off the shore the Antarctic Divergence area is located between the prevailing west and east winds. The dominant winds determine direction of wind-induced waves. South of 65°S the turbulence is usually minor; north of this latitude there are persistent ripples mostly from the north-west. From the early to mid austral summer (December and January, correspondingly) average wave height is growing from 0.75 to 1.2 m, receding to 0.35 m in February and drastically rising to 3-8 m in March.

Air temperature during the vegetation period displays regular changes dependent on the latitude. In the north (60° S) of the area the temperature is 0 to 1°C in November and December; in January – February the air warms to 2-3°C and then, in March – April, it cools to 1°C. At the ice margin the temperature keeps about –3°C during the entire summer season. In the northern Prudz Bay summer average for the air is about 0°C. Cooling begins from mid-February; by mid-March the air is –5°C and in some days –10°C and colder.

Among major factors which reduce natural light intensity in the sea surface during the vegetation season are clouds, fog and precipitation. North of 65° S the sky was usually (50% recurrency) obscured with sheet clouds (stratocumulus and nimbostratus), snow or wet snowfalls were frequent. Fair weather with few clouds are 11% of the observations; middle stratum (2000 - 6000 m) clouds prevail, upper stratum are very rare. South of 65° S sunny days are frequent in summer months (January – February); in March, with the beginning of autumn-winter season, their number sharply drops yielding to cloudy weather with fog, snow, wet snow and rain.

Ice cover of the region is mostly one-year and new ice. The northernmost (ca. 60° S) marginal ice is found in September, the southernmost (65 - 68° S) in March. North of the Antarctic divergence cyclones with a maximum recurrency line going 150-200 miles off the shore make ice drift eastward, south of the divergence ice moves west.

In the Indian sector of the Southern Ocean krill distribution area bordering 58-60 ° S in the north (McQuillan 1962; Yarogov 1969) occupies two of the three main zones of the Antarctic water circulation system identified by V.G. Neiman (1961) and Yu. A. Ivanov (1961): the Coastal (Western) Antarctic current going close to the shoreline, and the extensive zone of the eastern water transfer stretching to 52 ° S north in the west of the sector and to 57 ° S in the east. Longterm observations during our expeditions prove the distinct eastward water transfer at the northern periphery of the krill distribution area. This is where meanders are formed, the velocity of current fluctuating from 5 to 10-15 cm·sec^{-1} depending on the location. South of 60 - 62 ° S water circulation becomes more complicated due to local hydrometeorological and orographic conditions. Special feature of this vast part of the region which extends southward to the coastal waters are latitude-directed alternating cyclonic and anticyclonic eddies. Their position changes from year to year that is related to changes of generally heterogeneous baric field (In: Newton {ed.} 1976; Pomazanova et al 1983). Typical of the region are small local gyres of different directions persisting for a certain synoptic term within seasonally stationary extensive – hundreds miles in diameter – circulation systems. Velocity of the currents is not high (2 – 5 cm·sec^{-1}). The southern periphery of the cyclonic eddies gives rise to the Western Antarctic Coastal current directly in the near-shore zone. The core stream of the current has the velocity of 5 to 50 cm·sec^{-1}.

Water structure is composed of Antarctic surface, intermediate, deepwater circumpolar and near-bottom water masses. The first of them contains trophogenic layer and changes with season because of wind-induced mixing of water layers with different density that, in turn, determines seasonal changes over the entire ecosystem. In close proximity to the Antarctic continent the ecosystem subdivides into shelf and shallow ones. The former is largely above the continental shelf, its greatest depth is about 500 m. The sea water is cold (ca. –1.8° C) year through. Downwelling and mixing with deeper water results in the Antarctic near-bottom layer formation. The latter lies north of the shelf ecosystem; in the coastal zone its depth may reach 150 m, drastically decreasing above the elevations. The width of the coastal zone with the shelf and shallow waters is determined primarily by the width of the continental shelf. Warming of the upper surface layer and its desalination through ice melting during December – March result in the appearance of warm summer water layer separated from the residual cold water by thermocline (seasonal pycnocline). The lower boundary of the underlying intermediate Antarctic water mass goes 500-600 m deep within the Antarctic divergence area.

Surface water temperature is above 0°C year round for the larger part of the region between 60 ° and 65 ° 30'S. In austral summer the temperature is 0.7 to 1.7 ° C at 60 ° S, and –1.5 ° to –2.1 ° C near the marginal ice.

The warm summer water layer is 40-50 metres deep in the north of the water area and 10-20 metres deep in the south. Temperature gradient lying beneath has the lower boundary going at 30-50 m depths south of 65 ° S and at 70-90 m north of 62° S. Maximum vertical gradient does not exceed 0.18 ° C·m^{-1}. Measured in 50-150 m layer minimum temperature is –1.8 ° C. In deeper water the temperature is increasing to a maximum at 300 - 600 m. Between 62 ° and 65 ° S the measured maximum was 1.9 ° C.

During austral summer the salinity in the 10-20 metres deep surface layer varies from 33.3 to 33.9‰ displaying a tendency to increase northward with depth and reaching 33.8 – 34.6‰ at 100 m.

Hydrochemical background. Scientific observations made during the cruises by AzCherNIRO and the South Fisheries Scouting Agency (Khimitsa et al. 1983) show that during the entire navigation season the content of dissolved oxygen (DOC) in the ocean surface remains as high as 680-720 µg·at·l^{-1} (96-100% saturation) over the major part of the water area, and increasing southward; Prudz Bay is where maximum (760 µg·at·l^{-1}, 115% saturation) DOC was measured. Maximally oxygenated water layer goes 10-20 m deep in the south and 30-40 m deep in the north of the location. With depth the values are decreasing to a minimum (348-393 µg·at·l^{-1}) registered in warm water 400-600 m deep.

Most of the ocean surface is rich with nutrients over the vegetation period; phosphate content, for instance, is from 1.2 to 1.9 µg·at·l^{-1}; with greater depth it increases to 2.9 µg·at·l^{-1} at 400-800 m. Silicic acid measured in the upper 50-m layer in which it distributes relatively evenly varies between 20 and 50 µg·at·l^{-1} with several drops to 6 µg·at·l^{-1}. Depth increasing, silicic acid content elevates amounting 60 and 170 µg·at·l^{-1} at 200 and 2000 m depths, correspondingly.

Thus, according to the abiotic background the region under our investigations is a typical constituent part of the biotope of Antarctic pelagic ecosystem. This fact explains the adequacy of main features the community component manifests within the limits of the study area and permits to extrapolate results – at least for the majority of topics – to the entire distribution area of krill.

CHAPTER I

THE ANTARCTIC KRILL *EUPHAUSIA SUPERBA* DANA: MAIN BIOLOGICAL CHARACTERISTICS

Studies of krill have more than a century long history, yet major biological features of this small crustacean were not given serious concern of the researchers. Among the essential characteristics are life history, distribution, production and productivity, concentration and dimensional parameters of adult portion of krill population.

1.1 Krill eggs and larvae distribution and the functional structure of the distribution area

Until recently the concept of life history of *E. superba* has been based mostly on the *Discovery* Antarctic expedition data. According to the expedition results (Marr, 1962), spawned eggs sink into depth; later the growing eggs and hatched larvae are transported with the deepwater current southward to the continent where their uplift with the development takes place. The rest of its life the krill stays in surface water. This mode of spatial existence of plankton has been described for Antarctic zone by Mackintosh (1934). To some extent this proves the hypothesis cited above about the scenario of ontogenetic development of krill in space. Yet, as Marr emphasizes, it remains obscure where krill spawns – in neritic or in oceanic water at a large distance off the shore. High frequency of juvenile krill occurrence in near-continental water and even under the ice (Ruud, 1932) may be indicative of the probable spawning ground. Having large residual weight, the eggs sink into depth relatively fast, that allows to suggest that in the case of the above-shelf spawning the final stage of incubation takes place at the sea floor.

No convincing proof has been offered of the validity of "Large circle" concept which claimed that spawning in the deep-ocean zone might also be efficient. Having taken into consideration that only minor concentrations of the eggs were found in water column, Marr suggested that krill would spawn in deepwater localities. This hypothesis was criticized by Mauchline and Fisher (1964), who stated that eggs of euphausiids (boreal species) sank to the bottom rapidly due to large residual weight. For instance, sinking rate of eggs by *Thysanoessa rashii* and *Meganyctiphanes norvegica* is 5.5 – 7.5 $m \cdot h^{-1}$ at the salinity of sea water 33‰ and the temperature 15°C. Time interval measured from the beginning of spawning till the hatching of nauplii was 5-6 days in these species. In comparison with the two species, *E. superba* has eggs larger in size. The authors supposed that if *E. superba* spawned in deep water, its metanauplii, nauplii and calyptopis stage would have to make long upward migration to surface water rich in food.

Later a number of concepts appeared about the scenario of *E. superba* life cycle and they are worth of scrutinizing. In particular, direct and indirect evidences have been obtained which confirmed Marr's hypothesis about the separate existence of larval and adult krill (Beklemishev, 1959, 1961; Naumov, 1962). K.V. Beklemishev (1961) put forward a suggestion about the accumulating role of stationary cyclones which, on the one hand, evoke the ascent of juvenile crustaceans to the surface of the ocean and, on the other hand, foster generation of adult krill aggregations. N.A. Mackintosh (1972) and R.R. Makarov (1972) claimed that spawning of *E. superba* might go at any area of Antarctic. However, N.M. Voronina (1974) took note of the marked asymmetry in the distribution of larvae of *E. superba* shown in the map by Marr, the abundance of the larvae at the Atlantic sector of Antarctic and the scarcity at the Indian and Pacific sectors, and she made an assumption that effective spawning of the krill in the Atlantic sector might be owing to specific vertical water structure. This structure implies shallow (from 1800 m depth and up) position of transformed dense shelf water (near-bottom water) as the result of cyclonic circulation at the Weddel Sea area. This water prevents sinking of eggs into greater depth where from non-feeding larvae are incapable of floating up into photosynthetic layer. Larval retaining within the Atlantic sector is owing to the Antarctic Circumpolar Current and the Weddel Sea water circulations. Some part of krill population spreads over the Antarctic water expanse thanks to surface water transfer. Observations by V.V. Maslennikov, as cited in A.G. Naumov (1978), point out that the homeward drift of krill to high latitude (and therefore the decrease of expatriated crustacean share – E.S.) in the Scotia Sea and adjacent waters is provided by southward streams in surface currents. Having taken the Atlantic sector as an example, R.R. Makarov (1972) and N.M. Voronina (1977) made an assumption about the basic krill distribution area located within the Antarctic Circumpolar Current and the water circulation of the Weddel Sea.

Current investigations of the problem under consideration are confined to specific aspects: the term of krill egg incubation, the rate of egg sinking, egg and larval distribution in particular localities. Simultaneously, attempts were made to revise extant concepts of life history of krill.

In particular, it was reported (Kikuno Tsucasa, 1982; Ikeda, 1984; Marshall, Hirche, 1984) that according to experimental data the hatching of krill nauplii took place on the 5-8th day of incubation depending on water temperature within a narrow range (-1 - +1.5°C).

The share of spawned eggs from which larvae hatched during the experiment varied as broadly as from 0 to 100%, averaging 44% in some cases (Ross, Quetin, 1982) and 15% in other cases (Marshall, Hirche, 1984).

Hydrostatic pressure of 50 atm produced negative effect on the development of krill eggs which, because of the destruction of intercellular walls, "regressed" from the 2-nd and 4-th blastomere stages to the 1-st stage. The pressure load of 250 atm completely impeded egg development; normal gastrulation took place at 40 atm (George et al., 1982). Under 20 atm the egg develops to blastula; a drastic increase up to 200 atm ceases further growth (George, 1984). At the same time, as the cited authors reported, nauplii bear high pressure well: I stage endures up to 210 atm, II stage up to 150 atm. This feature is found in postlarval and juvenile (sexually immature) individuals, while egg-bearing females do not survive more than 25 atm that, as those authors claim, implies the possibility of spawning at depths not greater than 250 m.

Mean sinking rate of krill eggs is 211 $m \cdot d^{-1}$ at the temperature 1.8°C and the salinity 33.75‰, and 232.5 $m \cdot d^{-1}$ at 1.9°C and 33.9‰ (Marshall, 1983). According to Marshall, over incubation period the eggs may sink down to 1250-1850 m in the absence of turbulence events; their density (ca 1.50) keeps higher than the density of seawater at any depth. However, Ross and Quetin (1982) give data different from these. In particular, they measured the rate of krill egg sinking as 195 $m \cdot d^{-1}$ at the water temperature 2.0°C, salinity 36.2‰ and density 1.029 $g \cdot cm^{-3}$ during the first day. Between the 1.5 and 3 day of the incubation the rate decreases to 95 $m \cdot d^{-1}$, growing again by the time of hatching. For the 135-h long embryonal development the egg should sink to 700 m depth. Similar results were reported by George (1982, 1983). His experimental data point out that hydrostatic pressure has no influence on the sinking rate but accelerates development of krill eggs. Special experimental studies by Quetin and Ross (1982, 1983) have demonstrated that pressure is almost of no significance for the rate of egg development and nauplius hatching. Formally, the contradiction between results on the hydrostatic pressure effect on the rate of egg development may be explained: firstly, by errors of the experimental technique, and secondly, by inadequate response to pressure as related to different condition of the eggs (though the latter factor is dubious).

According to tentative experimental data (George et al., 1982), nauplii are sensitive to the content of some amino acids in sea water, and beginning from calyptopis stage I - to food composition and amount (Ikeda, 1984). The latter has been proved in experiments when the researcher succeeded in incubating about 200 eggs of the same hatch at 1°C and in maintaining their growth to furcilian stage VI. The overall term of the larval development until this stage was 127 days. Beginning from calyptopis stage I the larvae were fed on the brine-shrimp (*Artemia*) nauplii and diatom algae (*Phaedactylum*). Food concentration in the experiment was 2.7 – 11 times as large as that in nature; the preferable food item were the nauplii. When calyptopis I were placed and kept in filtered sea water, their swimming pattern changed to irregular moves in 6 days, ceased after 13 days and after 30 days the larvae became motionless. No moulting event took place during the experiment.

Comparison of experimental data on high mortality rate of eggs spawned by krill, high rate of egg sinking, the eggs sensitivity to incubation conditions (in particular, to hydrostatic pressure) and to the content of dissolved and suspended nutrients in sea water in larval krill makes the concept of "large circle" questionable rather than convincing. Fairly speaking, in recent years few attempts were made to furnish pertinent proofs; that the endeavours were unsuccessful (George, 1980; Deacon, 1984) predominantly due to the absence or deficiency of the knowledge about the matter and its aspects.

No doubt, finding the final solution of the problem will require both experimental and extensive field studies which would clearly show patterns of the distribution of krill as related to growth and development, primarily at the early developmental stages.

Cases of quantitative assessment of krill eggs and larvae by some investigators have not clarified the understanding of life cycle of this crustacean as they were endeavoured either in coastal location or in deep-ocean zone close to the continent, or near the underwater mountains and isles mostly in the western Atlantic sector of the Southern Ocean, in the Scotia and Weddel seas (Hempel, 1982; Hempel I., Hempel G., 1978; Hempel, 1979; Hempel et al., 1979; Nast, 1979; Fevolden, 1980; Siegel, 1982; Wormuth, 1983; Rakusa-Suszczewski, 1984; Loeb, Schulenberger, 1987). Findings of krill eggs and larvae (the former only in neritic zone at 50 to 400 m depths) in large amounts are not an artefact, these agree with the early hypotheses (Makarov, 1972; Voronina, 1974) about the core of krill distribution area located in the region. No regular observations of krill eggs and larvae distribution in water column over the vast expanses covering both coastal and deep-ocean zones were made in any sector of the Southern Ocean.

The yawning gap in the knowledge of the krill's life history is of principal importance because it hampers gaining understanding of a large number of problems including such subjects as the boundaries and the scale of the basic distribution area, the efficiency of population recruitment at different parts of the distribution area, population structure, etc. All these subjects are directly linked with commercial fishing of krill in general and with the localization and the scope of krill fishing in particular.

Material and methods

Net sampling (mesh N 49, the net opening 80 cm in diameter) of krill eggs and larvae was made simultaneously with mesozooplankton catches. The samples were collected during annual macroscale oceanological surveys at the main region during 1977-1986 and a mesoscale survey at the area (65-67° S, 57-63° E) where the krill swarms concentrated in 1980. During the macroscale oceanological surveys the step between stations was 1° latitude along the meridional transects with the step of 5°; net sampling of plankton at these stations was made to 2000 m depth at a standard series of depths (0-25, 25-50, 50-100, 100-200, 200-500, 500-1000, 1000-2000 m). The station grid during the mesoscale surveys was designed with the step 0°30' latitude and 1°20' longitude, plankton samples were taken by fractions down to 500 m in the water layers given above. Counts of the eggs and larvae of *E. superba* coupled with the determination of their developmental stages were made for the entire volume of each sample. 2300 samples were handled altogether.

In order to make the analysis comprehensive, a wide variety of data were involved: those obtained from continuous hydroacoustic estimation of the aggregations of adult *E. superba*, krill catches and also information about the water structure provided by V.I. Tsaturyan and V.A. Lednichenko. Another valuable contribution were results of the experimental measurement of krill egg sinking rate which A.I. Lushov and G.V. Voloshina performed following instructions of the author (E.S.) during the 19-th cruise of the *R/V Skif* (summer 1982/1983) to the Sea of Commonwealth.

Results and discussion

There are many intertwined factors which predetermine the distribution of krill eggs and larvae; most significant are the distribution of adult (spawning) portion of krill population; spawning intensity, i.e. the share of simultaneously spawning individuals; spawning location and time and, correspondingly, the place and time of observations; sinking rate of the eggs, the character of water circulation in the area, etc.

Our observations prove that the northern boundary of the distribution area of *E. superba* in the Indian sector of Antarctic never goes up beyond 58°S. Adult part of the krill population, which dwells in the Antarctic surface water mostly above the seasonal pycnocline, in the deep-ocean zone gets into a complicated combination of currents generated by atmospheric processes. Therefore, being common almost everywhere, the crustaceans seldom form large swarms at this zone because frequent storms and the currents drastically changing near the surface disperse these aggregations. The prevailing eastward and northeastward transfer of the surface sea water and adult krill accounts for changes in the size spectrum of krill from trawl catches: the large form fraction in the swarms regularly increases northward. The persistent dense swarms of the senior krill are typical of the near-shore locations with deeply indented coastline that is owing to gyre-stabilizing topogenic effect. Similar effects have been found above sea bottom elevations and around isles like, for instance, in the Scotia Sea and at some areas else.*

During our investigations we found that with the coming of austral summer – usually since mid-December – spawning season of the krill began in the ice-free north of the area (January) moving then to the south with the retreat of ice edge, and finishing in the southern part of the Sea of Commonwealth (March). Biotesting of krill taken from the trawl catches points out that the portion of spawning females is always within 4-5%,

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* More details about the distribution of adult krill fraction are given in the next section of this chapter.

i.e. the spawning period is strikingly long. Probably, this fact explains low concentrations of krill eggs in the sea water.

Examined in different years, krill distribution (eggs and larvae) over the region displays common features. Distinctions, which have been elicited, are associated with changes in specific conditions some year or other. A few relevant cases are given to illustrate this point.

Fig.2 demonstrates that in March (the early 2-nd decade, i.e. the end of austral summer) 1977 the major part of larvae concentrated in the southernmost coastal zone into which the sea-ice conditions permitted the *R/V* to have penetrated. The larvae, most of which were calyptopis stages I and II and the rest stage III, occupied the upper 0-500 m water layer above the shelf and the continental slope. Furcilians, predominantly stage I, were few; they located at the southernmost part of the transection at 50-100 depths. Neither eggs nor larvae at any developmental stage were detected in the deep-ocean zone and the sea surface despite the presence of adult krill (Fig. 13 A). The core of larval aggregation neighbouring the northern periphery in 100-200 m layer and at 63°S was certainly the result of water transfer from coastal zone. Krill eggs were solitary found at the southern stations in the depths from 50-100 to 1000-2000 m. The position of larval aggregations in the south of the area concurs with the position of persistent commercial swarms of krill in the central part of the Sea of Commonwealth (Table 2).

Through shifting surveys to earlier time, we succeeded in counting krill eggs and larvae during the spawning peak both in the coastal and deep-ocean zones, and in assessing the spawning efficiency.

Two consecutive surveys, one in the early summer (January, Fig. 3a) and the other in the late summer (February, Fig. 3b) 1978, have shown that the eggs, like adult krill, were commonly found over the studied area (Fig. 5,1). Maximums were measured in the upper 200-500 m water layer that confirmed the recent spawning. In January egg concentrations in the deep-ocean zone were conspicuously higher than in February; the spots of maximum egg abundance coincided with

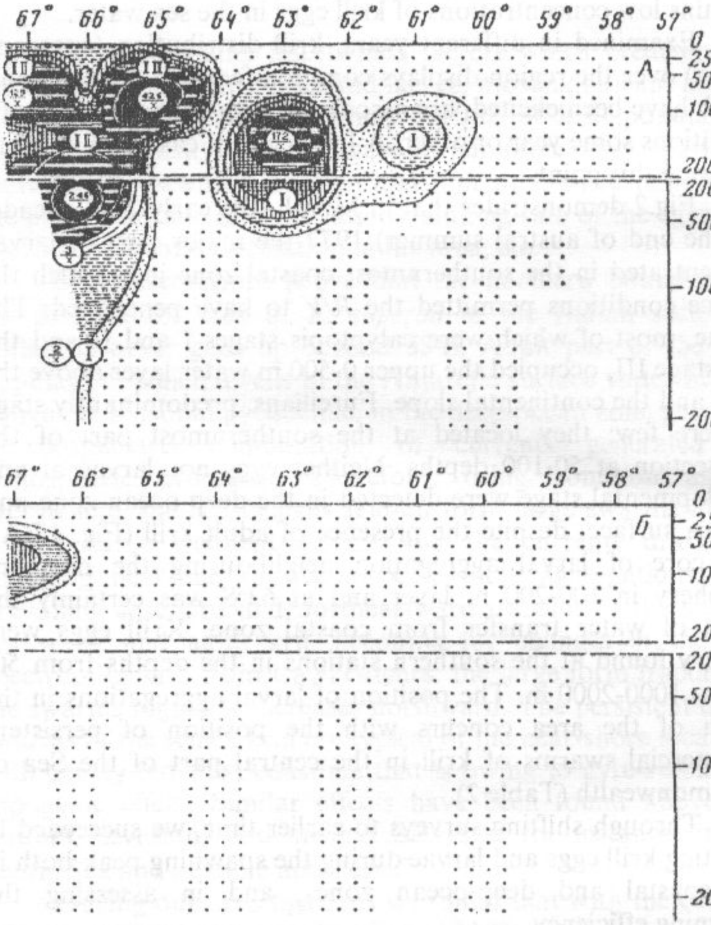

Fig. 2. The calyptopis (A) and furcilian (B) distribution in the transect along 75° E.

1 to 8: 0; 0-1; 1-10; 10-20; 20-50; 50-100; 100-200; >200 ind per 100 m^3, correspondingly. I, II, III – calyptopis developmental stages; x – the detected locations with krill eggs.

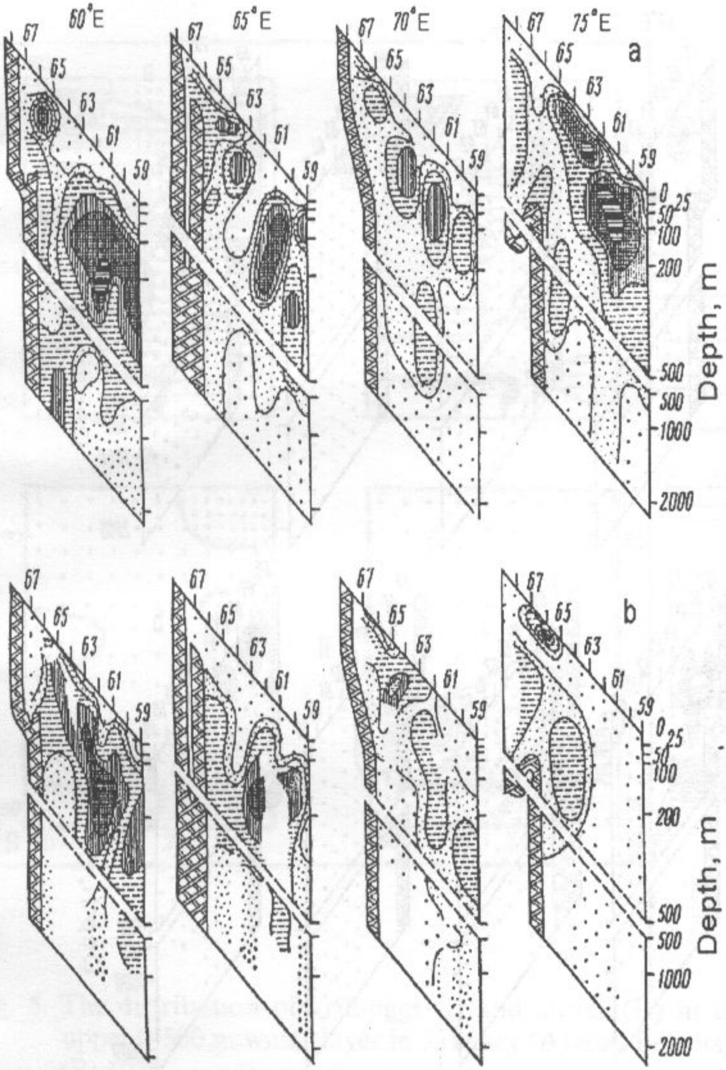

Fig. 3. The distribution of krill eggs in the meridional sections in January (a) and February (b) 1978. Designation marks as in Fig. 2.

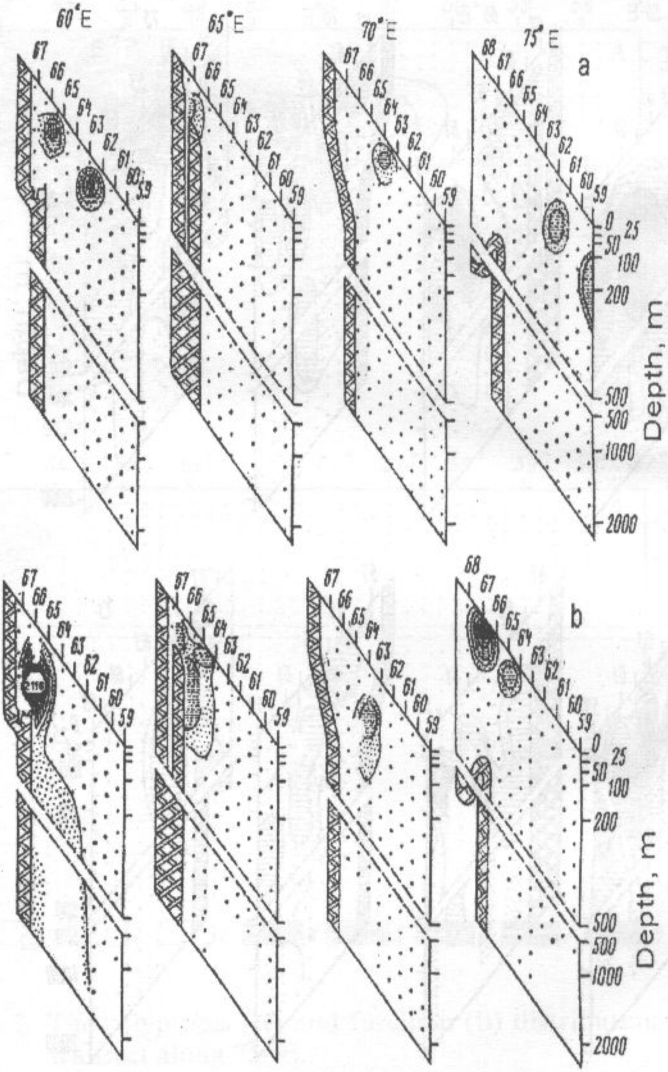

Fig. 4. The distribution of larval krill (predominantly calyptopis) in the meridional sections in January (a) and February (b) 1978. Designation marks as in Fig. 2.

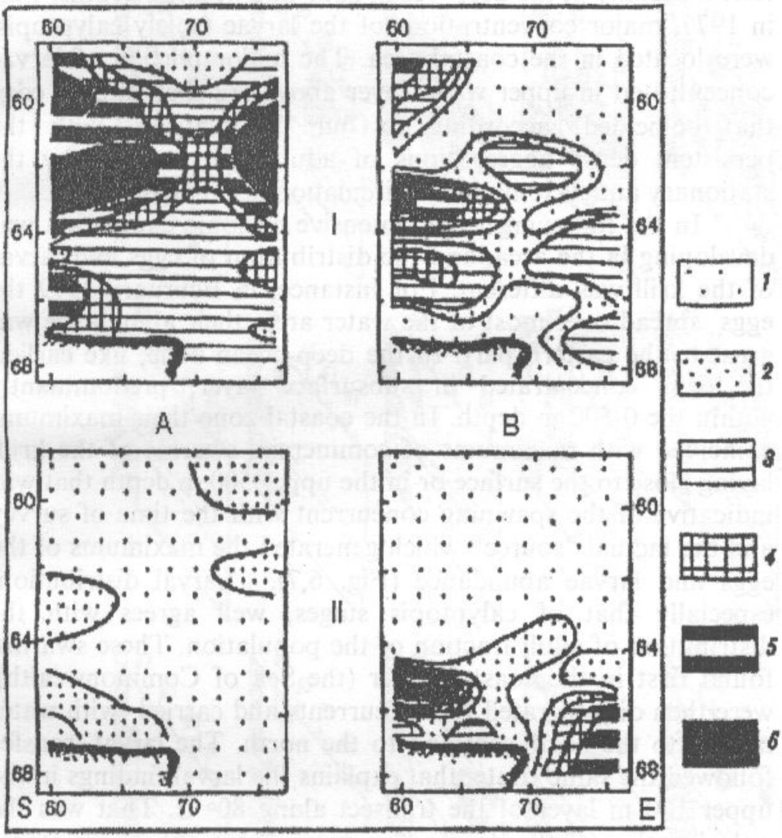

Fig. 5. The distribution of krill eggs (I) and larvae (II) in the upper 0-500 m water layer in January (A) and February (B) 1978.

1 to 6: I) 0; 0-1; 1-10; 10-20; 20-50; >50 eggs· m-², correspondingly; II) 0; 0-10; 10-50; 50-100; 100-500; >500 ind· m-², correspondingly.

large commercial swarms of the krill (Fig. 5,1). However, as Figs. 4; 5,II evidence, in January and February krill larvae were few, especially in the deep-ocean zone and at large depths. Like in 1977, major concentrations of the larvae (solely calyptopis) were located in the coastal area. The major portion of larvae concentrated in upper water layer above the shelf and its edge that coincided, according to our observations, with the persistent dense aggregations of adult krill retained by the stationary anticyclonic water circulation also like in 1977.

In the following years, intensive cyclonic circulation was developing in the area, and the distribution of eggs and larvae of the krill was different. For instance, in February 1979 the eggs spread over most of the water area, their abundance was great in the eastern part. In the deep-ocean zone, like earlier, the eggs concentrated in subsurface layer, predominantly within the 0-500 m depth. In the coastal zone their maximums coincided with maximums of commercial swarms of the krill, laying close to the surface or in the upper 500 m depth that was indicative of the spawning concurrent with the time of survey and the factual "source" which generated the maximums of the eggs and larvae abundance (Fig. 6,7). Larval distribution, especially that of calyptopis stages, well agrees with the distribution of adult fraction of the population. These swarms, found first in the coastal water (the Sea of Commonwealth), were then disintegrated by the currents and carried with water masses to the north-east and to the north. The larval transfer followed the same route, that explains the larval findings in the upper 100 m layer of the transect along 80° E. That was the only location of the deep-ocean zone where calyptopis stages was found; the minor amounts of furcilians (mostly stages I until III) at several sites were owing to their transfer from the coastal zone.

In other years krill eggs and larvae distributed over the area relatively evenly, without distinct maximums. For example, in January 1980 the eggs, though not abundantly, were found in the oceanic and coastal waters of the area under our investigation (Fig. 8). Rare patches of relatively high egg concentration overlapped those with high abundance of adult krill (64° S, 65° E). The larval krill

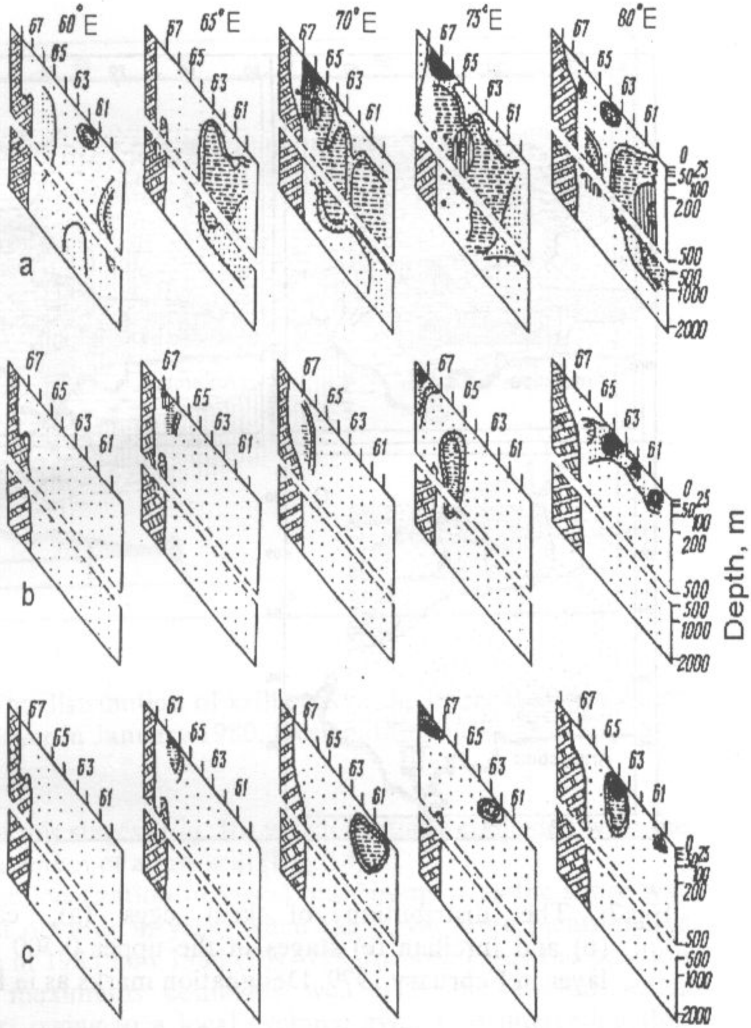

Fig. 6. Krill eggs (a), calyptopis (b) and furcilian (c) distribution in the meridional sections in February 1979. Designation as in Fig. 2.

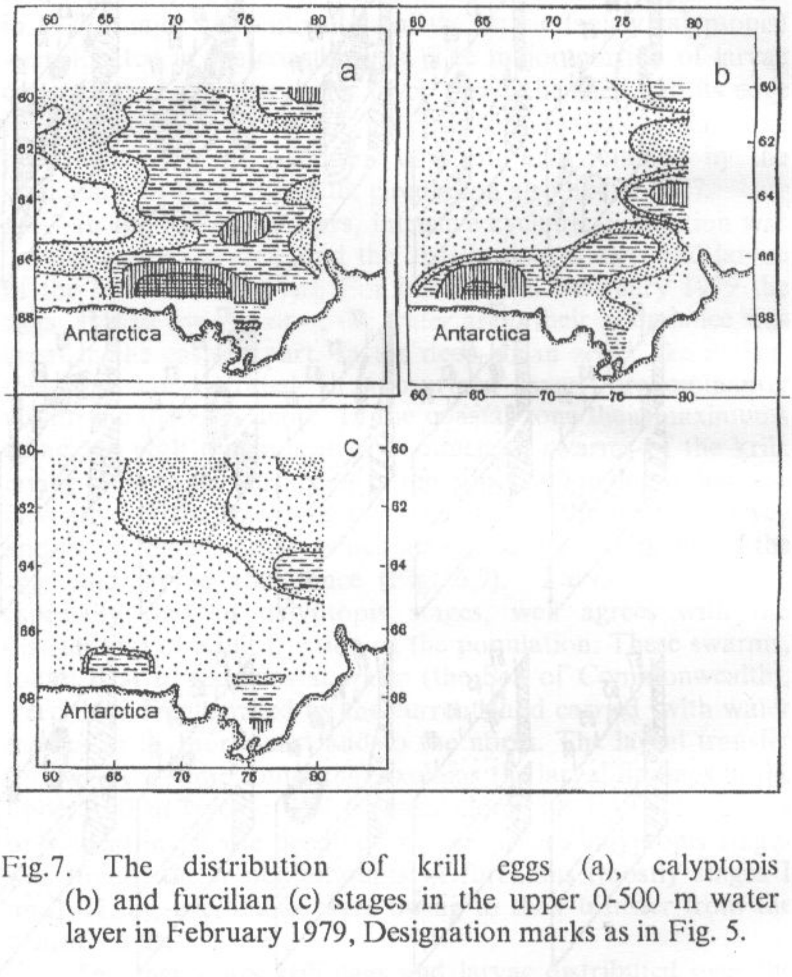

Fig.7. The distribution of krill eggs (a), calyptopis (b) and furcilian (c) stages in the upper 0-500 m water layer in February 1979, Designation marks as in Fig. 5.

(mostly calyptopis stages, with negligible inclusions of furcilian I to III stages) was scattered over the area with preference given to the upper 500-m layer (Fig. 9). Making a mesoscale survey in a near-shore commercial krill superswarm (Fig. 13) in February we had detected a larval aggregation predominantly

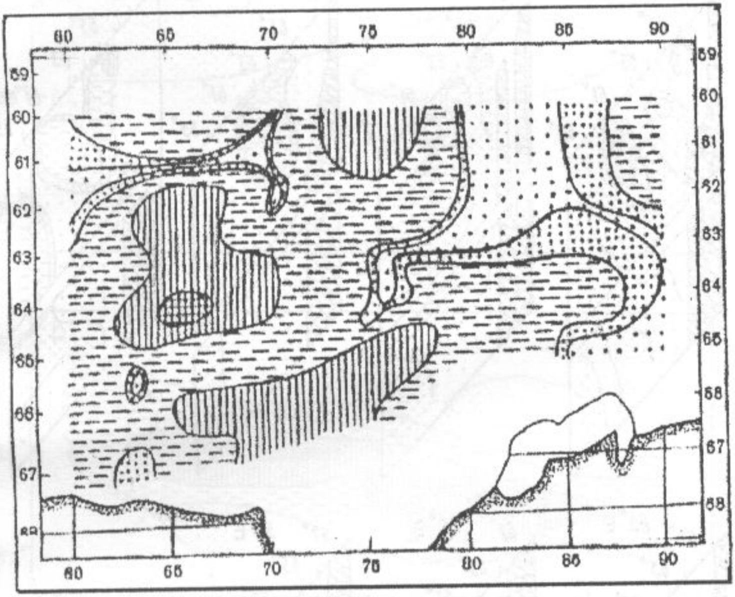

Fig. 8. The distribution of krill eggs in the upper 0-500 m water layer in January 1980. Designation marks as in Fig. 5.

of calyptopis stages (Fig. 10) which spatially coincided with the local maximum of adult krill (Fig. 14).

The localization of larval maximums near the shore was the most obvious in years when the larvae were plentiful, for instance in 1985 and 1986 (Fig. 11). In both cases the position of the maximums conforms well with the coastal water transport owing to a local cyclonic gyre. It is interesting that outside the area with the maximums not a single larva was found over the vast ocean zone.

These imply that the krill spawns at any part of the area, relatively high concentrations of its eggs may be found both in the oceanic and in the coastal zone. However, hatched larvae

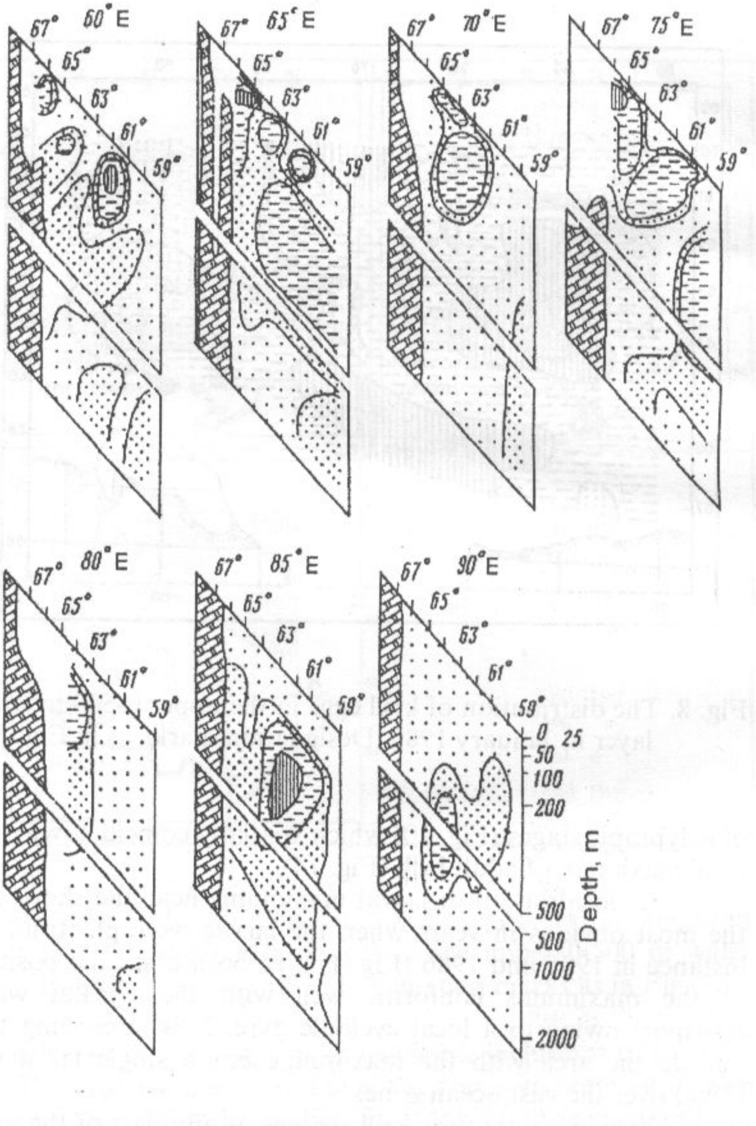

Fig. 9. The distribution of krill larvae (predominantly calyptopis) in the meridional sections in January 1980. Designation marks as in Fig. 2.

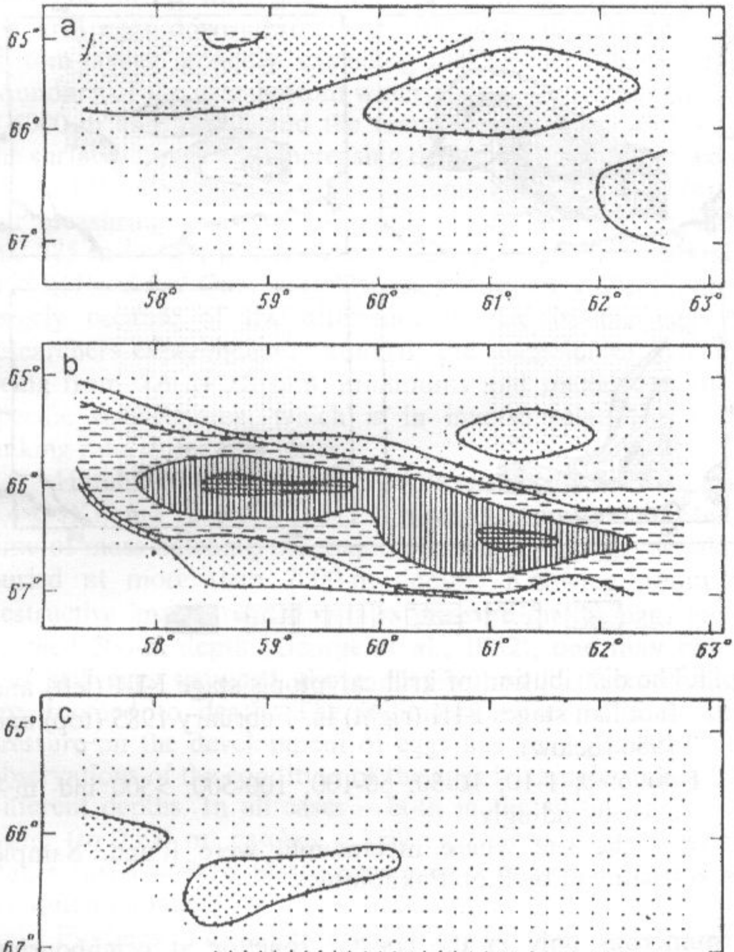

Fig. 10 The distribution of krill eggs (A), calyptopis (B) and furcilians (C) in the 0-500 m layer under a mesoscale survey conducted in the area of krill superswarm concentration in February 1980.
Designation as in Fig. 5.

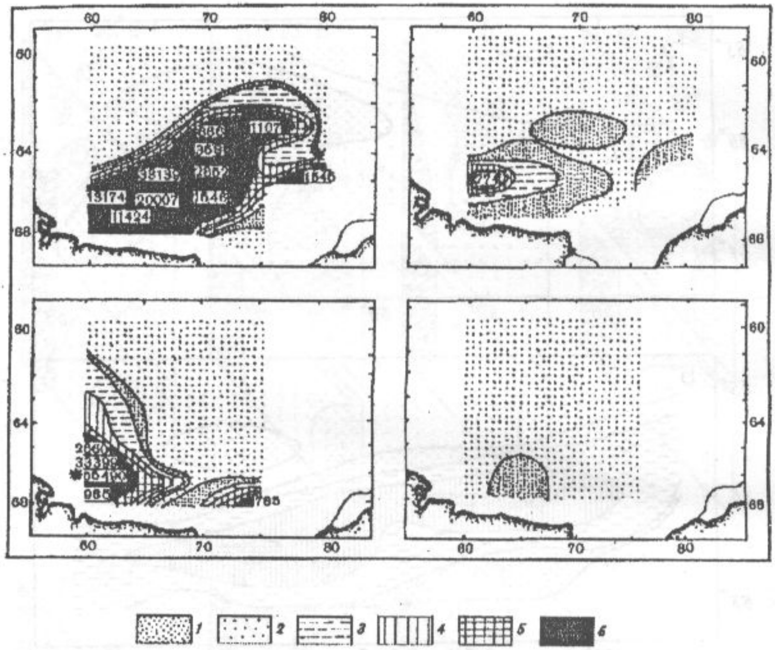

Fig.11.The distribution of krill calyptopis stage I-III (left) and furcilian stages I-III (right) in February 1985 (top) and 1986 (below).

1 to 6: 0; 1-10; 10-50; 50-100; 100-500; >500 ind· m^{-2}, correspondingly.

* - the site where metanauplii were found. Sample treatment by E.N. Pakhomov.

are numerous only in the coastal zone or at neighbouring locations. The appearance of the larvae in small or large quantities in the open ocean is related to their transport from shallow water. That the eggs and larvae vanish from the open ocean, as it was in 1978, may probably be explained by that all eggs spawned by the krill had sunk irretrievably.

Factors contributing to the phenomenon are, firstly, that vertical gradients at the borders of water masses (with the exception of seasonal pycnocline zone) are so negligible in the

Antarctic surface water that they can hardly obstruct sinking of the krill eggs down through transitional, abyssal and near-bottom layers; secondly, excluding the Weddel Sea, the upper boundary of the near-bottom water goes much deeper (to 3000 – 4000 m and more), and the temperature and salinity below the surface change with increasing depth in all Antarctic sectors of the krill distribution area (Demenitskaya et al., 1974). As our measurings show, the sinking rate of krill eggs at 0°C is 260-275 $m \cdot d^{-1}$ that is somewhat higher than given by Marshall (1983), Ross and Quetin (1982). The discrepancy of estimates is largely because of the difference in size of the eggs the researchers experimentally studied: the diameter of krill eggs being from 0.6 to 0.8 mm, minimums and maximums of the specific surface area, which is in inverse relationship with sinking rate, differ 1.33 times.

Hatching of nauplii begins 7 days after the incubation at 0.4°C (Kikuno Tsukasa, 1981). It is easy to compute that by the time of mass hatching the major portion of the eggs would be buried at more than 2000-m depths. Knowing about the destructive impact of hydrostatic pressure on the eggs having reached 500-m depth (George et al., 1982), one may be sure that krill eggs spawned above deep-waters far from shallows are doomed to death. The inhibitory effect of hydrostatic pressure on the development of eggs has been proved by our observations of the condition of the eggs in samples taken from different depths. In all cases – both in the surface and deep-water (to 2000 m) catches – krill eggs were at early division stages (usually 8-16 blastomere stage). Division process was without anomalies.

Findings of different larval stages far from their hatching grounds may be explained by long larval metamorphosis and by the transfer with currents. It has been reported (Ross, Quetin, 1982) that the duration of larval stages development is large in krill; the quoted estimates are within the following temporal range: the period from the spawning to hatching of nauplius I takes 5-6 days, nauplius II forms in 8-10 days, metanauplius in 15-18 days, calyptopis I in 21-25 days and calyptopis II in 32-37 days. According to L.A. Ponomaryova (1966), the metamorphosis from calyptopis I to furcilian VI is

90-120 d long. Having information about the direction and the velocity of water transfer, it is an easy task to figure out the distance from the hatching spot at which the larva at a particular stage of metamorphosis should be found. For instance, for the Sea of Commonwealth, assuming that actual velocity of meridional water transfer is 20 $cm \cdot s^{-1}$ and the prevailing wind 15 $m \cdot s^{-1}$, the larval drift per day would be 22 km, i.e. by the stage of calyptopis I, the larva would cover 270-330-km distance. It is staggering how huge distances the larvae at later stages or completing the development may be transported at, especially when cyclones and currents accelerate the transfer several times.

Estimates averaged for the concentration of krill eggs and larvae in different parts of the region lying at a distance from the neritic zone (Table 1) highlight the general trend of distribution: the abundance of the eggs almost does not depend on the fishing zone location. Maximums of the larval abundance were measured in the Sea of Commonwealth (the northern boundary of the sea going along 66° S) and adjacent waters verging in the north on the Antarctic divergence (AD); north of it the concentration of larvae drops drastically, often to absolute extinction.

It is also noteworthy that despite the repeated detailed examinations of the regional 2000-m water column we can not boast about a single finding of an early krill larva (nauplius, metanauplius) far off the neritic zone, that would point to the fact of efficient spawning of krill in those waters; however in the vicinity of or directly in the neritic zone the larvae, though seldom, were found. For example, in 1983, the nauplii were found in the Sea of Commonwealth (67° 34' S, 75° E) throughout the water column as 64 $ind \cdot m^{-2}$. In 1986, in the Sea of Commonwealth (66° S, 60° E) about 80 km off the neritic zone metanauplii were found, their concentration in the 0-500-m layer was estimated as 4320 $ind \cdot m^{-2}$. These findings as far from the neritic zone as that agree with the direction of water transfer under the development of cyclonic activity which took place in 1986; they also do not contradict the duration of larval

Table 1

The concentration (spec · m^{-2}) of krill eggs and larvae in 0 – 500-m layer in the Sea of Commonwealth and the adjoining water areas (1978-1986)

Year	Sea of Commonwealth			Between 66° S and Antarctic Divergence (AD)			Between AD and 60° S		
	Eggs	Calyptopis	Furcilian	Eggs	Calyptopis	Furcilian	Eggs	Calyptopis	Furcilian
1978	1.2	1.7	0	3.5	0.3	0.3	13.0	0	0.9
1979	11.5	7.4	6.5	4.0	12.6	3.6	3.8	1.1	0.4
1980	4.0	0	0	3.2	1.9	0	4.7	0	0
1981	0.5	4.1	34.0	0.1	16.2	0.3	0.1	0	0
1983	2.9	0.5	0	1.7	0.8	0	4.4	0	0
1984	0.4	4.8	1.0	1.2	0.1	0	0.5	0.1	0
1985	No data available	5195.3	88.7	No data available	4215.1	2.4	No data available	71.6	0
1986	-	6416.0	0.5	-	3711.0	0	-	182.6	0

metamorphosis and the velocity of local water transport.

These facts imply that the spawning of *E. superba* may be efficient only in the shallow coastal zone, where the scenario of "small circle" development with the incubation of eggs and the hatching of nauplii at the sea bottom (according to Marr) is implemented. This concept has been corroborated by an asymmetric distribution pattern disclosed by N.M. Voronina for the larvae and adults in the krill distribution area. This pattern implies concentration of the overwhelming part of the population in the western Atlantic sector of Antarctic where the orographic and hydrological conditions are the most favourable.

Statements about efficient spawning of the krill in oceanic zone (Aseyev et al., 1988) have not been provided with convincing proofs.

The knowledge we have obtained employing data on the regional water structure and the distribution of adult portion of the krill population shed more light on the extant notion about the functional structure of the krill area. The fact that the krill breeding grounds are located in shallow water is in strict conformity with the concept formulated by N.M. Voronina (1984) about location of the distribution core at the Antarctic Coastal Current circulation and in the Weddel Sea. However, taking into account the presence of more or less pronounced circulations in all Subantarctic seas and adjoining water areas south of the Antarctic Divergence (AD) which impede mass evacuation of the krill, the notion about the main distribution area may be widened. In our understanding, the basic area is where accumulative process prevails over dispersion as the result of intensive turbulence at the field of currents and the presence of quasi-stationary eddies. This is determined by topogenic and orographic effect along with the complication of the field of currents south of AD due to the currents of different direction, the factor that sustains existence of AD itself.

Most of the krill carried out of the limits of AD and transported with currents to the north are the expatriated part of population. Some of the expatriants may enter the core of krill distribution area and even the breeding ground owing to "return" streams of the currents: krill swarms drifting toward the continent were repeatedly observed from the R/Vs of AzCherNIRO.

Analysis of the larval and adult krill records made in different years has unveiled, firstly, a shockingly low spawning efficiency during 1974-1984 in comparison with 1985-1986 (the recent larval abundance in the region is two orders of magnitude greater than maximums registered in the preceding years), and, secondly, the absence of distinct relationship between the numbers of krill larvae and the overall stock of adult krill in the region. This leads to a conclusion that the efficiency of krill reproduction there depends on the amount of spawners, which succeeded in reaching the neritic zone during the spawning season, and on the rate of the spawners and eggs transport from the neritic zone rather than on the total abundance of spawning krill. Drastic fluctuations in the abundance of larvae may be due to too narrow neritic zone making the spawning efficiency problematic; above the narrow shelf the transfer of krill and its eggs would finish above abyssal zone within as short span of time as that for which the eggs would reach the bottom of neritic zone. There are some reasons allowing to suggest that the efficiency of krill reproduction depends also on the intensity of generation of the unfrozen water patches in the coastal sea-ice cover in early spring. Similar formations appear to be typical of many antarctic seas. This point, on the one hand, requires special investigation, and, on the other hand, studying this problem is compatible with the concept about the scenario of the krill life cycle I have portrayed before.

1.2. The distribution patterns of adult portion of the population and krill abundance estimates

Expedition records of *the Discovery* set the northern limit to the krill distribution area as going along the zone of Antarctic convergence (Mackintosh, 1934; Marr, 1962). From the catches with plankton net it is evident that spatial distribution of the krill is uneven (Marr, 1962); swarms generating is characteristic of this species. The swarms are formed during the larval development and remain relatively steady for long time. Drifting with currents, the euphausiids may crowd together at areas where the currents slow down, especially around the local eddies (Ruud, 1932; Marr, 1962). Mean density of krill aggregations computed from net sampling in the Weddel Sea is as high as over 29 $g \cdot m^{-3}$ (Marr, 1962).

Causes responsible for krill swarm formation in surface water have been considered in remarkably large number of articles; the growing popularity of the krill as a food item spurred the investigation. Following by Ruud (1932), most of the researchers emphasize the significance of dynamic factor. Some of them associate generation of the aggregations with frontal zones with higher gradient of oceanographic characteristics (Yarogov, 1969; Solyankin, 1969, 1972; Stein, Rakusa-Susczewski, 1984), others with the generation of quasi-stationary zones of high water turbidity (Bogdanov, Solyankin, 1970; Khvatsky, 1972; Witek et al., 1981; Kozlov et al., 1983; Poluyaktov et al., 1983; Solyankin et al., 1983) or with cyclonic-induced turbidity of surface water (Maslennikov, 1972; Latogursky et al., 1975; Makarov et al., 1980), or with anticyclone-induced turbidity (Yelizarov, 1971). S.S. Parfenovich (1982) has overviewed longterm data on krill swarm distribution in the field of hydrological characteristics and proposed a classification based on six regional-genetic types. Attempts were also made in order to elicit relation between krill aggregation formation and other factors; the result was a number of odd deductions.

Looking into factors of biological origin which determine the accumulation of krill, R.R. Makarov et al. (1980) underline quantitative unevenness of krill transport on temporal scale and phases of the reproductive cycle; in their interpretation the intrinsic stimulus which drives the formation of sex-mature euphausiid aggregations is sex and spawning instinct. However, as the authors do not have arguments which would explain juvenile krill aggregations, they admit that other factors may obstruct dispersal of those aggregations.

In the western Indian sector of Antarctica locations of high krill concentrations were characterized by low concentrations of phytoplankton (El-Sayed, Hampton, 1980). Other reports (Makarov et al., 1980; Kozlov et al., 1983) claim that with the intensive growth of planktonic algae (phytoplankton bloom) the euphausiids have higher mortality and scatter over the surface. Formation or disintegration of euphausiid swarms during the feeding period depends on the peculiar structure of their feeding apparatus (Neiman, 1980).

No correlation was found between krill superswarms in the zones of water mass interaction near the bottom elevations on the shelf of the Antarctic Peninsula and the distribution of temperature, salinity, DOC and phytoplankton (Witek et al., 1981). Neverthless, the events of high krill concentration in the Indian sector of Antarctic (61-68° S, 30-120° E) coincided with low (from 0° to 1.5°C) values of depth-averaged temperature for 0-200-m layer (Naganobu Mikio, Nirano Tosiyuki, 1982).

Round the Balleny Islands at the season of pack sea-ice a relation between krill concentrations and daily light intensity in the surface was noted (Takahashi Tadashi, 1979).

Vertical distribution of krill also displays a wide variety of patterns. From observations in the Scotia Sea (Latogursky et al., 1972), the majority (93.2%) of euphausiid aggregations spread above the lower boundary of thermocline in summer. Studies in the Indian sector brought in similar conclusion (Aseyev, Khimitsa, 1976).

Visual observations of krill swarms ("patches") visible in the surface have shown that their formation follows the daily rhythm (Ozawa, 1968, cited from Pavlov, 1972; Shust, 1969): they emerge in the morning and the evening. In mid-day and in midnight the euphausiids scatter over the surface. According to V.Y. Pavlov (1972) vertical migrations and swarm formation are linked with daily feeding rhythm: krill aggregations disperse during the period of active feeding; having finished with feeding, the euphausiids again gather in swarms and descend to subsurface water; under food deficiency the krill stay within the foragé ground for most of the day or do not leave it at all.

Further studies of krill vertical distribution were carried out assuming the daily variability as a starting point. Day-light conditions were taken as a formal cause determining a particular distribution pattern. Such a simplified approach to the complicated phenomenon could not but produce a lot of contradictions. Some authors reported that at different areas the euphausiids made daily vertical migrations, gathering at night in surface (0-200 m) layer and sinking in day time into depths varying from 50-200 m (Nast, 1979) to 20-40 m (Kubota Katsuhiko, 1981). A hydroacoustic survey in the western Scotia Sea registered at night hours 3-4 times as less frequency of krill aggregation findings as at day hours (Klindt, Zwack, 1983). Other papers (Witek et al., 1981; Roe, 1983) denied any clear relation between vertical distribution of the krill and day light. Along with this, special purposeful investigations of the variability of vertical distribution and swarm density, which involved employment of a calibrates echosounder and an echosounding indicator, have demonstrated considerable difference in the character of daily vertical migrations of the euphausiids (Everson, 1983; Kluzek, Godlewska, 1983). Accompanying changes in the configuration and density of the swarms were explained by different feeding rates of the krill (Godlewska, Kluzek, 1988).

Information about krill population size and concentration is as contradictory as that about the distribution mechanism and causes. Indirect computations based on the baleen whale ration and numbers estimated overall krill biomass as 1350 million t (Pequegnat, 1958). Later, many authors endeavoured similar or different indirect computations which brought estimates from 800 million t (McQuillan, 1962) to 6 billion t (Nemoto, 1968). With the trawl fishing development direct counting of krill became a reality. Data from trawling surveys evaluated total krill biomass for the Atlantic sector as 90-100 million t (Bogdanov, Lyubimova, 1978). Corresponding aggregation density estimates (2..5 g$\cdot$ m^{-3} at the highly productive localities and 0.5 g$\cdot$ m^{-3} at the fishing areas) were lower than those obtained from net sampling that evidenced imperfection and low fishing efficiency of the trawls and, therefore, potential underestimation of the total krill biomass in the area. Shortcomings inherent to a 31-m having been designed at PINRO and used for fishing krill in the Scotia Sea were discussed in M.Y. Groisman et al. (1969) and V.M. Tupolev (1969).

The hydroacoustic survey data we obtained during 1972-1973 estimated the total krill biomass in the Indian sector of Antarctic as more than 300 million t (Bogdanov, Lyubimova, 1978). Like for the Atlantic sector, the "bottleneck" in these computations were data about the population density.

The patchy distribution, the variable extent of krill aggregations and euphausiid concentration in the swarms are the factors which obstruct evaluation of krill abundance even today when more effective hydroacoustic devices equipped with echointegrators and considerably improved fishing and sampling tools are available. These explain why many results of the quantitative record at particular parts of the distribution areas are illustrations of a particular distribution but not the basis for a conclusion about overall krill stock in an area. Several examples may illustrate the incoherence of the resulting estimates. In the southern Weddell Sea (near Ice Harbour Atka) during January-February 1980-1981 the krill distributed evenly (without forming aggregations) over 4525 square miles (Siegel, 1982) and its total biomass was evaluated as 2.91 thousand t, or per area unit, 0.8 $g{\cdot}m^{-2}$. In the western Atlantic sector of Antarctic, in sea water around the isles and near the continent krill biomass in the superswarms may average 2-10 $kg{\cdot}m^{-3}$ with peak estimates approximating 30 $kg{\cdot}m^{-3}$ (Rakusa-Susczcewski, 1980; Shulenberger, 1983). A hydroacoustic survey (March 1981) at the eastern Bransfield Strait estimated krill biomass over the area of 1735 square miles 258 thousand t, with the average density 41.4 $g{\cdot}m^{-2}$ (Kalinowski, 1984).

Large-scale quantitative assessment surveys usually yield more comparable estimates. For instance, recording with the employment of SIMRAD hydroacoustic device resulted in the estimate of the krill stock in West Antarctic of 210 million t and that for the entire distribution area as large as 440 million t (Kalinowski, Witek, 1981). Acoustic surveys which were made during January-March 1981 within the framework of FIBEX (the first stage of the implementation of the BIOMASS programme) from 11 ships sent by 11 countries to the Pacific, Indian and West Atlantic sectors of Antarctic (Hampton, 1983), eventuated in having assessed the overall stock of krill for the 1.3 million square miles large water area under the investigation as 78 million t, with the average biomass of 17.5 g·m^{-2}. Most of the stock concentrated between 60 and 80° E; the total weight of krill in the distribution area during the studies was estimated 200-600 million t.

With the advancement of knowledge about the main components constituting Antarctic ecosystem, which are krill consumers, some researchers have tentatively determined their overall ration on more substantiated ground taking into consideration changes occurring in the ecosystem. The consumption of krill by whales and seals explored in detail by Laws (1977) was 43 and 64 million t annually. Before the whales had become an object of extermination to whaling industry, they ate away about 190 million t of krill a year; that is, the remainder of krill production was 147 million t a year, correspondingly. Antarctic birds ate 14.7 – 20.3 million t annually (Everson, 1977), fish and squids 28 and 50-54 million t, correspondingly. Total krill consumption by all the consumers (excluding baleen whales) calculated with reference to the literature about the rations of birds and seals is 166 million t (Lyubimova, Shust, 1980). The review by Odening and Bannasch (1981) estimates annual krill consumption by baleen whales as ranging from 174 to 190 million t in the past and from 33 to 43 million t after the whaling has reduced the whale population, by birds as 38.66 million t (of this 33.14 million t is the withdrawal by penguins), and by seals as 64 million t (that agrees with Laws). The authors deduce that the "unclaimed" krill – the result of overwhaling – may be estimated 131-157 million t a year, therefore, in accord with the current knowledge, fishing out 100 million t of the krill annually would not disturb the ecosystem of Antarctic.

N.M. Voronina (1981) made essential amendments to the extant knowledge about krill production. Her indirect computations, unlike those of other scientists, were based on the production generated by organisms of the same trophic level. According to these computations, krill production varies from 2.4 to 47 g·m^{-2} a year, and the average biomass from 13 to 25 g·m^{-2}.

Comparison of annual krill production per the distribution area evaluated from the data by Voronina with tentative estimates of the amount of krill eaten out by the main consumers as 200 million t a year leads to a conclusion about the underexploitation of krill production (Lubimova, 1983).

At the same time, a mathematical model of food web in Antarctic ecosystem (Nagata Takeshi, 1983) under given critical conditions – the krill population would not decrease - and the most probable values of krill biomass (1 billion t) and the grazing out by predators (110 million $t \cdot yr^{-1}$) sets the upper limit for commercial krill fishing equal 110 million t a year.

Later, the estimates of krill consumption by the major consumers have been revised (Laws, 1985): the escalating abundance of the consumers, especially birds and seals, has led to a rise of total krill uptake to 470 million t.

The scientific evidence available by today about the distribution and the stock of adult krill gives only general outline of the problem and, though being of indisputable value to the expertise, it does not suffice for more or less precise prognostication. The contradictory character of opinions about environmental (external) causes responsible for krill superswarm* generation and disintegration, concentration and stock at a particular area is, as we understand it, due to irregular, or rather occasional, observations and the narrow spatial scale they cover. The natural result is that the local events, e.g. changes of the position and abundance of superswarms on the spatial micro- and mesoscale, do not allow to reveal more or less general trends and patterns of the processes and their development. Recognizing the array of special features inherent to the krill – the huge distribution area and the corresponding extent of population, the diversity and changeability of ambient conditions and distribution patterns – and assuming that considerable fluctuations of the stock abundance and distribution depend primarily on mesoscale oceanological processes, it is a matter of time to have the

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* Here and further by superswarms we mean krill aggregations the extent of which is by far greater than a swarm; the latter is the result of particular behaviour of the euphausiids.

relevant regularities and trends elicited for the prognosis which would be based on the regular large-scale studies with oceanological, hydroacoustic and trawling surveys exerting control over the spatial and temporal aspects of the variability.

The target of our investigations was to find some logic in changes of the chorologic structure, extent and density of senior fraction of the population as determined by some probable factors unveiled by direct observations.

Material and methods

In doing this work we referred to the echosounder records and data on krill catches obtained from the regular surveys in the region during 1973 and 1977-1987 and from a fishing scouting expedition to the Cosmonaut Sea in 1983.

The continuous hydroacoustic search with echosounding recording was conducted during macroscale meridional oceanological surveys from the ice edge to 58-60° S with the step of 5° and during mesoscale surveys at the sea areas where krill superswarms concentrated. The continuous echo-sounding recording was also a component of the krill scouting (usually in the Sea of Commonwealth) and fishing activities. The surveys included regular check trawlings by Isaacs-Kidd trawl modified according to Samyshev and Aseyev* and by krill fishing trawls and were usually conducted in response to echosounding signals.

In the studies the sonic depth finders AG-331, OMAR and SARGAN (high frequency spectrum) were employed in the frequency range from 30 to 150 kHz.

The echolocation was conducted in 0-200 or 0-300 m water column because most of the krill superswarms concentrated within upper 50-70-m water layer. The density of krill aggregations was estimated from trawl catches with a necessary adjustment to the corresponding data of echosounding.

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* The net of the modified Isaak-Kidd trawl is a fine-mesh (3:5 mm) sieve; correspondingly, the trawl gets proportionally longer (29 m) and has a 5-m long replaceable sack from the kapron sieve N 7.

In evaluation of total krill biomass, initial parameters were the volume and density of superswarm; in determining the dimensions and volume, the type and extent of the aggregation were taken into account. Based on the echo-sounding records, 3 types of the superswarms were differentiated (Fig. 12):

- ♣ solitary swarms, 1.5 – 15 m thick, 10-30 m large; they have the highest density and are found at substantial distance one from another;
- ♣ extensive dense aggregations which, probably, are the result of merging of a large number of swarms (the echo-sounding indicates them with a densely toothed line); they are from several dozen metres to several kilometers large, and from several metres to 20-50 m and more thick;
- ♣ dispersed (rarefied) aggregations clearly registered by a sonic depth finder; these are up to several kilometers large and common in subsurface (0-20 m) layer.

Dimensional measurements were made in conformity with the earlier instructions for determining fish shoal parameters from echosounding records (Averkiyev, 1972).

The volume of small aggregations (swarms) which dimensionally "fit" the sonic beam scope was calculated by means of the equation for ellipsoid rotation volume (Aseyev, 1976). However, this is not valid for large aggregations (superswarms) because of complicated configuration of the latter. Therefore, superswarm volumes were computed only as a fragment of the aggregation got into the sonic beam field of vision, from the accurately measured length and height (thickness) and the diagram of echo-sounder antenna direction reflecting the width of the explored zone (and aggregation). The resulting measurements coupled with trawl catch data underlay calculations of the parameters and of the intervals between the aggregations, the biomass and total stock of the krill. Computer processing of the data was provided by G.S. Noshchenko, senior computer programmer from AzCherNIRO. In the analysis of krill distribution we used the maps of geostrophic currents drawn from the observations

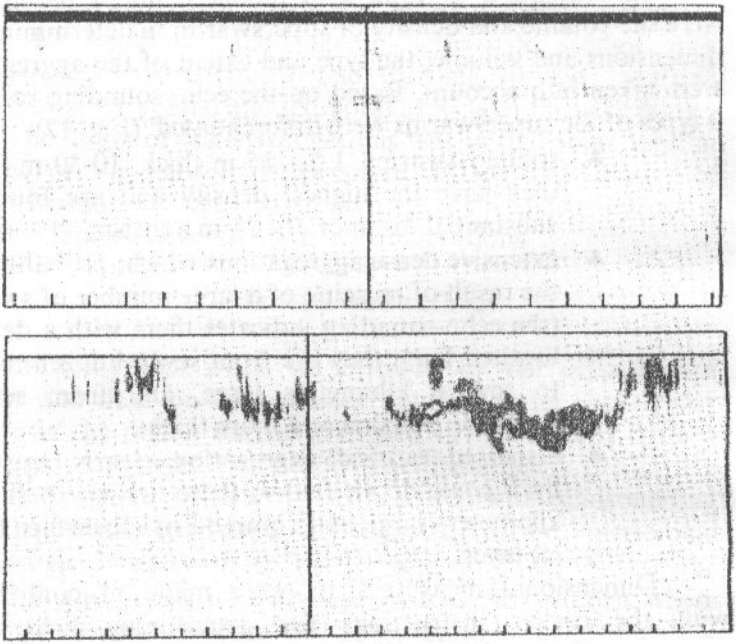

Fig.12. Some echosounding records of the krill obtained with sonic depth finder NA-331. The depth range 0-200 m; time interval 5 min; ship's speed about 9 knots.
Top: krill swarms and scattered aggregations.
Below: krill swarms and extensive dense aggregations.

having been conducted by V.A. Lednichenko, N.A. Ryabchikova and A.S. Pelevin.

Results and discussion

Dwelling in the sea surface, adult fraction of the krill population is transported over the investigated area by a complicated trajectory. The main drift is, apparently, clockwise (Maslennikov, 1980). The process of transport is complicated by local gyres of different directions which exist in the region.

Yet an established fact is the gradual transfer of euphausiids with northward water flows manifested as regular alteration of the type and size-age structure of the swarms.

Krill aggregations represented by swarms of all the three types were found in different localitions of the region. It was noted, however, that the share of euphausiids which compose solitary swarms and dispersed aggregations (III type) is increasing from south to north. In deep-ocean zone far from the coast these varieties of aggregations prevail. At commercial fishing areas, as observations show, the swarms are continuously changing; they might have disintegrated on the regional spatial scale in a few hours, irrespective of time of a day, under the influence of drastic changes of the baric field and storm wind. Apparently, the hypothesis advanced by Marr about swarm generation owing to larval krill, and the phenomenon of their sustained existence in time are strongly disputable; probably these may take place only in locations with very stable hydrological conditions. Swarm generation is certainly the result of high activity of the euphausiids (Marr, 1962); relatively homogeneous size composition of krill catches either with plankton net ("point" sampling) or from trawling individual swarms provides the evidence. V.V. Shevtsov and R.R.Makarov (1969) arrived to identical conclusion about the homogeneous composition of small krill aggregations after they had done pertinent studies in the Scotia Sea. Different aspects of the activity of euphausiids in swarms have been the object of Soviet and American underwater researches (Nesis, 1985). As submarine observations show, a typical activity is search for food that is a stimulus for euphausiids to make extended vertical and horizontal migrations. That krill swarms are formed of single-size individuals is related to difference in the swimming speed of different size classes: larger euphausiids with higher swimming velocity separate from smaller (and hence less motile) through natural mechanics.

As we have found, not all of the euphausiids make upward migrations to the surface at night hours; a conspicuous number of intact swarms are positioned in subsurface water layer. Yet, there is much in the behaviour of krill that remains still obscure. For instance, we did not find explanation to changes in the vertical distribution of euphausiids in Prudz Bay in late March-early April 1978. In the beginning of that period thermocline was going down until eventually it vanished. With the increase of thermocline depth krill swarms also descended deeper (to 150-180 m) than usually independent on time of day; as soon as the thermocline disappeared, cases were registered when the krill gathered in swarms at the surface at night.

From the state of hepatopancreas and the index of fullness, it is evident that feeding intensity was the highest when the euphausiids got into dense algal mats moving south with the retreat of sea-ice. The "green" krill, i.e. euphausiids with enlarged hepatopancreas of green colour because of the intensive feeding on phytolankton, is widely found over the regional coastal zone until late January-early February. Further, in accord with the receding phytoplankton bloom events which by that time are confined to occasional spots usually close to the ice-edge, the fullness of gastrointestinal tract decreases, and "red" krill again becomes dominant in the population.

A series of more than a hundred fatness determinations which we made in a krill aggregation at Prudz Bay (1300 km^2) in 1978 has pointed out that feeding rate of the euphausiids differed between different locations. Fat content of krill of one size group, sex and biological condition strikingly differs, with a minimum of 2.5 and a maximum of 57.0% (dry weight). We suppose that it is the difference in individual biological activity that is responsible for the fact. Small swarms distribute unevenly within the aggregations; similar lack of the consistency is found in the water structure and phytoplankton distribution.

Comparison of our data with those available from literature gives a key to inadequate behaviour of euphausiids under the same environmental conditions, and to qualitative distinctions – primarily fatness and fullness – between individuals over the observation period. If the fatness and fullness are insufficient, krill ventures active feeding migrations which are usually upward to the surface, but may also be downward, like in the case of sinking and degrading thermocline with the accompanying descent of phytoplankton described above. Having found the forage, the euphausiids scatter and feed to satiety; otherwise, the swarm keeps stick together in the subsurface layer. The patchiness of food distribution explains the asynchronous feeding activity by the krill at different parts of a swarm or an aggregation and its behaviour; that is why so many papers contradict one another about the relation between behaviour and environmental factors including nutrition.

Size range of adult fraction in the krill population as trawl catches in the region show is from 16 to 66 mm. Like the entire distribution area, the regional distribution follows a characteristic pattern at which the share of adults increases northward. There are also events of random distribution with the dominance of juvenile krill at the northern periphery and the prevalence of adults at the southern periphery.

Owing to the expedition materials the relation between krill distribution and water dynamics which was marked by many authors has been proved, and the effect of diverse shifts and movements of the surface water on the distribution have been proved.

The relevant cases we met during the studies may be confined to several typical examples. In February – March 1977 (Fig. 13 A) extensive krill aggregations, the target of commercial fishing, concentrated in Prudz Bay; with its distinct anticyclonic circulation in the sea surface persistent on time-scale. Most of the superswarms were the vast dense aggregations (type II). The population density was very high – mean biomass was over 1500 g· m^{-2} and total krill biomass 5 million in the most condensed part of the aggregation (Table 2). Another characteristic feature was very high spatial and temporal stability of the superswarms which sustained throughout the summer. In deep-ocean zone none of the superswarms was found. However, there was no clear relationship between characteristics of the aggregation distribution and the water circulation. Smaller swarms varying in density distributed over the bay relatively evenly, irrespective of the water circulation direction.

A situation resembling that described for the coastal zone emerged again in January 1978. In February – March, however, the anticyclone located at the Prudz Bay area in January yielded to cyclone. As a result, the krill superswarms of commercial interest were quantitatively inferior to those found in 1977; the biomass average was 260 $g \cdot m^{-2}$ in January and 380 $g \cdot m^{-2}$ in February – March.

During this period vast and dense krill aggregations were detected in the ocean far off the shore; however the first of local gales had broken up the superswarms. We repeatedly faced similar situations over the years of observations. Certainly, the longevity of extensive aggregations at this water area is not large and is commensurable with the synoptic period. The unstable hydrological structure in the deep-ocean zone is, probably, the key factor inducing the regular distribution of newly formed krill aggregations and their final dispersion along the distribution border.

During the following years cyclonic circulation prevailed in the coastal zone of the region. Superswarms were seen predominantly at the western part of the Sea of Commonwealth. During 1980 and 1981 less extensive aggregations gathered in the central part of the sea (Fig. 13 B). Being mostly vast and dense swarms (type II) – like in 1977 – these aggregations had remarkable density. In particular, in 1980 weighed mean of the krill biomass, like for the location I was two times and for the location II more than four times as less as that for the coastal aggregation generated during the anticyclonic circulation in 1977.

That the krill aggregations are regularly generated and persist for long in coastal waters of the region is certainly owing to orographic factor (mainly, the indented coastline) which makes the water circulation system especially stable. The distinctions we found in the location and character of the superswarms as related to specific types of the circulation are due to differences in the dynamic structure of the gyres (Bryantsev et al., 1983). Analysis of hydrological data shows that in comparison with cyclonic circulation anticyclonic water circulation more efficiently fosters formation of the tranquility zones inviting of plankters accumulation. Generation of those zones under the influence of cyclonic water circulation depends

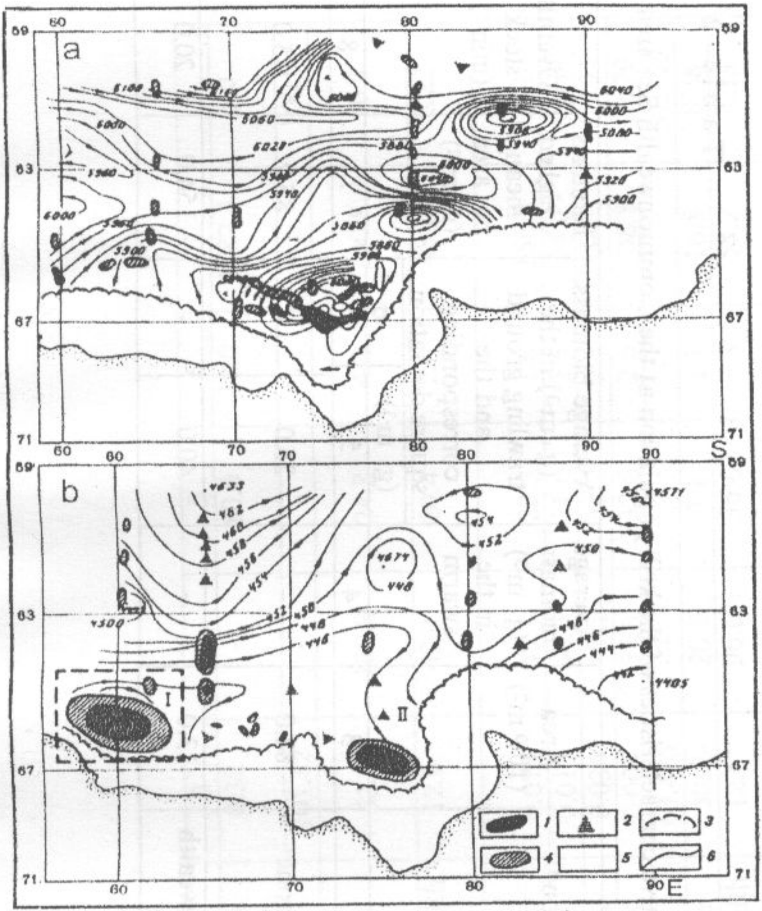

Fig.13. The distribution of krill superswarms and the dynamic map of currents for 1977 (A) and 1980 (B).

1 – dense extensive aggregations;

2 – dispersed aggregations;

3 – swarms;

4 – localities with commercial krill superswarm;

5 – ice-edge position;'

6 – isobars.

Dashed line: the mesoscale survey area.

Table 2

Quantitative characteristics of the krill population at the Commonwealth Sea area

Year, month	Location*)	Area (10^{10} m^2)	Average biomass (g · m^{-3}) in the swarm	Average biomass (g · m^{-3}) in the trawling ground and the corresponding square deviation		Biomass weighed mean per area (g · m^{-2})	Overall stock (mln t)
				(g · m^{-3})	σ		
1	2	3	4	5	6	7	8
1977, February-March	Ocean zone	88.0	-	25.0	-	85.2	75.0
	Commonwealth Sea	13.0	-	40.0	-	154.0	20.0

1	2	3	4	5	6	7	8
	Aggregation 75° E, 67° S	0.32	-	80.0	12.0	1587.3	5.0
	Total:	101.32	-	-	-	-	100.0
1977-1978,	Ocean zone	50.5	100.8	24.8	4.2	100.8	50.8
December-January	Commonwealth Sea	12.8	42.0	20.4	2.0	48.6	6.22
(1-st survey)	Aggregation: 74° E, 67° S	0.073	48.3	22.5	1.6	156.2	0.110
	75° E, 67° S	0.013	40.0	21.6	1.5	34.0	0.004
	74° E, 68° S	0.036	46.2	38.2	2.5	534.2	0.192
	63° E, 67° S	0.004	54.6	37.6	2.6	708.8	0.029
	Total:	63.426	-	-	-	-	57.355
1978,	Ocean zone	50.5	20.2	7.1	1.1	16.8	8.48
February-March	Commonwealth Sea	12.6	96.6	36.8	3.3	58.2	7.33

1	2	3	4	5	6	7	8
(2-nd survey)	Aggregation: 77° E, 67° S	0.06	86.5	27.7	1.7	178.5	0.107
	74° E, 68° S	0.24	47.9	22.5	1.4	437.4	1.05
	Total:	63.4	-	-	-	-	16.967
1979, February	Ocean zone	67.3	33.0	8.8	2.9	27.1	18.23
	Commonwealth Sea	10.5	48.4	12.8	9.0	34.0	3.57
	Aggregation: 72°30’E, 67° 30’ S	0.13	30.8	13.0	7.2	79.5	0.103
	79° E, 66° S	0.13	66.0	19.1	8.5	2200.0	2.86
	Total:	78.06	-	-	-	-	24.763
1980, January	Ocean zone	96.4	12.2	7.7	6.5	10.5	10.12

1	2	3	4	5	6	7	8
	Commonwealth Sea	11.8	12.2	8.7	13.9	16.6	1.96
	Aggregation: 60° E, 66° S	1.1	29.0	7.5	3.3	48.1	0.53
	75° E, 67° 30' S	0.4	15.6	8.0	3.5	57.8	0.23
	Total:	109.7	-	-	-	-	12.84
1981,	Ocean zone	117.7	56.1	5.4	4.3	14.0	16.48
January-March	Commonwealth Sea	10.9	119.0	7.1	-	18.6	2.02
	Aggregation: 65° E, 67° S	0.2	143.0	5.4	4.7	42.5	0.085
	70° E, 67° S	0.11	30.6	6.0	5.2	123.6	0.136
	73° E, 67° S	0.03	90.1	9.0	7.8	28.3	0.009
	Total:	128.94	-	-	-	-	18.73

1	2	3	4	5	6	7	8
1981-1982,	Ocean zone	67.3	68.0	6.2	5.3	12.7	8.56
December-January	Commonwealth Sea	15.7	22.0	10.0	-	21.7	3.41
	Aggregation: 62° E, 66° 30’ S	0.7	27.7	8.2	1.9	34.0	0.238
	67° E, 66° 30’ S	0.4	39.8	8.8	2.0	38.3	0.153
	Total:	84.1	-	-	-	-	12.351
1982-1983	Ocean zone	100	70.0	3.4	-	50.4	50.4
December-January	Commonwealth Sea	12.6	90.0	12.8	-	21.0	2.65
	Aggregation: 70° E, 67° S	0.08	117.8	30.6	-	58.4	0.047
	Total:	112.68	-	-	-	-	53.097
1983-1984,	Ocean zone	66.9	144.0	1.4	-	24.2	12.3
December-February	Commonwealth Sea	11.9	143.0	2.4	-	67.6	8.04

1	2	3	4	5	6	7	8
	Aggregation: 70° E, 67° S	0.5	175.0	10.0	-	153.4	0.77
	Total:	79.3	-	-	-	-	21.11
1985, February	Commonwealth Sea**)	12.3	-	2.7	-	41.1	5.1
1986, February	Commonwealth Sea**)	9.4	-	4.7	-	36.6	3.44
1987, February	Commonwealth Sea**)	10.5	-	4.5	-	18.3	1.92

*) The northern boundary of the Sea of Commonwealth goes along 66° 00' S, north of it (to 60° S) the regional ocean zones lies. In locating the aggregations we used central coordinates. Estimates for the ocean zone and the Sea of Commonwealth are given without taking aggregations into account.

**) No studies were conducted at the ocean zone; no superswarms of interest to fishery were found.

on cyclon development rate. When the rate is high, the krill aggregations disintegrate very rapidly. In zones where straight currents prevail the probability of sustaining the swarms intact is even lesser. Now it is clear why most of the aggregations having been detected over the deep-ocean zone broke up too soon.

Using formal logic for summing up the array of facts would lead to a conclusion that the steady anticyclonic circulation favours the generation of extensive aggregations (superswarms), while the cyclonic circulation obstructs it; the aggregations are breaking up within straight currents under the influence of storms; the probability is the highest in the ocean zone. However, this explanation discards such factor as krill itself which is capable of making active migrations and hence generating swarms and superswarms.

In 1980 a series of macroscale surveys, mesoscale hydroacoustic and trawling surveys in krill aggregations of commercial interest and a complex mesoscale survey at the locality I were conducted. Resulting data about the distribution of krill and phytoplankton had highlighted distinct relation between phytoplankton concentration and forming of euphausiid swarms. At the zones populated by krill superswarms the abundance of phytoplankton was 3-5 times as large as that in adjacent waters. Within the huge and stable aggregations phytoplankton biomass was always over 1000 mg$\cdot$ m^{-3} (including "lenses", i.e. peak concentrations registered at some depths within the 0-100-m layer). The aggregations broke up or were missing in locations of the sea with phytoplankton biomass less than 500 g$\cdot$ m^{-3}. Therefore, the duration of aggregation life depends on the ratio between the forage (phytoplankton) recruitment and the nutritional requirement of krill. Being demanding of food concentration, the euphausiids, however, do not eat much: in adult krill, which is the major component of population, daily consumption does not exceed 2%.

Assuming the range of average biomass fluctuations in the krill aggregations from 35 to 1500 g$\cdot$ m^{-2}, the essential daily food replenishment which would maximally satisfy the daily food requirement of aggregated euphausiids is 700 and 30000 mg$\cdot$

m^{-2}, or, with the mean thickness of photic layer of about 45 m (see Chapter III), it is 16 and 670 $mg \cdot m^{-3}$.

Knowing from our computations given further in Chapter III that in summer the daily production to biomass (P/B) ratio in microalgae, especially in coastal waters of the region, is 1.0 and more on the average, we arrived to a conclusion that the zones of phytoplankton abundance are remarkably steady in terms of time, i.e. when hydrological conditions (water circulation) get stable in the locations with mictoalgal biomass greater than 1000 $mg \cdot m^{-3}$, the recruitment of phytoplankton in comparison with the nutritional demand of the krill is high enough to sustain the swarm for long. Most probably, it is this fact that explains the longevity of nearly all coastal superswarms during the years of our investigations. Then the disintegration begins with the progressing grazing or with the dispersion of phytoplankton through changes in the water structure. Fig. 14 shows that at the area covered by the mesoscale oceanological survey the krill superswarm is situated at a site with the specific water circulation and the reduced stock of phytoplankton which is the result of progressing grazing. In tightly concentrated krill aggregations phytoplankton biomass was estimated 400-600 $mg \cdot m^{-3}$ while around the aggregation it was as large as over 1000 $mg \cdot m^{-3}$ and at some spots within the 0-100 m layer even more than 3000 $mg \cdot m^{-3}$. Comparison of the overall ration of krill with ^{14}C measurements of phytoplankton production reveals a food deficiency developing within the aggregation limits: with the daily food demand over 300 $mg \cdot m^{-3}$ (the aggregation density is 29 $g \cdot m^{-3}$), the recruitment of the forage during the observation time was about 120 $mg \cdot m^{-3}$, or 6 $mg\ C \cdot m^{-3}$. In March the swarms dissociated because the nutritive base had been depleted through overgrazing.

Certainly, it is active feeding bechaviour of the krill that along with a number of biological factors not discussed here plays the leading role in generation and disintegration of the aggregations.

Longterm observations of a krill superswarm detected in the Cosmonaut Sea in 1983 have elicited curious details of its location and characteristics which were decisively owing to

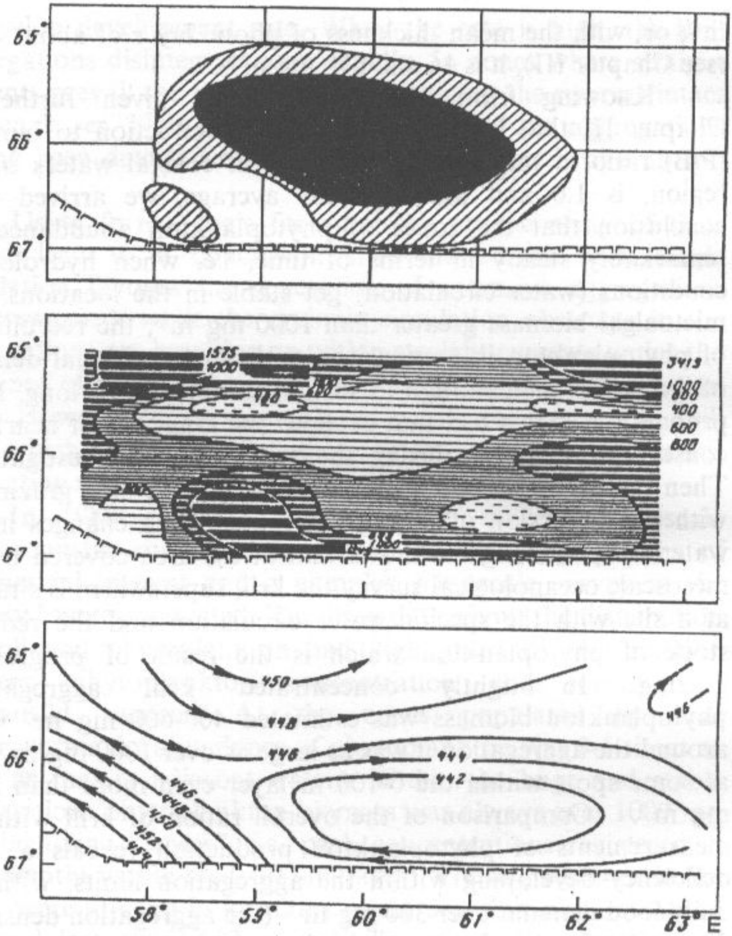

Fig.14. The distribution of krill aggregations (top) and phytoplankton biomass (mg. m-3) in 0-100 m layer (center) and the map of geostrophic currents in the surface layer at the area of krill aggregation I in 1980 (cf. Fig. 13) as depicted by the mesoscale survey.

More shaded and less shaded areas reflect the corresponding density of krill aggregations.

feeding bechaviour (Fig. 15). From January to March, as the phytoplankton bloom advanced southward following the retreat of sea-ice, the superswarm moved accordingly, close to the outer boundary of the vegetation zone. For that period the initial aggregation area of 200 km^2 had increased 6 times and the initial total biomass of 10 thousand t – 10 times; in 55 days the euphausiids had covered 80 km, their mean biomass was estimated as about 100 g·m^{-2}.

The structure of krill aggregations poses both scientific and practical interest. Looking at a commercial superswarm detected in Prudz Bay in 1977 (Fig. 16) one finds that particular groups of the krill aggregations (mostly of types I and II) spatially differ an order of magnitude over the area on the whole but not more than 3 - 4 times in the majority of cases. At the same time, estimates of the swarm volume fluctuate in a considerably wider range: extreme values differ 3 orders of magnitude and the most common – an order of magnitude at the least. The volumetric disparity between the groups, even those neighbouring each other, indicates that the hydrological field is heterogeneous on microscale that, in its turn, predetermines heterogeneous biotic (including nutritional) conditions. Nevertheless, groups which comprise krill swarms both of very small and very large volumes may concur at any part of a fishing ground that evidences relatively even spatial alternation of trophic and hydrological conditions favoring or impeding krill accumulation as in the case of the tranquility zones discussed above.

That the krill distributes over the examined fishing area in accordance with the disclosed pattern may imply equal possibility for good or poor krill catches at any part of the fishing ground; therefore, knowing the bounds of the area, a fishing vessel should not scout around for the krill too far. This circumstance must be borne in mind when a large number of ships must be positioned in the most efficient way at a fishing area.

Thus, we suppose that vast aggregations of the krill form only given a favourable combination of factors of which the basic are the activity in generating swarms and finding optimal environment with a rich nutritive base and the water dynamics which would either stimulate or hamper the aggregation process (direct influence) and the availability of food (indirect influence). The clarified connection between the fluctuations in the distribution of dense superswarms and the fluctuations in the position of phytoplankton intensive growth patches (mostly in the coastal zone) is of strong interest as it enlarges the possibility of successful scouting for the potential localities at which the aggregations are generating and of more accurate predicting. The scouting for krill superswarms is to be done by means of remote-operated pigment recorders installed in an artificial satellite or some other flying apparatus. Positive experience has been gained both in Russia and abroad (Pelevin,

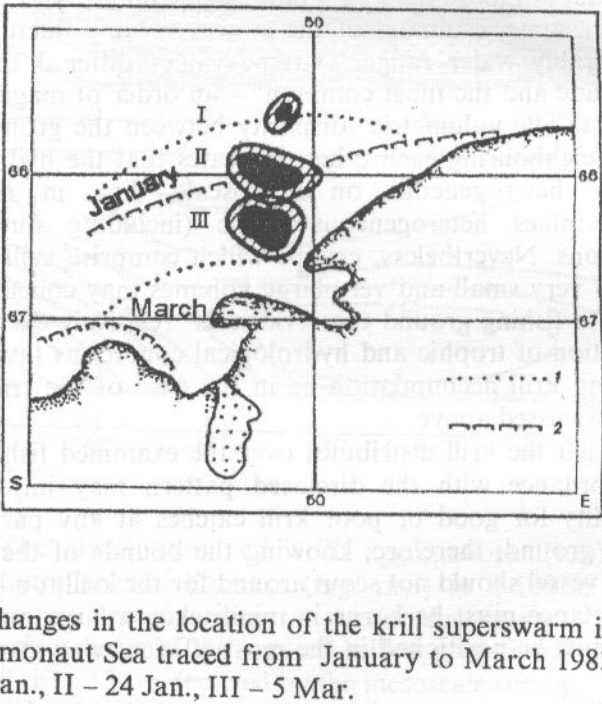

Fig.15. Changes in the location of the krill superswarm in the Cosmonaut Sea traced from January to March 1983: I – 11 Jan., II – 24 Jan., III – 5 Mar.
1 – the zone of phytoplankton bloom; 2 – the ice edge.

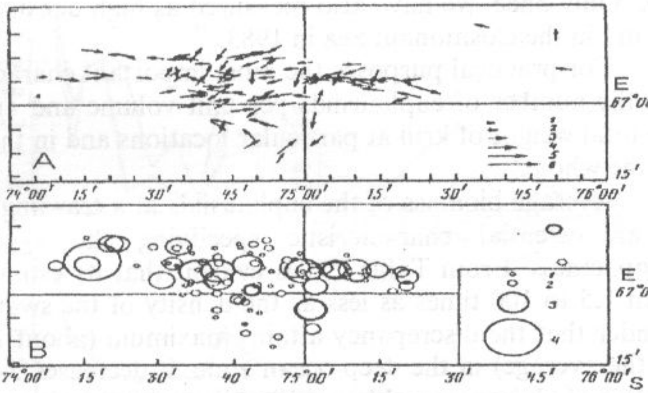

Fig. 16. The length (A) and the volume (B) of krill swarms in the commercial aggregation located in Prudz Bay in 1977.

Extent: 1 - <400; 2 – 400-1000; 3 - 1000-3000; 4 – 3000-4000; 5 – 4000-6000; 6 - >6000 m.

Volume: 1-1000; 2 – 10000; 3 – 100000; 4 – 1000000 m^3.

1978; Vanyushin, 1978; Suetin et al., 1983; Muralikrishna, 1983) in determining phytoplankton concentration using aerial surveys and satellite imagery. Conversely, the absence of the discussed relation in the ocean zone, that is primarily due to wind-induced mosaic water circulation in the surface layer, obstructs any scouting or prediction there, at least in the nearest future.

Results of the quantitative counts of krill made in the region during the surveys of 1977-1987 are presented in Table 2. The data tabulated indicate striking variability even of the averaged estimates which portray krill aggregations on different scales – from a particular swarm to the region on the whole.

The density of krill aggregations measured in different years varied for the region from several grams to 6.8 kg· m^{-3}; in the majority of cases from 12 to 320 g· m^{-3}, the mean was several dozen grams per cubic metre. Swarms with the density from 15 to 75 kg· m^{-3} reported elsewhere (Makarov, Shevtsov, 1971; Nesis, 1985) are, apparently, an exception rather than a rule. Only once we have also measured as high density as 73.4 kg$\cdot$ m^{-3} in the Cosmonaut Sea in 1983.

For practical purposes the most important characteristics are the number of euphausiids per unit volume and area, and the total weight of krill at particular locations and in the region on the whole.

Average biomass of the euphausiids at a trawling ground is an essential characteristic specifying the aggregation compactness. From Table 2 it is evident that its estimates are from 1.5 to 100 times as less as the density of the swarms. No wonder that the discrepancy attains maximum (about 10 times on the average) in the deep-ocean zone, it decreases 5-fold for the Sea of Commonwealth and is minimum (ca. 3 times) for the krill aggregations. Interannual variability of the estimates of average krill biomass in the trawling grounds of all the three locations of the region was generally similar to the variability of krill biomass averages for the locations at large.

The weighed means of krill biomass per unit area characterize the abundance taking into account vertical distribution of the euphausiids. In fact, the ratio of weighted means to krill biomass per unit volume represents average height of the aggregation, which, irrespective of the examined location, varied as widely as from 1.5 to 20 m.

Total biomass of the krill also varied considerably between the years. In order to have comparable biomass weighed means and krill stock estimates for different years, the corresponding computations were made for an area common to all the surveys (between 60 and 75^{0} E, with the invariable northern and southern borders). As Fig. 17,I demonstrates, these quantitative characteristics of the population have interannual variability generally similar for both the regional ocean zone and the Commonwealth Sea. Since the late 1970s the abundance of krill had been dramatically reducing first in the Sea of Commonwealth and a year later in the ocean zone of the region. The biomass and stock estimates fluctuated within an order of magnitude. In commercial superswarms the euphausiid numbers altered differently, with a distinct drop by 1983, a substantial rise in 1984 and the following stagnation during 1985-1987 (Table 2).

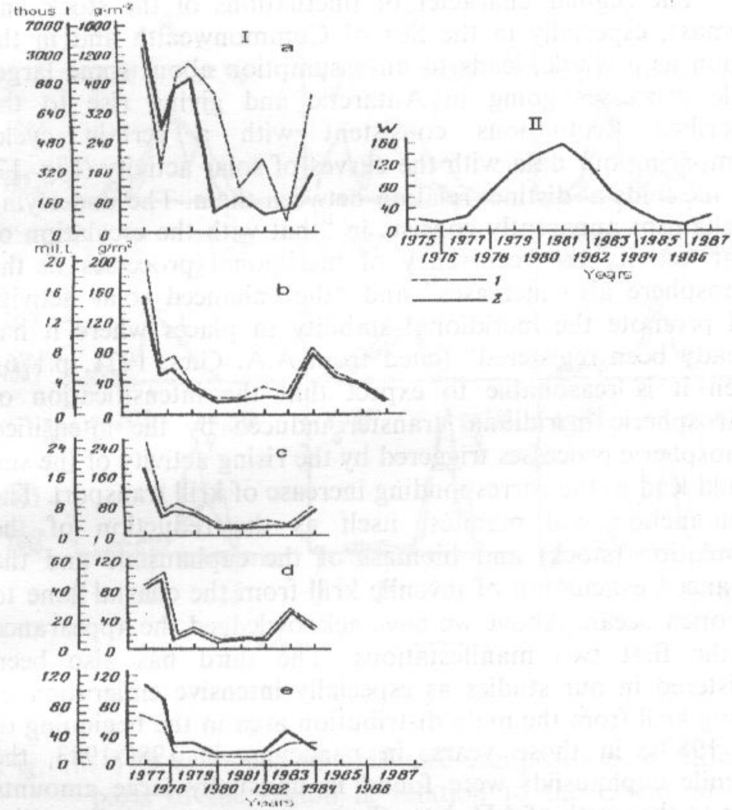

Fig. 17. Interannual variations of the krill stock and biomass in different parts of the region between 60 – 75° E and 60° S, of the ice-edge position in the south (I) and of the solar activity (II).

a – commercial aggregations of the krill in the Sea of Commonwealth; b – the Sea of Commonwealth without the aggregations; c – the Sea of Commonwealth including the commercial superswarms; d – ocean zone; e – the region on the whole;

w – Wolf number;

1 – krill stock, million or thousand t;

2 – krill biomass, g. m^{-2}.

The regular character of fluctuations of the stock and biomass, especially in the Sea of Commonwealth and in the region as a whole, leads to an assumption about some large-scale processes going in Antarctic and giving rise to the described fluctuations consistent with a certain cycle. Comparing our data with the curves of solar activity (Fig. 17, II) one finds a distinct relation between them. The underlying mechanism apparently consists in "that with the escalation of solar activity the recurrency of meridional processes in the atmosphere also increases" and "the enhanced solar activity will promote the meridional stability in places where it has already been registered" (cited from A.A. Girs, 1971, p.176). Then it is reasonable to expect that the intensification of hydrospheric meridional transfer induced by the intensified atmospheric processes triggered by the rising activity of the sun would lead to the corresponding increase of krill transport. The phenomenon will manifest itself as the reduction of the population (stock) and biomass of the euphausiids and the enhanced evacuation of juvenile krill from the coastal zone to the open ocean. Above we have acknowledged the appearance of the first two manifestations. The third has also been registered in our studies as especially intensive emigration of young krill from the main distribution area in the beginning of the 1980s; in those years, in particular in 1982-1983, the juvenile euphausiids were found in unusually large amounts even to the north of AD; later the transport was receding (Fig. 18).

To check our hypothesis, V.A. Bryantsev have calculated indices characterizing the water transfer intensity as related to the intensity of solar activity (Samyshev et al., 1987). The computations were made for the years during which our investigations were conducted and for the preceding and the following solar cycle. It was found that the variations in krill stock and biomass were associated with the changeable system of water transfer strongly dependent on the complicate and variable baric field. The analysis of complex relation with the use of matrices of state-to-state transition probabilities (similar

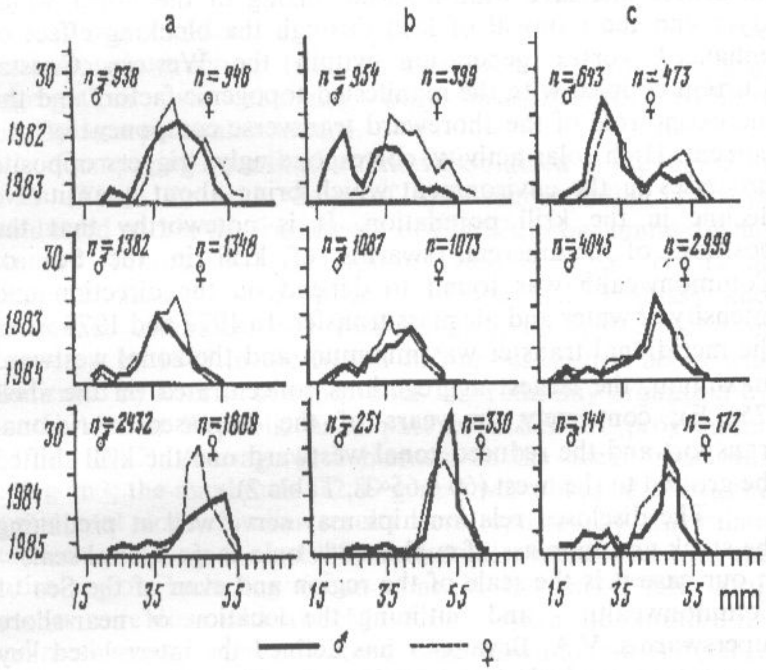

Fig. 18. The examples of krill size composition in different parts of the region in relation to the extent of krill transport from the distribution core (extensive during 1982-1983 and moderate in subsequent years).

a – Commonwealth Sea;

b – between 66° S and Antarctic Divergence (AD) zone;

c – between AD and 60° S.

to Markov's) showed that the quantitative rise of krill is logically linked with a series of interplaying factors – solar activity reduction, intensive zonal water transport from the east to the west, weak meridional transfer and exchange of air masses. Mechanism underlying the linkage is as follows. Low and moderate activity of the sun slows down the meridional transfer but increases the westward one. In its turn, the latter influences intensive wind-induced mixing of the upper water layer and the removal of krill through the blocking effect of enhanced vortex generation within the Western Coastal Current coupled with the manifested topogenic factors and the increasing role of the shoreward transverse component of this current. High solar activity, correspondingly, triggers opposite processes in the environment which bring about quantitative decline in the krill population. It is noteworthy that the position of commercial swarms of krill in the Sea of Commonwealth was found to depend on the direction and intensity of water and air mass transfer. In 1977 and 1978 when the meridional transfer was minimum and the zonal westward maximum, the largest aggregations concentrated on the shelf (75° E); conversely, in years of the increased meridional transport and the reduced zonal westward one the krill shifted the ground to the west (60 – 65° E; Table 2).

The disclosed relationships may serve well at predicting the stock and biomass of euphausiids on a large spatial scale – in our case it is the scale of the region and even of the Sea of Commonwealth – and outlining the location of near-shore superswarms. V.A. Bryantsev has defined the interrelated key parameters on which the prediction is based as follows:

- ♣ solar activity estimate which is easy to extrapolate with high precision to more or less distant future;
- ♣ the direction of the meridional and zonal transfer which may be predicted given a relevant method for atmospheric circulation forecasting;
- ♣ the difference between temperature estimates measured at Novolazarevskaya and SANAE stations.

As for the superswarms targeted for fishing, the individual quantitative characteristics of euphausiids in them are influenced by intrapopulation changes as well as by local conditions in the ocean. Traits listed above as indicative of the escalated krill transport manifested themselves during the regular observations only as shifted on the time scale. For instance, a conspicuous reduction of the collective stock of commercial superswarms in the Commonwealth Sea became evident only in 1981, while in the sea manifestations of this process were noticed a few years earlier (1978-1979). The dimensional structure (size groups of the krill) of those aggregations was changing only insignificantly without displaying a particular pattern.

Comparing quantitative data we obtained in the region in 1981 (Table 2) with data of the echosounding surveys conducted within the framework of FIBEX programme during January -March 1981 (Hampton, 1983) in three sectors of Antarctic shows the conformity of the krill biomass and abundance estimates. The marked drop of krill population registered by 1985 in the region of our research concern was confirmed by a series of expeditions to Prudz Bay organized by South African Republic as a part of SIBEX-II programme (Miller, 1987). Average krill biomass in the ocean zone was 0.48 g· m^{-2}; the maximum (12.89 g· m^{-2}) was obtained above the continental slope. Similar results were reported by Australian researchers (Hosie et al., 1988) from studies conducted over the entire region including ocean zone in the mid-1980s. Krill catches were done with an RMT-8 trawl (with the mouth 8 m^2 and mesh size 4.5 mm) in water column down to 200 or 1000 m depth. Like in the case we discussed before, in January 1985 the krill distributed in patches and had numbers not larger than 1 euphausiid per 1000 m^3 at the majority of stations; the average estimate for the 0-200 m layer was 6 euphausiids per 1000 m^3 (2 g wet weight · 1000 m^{-3}), or in other terms 3.4% of the total zooplankton biomass.

These facts prove, on the one hand, that the results are representative enough, and, on the other hand, that the idea about the comparability of data surveys has received confirmation.

The noticed fluctuations in the stock over as vast region as that cast doubt on the validity of the data on population size extrapolated from one or several surveys at a particular area as some authors did in a number of publications including those based on the survey within the FIBEX programme. Apparently, even a conventional average of the krill stock and biomass under the discussed fluctuations would be correct only given that longterm observations of the full cycle of those fluctuations underlay the corresponding computations.

Otherwise, it is correct to conclude about quantitative characteristics of a particular year and nothing else. In our case computing such an average estimate is of interest for the comparison with estimates given by other researchers. Our tentative computations yielded the average of krill biomass equal 40 g· m^{-2}, that is close to the estimate (13-25 g· m^{-2}) given by N.M. Voronina for a zone of euphausiid abundance. The similarity is even greater if in the computations by Voronina we assume the value of annual P/B coefficient not 1.86 (Allen, 1971) but 1.0 (from our experimental data given in the next section); then the resulting estimate is 24-46 g· m^{-2}, i.e. the mean is 35 g· m^{-2}. Judging from the average biomass estimates and the krill dominance in the total zooplankton, the region we explored falls within the distribution range as a zone of mass abundance. There is much uncertainty about the limits of this zone; the literature available defines the area as from a minimum of 5 million km^2 (Voronina, 1987) to a maximum of 19 million km^2 (Lyubimova, 1985). The krill stock hypothetically evaluated for the areas of the minimum and the maximum is 200 and 760 million t, respectively. Most of the stock estimates proposed by different authors on the basis of large-scale hydroacoustic surveys or computations are precisely within the numerical limits pointed above. The highest of the estimates we obtained may be admitted as a maximum possible for the extent (size) of krill population. We agree with N.M. Voronina (1981) that the krill stock evaluated in some publications as 2000 million t and more is a flagrant overestimation.

1.3 The ration and food balance elements

The information about krill production obtained through indirect calculations, though positively interesting and valuable for tentative assessment of the functional role of the entire population and the allowable commercial withdrawal, does not suffice to provide accurate prognosis. The more reliable alternative is direct computation based on the quantification data and preliminary analysis of productivity characteristics.

By the time we began our investigations, the knowledge about Antarctic krill production (energy) characteristics rested upon few fragmentary data about metabolic characteristics alone (McWhinnie, Marciniac, 1964) or combined with computations from growth curves (Chekunova, Rykova, 1974). M.A. McWhinnie and P. Marciniac focused mainly on ascertaining the response of euphausiids to changes of temperature; therefore the results are of interest in point of methodology. V.I. Chekunova and T.I. Rykova (1974) had experimentally determined the rate of oxygen consumption by the krill kept at 5° C as approximated by the following equation:

$$Q = 0.121\, w^{0.965},$$

where Q is expressed in ml O_2. $spec^{-1} \cdot h^{-1}$ and w is the weight in g wet weight for a relatively broad range of resulting estimates. The authors employed the data on the metabolism and evaluated weight increment of the krill from the growth curves in order to tentatively estimate possible growth and metabolic expenditures and the rations associated with particular stages of exogenous nutrition and with the life expectancy of 2.5 years. Total weight of phytoplankton eaten by the euphausiid over the life time is 60 g wet weight.

Afterwards, experimental studies of krill bioenergy characteristics were given a growing concern of researchers, among which is the author of this book.

Compared with standard metabolism estimates given by McWhinnie and Marciniac (1964), the metabolic rate of krill performing active locomotion is 40% higher (Kils, 1978). U. Kils underlines high sensitivity of the krill to growing oxygen deficiency in the water and the ability to adapt to low DOC.

Polish researchers (Rakusa-Suszczewski, Opalinski, 1978) measured the rate of oxygen uptake as dependent on temperature. Resulting equations ($Q = 0.116\, w^{0.950}$ at –1° C, $Q = 0.551\, w^{0.74}$ at –1.5° C, and $Q = 2.09\, w^{0.50}$ at –2.4° C) imply that the authors manipulated with krill insufficiently acclimated to the experimental conditions, that may be deduced from a staggering – over an order of magnitude – difference between the estimates of metabolic rate obtained in the narrow temperature range.

On the contrary, continuing his studies K.V. Opalinski (1979) found only insignificant difference in the cardiac contraction frequency of euphausiids kept at the temperature from –1.4 to +2.4° C. Within this range of temperatures Q_{10} was evaluated as 1.3 for the juvenile krill and 1.6 for the adults.

According to A.G. Naumov and V.I. Chekunova (1980), under different temperature conditions the oxygen consumption rate depending on body weight of the krill is approximated by the following set of equations:

$Q = 0.142\, w^{0.851}$ at 2° C,
$Q = 0.210\, w^{0.683}$ at 5° C, and
$Q = 0.752\, w^{0.400}$ at 7° C.

In doing these calculations, the authors followed the earlier pattern (Chekunova, Rykova, 1974) with some amendments made; they evaluated the amount of phytoplankton consumed for the life term as 62 g for males and 91 g for females. Comparing these values with those by A.G. Naumov and V.I. Chekunova, one finds that in the latter case the metabolic rate measured at 5° C is about two times and the total ration of females 1.5 times as large as in the former.

Experimental studies within the BIOMASS/FIBEX programme (the cruise of the *Umitaka Maru III*, the austral summer 1980-1981) and at the University of Tokyo are worthy of special consideration. Respiration rate of euphausiids with dry weight from 6.1 to 385.4 mg was determined by Winkler method, the krill was kept in 300- and 1000-ml or in 12-l containers at 0° C (Segawa Susumi et al., 1982). The acclimation lasted for 8-12 h. The relationship between respiration rate and dry weight was described by equation $Q = 0.0259\, w^{08331}$. Converted to wet weight (the average content of dry matter in the krill was estimated as 26%; see Chekunova, Rykova, 1974), the equation looks as follows: $Q = 0.1000\, w^{08331}$. Filtering and feeding rates were measured in the 19-55-mm long euphausiids with dry weight from 7 to 400 mg which were fed on *Dunaliella* culture given in varying concentrations (Kato Mitsuo et al., 1982). The relationship between filtration rate and the weight of euphausiid was described by the equation

$Y = 16.4 + 0.205\,X$ (r = 0.654), where Y is the filtering rate in ml· spec^{-1}· h^{-1}, and X is the dry weight in mg. The authors supposed that taking into consideration the metabolic expenditure for respiration and moulting, the krill, under the shortage of phytoplankton, turns to predation and sometimes to cannibalism (that was occasionally registered during the cruise). Of the suspended particles 4.8 – 83 μm in size the krill chose particles larger than 8 μm; however, having restored its dominance, the krill fed on particles smaller than 8 μm (Segawa Susumi et al., 1983). The buccal apparatus enables the euphausiids to capture suspended particles as small as 2 μm, however the preferable dimensional range is from 10 to 30 μm and larger (McClatchie, Boyd, 1983). The Japanese investigators to whom we were referring above emphasized that when food was in plenty, the krill had greater filtration rate than in cases of food deficiency. Under the shortage of phytoplankton the euphausiids lost activity and could not compensate for the metabolic expenditure.

The increase of feeding rate leads to the growth of dynamic activity and oxygen consumption rate in the krill (Ikeda, Dixon, 1984).

Laboratory observations (Morris et al., 1983) show that krill feeds all day long, the peak of feeding is at night hours; during day time the filtering activity also has rises and falls. An indirect manifestation of the nocturnal feeding activity in upper water layer is high rate of lipid synthesis in the natural environment. Index of fullness of stomach was decreasing in day hours and with depth. Krill population density strongly influences the rate of filtration: experimental increase of the density from 0.5 to 9.5 ind· l^{-1} brought about the deceleration of filtration from 30 to 5-7 l· h^{-1}· g^{-1} dry weight.

Studying the daily feeding activity of *E. superba* from the index of fullness of stomach and intestines (Pavlov, 1972; Sawamoto Shozo et al., 1983) had produced dim results. Pavlov claimed that feeding of the krill had a distinct daily rhythm with two peaks, one at midnight and the other at midday; he associated active vertical migrations of the euphausiids with this rhythm. Sawamoto Shozo with the co-authors reported about the daily feeding rhythm with the peaks at about 0-3.00 a.m. and 12.00-15.00 p.m. for some cases and without a peak for other cases.

Day-long observations over the variation of glucose and lactate content in the hemolymph and alimentary gland and of glycogen content in the alimentary gland of the krill revealed a nocturnal maximum in the feeding activity (Mezykowski, Rakusa-Susczcewski, 1979).

A review (Clarke, Morris, 1983) of the field of data having been gained about bioenergy characteristics of Antarctic krill subjected to criticism methodological aspects of the experiments and explored the applicability of results from the literature for calculating "energy budget" of the euphausiids. The authors asserted that the proposed estimates of oxygen uptake obscured rather than clarified understanding of basal (standard) metabolism of the krill. The krill is tolerant towards hypoxia; its oxygen consumption reaches maximum at 85% saturation. Generally, the oxygen uptake rate is not high, its dependence on fresh weight of the krill may be described by equation $Q = 0.813\ w^{0.88}$. Krill can filter particles about 3 μm large, however, the filtration goes especially active in the size range of 20-30 μm. Measured in flow-through tanks, the filtering rate was 100-1000 cell· h^{-1}. Probably, the feeding process continues for 24 h developing a peak at night (as it was at South Georgia). Proceeding from the krill energy budget reconstruction at the Island of South Georgia, it was determined that for the summer (190 days) in the males energy expenditure for growth was 4.5 Kjoule and for moulting 0.56 Kjoule, in females there was an extra expenditure for the development of ovary. Nothing is known about metabolic expenditures for tissue generation, swimming and feeding. In summer time the daily energy consumption of krill males may be tentatively evaluated as 5% and that of females as 6% of their body weight.

Active metabolism, i.e. metabolism during prolonged active motion, investigated in *Euphausia pacifica* (Torres, Childress, 1983) slightly exceeds the level the two authors referred to as standard but which in fact was "normal" (routine metabolism), representing the total of standard metabolism and metabolic extra-expenditure at usual spontaneous activity. Experiments on the "standard" (which is virtually normal) metabolism determinations under group maintenance of animals may result in overestimation. Metabolic rate strongly depends on temperature; in its turn the effect of temperature depends on the speed at which krill moves. For instance, at high velocity (112 m· h^{-1}) $Q_{10} = 2.8$, and at standard metabolism (0 m· h^{-1}) $Q_{10} = 2.0$. Increasing pressure may induce a slight, though meaningful, rise of oxygen consumption. The krill can develop temperature acclimation.

Experiments prove that energy characteristics of krill may widely vary depending on physiological condition and food supply. In euphausiids placed in an aquarium energy consumption rate determined from faecal excretion rate was 17-28% of the body weight a day (Clarke et al., 1988); these experiments had not corroborated the hypothesis about excessive feeding of krill. Depending on feeding schedule, the metabolic expenditure for moulting may fluctuate from –15 to +21% (Buchholz, 1988), while annual P/B coefficient of the krill was estimated as low as 1.8 (Ross, Quetin, 1988).

Material and methods

Ration and food balance of the Antarctic krill were experimentally studied during the cruises to the Commonwealth Sea region (Antarctic summer of 1976-1977, 1977-1978 and 1979-1980). Krill of different size groups was fished in upper 0-200 m layer by Isaac-Kidd trawl modified according to instructions by Samyshev and by a plankton net with the diameter of rings of 80 and 113 cm and capron sieve N 49. To provide acclimation of captured euphausiids, they were placed in a 320-l flow-through tank for a period of 1 to 5-6 days; water temperature in the aquarium was 0-2° C. Under the long-term maintenance the krill was fed on microalgal cultures grown in the ship laboratory.

Ration of the krill was defined from the total of balance components: $C = R + P + F$, where C, R, P and F are values of the daily ration, metabolic expenditure, increment and non-assimilated food (feaces). In our computations we discarded excreted liquid as its share in the balance is negligible (Sorokin, 1966).

Depending on experimental purposes, the food balance elements were determined by radiocarbon method proposed by Y.I. Sorokin (1966) or by applying it in combination with oxygen method. The first set of experiments was targeted at evaluating threshold and maximum food concentrations in euphausiids of the same dimensional group. The combined approach, whereby P and F were determined by the radiocarbon method and R by oxygen method, was used in conducting experiments with the krill of identical size in order to specify values of the balance components and K_2 coefficient in relation to the weight of body.

In the experiments we employed radiocarbon-labelled phytoplankton cultures grown in artificial nutrient medium into which ^{14}C was injected (200 μCurie per 1 l). Having reached constant level in 7-10 days as a rule, the culture was condensed, rinsed and kept on at about 0° C in the dark. Carbon content of the cultured phytoplankton (in order to learn its inverse negative specific activity, C_r) and the euphausiid body was measured by means of wet burning method (Karzinkin, Tarkovskaya, 1972) with the following calculating of its amount through oxicaloric coefficient 3.34 (Ivlev, 1934) and the energy equivalent 10 cal mg^{-1} C (Platt, Irwin, 1973, Winberg, 1983)[*]. The menu offered to the krill consisted of several phytoplankton species and dinoflagellate detritus (Table 3). Food preference was deduced from results of the determination of food assimilation index (C_{ass}/ C). Exposition time for the animals fed on the labelled forage was from 6 to 12 h depending on the initial food concentration. Time required for food to have passed through the intestines was determined from faecal mark reduction: the euphausiids fed on the labelled forage were carried in succession from one vial with non-labeled nutrition into next with the time interval of 10-20 min until the extinction of the radioactive mark. In

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[*] It is noteworthy that estimates of the krill carbon content obtained through this method (Table 4) are in agreement with direct measurement estimates (Kotori et al., 1986).

experiments concentrated on defining balance estimates the radioactive CO_2 exhaled by the krill was bound by $BaSO_4$ and settled onto a filter as well as the faeces. In estimating the assimilated carbon the animals were dried at 65° C, and ground; after that a suspension was made of the resulting particulate matter. One-tenth, one-fifth and one-third of the full volume of the suspension, depending on the size of ground euphausiids, were settled onto the filter. Radioactivity of the residue was measured by means of a BFL-25 torsion counter and a radioactivity recorder DP-100, 1 - 3-l laboratory vials were used.

Oxygen consumption rate measurements were made with a lead-and-silver sensory unit following the instructions specified in L.B. Klyashtorin and E.I. Musayeva (1977); we employed 1-l respirometers in which the stocking density of krill was from 3 to 5 ind$\cdot$ l^{-1} depending on the length of the animals. Along with the daily metabolic expenditure, our interest focused on the duration of the adaptation to experimental conditions and the daily rhythm (regularity) of biological activity of the euphausiids. Resulting data would permit to clarify and then exclude the effect of stress during acclimation, and to compute daily food balance and daily ration from the short-term (1-2 h) experiments in which conversion factors applicable to particular time of a day would be obtained.

All the experiments approximated the temperature of the natural environment (0-2° C). 120 experiments estimated the food balance by radiocarbon method; over 150 determinations of metabolic rate were made by oxygen method.

Results and discussion

In studying the respiration we used oxygen data units; after 5 - 6-h long fasting the euphausiids were placed in respirometers and examined. The continuous observations had showen a pronounced increase of the metabolic rate as the result of excitation during the first 6-12 h after putting into respirometer; then the metabolism maintained stable at a level

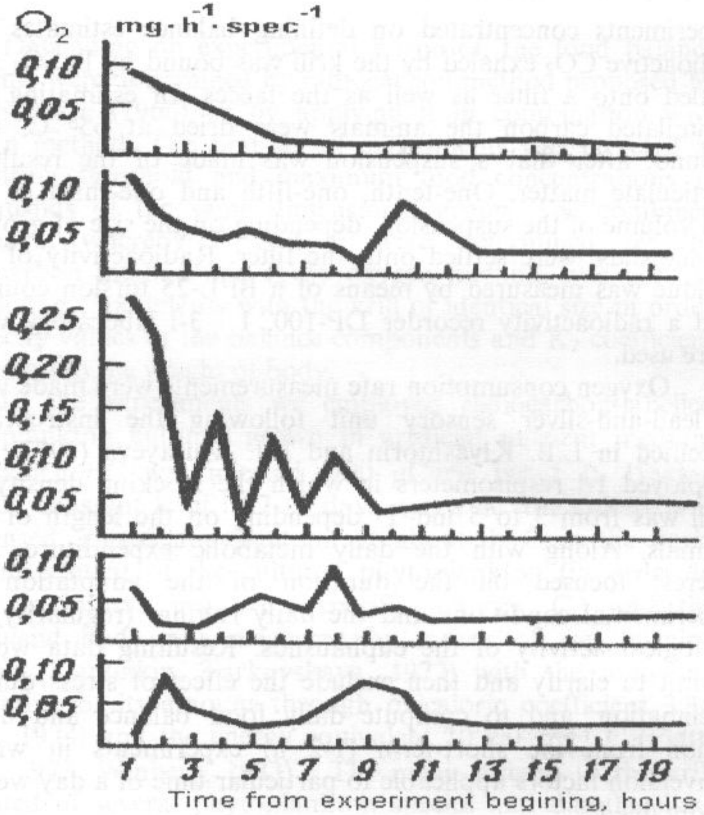


Fig. 19. Typical curves of the variation in oxygen consumption rate of the krill during the acclimation to experimental conditions.

which depended on the weight of animals (Fig. 19). It may be presumed that this period of time is a temporal minimum for the acclimation to experimental conditions in euphausiids with the body weight from 68.0 to 1200.0 mg (7.6 – 120 mg C). The acclimation was going differently in different groups irrespective of the body weight that is evident from the curves of metabolic rate oscillations. The diversity of acclimation patterns may be explained by distinctions in physiological condition of the euphausiids; the nature of these

Table 3

The results of nutritive value determinations in the food items of krill

Food item	Food concentration, mg· l-1	Cr of the food, 10^{-6} mg C· spec^{-1}	K = 24*/ t**	Radioactivity, imp· min^{-1}· Spec^{-1}	Carbon assimilation, 10^{-6} mg C· spec^{-1}	Weight, mg C· spec^{-1}	Assimilation index (Cass / C), % per day
Detritus	81.90	15.79	2.00	1290.00	20369.10	60.900	0.0669
Gymnodinium lanskoii	20.38	5.02	2.00	6488.00	32569.76	57.640	0.1130
Platymonas viridis	96.25	2.92	2.00	2136.00	6237.12	54.230	0.0230
Dunaliella tertiolecta	65.32	4.77	2.00	2556.00	12192.12	52.690	0.0463
Sceletonema costatum	30.00	4.13	4.00	6253.00	25824.89	80.100	0.1290
Nephrochloris salina	30.00	2.80	4.00	370.00	1036.00	73.340	0.0057

* - day, 24 h

** - feeding duration, h

distinctions is still unclear. The necessity of pre-experimental acclimation of hydrobionts is well-documented (Winberg, 1956) and generally recognized. In our case, the subject of interest was the time span required to the euphausiids for complete acclimation. Scientific works specialized in the temporal aspect of hydrobiont acclimation to experimental conditions are regrettably few; therefore, it is not possible to make a comprehensive comparative analysis of our data and those reported elsewhere. What we may state is that in the term of acclimation the krill stands between plankton copepods (Kuzmichyova, Sharf, 1978) and isopods (Samyshev et al., 1980) from the Black Sea.

During the observations of acclimated adult krill kept in the respirometers under natural light conditions we registered daily changes in the oxygen consumption rate. It was found that peaks of the respiration which emerged during a day were distinctly individual. Most of the euphausiids had been increasing the rate of oxygen consumption at noon or at midnight irrespective of the month (Fig. 20). Probably, the idea about the midday and midnight enhancement of feeding and motor activity which had originated as a result of studying the digestive tract fullness through integrated sampling (Pavlov, 1969), rested on the levelling of individual distinctions in the feeding behaviour (and even in behaviour at large) inherent in that method. Most probably, in the natural environment the daily biological rhythm (feeding and motion rates) is generally synchronized between different parts of krill population that is owing to an array of factors, e.g. fatness, fullness and physiological conditions, time of a day, etc. The above-mentioned individual variability of the fatness of euphausiids from the point catches made in day time is another proof to this suggestion.

An experiment with euphausiids with the length from 16 to 50 mm and the weight from 68.0 to 1200.0 mg (or from 7.65 to 120.8 mg C· ind^{-1} when converted) has elucidated the relationship between the rate of metabolism and the weight of body (Fig. 21, a). Depending on the length of krill, their metabolic rate was from 1.37 to 0.61% of body weight. In terms of power equation it may be described as:

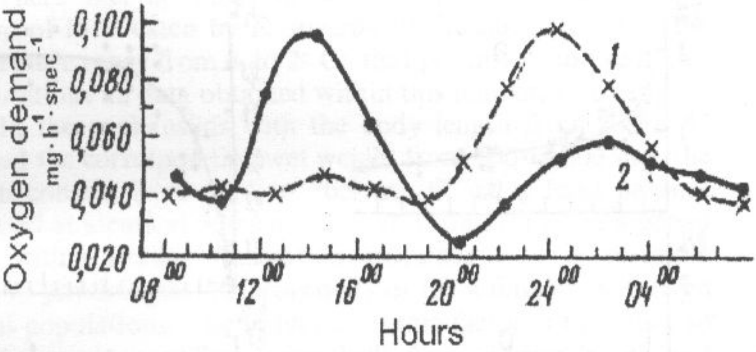


Fig. 20. The daily rhythmicity of krill respiration rate: 1 – January, 2 – February.

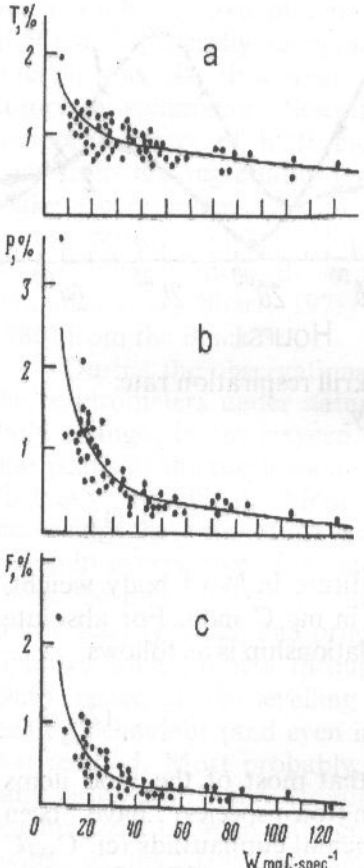
$$R = 2.45\, w^{-0.29}, \qquad (1)$$

where R is daily metabolic expenditure in % of body weight, and w is the weight of euphausiid in mg C· ind^{-1}. For absolute values of R (mg C· ind^{-1}· d^{-1}) this relationship is as follows:

$$R = 0.0245\, w^{0.71}. \qquad (2)$$

Food tests (Table 3) show that most of the food items (detritus and several phytoplankton species) have been successfully assimilated by experimental euphausiids (cf. C_{ass}/C data for tropical zooplankton in Petipa et al., 1971). However, the highest assimilation efficiency was measured at feeding on the cultivated *Sceletonema costatum*; for this reason this diatom was used in further experiments as the forage.

Time for which food would have passed through the digestive tract depended on the body weight. The time/body weight series is as follows: 3.0-3.5 h for 70-150 mg wet weight, 4.0 f – 200-400 mg, 4.5-5.0 h for 500-1000 mg wet weight and more. Proceeding from the results obtained, we learnt about the duration of particular feeding phases in the food balance experiments by radiocarbon method.



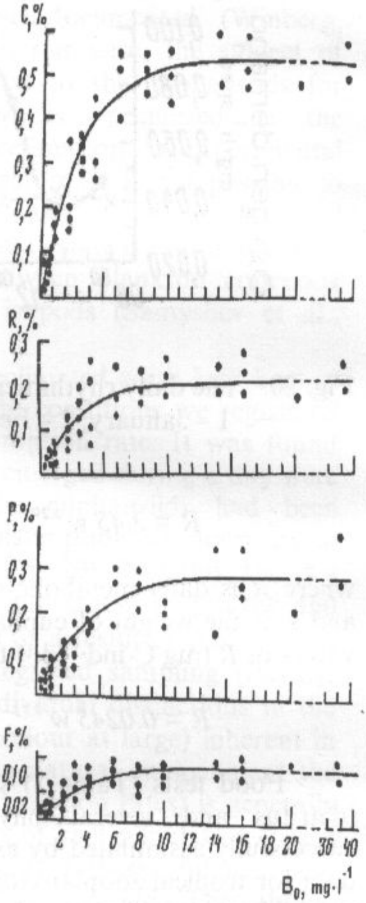


Fig. 21. Relationship between daily metabolic expenditure (a), food increment (b), non-assimilated food (c) and the body weight of krill (w) under the nutrient concentration of 10 mg·l^{-1}.

Fig. 22. Relationship between the euphausiid ration (C), metabolic expenditure (R), food replenishment (P), non-assimilated food (F) and the concentration of food (B_o).

There was no more or less regular variability in the amount of food eaten by *E. superba* of the same length in the temperature range from 0 to 2° C; that permitted to use in the computations all data obtained within this temperature range.

In the euphausiids with the body length from 37 to 42 mm and the corresponding wet weight from 500 to 600 mg (the carbon content from 60.4 to 76.9 mg C· ind^{-1}) food balance estimated at identical nutrient concentrations varied in a broad range within similar fluctuation extremes that is certainly owing to physiological heterogeneity of the animals taken from natural populations. The influence of this factor is the more so strong that the trawlings seize krill from diverse spots and swarms all at once. Bearing this in mind, we studied the dependence of rations and their balance values on the amount of forage for the krill at large, irrespective of the individual body weight. As Fig. 22 demonstrates, this dependence manifests itself clearly. It is pertinent to note that from our observations *E. superba* may feed at very low (0.005 mg· l^{-1}) food concentrations. As the food supply gets better, an asymptotic increase of the ration and balance estimates is developing. The corresponding curve "flattens", like in the majority of planktonic crustaceans (Sushchenya, 1969, 1975), when the concentration of food is 6-8 mg· l^{-1}. The relation between daily ration and available food concentration is described by modified Ivlev's equation (Ivlev, 1955):

$$C = 0.5400\,(1 - 0.5400\;10^{-0.1295\,Bo}) \text{ with } \sigma = 0.041, \qquad (3)$$

where C is the daily ration as % of the weight of body under some or other initial food concentration; B_o is the initial food concentration (mg· l^{-1}); 0.5400 is maximum ration corresponding to "plateau" at the curve (% of body weight), and σ is root-mean-square deviation.

For the food balance components this relationship is approximated with the following equations:

$$C = 0.2100\,(1 - 10^{-0.1320\,Bo}) \text{ with } \sigma = 0.013, \qquad (4)$$

$$P = 0.2870\,(1 - 10^{-0.1015\,Bo}) \text{ with } \sigma = 0.042, \qquad (5)$$

$$F = 0.1292\,(1 - 10^{-0.1261\,Bo}) \text{ with } \sigma = 0.016, \qquad (6)$$

Where *R*, *P* and *F* are the metabolic expenditure determined by radiocarbon method, the growth (increment) and non-assimilated food as % of the body weight, correspondingly; their approximated maximums are 0.21, 0.29 and 0.13%, respectively.

Maximums of the metabolic rate measured with ^{14}C method within the size group with the body weight equivalent to 60-70 mg C· ind^{-1} were more than three times as low as those yielded by oxygen method (cf. Figs. 21a, 22). Apparently, the underestimation ensued from the radiocarbon measurements was due to unusually abundant residue of $BaCO_3$ from the reaction between CO_2 and barium sulphate during the experiments. The residue of $BaCO_3$ was several times as large as the corresponding maximum given by Y.I. Sorokin (1966) in the table of self-absorption correction estimates; the coefficient of residue self-absorption which we had determined employing the proposed extrapolation technique also did not correspond to its actual value. Thus, the results obtained are but of narrow interest, namely, in the context of specifying food concentration extremes – a minimum, at which feeding would take place, and a maximum, when further increase of nutrient concentration would not lead to a rise of food balance estimates and the ration in general. In consideration of these reasons, in further computations of the ration and K_2 coefficient we referred to data obtained by oxygen method.

There was a regular decline of maximums of the daily increment and non-assimilated food in the euphausiids with the length varying from 16 to 50 mm and the body weight equivalent to 7.65 to 120.8 mg C· ind^{-1} when the concentration of food was 10 mg· l^{-1}; it was found that the maximums were T decreasing with the increase of the euphausiid body weight (Fig. 21 b, c). Within the examined size group the extremes of the daily increment and non-assimilated forage fluctuated from 2.48 to 0.16% and from 1.78 to 0.09% body weight, correspondingly. The relation between these food balance estimates and body weight of the krill is approximated by the power equations:

$$R = 18.6\, w^{-0.98} \tag{7}$$
$$F = 16.35\, w^{-1.09} \tag{8}$$

where R and F are the increment and non-assimilated food maximums expressed as % of the body weight, and w is the body weight of krill in mg C· ind^{-1}.

Equations 1, 7 and 8 help evaluate maximums of the daily food balance components for particular weight groups of the euphausiids and, through summing up, maximum daily ration; they also apply to tracking down changes of coefficient K_2 linked with size, i.e. growth, increase in the krill. The computations are given in Table 4. For the body weight range of the 16-50-mm long animals the maximum daily ration makes up from 5.63 to 0.86% of the body weight.

Evidently, the results of our experiments are not in absolute harmony with cited by other authors.

Switching to the daily rhythm of krill bioactivity, we find no such discord: both our experiments and the relevant literature prove that the rhythm actually exists and may have peaks at midnight and/or at mid-day, that conforms with field observations.

The commonality of opinions has also been reached about the amazingly broad food spectrum of the krill, its ability to capture both food particles (including detritus) as small as 8-10 μm and less, and large phyto- and zooplankton. Underwater observations (Nesis, 1985) considerably contributed to the knowledge about feeding patterns of the krill. The scientific evidence available points out high feeding activity of the euphausiids and the capacity to adapt to unfavourable food background. The fact of the high feeding activity has been conformed by the wide amplitude of fluctuations between the threshold food concentration (0.005 mg· l^{-1}) and the concentration of food (6-8 mg· l^{-1}) under which the ration curve would attain "plateau".

Table 4

Numerical values of the daily ration, its balance estimates and coefficient K_2 in different size-weight groups of the krill

Length, mm	Body weight		Increment P, %	Non-assimilated food F, %	Metabolic expenditure R, %	Ration C, %	K_2
	mg wet weight spec^{-1}	mg C spec^{-1}					
1	2	3	4	5	6	7	8
16	67.6	7.65	2.48	1.780	1.37	5.63	0.644
18	96.0	10.40	1.84	1.270	1.25	4.36	0.595
19	115.6	13.20	1.45	0.980	1.16	3.59	0.556
22	128.0	15.00	1.28	0.850	1.12	3.25	0.533
22	136.0	17.00	1.13	0.740	1.08	2.95	0.511
23	148.0	19.00	1.02	0.650	1.05	2.72	0.493
24	162.5	21.00	0.92	0.590	1.01	2.52	0.477
26	188.3	25.00	0.78	0.48	0.96	2.22	0.448
27	206.9	27.00	0.72	0.45	0.94	2.11	0.434

1	2	3	4	5	6	7	8
27	220.5	29.00	0.67	0.41	0.92	2.00	0.421
29	258.6	34.00	0.59	0.35	0.88	1.82	0.401
29	265.2	35.00	0.56	0.34	0.87	1.77	0.392
31	279.2	37.00	0.53	0.32	0.85	1.70	0.384
33	324.5	43.00	0.45	0.27	0.82	1.54	0.354
33	335.8	45.00	0.44	0.25	0.81	1.50	0.352
33	347.8	46.60	0.42	0.25	0.80	1.47	0.344
34	369.0	49.00	0.40	0.25	0.79	1.42	0.336
35	389.0	52.00	0.38	0.22	0.78	1.38	0.328
36	412.5	55.00	0.36	0.20	0.77	1.33	0.319
37	441.2	60.00	0.33	0.19	0.75	1.27	0.306
40	550.0	71.00	0.28	0.16	0.71	1.15	0.283
41	585.6	73.00	0.27	0.15	0.71	1.12	0.276
42	640.0	77.00	0.26	0.14	0.70	1.10	0.271
42	685.0	79.00	0.25	0.14	0.69	1.08	0.266
44	845.5	85.00	0.23	0.13	0.68	1.04	0.253
48	1020.0	105.00	0.19	0.10	0.64	0.93	0.229
50	1200.0	120.80	0.16	0.09	0.61	0.86	0.208

Our estimates of the food balance and the ration differ from those in the literature. To compare data from the metabolic rate measurements let us have the equation (2) formulated in terms acknowledged in the majority of pertinent papers, i.e.

$$R = 0.052\, w^{0.71}; \qquad (9)$$

Simultaneously, equations given by other authors are to be adjusted to 0° C, assuming that $Q_{10} = 2.25$ (Vinberg, 1983) (see Table 5).

Before bringing results obtained up for discussion, we should emphasize the significance of the parameter Q_{10}, because its values reported from a variety of experiments by different authors are of keen interest. For instance, it was shown (Ivleva, 1981) that metabolic rate of poikilotherms having completely acclimated to a temperature equally depends on the temperature at $Q_{10} = 2.0 - 2.5$. In this connection, G.G. Vinberg (1983) proposed assuming $Q_{10} = 2.25$ in order to adjust metabolic rate of poikilothermal animals to a certain temperature until more precise knowledge about the topic would have been gained.

From Table 5 it is evident that metabolic rate of the krill from our determinations is always lower in comparison with cited elsewhere. Judging from the equations, even the minimums given by other researchers are 1.5 to 2 times as large as out estimates. In making this comparison we used data by V.I. Chekunova and T.I. Rykova (1974) and A.G. Naumov and V.I. Chekunova (1980) who made the measurements at 5° and 2° C, correspondingly; and by Segawa Susumi et al. (1982) and Clarke and Morris (1983). Values reported in Rakusa-Susczcewski and Opalinski (1978) and in Naumov and Chekunova (1980) are 3-10 times higher than ours. Most probably, as wide discrepancy as that is due to the diversity of experimental techniques employed and the related distinctions in the success of the acclimation to experimental conditions. In contrast to our investigations all the authors we are referring to studied the rate of oxygen consumption by using bottle method which entails determinations of oxygen content by Winkler that

Table 5

Equations approximating the relation between oxygen consumption rate (P, ml $O_2 \cdot spec^{-1} \cdot h^{-1}$) and body weight (w, g wet weight) of the krill as cited in some publications

Authors	Experimental temperature, °C	Equation	
		Formulated from the experiments	Adjusted to 0° C
Chekunova, Rykova, 1974	5	$R = 0.121\ w^{0.965}$	$R = 0.088\ w^{0.965}$
Rakusa-Susczcewski, Opalinski, 1978	-1	$R = 0.116\ w^{0.95}$	$R = 0.130\ w^{0.95}$
	1.5	$R = 0.551\ w^{0.74}$	$R = 0.505\ w^{0.74}$
	2.4	$R = 2.09\ w^{0.50}$	$R = 1.82\ w^{0.50}$
Naumov, Chekunova, 1980	2	$R = 0.142\ w^{0.851}$	$R = 0.102\ w^{0.851}$
	5	$R = 0.210\ w^{0.683}$	$R = 0.151\ w^{0.683}$
	7	$R = 0.752\ w^{0.400}$	$R = 0.459\ w^{0.400}$
Segawa Susumi et al., 1982	0	$R = 0.0259\ w^{0.8331}$ (w – dry weight)	$R = 0.100\ w^{0.8331}$ (w – wet weight)
Clarke, Morris, 1983	?	$R = 0.0813\ w^{0.88}$ (admitted as a result of reviewing)	-
Samyshev, own data	0	$R = 0.052\ W^{0,71}$	$R = 0.052\ W^{0,71}$

is less accurate in maintaining control over the acclimation progress and oxygen consumption record in comparison with polarographic method.

The Polish researchers experimented with the least acclimated animals; this deduction is based on the fantastically overestimated respiration rate and Q_{10} within the experimental temperature ranges. For instance, tentative computations we made relying on the results by the Polish scholars show that at the temperature interval from –1° to +1.5° C Q_{10} equals 16 (!), at +1.5° – 2.4° C it is about 32 (!) and at –1° to +2.4° C it is close to 50 (!).

Though less exorbitant, the overestimation manifested itself in Soviet papers, too. The suggestion about the insufficient acclimation of experimental animals rests on too great difference in the estimates of metabolic rate (Chekunova, Rykova, 1974), too high estimates – including those obtained under similar (5° C) temperature – and too high values of Q_{10} (Naumov, Chekunova, 1980): close to 13 (!) at 5-7° C, about 10 (!) at 2-7° C, approximating the actual (ca. 2.5) value only at 2-5° C with other parameters also far overestimated.

Flaws in the methods linked with the acclimation distorted evaluation of Q_{10} in a number of works. McWhinnie and Marciniac (1964) did not find significant distinctions in the rate of metabolism at studying the krill at a series of temperatures and gave Q_{10} = 1.1 – 1.3 while in the temperature range from 5 to 15° C Q_{10} was estimated as 2.1. Certainly low are the estimates of Q_{10} cited in Opalinski (1979) as measured from heart contraction frequency in the krill: in the temperature interval from –1.4° to +2.4° C it is 1.3 (juveniles) and 1.6 (adults). Then one can hardly argue against the inference having been drawn by Torres and Childress (1983) from their study of *E. pacifica* that Q_{10} of the euphausiids is 2.0 under the standard metabolism and 2.8 under the active metabolism, that agrees with the value suggested by G.G. Vinberg. Therefore, Q_{10} values may serve as an extra criterion in assessing the validity of experimental data.

Serious arguments proving the reliability of experimental data on krill metabolism are their distinct correlation with body weight and other food balance parameters of the euphausiids and, as the result, the regular character of changes of coefficient K_2 over the ontogenesis. It is known that the product of powers of the equations approximating the relationships between metabolism and body weight and between body weight and length equals 2 (Tseitlin, 1984). The approximation is the closest for the power from our equation (2) describing the relation of metabolism with body weight and for the power from another our equation, which reflects the relation between body weight and length (with $w = 0.0226 L^{2.78}$), and that offered by Locker (1973) and corroborated by Sarchage (1978) with $w = 0.001798 L^{3.3436}$, where w is the weight of a euphausiid in mg wet weight and L is the length in mm. The products of powers from equations of other authors far exceed 2. Krill rations which we had figured out from the balance estimates were proved in experiments through recording the rate of phytoplankton grazing (Kato Mitsuo et al., 1982). According to the Japanese authors, placed in the sea water with high (4.93 μg chl "a"$\cdot l^{-1}$) concentration of phytoplankton, large euphausiids (240.7 – 247.9 mg dry weight of the body) had food consumption evaluated as 1468 – 1915 $\mu g\ C \cdot ind^{-1}$ while small (10.1 – 13.4 mg dry weight of the body) 183 - 211 $\mu g\ C \cdot ind^{-1}$. With mean krill caloric content we determined as 5.0 $cal \cdot mg^{-1}$ dry weight and the energy equivalent of carbon 9.3 $cal \cdot mg^{-1}$ (Vinberg, 1960), 1 mg dry weight of the euphausiid corresponds to 0.53 mg C. Calculations with the involvement of these equations show that daily ration of large (body weight equal in value to 128 –131 mg C) euphausiids may be estimated as 1.1 – 1.5% of the body weight, and that of small (5.4 – 7.1 mg C) as 3.4 – 3.0%. It follows from our measurements that in the euphausiids with the weight of body corresponding to 120.8 mg C daily ration was estimated as about 0.9% and with the weight of 7.65 mg C as 5.63%. The discrepancy between our and the Japanese results may be explained by some differences in research methods. In particular, in their experiments the Japanese investigators determined the rate of food consumption by means of computations based on Paffenhofer equation (Paffenhofer, 1971, cited from Kato Mitsuo et al., 1982). The elicited distinctions may also be due to differences in the energy value of the body and the related imprecision of calculations. The coherence between ration and body weight estimates we attained in our studies is definitely owing to the accuracy inherent in the methods we employed. Comparison between our results and krill rations defined from measurements of the fullness of stomach in the natural environment and by laser method (Ponomaryova, 1987) shows their similarity.

Our data on metabolic rates of the krill well agree with those for the metabolism of active (mobile) crustaceans ($Q = 0.232\ w^{0.875}$; Sushchenya, 1972) given that the equation was adjusted to 0° C instead of 20° C. Hence, a priori admitted or resulting from fallaciously high metabolic estimates the daily rations of krill about 5 – 6% are a three-time overestimation.

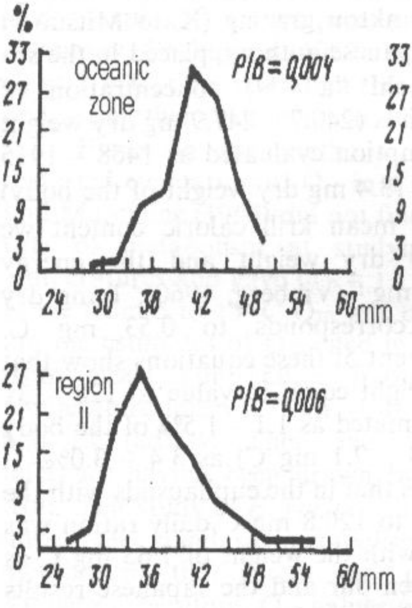


Fig. 23. Daily production-to-biomass (P/B) ratios in the krill populations with different size structure from different locations of the region (1980).

Rather interesting are values obtained from the computation of coefficient K_2 and its variability as dependent on the weight of krill body. Table 4 demonstrates that as the body weight increases, K_2 estimates decrease from 0.64 (with the weight of euphausiid equivalent to 7.65 mg C) to 0.21 (with the weight corresponding to 120.8 mg C). The parameter K_2 alters following the S-shaped curve of the euphausiid growth (Chekunova, Rykova, 1974). It may be presumed that in the youngest and in the oldest euphausiids the difference between K_2 values will be far greater. Therefore, in computation of krill production, which entails taking into account the production generated by the early developmental stages including larvae, routine methods will fit well (A guidebook in methods. Ed. G. Vinberg. 1968); otherwise the computation requires a series of K_2 determinations to be made at least for all juvenile age groups that implies solely experimental measuring of the growth. For practical purposes, evaluation of the adult portion of krill population at trawl fishing can be made proceeding from the tabulated averages (Table 4) with corresponding adjustments to the particular size structure. As our experience shows, in large samplings overall daily P/B coefficient depending on the size structure is from 0.002 to 0.006 (Fig. 23); the average for the region was determined as 0.003. Tentatively evaluated P/B coefficient of the krill approximates 1.0 assuming that the feeding is extended over a year and has seasonal peaks and declines. This estimate is almost three theoretically computed by Allen (1971), and it is two times as large as that by Tseitlin (1978) who applied a different method. Having in mind the demand for assessing an average for a population fluctuating in time (i.e. generally sustaining a certain level), it would be correct to assume annual P/B coefficient equal 1.0.

CHAPTER II

PHYTOPLANKTON: SPECIES COMPOSITION, SUCCESSION CHARACTERISTICS, DISTRIBUTION AND ABUNDANCE

Scientific evidence available from the literature about Antarctic phytoplankton was repeatedly analyzed by N.M. Voronina (Voronina, 1977, 1981, 1984). The materials analyzed had been gained from occasional local observations, therefore they allow only very general insight into the taxonomic composition and growth patterns of microalgae in Antarctica.

The flora is relatively diverse: microscopic counts have identified 260 species in waters of the Southern Ocean: 180 are diatoms, 70 dinoflagellates, 5 coccolithophorids and 5 silicoflagellates; about 30% of 77 phytoplankton species under our consideration are endemic to the region. The list of species is still updated. In phytoplankton of Antarctic zone the dominance of diatoms is almost absolute (99.9% of the abundance). Phytoplankton growth scenario always entails an abundance maximum by a few species of which one or two generate over half of the total abundance. Species prevailing in Antarctic are *Fragilariopsis nana, F. Curta, F. Cylindrus, Chaetoceros dichaeta, Ch. neglectus, Nitzschia subcurvata, N. closterioides.* Index of diversity is low in the southern part of Antarctic because of the steady dominance of a few microalgae; in the zone of Antarctic convergence values of the index are substantially higher.

Luminescent microscopy has shown that the quantity of small flagellated microalgae in the phytoplankton is very large; however their functional role in the community of plankton is obscure.

Seasonal changes in the abundance of phytoplankton are linked with regular alteration of dominant species.

Nutrients are not among factors which limit phytoplankton abundance. Opinions about the limiting effect of microelements or vitamins differ; some authors claim that the effect is profound, others that it is negligible. The majority of authors stress the overwhelming importance of light and water stratification in the surface layer (formation of seasonal pycnocline) which eventually account for the abundance of phytoplankton. A contributing factor is the temperature in photic layer. At the same time, in Antarctic the influence of temperature on the abundance was defined as insignificant (Voronina, 1984) and usually blocked by other factors. The persistence of surface water stratification depends on sea ice condition and varies from 6 months in the convergence area to 1-2 months in the south of Antarctic. Depending on the location of compensation point (1% light in the surface), photic layer depth varies from 7 to 95 m.

From pigment measurings it was found that seasonal rhythm of phytoplankton quantitative characteristics in Antarctic depends on the latitude. The character of the curve describing the northern part resembles seasonal variation of the phytoplankton abundance during the growing period in boreal zone: the population density increases in September – October, reaches a peak in December, then it gradually decreases by March, and after an "animation" in April it drops to minimum in June; in the mid-part lying between the northern and the southern the start of vegetation and the first maximum are shifted on the time-scale for a month; the late-summer maximum in May is insignificant; in the southern part the vegetation term is confined to from December to April with a maximum in February.

Similar changes of phytoplankton concentration expressed in traditional terms (biomass wet weight in 0-100 m water layer) were reported by V.V. Zernova (1983) who overviewed her own data and those available from literature as referring to the latitudinal zones between 50-60° and 60-70° S explored during December – May and December – April correspondingly. With the average biomass making up 390 mg $\cdot$ m^{-3} in the first zone and 480 mg $\cdot$ m^{-3} in the second, peaks (500 and 990 mg $\cdot$ m^{-3}) and minimums were in May and in April (13 mg $\cdot$ m^{-3} in the first area and 160 mg$\cdot$m^{-3} in the other, correspondingly). As no data are available about the winter period, it may be hypothesized that the biomass of phytoplankton decreases to a level estimated as several mg $\cdot$ m^{-3}; for convenience, the author assumes it to be 5 mg $\cdot$ m^{-3}.

This is the general outline showing the term and the course of seasonal changes in the abundance of phytoplankton depending on latitude. Temporal and spatial fluctuations of the hydrometeorological, including sea ice, conditions and special features of local hydrographic situation, e.g. specific coast line, may happen to cause serious departure from the normal scenario and disrupt usual development of biological season in a particular location (cited from Voronina, 1977, 1984). The amplitude of changes in the phytoplankton biomass on time scale is very broad. For example, peak numbers may keep up for a period from 10 days, as at the Soviet Antarctic station Mirniy (Klyashtorin, 1964), to 3 weeks, as around South Orkney Islands; in the last case the rate of microalgal production maintained high for 2 weeks. In local zones there were events of a short-term (3 days) alteration of dominant species, and the retrogression of phytoplankton abundance from "bloom" to oligotrophic status. As the decline is coupled with high content of nutrients in the sea water, a suggestion was made that causes generating the phenomenon are water mixing and grazing by phytoplankton organisms. Validity of the "grazing" hypotesis for Antarctic locations was proved through tentative calculations pertaining to formation of high concentrations of mesozooplankters (Voronina, 1984) and krill (Samyshev, 1985). It was suggested (Voronina, 1984) that the imbalance between food relations of phyto- and zooplankton, which is generally typical of Antarctic and caused primarily by spatial-temporal imbalance of the corresponding productivity cycles, manifests itself more or less distinctly over the region. During the vegetation season phytoplankton concentration varies on spatial scale as large as two-three orders of magnitude with maximums situated usually in 10-25 m subsurface layer that is mostly due to stratification of sea waters with different density. When the intensive vertical stratification takes place the phytoplankton distributes relatively evenly throughout the water column; at late succession stages the majority of phytoplankton cells sinks to depth greater than the compensation point (Voronina, 1977, 1984).

In sustaining Antarctic plankton communities ice flora plays its part. Diatoms are represented by ecologically different groups; one is attached and the other permanent planktonic. Despite low recruitment rate, the ice flora may generate high population density and numbers owing to the adaptation to low light and the absence of natural elimination e.g. through sinking to the depth and/or grazing by predators. There is an opinion (Voronina, 1977, 1984) that because of high chlorophyll content in the ice flora its role in the community life was exaggerated. More recent investigations (Fucuda Yasuchi et al., 1986; Ligowski, 1987) indicate also the abundance of glacial flora which may provide a substantial source of food for heterotrophs. However, its significance as the forage is relatively high only when it is found as aggregations incorporated in the ice; then krill would scratch the tiny algae out from the melting ice (Nesis, 1985). As the ice is melting relatively slowly, the released phytoplankton is sparse throughout the water column, the more so that some part, which are attached forms, immediately sinks to the depth and the other, which are permanent planktonic forms, is carried away with the currents.

Though studies conducted at different parts of the Southern Ocean were numerous, they produced only the very general and sometimes contradictory knowledge about regional distinctions in the abundance and species composition of phytoplankton. Data available from the literature on the composition and quantitative development cover almost all sectors of the Southern Ocean. However, making a comparative description of particular areas is a difficult task because of too huge water expanse and the heterogeneous water structure which determines the state of phytocenoses in different locations and the changeable and uneven distribution. There is no concord about the latitudinal distinctions in phytoplankton abundance; some researchers are unanimous in their opinion that Antarctic zone is richer in phytoplankton than Subantarctic, others claim quite opposite. N.M. Voronina (1984) explains this discord by zonal distinctions in the term of identical seasonal cycles in the phytoplankton. She supposed that during the vegetation period phytoplankton numbers alternately prevails in the following zonal succession: Subantarctic (October) – Antarctic (December – January) – Subantarctic (autumn). The annual average of plant pigment content N.M. Voronina has computed for different latitudes of Antarctica from data by Hart displays a tendency to decrease from the north to the south; the difference between pigment content measured at the northernmost and southernmost latitudes makes up 40%. Proceeding from the pertinent scientific evidence about huge amounts of phytoplankton in the sea water adjacent to the ice cover, N.M. Voronina advanced a hypothesis that the Atlantic sector is richer in phytoplankton because the boundary of the regional ice cover goes far northerly than in other sectors. Along with that the same review claims that phytoplankton is more abundant in neritic water compared with open ocean; water stratification is more distinct and persists longer in the former than in the latter. Therefore, it is reasonable to suggest that the dominance of certain ecological groups and the general level of phytoplankton growth at a particular sector of the Southern Ocean would depend on the extent of local neritic zone. Besides, the indented coastline and local sea-bottom elevations (shallows) contribute to the specific composition and abundance of phytoplankton through topogenic effect. Apparently, the above-listed distinctions in phytoplankton numbers measured in different sectors of the Southern Ocean at large and its Antarctic zone in particular are also influenced by these factors. Differences between regional atmospheric processes, which determine the water structure (including stratification) and natural illumination, also have influence on the distinctions in the numbers and species composition of phytoplankton.

Studying phytoplankton as the major component of the community specially focused on its main characteristics – taxonomic composition, growth extent, chorological structure and features of the succession in relation to the most significant determining factors – which were investigated based on regular many-sided observations made for the most part employing a single method.

Material and methods

Material for the study was gathered during macroscale surveys conducted over the entire region during 1973 – 1983 and at the Cosmonaut Sea area lying between 30° and 60° E, and from a mesoscale survey at the location where krill aggregation (I) concentrated in 1980 (Fig. 13). Samples were taken with water bottles from the standard series of depths (0, 10, 25, 50 and 100 m); for measurement of the primary production samples were taken from depths in which natural illumination corresponded to 100, 50, 25, 10 and 1% of sun light in the surface. In handling of the samples fixed by phormaldehyde and condensed through settling we used traditional method. Species structure and numbers of the phytoplankton were determined with the employment of traditional methods of mathematical statistics. Dominance of a particular species was defined from the computed estimates of the occurrence and the percentage in total biomass, and species diversity from Shannon index (Shannon, 1948).

Results and discussion

The heterogeneity of the regional hydrological structure explains the striking diversity of phytoplankton there. The list of all specimens identified consists of 210 species and varieties, among them 138 are diatoms, 63 peridineans, 6 chrysophytae and 3 cyanophytae.

The dominance of diatoms at large and their particular species depended on the phase of succession. In summer, at early (I-II) succession stages (according to Margaleff) diatoms contributed about 95% of total phytoplankton biomass (Table 6). The share of peridineans made up 4-6%, other contributors were estimated only as negligible. By the beginning of winter the portion of phytoplankton species characteristic of the succession stages III and IV became slightly larger than in summer; like in summer, their growth proceeded along with the dominance of diatoms, which generated as much as about 80% of the phytoplankton biomass at that period. Values of species diversity index indicate that phases of the Antarctic phytoplankton succession differ between seasons only slightly: estimated for the entire region in summer and in winter it was 3.9 – 4.0 and 4.2, correspondingly[•]. Seasonal distinctions in the condition of the Antarctic flora are the most evident at the examination of its growth extent and species number. The number of species decreased by winter as the result of generally depressed development and ice formation. For example, species found at particular water areas of the region during a summer survey numbered from 130 to 160; in winter time the diversity reduced to 93 species in the area lying between 30° and 60° E. Along with this the dominance of diatoms including those characteristic of the succession phases I and II, both in summer and in winter is certainly owing to instability of the water area, the continual wind-induced (in summer and winter) and convective (in winter) water mixing, which disrupts the normal course of succession by periods of more or less pronounced growth of these microalgae.

Genera *Fragilariopsis* and *Chaetoceros* are the most common and mass representatives of the phytoplankton succession phase I, the genus *Rhizosolenia* and the species *Dactyliosolen antarctica, Corethron criophylum* and *Thalassiothrix antarctica* of the phase II (Tables 6, 7). The portion of small diatoms, as the regional surveys show, is not

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[•] These estimates were obtained from the totality of samplings brought by the surveys; for individual samplings (samples, stations) they make up about 2.0 on the average for the region.

Table 6

The percentage of mass species in winter and summer phytoplankton (30 – 60° E)

Division, species	% biomass	
	June- July 1973	January – February, 1979*
Bacillariophyta	81.2	95.2
Dactyliliosolen antarctica	18.0	19.0
Fragilariopsis antarctica	15.0	4.0
Coscinodiscus sp.	5.0	6.0
Rhizosolenia sp.	5.0	0.4
Rh. hebetata f. semispina	3.0	14.0
Fragilariopsis rhombica	3.0	2.0
Thalassiothrix antarctica	2.0	20.0
Corethron criophilum	0.4	5.5
Pyrrhophyta	9.0	4.3
Exuviella cordata	2.0	1.0
Chrysophyta	1.7	0.3
Distephanus speculum	1.6	0.2
Cyanophyta	8.1	0.2
Oscillatoria thiebautii	5.2	0.2

[1*] The computations were made by M.S. Savich

Table 7

The average biomass and percentage (mg · m^{-3} / %) of mass diatoms in the phytoplankton of the explored region in different years

Species, its geographical origin and ecological nature*	1978		1979	1980	1981	1982	1982-1983
	Jan.	Feb.- Mar.	Feb.	Jan.	Feb.- Mar.	Jan.	Dec.– Jan.
Rhizosolenia hebetata f. semispina, tropical-Antarctic, open ocean	153/27	96/24	558/49	282/51	12/2	29/2	143/26
Rh. alata f. inermis, Antarctic, open ocea	109/19	68/17	27/2.4	46/8.4	70.12	41/2.7	75/13.7
Dactylosolen antarctica, Subantarctic, open-ocean	54/9	57/15	102/9	39/7	185/31	336/22	106/19
Corethron criophilum, cosmopolitan, neritic	41/7	15/4	90/8	67/12	33/5.6	261/17	27/5
Thalassiothrix antarctica, Antarctic, open-ocean	11/2	4/1	77/6.8	26/4.7	21/3.5	34/2.2	95/17.3

Species, its geographical origin and ecological nature*	1978		1979	1980	1981	1982	1982-1983
	Jan.	Feb.- Mar.	Feb.	Jan.	Feb.- Mar.	Jan.	Dec.– Jan.
Chaetoceros dichaeta, Antarctic, neritic	1.4/0.2	4/1	11/1	6/1	5/0.9	71/4.6	7/1.3
Fragilariopsis antarctica, Subantarctic, open-ocean	15/3	14/4	15/1.4	24/4.3	24/4	34/2	4/0.7
Fr. curta, Antarctic, neritic	13/2	3/1	8/0.7	1.7/0.3	30/5	41/2.7	5/0.3
Fr. rhombica, Antarctic, neritic	6/1	2/0.5	26/2.3	1.7/0.3	10/1.6	28/2	2/0.4
Synedra spatulata, Antarctic, neritic	12/2	36/9	60/5.3	20/3.6	23/4	50/3.2	8/1.5
Nitzschia barkleyi, Antarctic, neritic	10/2	6/1.5	14/1.3	6/1	5/1	23/1.5	7/1.3

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* Cited from Kozlova (1964) and Hasle (1969)

large in summer, being usually about 5% of total phytoplankton biomass. During all studies over the region and for the majority of stations under the surveys it was registered that the succession developed another stage at which large forms prevailed. Gaps in the observations of succession phase I were the result of imperfect research methods; in particular, the surveys were too extended on the time scale. Simultaneously, the heterogeneous regional hydrostructure makes the possibility to have this phase registered over the entire region very problematic. Apparently, development of the phase is fast and local, that may be deduced from a few facts. In summer, peak estimates yielded by main participants in the succession phase I concentrate at local sites, not only at those lying close to the ice edge where its presence is logical and the most probable but also at a distance, in locations free from ice. In all probability, in the last case there was a coincidence or a "superposition" between phases: while phase II was developing as the result of water mixing, vertical stratification disturbance and the eventual disorganization, the community regressed to initial stage (succession renewal). In winter, in the absence of seasonal pycnocline, these phenomena manifest themselves more markedly because the continuous diffusion of community components going on under the intensive non-stopping chaotic water transfer obstructs development of flora characteristic of the succession phase II. That is why in the winter 1973 (Table 6) the biomass generated by the small diatom *Fragilariopsis antarctica* made up 15% of total phytoplankton biomass in the region. The "retreat" of the succession to initial stage, that takes place at particular sites, is realized through intensified growth of a variety of representatives typical of the succession with the dominance of limited number of species. The latter is determined primary by uneven distribution of populations the initial concentration of organisms in some or other part of the distribution area. In some cases neighbouring communities at different succession phases were found at one and the same station; the neighbourhood manifested itself as the dominance of characteristic taxa at different depths. Depending on the position the community occupied vertically, it was easy to find out the direction of succession course in the community at a particular point: findings of a maximum number of forms characteristic of phase I at depths of 50 and 100 m, i.e. below the compensation point (that is of special importance in our reasoning because at this depth population growth does not take place at all), and forms characteristic of consecutive "direct" process at which some or other driving factors (e.g., sinking under the impact of the force of gravity or of a downwelling event) made "aging" fraction of the population of small diatoms to descend to depth, leaving intensively growing portion of the population of large diatoms above them; conversely, given different vertical arrangement of species typical of these phases, one may presume the "retreat" of the succession to initial stage.

Total share of the taxa characteristic of the succession phase I usually did not exceed 10-11% of the total diatom biomass in summer; the exception were the years 1977, 1981 and 1982 when the percentage increased to 17-25%. Interestingly, in the winter 1973, the estimate obtained for the area between 30° and 60° E was as high as 30%.

That one or another succession phase is clearly manifested, depends on the stability of favourable factors – day light stratification). In summer, when seasonal pycnocline. is forming, the unsteadiness of overlying water mass and the more or less pronounced, wind-induced vertical water transport lead to levelling of the differentiated succession development. As the result, firstly, the entire process looks obscure; secondly, relatively long exposition of the initial forms (taxa) in photic layer allows large diatoms, which represent the succession phase II, to advance and dominate the phytoplankton during most of the summer period and even later.

It is seen from Table 7 that the dominant species were altering from year to year over the explored region. Depending on the year, a 50% minimum of total phytoplankton biomass was composed of maximums of the relative biomass generated by two-three representatives of the dominant species (*Rhizosolenia hebetata f. semispina, Rh. Alata f. inermis, Dactyliosolen antarctica, Chaetoceros dichaeta, Corethron criophilum*). Despite different geographical nature of these taxa, it is difficult to find an explanation of the replacement of the leaders, especially for forms of similar nature. At the same time, some tendencies inherent in the phenomenon conform with large-scale changes in the regional hydrostructure. In particular, a noteworthy fact are changes in the share contributed by two species of the ocean phytoplankton – the tropico-antarctic *Rhizosolenia hebetata f. semispina* and the subantarctic Dactylosolen antarctica - over the years of our research. The portion of the former had considerably increased by 1980; after that, in 1981 and 1982, it dropped drastically; simultaneously, the share of the latter had risen 2 – 3 times. During the season of 1982/1983 *D. antarctica* was holding its position, while *Rh. hebetata f. semispina* had restored to the estimates measured in 1978. Along with these fluctuations, beginning from 1979 the portion of the antarctic species *Rh. alata f. inermis* had been reducing, the decline was especially obvious in 1979, 1980 and 1982. Simultaneously, in 1980 and 1982 there were several events of population increase in the cosmopolitan *Corethron criophilum*. The alterating abundance of the prevailing species having differ geographical origin was found to be linked with fluctuations in the intensity of meridional water transfer, which determined also the position of peaks generated by the species typical of open ocean and coastal zone – *D. antarctica* and *C. criophilum*, correspondingly (the latter is an indicator species of the Western Coastal Current). When the transport attenuated, as it was in 1979 (Fig. 24), the maximums concentrated in their usual zones; with the increase of water transfer intensity, as it was in the season of 1982/1983 (Fig. 25), maximums of the oceanic species penetrated the neritic zone and, vice versa, the maximums of the neritic species – the open ocean. It was found that the enlargement of the influence of tropico-antarctic oceanic forms in the coastal water and coastal forms in the open ocean owing

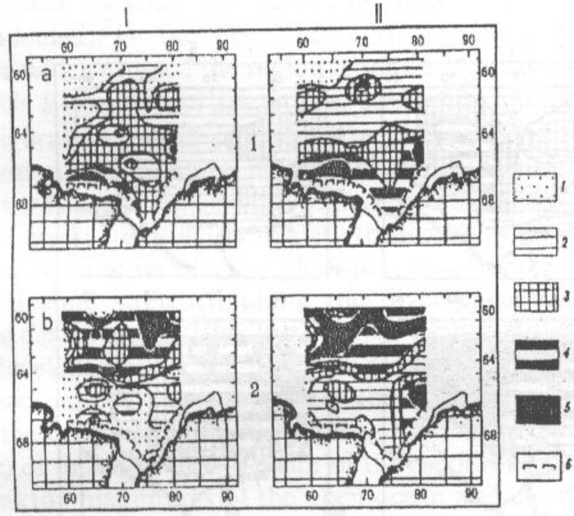

Fig. 24. The distribution of *Corethron cryophilum* (a) and *Dactyliosolen antarctica* (b) biomass (I) and the percentage (II) of their biomass in total phytoplankton biomass.
I: 1 – 0-50; 2 50-100; 3 – 100-500; 4 – 500-1000; 5 - >1000 mg $\cdot$ m^{-3}; II: 1 0-1; 2 1-10; 3 – 10-25; 4 – 25-50; 5 - > 50%; 6 – ice-edge

to the intensive meridional transfer correlates well with the reduction of the krill stock and biomass in the region provoked by the intensive expatriation (see Chapter I).

The list of species we identified as dominating Antarctic phytoplankton differs from that given in literature (Hasle, 1969); the latter misses some mass species characteristic of the succession phase II. Most of Antarctic zone provides conditions favouring this phase. It is also hardly reasonable to treat this species composition as something unchangeable. The diverse and varying character of water transport along with uneven distribution of the populations having different

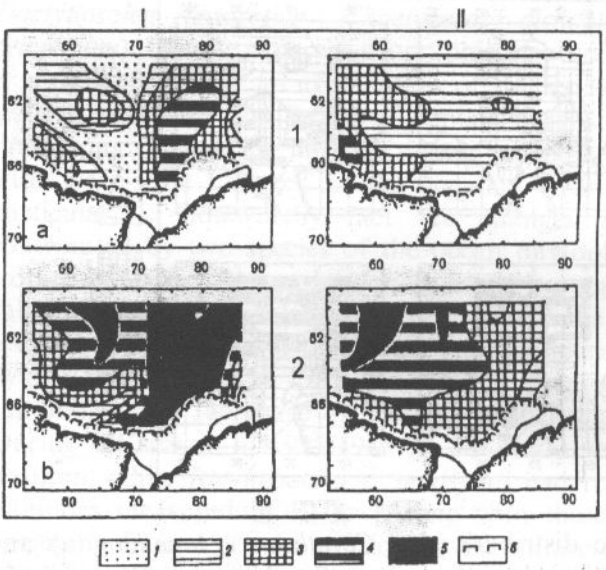

Fig. 25. The distribution of *Corethron cryophilum* (a) *Dactyliosolen antarctica* (b) biomass (I) and its relative portion (II) in the total phytoplankton biomass for the region (December 1982 – January 1983).
Conventional marks as in Fig. 24

geographical origin will certainly induce changes in the source of the taxa which become mass given favourable combination of factors.

In conformity with the fact that succession processes develop asynchronously at different locations we observed uneven distribution of phytoplankton abundance. It is noteworthy that the situation had been changing kaleidoscopically over the season as well as between the years. Discarding insignificant details, in general, the quantitative distribution of phytoplankton in the region looks as follows. The phytoplankton was abundant (the biomass over 1000 mg · m^{-3} in the 0-100 m water layer) both in the coastal (near-ice edge) and in the open ocean zones. In the coastal water this phenomenon was owing to a propitious topogenic effect appearing near the shore (ice edge) especially if the coastline is deeply indented; in the open ocean it was owing to the divergence which crossed the region from the south-west (ca. 61 – 65° S, 55° E) to the north-east (ca. 62° S, 90° E). The extent and configuration of the peaks of abundance were obviously related with the prevailing pattern of water transfer elicited from the analysis of representative species distribution. In cases when the main (eastward) water transport was distinctly manifested maximums of the phytoplankton biomass in the deep-ocean zone stretched along the divergence toward the water transfer direction (Fig. 26 a). When the meridional water transfer developed under the influence of large-scale cyclonic or anticyclonic eddies, phytoplankton biomass peaks located either in the centre (Fig. 26 b) or along the outward periphery (Fig. 26 c) of the eddies. As a result of the meridional transport, phytoplankton maximums of the open-ocean and coastal zones merged, especially if they concentrated along the outward periphery and their common axis lay meridionally.

Numerous observations show that in characterizing regional distinction in the abundance of phytoplankton in Antarctic zone, one has no grounds to categorically define either the divergence-influenced (Kozlova, 1964) or the near-ice (Kozlova, 1984) area as the richest one. The abundance of phytoplankton in them is determined by the character of circulation in the system of currents under the impact of atmospheric processes changeable in time and space.

More detailed examination of the distribution of phytoplankton biomass under different oceanographic conditions provided a deeper insight into the mechanisms responsible for generation of the biomass maximums (and hence the cause bringing about spatial heterogeneity of the quantitative distribution of phytoplankton) and the temporal variability of the abundance over the region.

The well-known limiting effect of water stratification on phytoplankton accumulation is seen from the character of phytoplankton distribution in winter period (Fig. 27). In the absence of seasonal pycnocline and the related vertical mixing of water masses, phytoplankton growing in ice-free sea water distributes relatively evenly throughout the entire 100-m water column inspected at several stations. Curves which describe its biomass are predominantly vertically stretched. Despite the deficiency of sun light in the region at large, that we a priori admitted for the winter period, and the generally low numbers of phytoplankton, the spatial heterogeneity of biomass distribution, especially on horizontal plane, took place.

From the concord between the horizontal distribution of phytoplankton biomass and of the salinity in near-surface water during the observation period (phytoplankton maximums agreed with salinity minimums) it follows that

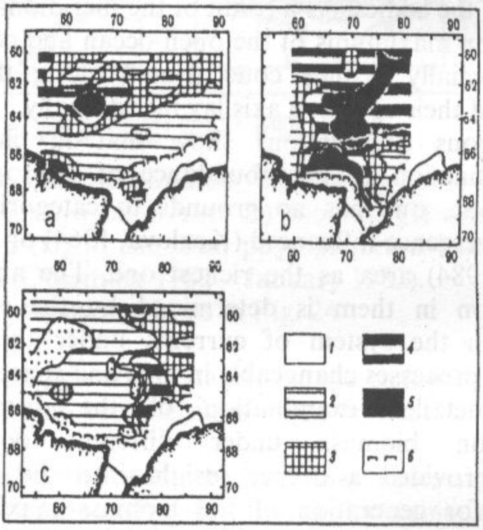

Fig. 26. Examples of the distribution of phytoplankton biomass in the main region of the study (0-100 m water layer) in February 1981 (a), February 1982 (b) and December-January 1982-1983 (c). 1 - < 100; 2 – 100-500; 3 – 500-1000; 4 – 1000-2000; 5 - >2000 $mg \cdot m^{-3}$; 6 – ice-edge

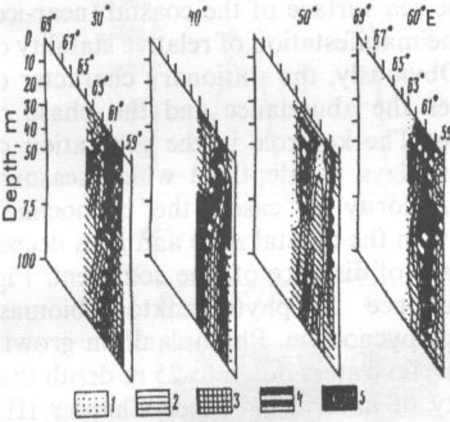

Fig. 27. Typical vertical distribution of the biomass of phytoplankton in the meridional sections made in austral winter (June – July 1973, Cosmonaut Sea).
1 - < 10; 2 – 10-20; 3 – 20-30; 4 – 30-40; 5 - > 40 mg · m^{-3}

during the winter period the levelling of oceanographic characteristics measured in different parts of the water area free from ice goes asynchronously because of the spatial heterogeneity of atmospheric processes. Patches of low salinity near the surface should then be considered as an after-effect of the summer stratification with the corresponding effect of relative abundance of phytoplankton in them. The appearance of phytoplankton biomass maximums below the compensation point indicates that the phytoplankton sinks into deeper water in the process of natural growth and death under the effect of gravity and convective mixing of water masses. Simultaneously, both microalgal accumulation and the development of succession were limited that stimulated the continuous "retreat" to the initial stage.

During summer period, when seasonal pycnocline is forming over most of the region, uneven distribution of phytoplankton is, as in winter period, due to local gyres which, unlike in winter, develop under relatively vertical water stratification. That the maximums of phytoplankton biomass coincide with eddies in the sea surface of the coastal (near-ice) and open-ocean areas is the manifestation of relative stability of these water formations. Obviously, the stationary character of the eddies often influences the abundance and the phase of succession of phytocenosis. The key role in the generation of phytoplankton maximums plays the depth at which seasonal pycnocline lies. In the majority of cases, the pycnocline's position is the most shallow in the coastal zone and goes deeper and deeper with the increase of distance off the continent. Fig. 28 illustrates the dependence of phytoplankton biomass maximums on the depth of pycnocline. Phytoplankton growth goes most actively in Antarctic waters down to 25 m depth that is owing to the availability of natural light (see Chapter III). With the general tendency toward the along-meridional change of pycnocline depth, optimal position of the upper boundary (to 25 m) of the pycnocline was usually either at the ice edge or at the zone of Antarctic divergence. As favourable situation as that occurred only in the presence of stationary gyres which blocked the diffusion of phytoplankton cells in the currents. Otherwise, though the pycnocline was developing phytoplankton accumulation did not take place. The favourable combination of factors (the shallow 0 to 25 m - upper boundary of phytoplankton and the stationary gyres) explains why phytoplankton production was similarly high in the coastal in zone and in the zone of Antarctic divergence. The penetration of phytoplankton biomass maximums into deep-water layers of the near-shore zone was owing to shelf water downwelling; their appearance in a few locations below pycnocline might be the result of horizontal drift from the neighbouring water areas at which pycnocline lay deeper.

High concentrations of phytoplankton in the north of the region, sometimes over vast areas, certainly were owing to the transport of phytoplankton from the eddies of AD. With deepening of pycnocline, deepening of phytoplankton maximums was also registered.

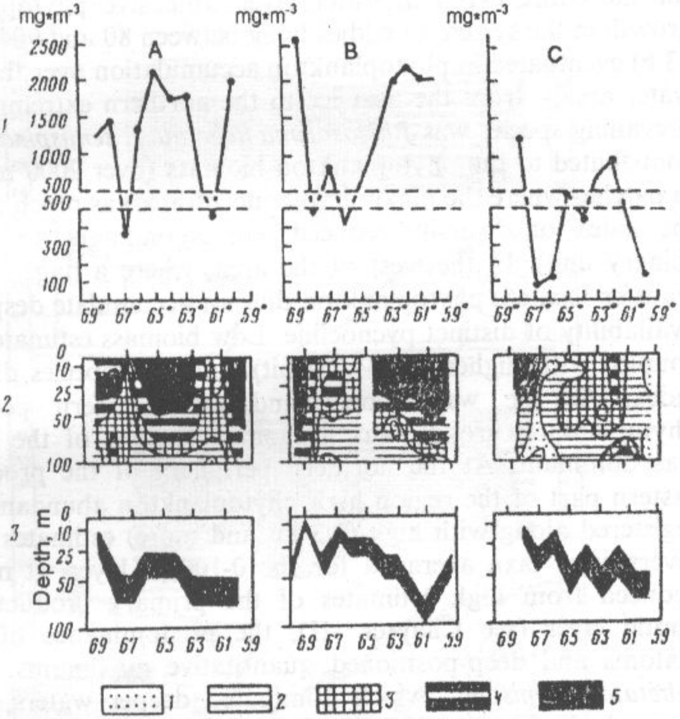

Fig. 28. Average phytoplankton biomass (mg · m^{-3}) for 0-100 m layer (1); its distribution in the water column (2) and the position of pycnocline (3) at a transect along 75° E in February 1979 (A), in 1982 (B) and 1981 (C).

Taking into consideration the mechanism governing and regulating the regional processes, it is possible to find manifestations of different stages of the transformation of phytoplankton aggregations at corresponding sites – from generation of maximums to their dispersion. This may be represented more or less universally (integrally) with the involvement of Shannon index of diversity, using our observations in January 1980 (Fig. 29) as an example. One cannot but notice harmonic distribution of estimates obtained for the index and phytoplankton biomass that is evident even for the entire 0-100 m water layer. Intensive phytoplankton growth in the system of eddies lying between 80 and 90° E (Fig. 13 b) eventuated in phytoplankton accumulation over the entire water area – from the near-ice to the northern extremity. The prevailing species was *Rhizosolenia hebetata f. semispina*, which contributed to the phytoplankton biomass (over 2000 mg · m^{-3} in patches where the maximums concentrated) as much as 93%; the index of diversity reduced, correspondingly, to 0.5 bit (binary unit). In the west of the area, where a huge cyclonic transfer located, phytoplankton did not accumulate despite the availability of distinct pycnocline. Low biomass estimates were coupled with higher (1.5 – 2.0 bit) values of species diversity index. At the westernmost and the northern periphery phytoplankton growth was insignificant, none of the species was dominant. At the northern periphery of the productive eastern part of the region high phytoplankton abundance was registered along with high (2.5 bit and more) estimates of the diversity of taxa averaged for the 0-100 m layer. It may be deduced from high estimates of the primary production in photic layer (see Chapter III), the predominance of small diatoms and deep-positioned quantitative maximums of *Rh. hebetata f. semispina*, which dominated deeper waters, that a renewal of succession process developed there in the surface.

The effect of sun light (illumination) on phytoplanktón distribution may be indirect, through the influence of water structure. Certainly, grazing may have effect on the quantitative distribution of phytoplankton. Marked impact of phytophagous organisms on the abundance of phytoplankton during summer blooms is possible only under high concentrations of phytoplankton-feeders at particular locations, as we showed early for the krill. Seasonal changes in phytoplankton numbers over the vast water expanse under the study may be described and explained only in very broad outline. The difference in the abundance of phytoplankton and concomitant parameters is especially great if compared between summer and winter estimates.

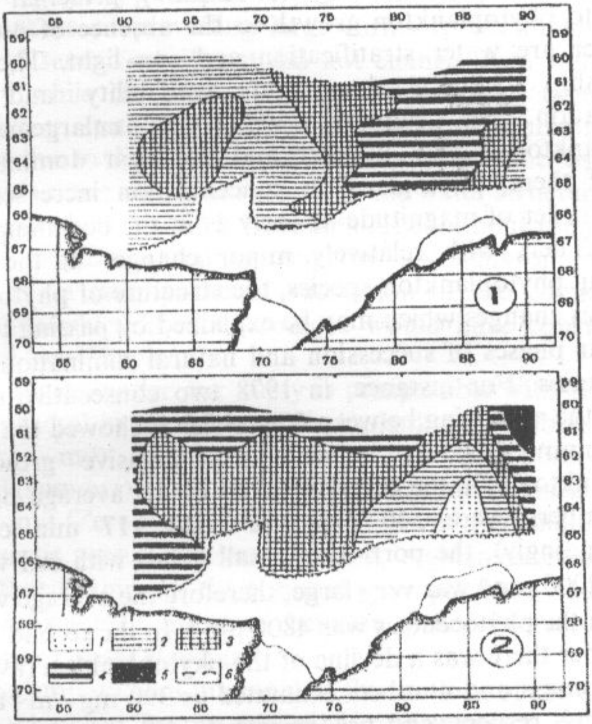

Fig. 29. The distribution of phytoplankton biomass (1) and phytoplankton diversity indices (2) as averaged for 0-100 m layer (January 1980).

1: 1 - < 100; 2 – 100-500; 3 – 500-1000; 4 – 1000-2000; 5 - > 2000 mg · m^{-3}; 2: 1 - < 1.0; 2 – 1.0-1.5; 3 – 1.5-2.0; 4 – 2.0-2.5; 5 - > 2.5 bit · ind^{-1}; 6 – ice-edge

In the case referring to the area stretching between 30 and 60° E, the species diversity was relatively limited and the dominance of particular species less pronounced; however mean biomass and numbers of the phytoplankton in 0-100 m layer were 34 mg · m^{-3} and 6.4 mln cell·m^{-3}, correspondingly.

Due to the recurrent renewal of succession in the community mean cell volume is not large (5300 μm^{-3}); principal limiting factors to phytoplankton growth in the absence of numerous consumer are water stratification and sun light. There is a relationship between day light availability and water stratification. In summer, with the enlargement of phytoplankton species number and the clear dominance of some of them, phytoplankton concentration increases more than an order of magnitude as early as in the beginning of the season. Then, with relatively minor changes in the set of prevailing phytoplankton species, the structure of phytocenosis undergoes changes which may be explained by passing through particular phases of succession and natural elimination of the mass species. For instance, in 1978 two consecutive surveys made in the area lying between 60 and 75° E showed that in the early summer (January), whit the intensive growth of phytoplankton (for the layer of 0-100 m the average biomass and numbers were 560 mg · m^{-3} and 117 mln cell·m^{-3}, correspondingly), the portion of small forms with cell volume to 1000-2000 μm^{-3} was very large, therefore the average volume of cells in the phytocenosis was 4800 μm^{-3}. In the second half of the summer there was a decline of the phytoplankton (averages of the biomass and numbers estimated as 390 mg · m^{-3} and 46 mln cell·m^{-3}, respectively) predominantly due to species which had been prevailing in the first half of the summer. Simultaneously, the set of minor species changed also; the index of phytocenotic diversity slightly grew (from 3.9 to 4 bit), the large cell fraction ($10^4 - 10^5$ μm^3) considerably increased mostly owing to the dominant species, and mean cell volume increased almost twice (8500 μm^3).

The described changes of the phytoplankton structure were developing in the area when the main consumers – krill and macrozooplankton – were very abundant, and the regional water structure was also changing. The effect of each of the factors may be assessed only approximately. For example, taking into consideration that grazing of the phytoplankton by the krill and mesozooplankton accounts far a small part of the computed primary production (see Chapters IV and IX) and that the share of prevailing large forms (predominantly *Rh. hebetata f. semispina*) almost did not change from January to February while the total numbers dropped two times, it is reasonable to state that total phytoplankton elimination was primarily due to die-off of those large forms and the dispersion of phytoplankton owing to changes in the water structure in the area. Conclusions by N.M. Voronina (1984) about the possible effect of phytoplankton grazing by zooplankton may be justified for a later phase of succession of the communities when the production of microalgae would have considerably decreased (see Chapter IX).

The region under our study is comparable with Antarctic zone in general in averages of phytoplankton numbers (about 550 mg · m^{-3}) calculated from many-year observations. Seasonal (summer) mean of the phytoplankton biomass is from 480 mg · m^{-3} (Zernova, 1983) to 600 mg · m^{-3} (Voronina, 1984) for Antarctic zone. However, from our regular observations it follows that in summer the regional phytoplankton abundance may conspicuously fluctuate between years in response to alterations of water structure.

The amplitude of interannual fluctuations of the numbers of phytoplankton in the region during summer period far exceeds the amplitude of intraseasonal fluctuations of a particular year, reaching 300% (Fig. 30). Interannual distinctions in the abundance cannot be explained by different condition of phytoplankton succession in different months: as the amplitude of these distinctions does not differ between the first and the second half of summer period. Taking into consideration that phytoplankton grazing by phytophagous organisms is insignificant during these months (Chapter IX), the fluctuations may be explained by fluctuations of the abiotic background, primarily by factors which determine the level of phytoplankton accumulation – shallow position of pycnocline and the presence of stationary gyres. The optimal combination took place in 1979 and in 1982. A pertinent illustration may serve our observations of a meridional transection along 75° E (Fig. 28). High turbulance of the field and the related shallow

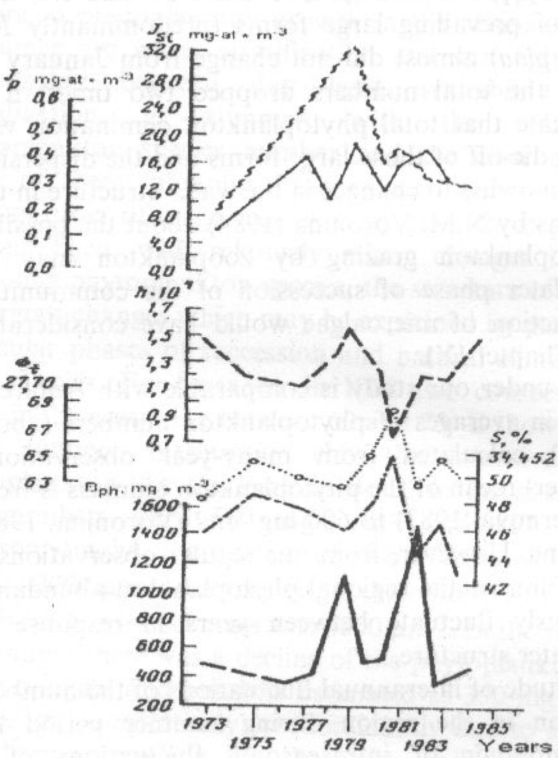

Fig. 30. The interannual variability at the Sea of Commonwealth.
1 – the biomass of phytoplankton in 0-100 m layer (B_{ph}); 2 - salinity (S, ‰); 3 – specific density (σ_t); 4 – homogeneity index (h – 104) for 0-500 m layer; 5 – the content of phosphates consumed by phytoplankton (J_p); 6 – SiO_2 consumption (J_{si}) by phytoplankton in photic layer.

position of pycnocline predetermined the events of phytoplankton accumulation in 1979 and 1982 when the average biomass in 0-100 m layer was 1300 and 1500 mg · m-^{3}, correspondingly. In 1981, when the condition were less favourable, the phytoplankton biomass average was only 480 mg· m^{-3}.

There is one more associated factor which also accounts for the extent of phytoplankton growth and explains the mechamism of the accumulation. It is the intensity of vertical water mixing above seasonal pycnocline. Owing to the intensive vertical mixing phytoplankton cells stay in well-illuminated water layer longer than when water stratification is steady and phytoplankton inevitably sinks to dark depth under the force of gravity. Simultaneously, nutrients are carried out from less illuminated depths of the photic zone to waters receiving more light. As the result, the biomass of phytoplankton is increasing more efficiently. The influence of the described factor on interannual variability of quantitative characteristics of the phytoplankton reveals itself as relationship between phytoplankton biomass estimates with values of the intensity of vertical water mixing, which is inverse to average salinity and water density estimates and direct to the index of water homogeneity for 0-500 m layer (Fig. 30; see also Bryantsev, Sobolev, 1983). Thus, in Antarctic zone the well-recognized dependence of phytoplankton abundance on water stratification and sun light availability is not in essence as obvious as it is traditionally believed to be. Manifestations of this relationship depend, in their turn, on the availability of several positive factors which are 1) shallow-lying pycnocline, 2) the development of a system of stationary gyres obstructing the drift and dispersion of reproducing phytoplankton, and 3) the intensity of vertical mixing of water masses above pycnocline. Certainly, these specific details account for successful realization of the debated relationship and also for phytoplankton abundance in Antarctic zone.

CHAPTER III
PRIMARY PRODUCTION

Many authors addressed the problem of phytoplankton production in Antarctic. The rewiev of the most significant works was made by N.M. Voronina (1984). Analysis of the literature available had elicited an annoying discord between the measurements and computations of the primary production in this geographical region. Depending on the spatial and temporal scale, estimates of the primary production differ 2 – 3 orders of magnitude. Annual phytoplankton production in the Southern Ocean evaluated by different authors differs an order of magnitude (from 16 to 180 g C · m^{-2}, cited from Voronina (1984). Therefore, discussion of the results available will lead to nothing unless the aspect related to methods and techniques is given due concern.

Many researchers underlined the possibility of underestimating primary production in the ocean when the study was made applying radiocarbon bottle method (see in Y.I. Sorokin, 1971 a). Causes which generate the errors may be divided into two groups: 1) those due to measuring procedure, and 2) those related to the reliability of sampling. Y.I. Sorokin supposed that the elicited errors might eventuate in 3 – 4 times as large distortion of the annual primary production. In the opinion of O.I. Koblentz-Mishke and V.I. Vedernikov (1977), the procedure-related errors in primary production measuring by ^{14}C bottle method are not as large as that.

Underestimation of the primary production in the tropical Atlantic as considerable as 4 – 10 times is associated with the use of small-volume (< 4 l) bottles and long (12 h) exposure time (Gieskes et al., 1979; Baars, 1980). However, experiments conducted in coastal waters of South Africa with 125- to 1000-ml bottles had shown little difference in the corresponding results of phytoplankton production measurements (Brown, 1982). Similar results were obtained during determination of primary production by oxygen method in a hypereutrophic lake (Berger, 1984). Data of primary production measurement are influenced by the type of glass of culture bottles (Smith, Baker, 1980; Worrest et al., 1980). According to Smith and Baker, biology effective dose of UV radiation decreased by 6% when quartz glass was used, by 13% in case of pyrex and by 22% in case of viton glass bottles. In the experiments the effect of glass reduced with greater depth. Worrest and his co-authors also pointed out different ultraviolet permeability of the examined types of glass; the assimilation of radiocarbon by the culture of the diatom *Thalassiosira pseudonana* in quartz, pyrex and glass bottles depended on the type of illumination. Under illumination with white luminescence lamp the assimilation developed evenly independent of the type of glass of the bottles; under combined illumination (a sun-light lamp and a system of UV (290-320 nm) filters) it was different depending on the sort of glass. Comparing the amount of carbon uptaken by phytoplankton and determined by direct measurement of method, a team of researchers (Öquist et al., 1982) arrived to a conclusion that ^{14}C method underestimated carbon assimilation in phytoplankton with high respiration rate. Pertinent experiments revealed distinctions in phytoplankton production depending on light (Hitchcock, 1980; Krupatkina, 1980; Perry et al., 1981; Marra, Heinemann, 1982; Harding et al., 1982), the content and composition of nutrients (Slawyk, 1979; Terry, Caperon, 1982 a, b) and some other factors (Holm-Hansen, 1987; Rivkin, 1987; Spies, 1987); discarding these factors would lead to incorrect results.

Thus, the contradiction between the primary production data in Antarctic and in the World Ocean roots in the lack of a common approach to the problem. Similar situation was met in estimating phytoplankton production by means of oxygen bottle method (Ivanenkov, 1983). A number of methods were proposed as an alternative: marking additional measurements of some physiological characteristics of phytoplankton coupled with phytoplankton production determination (Eppley, 1981), evaluating total oxygen production in water body (Ivanenkov, 1983), employing computation methods for phytoplankton production assessment from data about chlorophyll content, light and temperature (Smith, 1980) of from the estimate of chlorophyll fluorescene (Öquist et al., 1982).

In course of our investigation we have also faced the problem of primary production underestimation when determining the production by radio-carbon method. In order to approximate the phytoplankton production estimates close to real, the computation was made using two ways – by employing a mathematical model by L.A. Vinogradova and L.P. Fetisov (1986)* and from the replenishment of particulate organic matter (POM) during the summer in the studied region.

Material and methods

Materials were collected during three oceanographic surveys conducted at the basic area during 1 – 26 January 1980, 1 February – 7 march 1981 and 20 December 1982 - 14 January 1983, respectively.

Primary production was determined by modified radiocarbon method (Newhouse, 1967).

Model estimation of the primary production was made based on a survey conducted at the Commonwealth Sea in the season of 1982/1983, the POM replenishment was evaluated from the regional observations during 1980-1985 (see Chapter VIII).

Results and discussion

During the years of the study of primary production oceanographic and hydrobiological conditions and the light conditions during phytoplankton growth differed insignificantly over the region; all essential characteristics of

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* The corresponding calculations cited in this book are owing to the courtesy of L.A. Vinogradova and L.P. Fetisov.

plankton (except krill biomass and stock) were within the range of averages derived from many-year observations. In January 1980 the depth of photic layer was 53 m on the average, varying from 39 to 78 m; in February – March 1981 and in December 1982 – January 1983 the averages were 45 and 44 m, correspondingly, with the variation from 36 to 52 m and from 20 to 90 m, correspondingly.

Daily primary production estimates differed only inconsiderably between the years. In January 1980 the primary production varied from 68 to 314 mg C · m^{-2} in photic layer at some stations, in February – March 1981 it was from 46 to 506 mg C · m^{-2} and in December 1982 – January 1983 from 28 to 314 mg C · m^{-2}, with the average of 150, 140 and 136 mg C · m^{-2} · d $^{-1}$, correspondingly. Similar situation was found about high primary production. The percentage of stations with primary production estimated < 100, < 200 and < 300 mg C · m^{-2} · d $^{-1}$ was 35-40, 15-20 and 5-10%, correspondingly.

These estimates agree with Antarctic phytoplankton production measured by some researchers (Klyashtorin, 1964); at the same time, they are lower than given in Kabanova et al. (1974) and Jacques et al. (1982), and substantially (6 times on the average) lower compared with cited in El-Sayed (1966). Inasmuch as errors related to determination technique of radiocarbon method are not too serious, it is logical to assume that the conspicuous difference between data given by several authors for a particular area, as well as too wide amplitude of fluctuations of the measured parameters, are caused by natural factors (using more accurate terms, it is the degree of natural factors realization during the period of measuring). In Antarctic zone factors of utmost significance are light, water stratification and the abundance of phytoplankton (El-Sayed, 1966).

Let us investigate how strong is the effect of these factors on primary production estimates in our case.

Over the entire region, during the late spring – the early summer (December – January)*, when the first phase of phytoplankton succession goes to the end and the second phase begins, maximums of the primary production concentrated in the layer with 50% illumination (Fig. 31, 1), i.e. the light was not a limiting factor for phytoplankton growth at that time. In the mid- and late summer (January and February – March, correspondingly) the photic optimum zone lifts up to the surface. In the first case, this conforms with the succession phase: plankton is dominated by large-size forms for which the adaptation to the high light intensity favours better growth in comparison with small forms (Krupatkina, 1980). In the second case, despite the predominance of small diatoms (the first stage of the second succession) the zone of photic optimum was also in the subsurface water in conformance with the reduction of solar radiation (PAR) 1.5 times on the average and with the three time increase of POM content (which is also associated with the light conditions) in comparison with early-summer estimates (see Chapter VIII). As it has been shown before, primary production estimates measured at different spans of the vegetation season differed insignificantly over the region, while the numbers of phytoplankton in the mid- and late summer was 1.5 times as large as that in the beginning of summer. Correspondingly, the daily P/B ratios differed as 0.19 in the early summer vs 0.13 in the mid- and late summer. At some stations the relation between the distribution of primary production estimates and factors influencing them is even more complicated, that is explained by asynchronous course of the processes going at different locations of the investigated region. As the stage of intensive growth comes to the end (usually in the north of the area which is among first getting clear of ice) with the abundance of phytoplankton and high solar radiation,

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* The similarity of regional oceanographic conditions during the years of our studies and the regular changes in seston components give a reason for considering these as a seasonal phenomenon.

the production is relatively low (Fig. 31, 2; stations 45/217, 31/203). Large diatoms predominate (second phase of the succession); daily P/B ratios are not high, being generally characteristic of background ones for the photic layer and dropping to around one-thousandth when the phytoplankton sank to depths with 1% -illumination. Knowing about the associated high concentrations of phosphorus and silicon (50-70 and 1000-2000 μg $\cdot$ l^{-1} and more, correspondingly), it may be hypothesized that among limiting factors might also be iron and microelements as it was in locations with intensive upwelling events (Koblentz-Mishke, Vedernikov, 1977).

Conversely, at early stages of the growth, which were most frequently found in the south close to the ice-edge, the level of measured primary production kept high under moderate light conditions (Fig. 31, 2; stations 21/191, 40/212). From these examples it is evident that at the station 21/191 the first stage of the first succession (small diatoms dominated the phytoplankton) was registered: despite very low biomass of the phytoplankton cells their production in photic water layer was 3 times as large as at the station 45/217 (10.2 vs 3.4 mg $C{\cdot}m^{-3}$, correspondingly), and the daily P/B ratio was 24 times as large (5.05 vs 0.21, correspondingly). At the station 40/212 succession phase was more advanced (the final of the first – the beginning of the second) in comparison with the station 21/191, the biomass was considerably greater. Accordingly, primary production estimates were also high and exceeded those in the photic layer at the station 45/217 4.7 times (15.7 vs 3.4 mg $C{\cdot}m^{-3}$, correspondingly); the daily P/B ratios, however, differed only 2 times (0.40 vs 0.21, correspondingly).

Manifestations of the absence of formal linkage between the primary production estimates on the one hand and the abundance of phytoplankton and the intensity of solar radiation on the other hand were also noticed at some stations in December – January when the maps showing distribution of the corresponding estimates were drawn. In the end of the summer, with the reduction of solar radiation, the map of

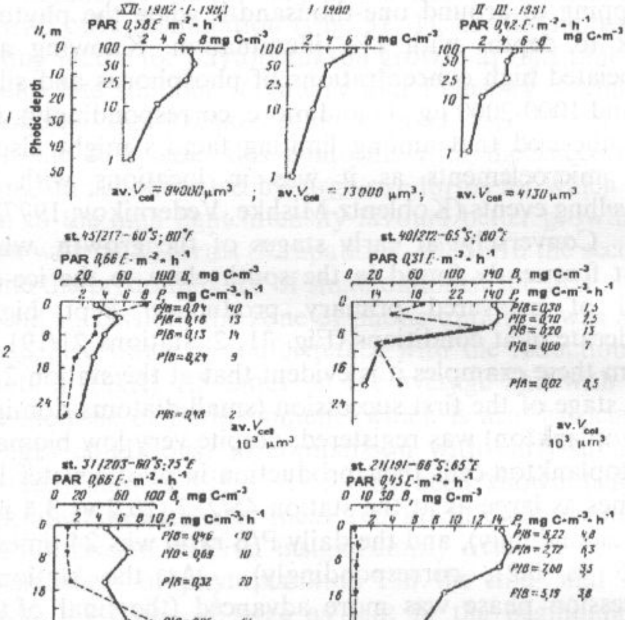

Fig. 31. Vertical distribution of the quantitative characteristics of phytoplankton (production – P, mg C · m⁻³ · d⁻¹, biomass – B, mg C · m⁻³, cell volume and sea surface illumination – J, E·m⁻²·h⁻¹) for the entire region during the summer (1) and at the stations with typical phytocenoses in December 1982 – January 1983 (2).

Photic depth – as per cent of the illumination on the surface.

primary production distribution well agreed with the distribution of PAR estimates in the surface but, as in the early summer, had nothing in common with the map of phytoplankton biomass distribution.

The fact that the low values of primary production couple with the high phytoplankton numbers leads to a suggestion that the level of primary production in Antarctic waters is determined by short-time outbreaks of phytoplankton in locations at which favourable conditions (light intensity, water stratification) have developed. The possibility of detection of such maximums is extraordinary low because of too extended term of the surveys and huge distances between the stations. Therefore in the majority of cases the rate of phytoplankton production was measured at phases of succession more or less "temporally remote" from the peak (outbreak). The measured production estimates are closely related with the extent of this remoteness. Possibly, the substantial difference found between primary production measurements (which are predominantly underestimates) cited by different authors for one and same water area is due to different degree of realization of error (deviation) factors discussed above, i.e. due to the degree of incorrectness of the samplings.

Values of the primary production calculated by means of a mathematical model varied in a broad range, much broader than that of the measured estimates. It was noticed that the calculated estimates were lower than the measured only in those rare cases when the measurement was made in locations with the intensive photosynthesis observed at the initial phase of phytoplankton succession, for instance, at the already mentioned stations 21/191, 40/212 (Table 8). Conversely, in locations with high biomass and low photosynthetic rate (as the measurements showed), where the phytocenosis went through the second or third phase, computed values of the primary production were larger than measured maximums (stations 31/203, 45/217). In all other cases the computed estimates always exceeded those measured, the degree of the difference

Table 8

The comparative characteristic of measured and calculated daily estimates of the primary production for stations given in Figure 31

Station NN	Sampling depth, m	Primary production				The ratio of calculated to measured production	
		measured		calculated			
		at the sampling depth, mg C · m^{-3}	in the photic layer, mg C · m^{-2}	at the sampling depth, mg C · m^{-3}	in the photic layer, mg C · m^{-2}	at the sampling depth	in the photic layer
21/191	0.0	14.55	315	21.70	165	1.49	0.5
	4.7	15.37		22.90		1.49	
	9.5	14.60		2.24		0.15	
	15.5	9.20		4.82		0.52	
	31.0	4.88				0.04	
40/212	0.0	25.85	314	8.21	117	0.32	0.4
	3.0	26.61		8.45		0.32	
	6.0	25.62		21.14		0.83	
	10.0	14.43		0.68		0.05	
	20.0	0.97		0.08		0.08	
31/203	0.0	4.64	195	182.30	3227	39.29	16.6
	7.0	7.26		285.27		39.29	
	14.0	4.92		32.78		6.66	
	23.0	5.25		20.08		3.82	
	46.0	0.63		0.75		1.19	
45/217	0.0	3.14	93	249.87	2567	79.58	27.5
	4.0	5.70		453.60		79.58	
	8.0	4.22		36.90		8.74	
	13.5	3.2		7.86		2.46	
	27.5	1.87		0.09		0.05	

depended mainly on phytoplankton abundance. Therefore, the map showing the calculated phytoplankton production distribution coheres with that of the phytoplankton biomass distribution. Thus, the computed estimates better represent the level of primary production as it was in the recent past than by the moment of sample taking.

For the estimates fluctuating from 0.14 to 27.5 average ratio between calculated estimates of the primary production and measured in photic layer of the area covered by the survey was 7.5; without the stations at which this ratio was less than 1.0 the average was 9.4 (Table 9).

The reliability of the calculated values was also proved by results of tentative evaluation of the rate of POM replenishment in the region owing to phytoplankton (even without the portion assimilated by consumers). For the seasonal surveys (1980, 1981 and 1982-1983), when owing to the similarity of environmental conditions the structure of the regional community also displayed relative similarity (see Chapters I, II, IV – VIII), computed values of the primary production and POM replenishment were within the same range. In the season of 1983-1984, POM replenishment was only 4 times as high as the average of measured phytoplankton production. The generally low POM content and accumulation rate during the season of 1983-1984 were related to reduced phytoplankton stock in the region that was because of excessive phytoplankton transport with the currents. This eventuated, in particular, in a drastic drop of mesozooplankton biomass in this season (Chapter V).

Similar discrepancy between measured and calculated primary production was also revealed for Antarctic (Slawyk, 1979) and tropical (Baars, 1980) waters. Employment of the method of total oxygen production assessment yielded similar results (Ivanenkov, 1983). Such a coincidence of results suggests that the knowledge which has been gained by now about the primary production of the World Ocean through the traditional radiocarbon or oxygen measurements (this also

Table 9

Average estimates of the primary production obtained through different methods and the replenishment of POM (mg C · m^{-2} · d^{-1}) at the Commonwealth Sea

The date of survey	Primary production estimates in the photic layer		POM replenishment owing to phytoplankton [•] in 0-100 m water layer
	measured by ^{14}C-method	computed from a model	
20.XII 1982 - 14.I 1983	136	1280	-
1-26.I 1980	150	-	1300[i]
1.II – 7.III 1981	140	-	2530
2-24.XII 1983	126	-	-
2-26.II 1984	41	-	330

refers to the method of pigment content measurement) is based predominantly on underestimation; hence, it is far from truth. The amplitude of differences between the factual and measured estimates is very large and looks similar in all the authors who dealt with huge data sets. The discrepancy between data given

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[•] Without the portion of consumed phytoplankton which had been assimilated by heterotrophic organisms by one or another researcher may be explained by a number of possible technical errors. What is of much greater significance is the very fact that the considerable discrepancy between measured and actual primary production has been elicited.

In this context it is interesting to compare our data in this field with those cited in other authors as comparable in the range. Our estimate of the actual primary production averaged for the growth season in the region as 1500 mg C $\cdot$ m^{-2} $\cdot$ d^{-1} most closely approximates that given in El-Sayed (1966) which is only 1.5 times as less as ours.

Proceeding from this estimate (1500 mg C $\cdot$ m^{-2} $\cdot$ d^{-1}) it is easy to compute the overall summer production in the region:

1.5 mg C $\cdot$ m^{-2} $\cdot$ 100 d^{-1} = 150 mg C $\cdot$ m^{-2}.

In essence, this estimate approximates that per year because the ice-cover lies over most of the region, including coastal and AD zones. At the same time, it may be presumed that in ice-free part of the region primary production will be lower in winter than in summer (that is inconsistent with phytoplankton numbers, because the phytoplankton is continuously carried away to depth and therefore cannot be measured precisely. Nevertheless, this part of the region contributes only insignificant share in total regional phytoplankton production. Assuming that the average daily production is 10 times less in winter than in summer, and knowing that this water area makes up 25% of the regional, the portion contributed to the total production for the rest of a year is 10 g C $\cdot$ m^{-2}. Then total annual primary production in the region is 160 g C $\cdot$ m^{-2}, that is within the range of known estimates (16-180 g C $\cdot$ m^{-2}) and close to the maximum of 50-180 g C $\cdot$ m^{-2} according to Sorokin (1973).

CHAPTER IV

BACTERIOPLANKTON: CONCENTRATION, PRODUCTION, BACTERIAL DESTRUCTION

The knowledge about quantitative characteristics of bacterioplankton from Antarctic zone of the ocean was and is regrettably insufficient.

Studies undertaken by some researchers (Melnikov, 1972; Kriss, 1973; Mitskevich, Kriss, 1975) have demonstrated that bacterial numbers and heterotrophic activity are extremely low in Antarctic waters. According to these authors, in surface water of Antarctic bacterial content was estimated as about $4 \cdot 10^3$ cell·ml^{-1}, biomass about 0.1 mg C· m^{-3} and production (from biomass measurements) 0.03 mg C· m^{-3} that is two orders of magnitude less than in mesotrophic boreal waters of the ocean.

Critical revision of these data was given by Y.I. Sorokin and V.K. Fyodorov (1978). They explained the considerable underestimation by errors related to technical aspects; in particular, by bacterial losses at filtering onto membrane filters. The abundance and biomass determined from direct bacterial counts on membrane filters for the Antarctic zone at the transects along 148 and 158° E in January varied within 30-$175 \cdot 10^3$ cell·ml^{-1} and 0.8-2.1 mg C· m^{-3}, correspondingly; the production measured by radiocarbon method made up 10-20% of the biomass.

According to Hanson (1980), the numbers and biomass of microorganisms measured in January in the surface of the Drake Passage were 10-30 $\cdot 10^3$ cell·ml^{-1} and 20-30 ng ATP·l^{-1}, correspondingly; deeper, at 50 and 100 m these parameters were three times as high. Below 200-m depth bacterial biomass decreased to 5 ng ATP·l^{-1}. Heterotrophic activity of the microflora was generally three orders of magnitude as less as that in temperate zone of the ocean.

In a later work by Hanson and co-authors (1983) estimates differed from those above; by the end of Antarctic winter maximum bacterial abundance and the frequency of dividing cells were 200-350 $\cdot 10^3$ cell$\cdot$ml^{-1} and 11%, respectively, in waters of Antarctic Divergence; north of the Polar front they were 100-200 $\cdot 10^3$ cell$\cdot$ml^{-1} and 3-5%, correspondingly. In the Drake Passage bacterial concentration was 2-3 times as large as that. The corresponding maximums ($1 \cdot 10^6$ cell$\cdot$ml^{-1} and 16%) were measured south of the Polar front and near the ice-edge. In the south-eastern Pacific, bacterial production varied from 0.62 to 4.1 µg C-l^{-1} and in the Drake Passage from 2.6 to 17.1 µg C-l^{-1} a day. Bacterioplankton production made up 15-45% of primary production.

Similar results were reported later for these and other water areas of Antarctic (Bailiff et al., 1987; Mulling, Priddle, 1987; Delille et al., 1988).

Our study of Antarctic bacterioplankton focused primarily on determining the abundance, biomass, production and the decomposition of organic matter by bacteria.

Material and methods

In the basic region material was collected during oceanographic surveys, simultaneously with making measurements of primary production in 1980-1983 (Chapter III). In 1980 and 1981 we measured bacterial production; during the season of 1982-1983 samples of bacterioplankton were also taken in order to assess its numbers and biomass. In our investigation we also used material collected in 1981 for quantification of bacteria and for evaluation of their production in the Atlantic sector of Antarctic.

Samples collected taken from 100, 25 and 1%-illuminated depths in the main region; in the Atlantic sector they were also taken from 50 and 10%-illuminated water layers. Over the main region bacterioplankton was studied at each of the depths separately, in the Atlantic sector equal portions of samples from different depths were mixed in different proportion before examination.

Total bacterial abundance was assessed from direct count according to A.S. Razumov (1932, 1955) on Synpore membrane filters with the pore size 0.1-0.3 μm. In determining bacterial production we used radiocarbon method by V.I. Romanenko (Romanenko, 1964; Romanenko, Kuznetsov, 1974).

During the season of 1982 - 1983 at some stations size fraction predominant in the bacterioplankton was determined through simultaneous measurement of bacterial production in sea water samples to different degree purified of seston. One set of samples was obtained from filtering the sea water through capron sieve N 70 (≤ 70 μm fraction); another was first filtered through the sieve N 70 and then through Nucleopore filter with the pore size 2 μm (≤ 2 μm fraction). Relative share of these fractions was defined from the result of radioactivity measurements.

Assuming that K_2 is 0.32 (Sorokin, Mamayeva, 1980), bacterial destruction was determined from the equation proposed by these authors:

$$D = P \times 2.125,$$

where D is destruction and P – production.

In converting bacterial biomass expressed as wet weight and organic carbon content we used coefficient 10 (Troitskiy, Sorokin, 1967). In the final analysis we also employed materials gathered during other observations and surveys conducted in the research cruises.

Results and discussion

In the basic region and in the Atlantic sector of Antarctic bacterioplankton consisted mostly of cocci, rod-like forms had always been within 10% of the bacterioplankton abundance in the series of samples examined.

Bacterial heterotropic activity measured in parallel samples filtered through the sieve N 70 and Nucleopore filters almost did not differ (Table 10); the radioactivity fluctuated within ± 25%, or 14.5% on the average. Values of the deviation were within the limits of radiocarbon method accuracy. All this

Table 10

The heterotrophic activity of bacteria in the seawater samples having been filtered through sieve N 70 (A) and Nucleopore filters (B) at the Commonwealth Sea

Latitude S°	Longitude E°	Depth of sampling, m	Radioactivity Imp·min^{-1}		The deviation of A from B, %
			A	B	
63°00	55° 00	0.0	25.3	21.0	+20.5
		18.0	25.3	28.4	-10.9
		62.0	15.7	14.5	+7.6
65°00	“ – “	0.0	16.6	18.6	-12.0
		14.0	9.3	10.6	-14.0
		46.0	9.3	11.0	-18.3
66°00	60° 00	0.0	11.6	14.2	-22.4
		12.5	10.9	8.2	+24.8
		39.0	7.2	9.0	-25.0
67° 00	70° 00	0.0	9.8	10.5	-7.1
		9.5	18.2	19.2	-5.5
		31.0	30.2	25.5	+15.6
65°00	“ – “	0.0	26.8	32.5	-9.8
		11.6	33.2	35.5	-6.9
		39.0	24.2	22.8	+5.8
62°00	“ – “	0.0	36.2	34.1	+5.8
		14.0	22.1	27.4	-24.0
		46.0	30.2	29.2	+3.3
60°00	75° 00	0.0	16.3	17.7	-8.6
		14.0	15.6	17.3	-10.9
		46.0	27.2	24.4	+8.1
63° 00	“ – “	0.0	6.7	5.5	+17.9
		6.0	14.8	12.8	+13.5
		20.0	10.2	12.8	-23.5
65° 00	80° 00	0.0	13.0	15.3	-17.7
		6.0	30.0	26.7	+11.0
		20.0	27.0	23.3	+13.7
60° 00	“ – “	0.0	13.7	13.0	+5.1
		8.0	15.3	12.5	+18.3
		27.5	38.3	40.0	-4.4
61° 00	85° 00	0.0	6.0	5.5	+8.3
		10.0	6.0	7.0	-16.7
		33.0	17.0	20.1	-24.1

indicates that in the studied photic water layer size fraction up to 2 μm large dominated the bacterioplankton.

From the determinations, in some samples quantitative characteristics of bacteria from the Commonwealth Sea varied in December – January 1982-1983 very broadly – the abundance from 150 to $1770 \cdot 10^3$ cell·ml^{-1}, the biomass from 6.0 to 40 mg C· m^{-3}, the daily production from 0.07 to 3.49 mg C· m^{-3}, the daily P/B coefficient from 0.02 to 0.31, the daily bacterial destruction from 0.15 to 7.42 mg C· m^{-3}. Estimates for the stations positioned in photic layer (Table 11) differed to lesser extent, with 5 times as large difference between extreme values, and 2-3 times difference in the majority of cases. Averaged for the region, the abundance of bacteria was $427 \cdot 10^3$ cell·ml^{-1}, the biomass 9.8 mg C·m^{-3}, or 438 mg C· m^{-2} in the photic layer; the daily production 1.09 mg C· m^{-3}, or 50 mg C· m^{-2}; the daily P/B coefficient 0.12, and the bacterial destruction 2.3 mg C·m^{-3}, or 104 mg C·m^{-2} a day.

Maximums of the abundance and production of microorganisms concentrated above seasonal pycnocline in the zone of Antarctic divergence (Fig. 32). When the pycnocline was not well-developed and when it was situated deeper than usual (that was usually north of the border line of the front), bacterial abundance and production decreased 2-5 times and more, remaining the same or changing insignificantly with increase of depth. Then the typical estimate was about 100-$200 \cdot 10^3$ cell·ml^{-1}.

In the Atlantic sector, quantitative characteristics evaluated in 1981 (Table 12) were not as high as those in the Commonwealth Sea in December 1982 – January 1983. However, the range within which estimates fluctuated was very similar. Average bacterial abundance was $313 \cdot 10^3$ cell·ml^{-1}; biomass 9.7 mg C·m^{-3}, or 425 mg C· m^{-2}; daily production 0.85 mg C·m^{-3}, or 37.5 mg C· m^{-2}; P/B coefficient 0.09, and bacterial destruction 1.8 mg C·m^{-3}, or 80.0 mg C· m^{-2} a day.

Bacterial production at the Sea of Commonwealth in January 1980 and in February 1981 was even higher than the cited. In 1980 and 1981 its average estimate for the photic layer

Table 11

The content and production of bacteria and the bacterial destruction in photic layer of the Commonwealth Sea (December 1982 – January 1983)

Latitude S°	Longitude E°	Abundance, $1 \cdot 10^3$ cell·ml^{-1}	Biomass, mg C·m^{-2}	Production		Daily P/B coefficient	Destruction, mg C·m^{-2}
				mg C·m^{-2}·d^{-1}	mg C·m^{-3}·d^{-1}		
61°00	55°00	336	514	40	0.64	0.08	85
63°00	“ – “	426	540	100	1.62	0.19	213
65°00	“ – “	249	283	35	0.77	0.12	74
66°00	60°00	289	273	30	0.77	0.11	64
64°00	“ – “	414	372	27	0.70	0.07	57
62°00	“ – “	214	347	23	0.35	0.07	49
“ – “	65°00	320	734	37	0.41	0.05	79
63°00	“ – “	617	1146	99	1.38	0.09	210
66°00	“ – “	643	513	22	0.71	0.04	47
67°00	70°00	354	270	44	1.42	0.16	94
65°00	“ – “	579	544	82	2.10	0.15	174
62°00	“ – “	545	360	72	1.55	0.20	153
60°00	“ – “	282	500	64	0.82	0.13	136
“ – “	75°00	405	425	63	1.38	0.15	134
63°00	“ – “	621	290	16	0.79	0.06	34
66°00	“ – “	429	432	54	1.38	0.13	115
65°00	80°00	409	234	34	1.70	0.15	72
62°00	“ – “	550	403	31	1.13	0.08	66
60°00	“ – “	553	408	74	2.70	0.18	157
61°00	85°00	267	221	24	0.73	0.11	51
63°00	“ – “	776	695	101	2.81	0.15	215
65°00	“ – “	297	253	21	0.64	0.08	45
Average		427	438	49	1.09	0.12	104

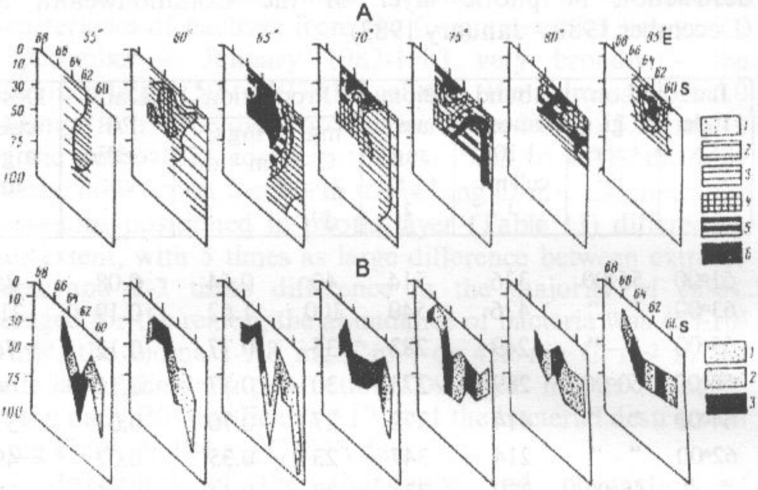

Fig. 32. The distribution of bacterioplankton abundance (A) and the position of the maximums of specific density gradient (B) in meridional sections at the Commonwealth Sea (December 1982 – January 1983).

A: 1 - < 200; 2 – 200-300; 3 – 300-400; 4 – 400-500; 5 – 500-600; 6 - > 600 thousand cell·ml^{-1}

B: 1 < 0.01; 2 – 0.02-0.03; 3 - > 0.03 conventional unit σ STP·m^{-1}.

was almost identical – 85 and 88 mg C· m^{-2}· d $^{-1}$, correspondingly; calculated per 1 m^3 it was 1.6 mg C in 1980 and 2.0 mg C in 1981; the range of fluctuation of individual estimates obtained was also very wide. Average biomass of bacterioplankton computed with the employment of the P/B coefficient equal 0.1 was 16.0 mg C· m^{-3}, or 720 mg C· m^{-2} in January 1980, and 20.0 mg C· m^{-3}, or 900 mg C· m^{-2} in February 1981.

In assessing quantitative characteristics of bacterioplankton in Antarctic zone on the whole, special

Table 12

The content and production of bacteria and the bacterial destruction in Antarctic zone of the Atlantic Ocean

Date	Latitude S°	Longitude E°	Sampling depth, m	Abundance, $1 \cdot 10^3$ cell$\cdot$ml^{-1}	Biomass, mg C$\cdot$m^{-2}	Daily production		Daily P/B coefficient	Daily bacterial destruction, mg C$\cdot$m^{-2}	Daily primary production, mg C$\cdot$m^{-2}	Sea water temperature (°C) at the surface (0 m)
						mg C$\cdot$m^{-2}	mg C$\cdot$m^{-3}				
1	2	3	4	5	6	7	8	9	10	11	12
25.01.81	58°30'	07°28'	0;4;8;14;28	153	128.8	20.1	0.72	0.15	427	237.1	1.02
28.01.81	63°00'	05°00'	0;4;8;14;28	234	196.0	23.7	0.85	0.12	50.4	183.3	1.42
31.01.81	65°22'	02°39'	0;4.5;9;14.5;29	106	92.8	20.4	0.70	0.22	43.4	385.3	1.89
4.02.81	68°13'	03°59'	0;5.5;11;18;36	305	331.2	12.4	0.34	0.04	26.4	210.1	1.16

1	2	3	4	5	6	7	8	9	10	11	12
8.02.81	60°05’	21°27’	0;6.5;13;22;44	307	404.8	20.6	0.47	0.05	43.8	291.6	0.54
11.02.81	55°32’	30°15’	0;6;12;19.5;39	131	152.1	27.8	0.71	0.18	59.1	259.4	1.14
16.02.81	57°31’	32°59’	0;9;17.5;29;58	340	591.6	38.6	0.67	0.07	82.0	193.7	1.06
19.02.81	61°25’	32°50’	0;6;12;19.5;39	64	74.1	-	-	-	-	203.2	-0.10
22.02.81	68°47’	31°00’	0;4.5;9;14.5;29	474	411.8	14.1	0.40	0.03	30.00	217.1	-0.21
25.02.81	69°52’	07°02’	0;6.5;13;21;42	175	222.6	5.8	1.09	0.20	97.3	211.5	0.13
28.02.81	70°00’	02°59’	0;8.5;17;28;56	561	940.8	47.2	0.84	0.05	100.3	254.8	-1.42
9.03.81	69°10’	12°58’	0;7.7;15.4;26;52	648	1008.8	143.7	2.76	0.14	305.4	248.1	-1.29
13.02.81	64°24’	12°00’	0;8.7;17.4;29;58	571	974.4	35.0	0.60	0.04	74.4	90.5	1.26
Average				313	425.3	37.5	0.85	0.09	79.7	229.7	0.51
16.03.81	52°08’	14°00’	0;6;12;20;40	510	612.0	22.1	0.55	0.04	47.0	131.5	2.22
19.03.81	48°18’	07°50’	0;6.5;13;22;44	168	220.0	15.7	0.36	0.07	33.4	139.8	5.08
54.03.81	46°39’	07°02’	0;7;13;23;26	115	161.0	37.3	0.81	0.23	79.3	210.5	6.31
25.03.81	44°43’	03°53’	0;6.5;15;22;44	-	-	58.7	1.33	-	124.7	293.2	13.50
2.04.81	41°54’	01°10’	0;5;10;16.5;33	88	85.8	83.4	2.53	0.97	177.2	316.1	11.92
5.04.81	41°53’	01°08’	0;5.5;11;18;36	87	93.6	71.5	1.99	0.76	151.9	325.3	11.73

emphasis should be placed on a few aspects. In particular, with relatively low P/B coefficient, that is sea water, bacterial abundance in the areas under the study approximates that characteristic of mesotrophic waters and the biomass is comparable with that of mesozooplankton from Antarctic zone (Samyshev, 1983).

The data on the abundance and production generally agree with the later studies (Sorokin, Fyodorov, 1978; Hanson et al., 1983); at the same time, they imply that the estimates obtained may substantially fluctuate on the temporal and spatial scale depending on water productivity and the phase of community succession. In particular, higher quantitative characteristics at the Sea of Commonwealth in comparison with the Atlantic sector of Antarctic are owing to that the community of phytoplankton in the latter was at an earlier phase of succession. This distinction clearly indicates the correlation of bacterial and phytoplankton production: in the Atlantic sector the production of bacteria made up 16% of the primary production ; in the Commonwealth Sea it was estimated as 37.57 and 63% in December 1982 – January 1983, and in January 1980 - February 1981, correspondingly. Comparing between the maps of the distribution of bacterioplankton and other living components drawn in different years has shown inner logic in the position of maximums measured under particular state of the community. For instance, in December 1982 – January 1983 (Fig. 33) the bacterial maximums did not coincide with those of phytoplankton and primary production but they cohered with the zones of plentiful particulate organic matter. Maximums of all components composing seston were situated either along the periphery of cyclonic gyres or lower downstream. In January 1980 (Fig. 34), at the height of the summer season, peaks of bacterial production tended to coincide with maximums of primary production, phytoplankton biomass and POM. Characteristic features of the region were the relatively homogeneous field of currents, the predominantly eastward water transfer and formation of a huge cyclonic gyre only at the southern-central part. The transport of seston components

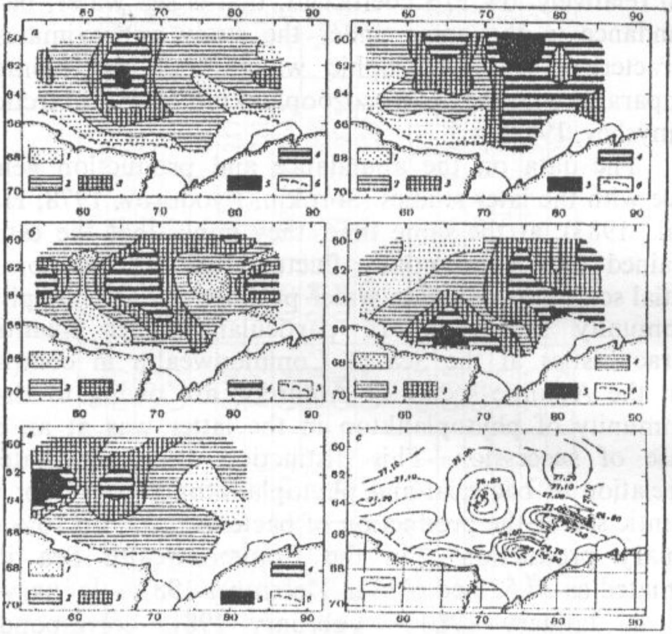

Fig. 33. Horizontal distribution of the bacterial biomass (a) and production (b), particulate organic matter (c), phytoplankton (d), primary production (e) in photic layer and the geostrophic circulation of surface sea water (f) at the Commonwealth Sea

a: 1 - < 300; 2 – 300-500; 3 – 500-700; 4 – 700-1000; 5 - > 1000 mg C·m^{-2} ; 6 – ice-edge

b: 1 - < 30; 2 - 30-50; 3 - 50-70; 4 - > 70 mg C·m^{-2}; 5 – ice-edge;

c: 1 - < 50; 2 – 50-100; 3 – 100-150; 4 – 150-200; 5 - > 200 g·m^{-2}; 6 –ice-edge;

d: 1 - 1 - < 500; 2 – 500-1000; 3 – 1000-2000; 4 – 2000-5000; 5 - > 5000 mg C·m^{-2}; 6 – ice-edge;

e: 1 - < 50; 2 – 50-100; 3 – 100-200; 4 – 200-300; 5 - >300 mg C·m^{-2}; 6 – ice-edge;

f: specific density isolines.

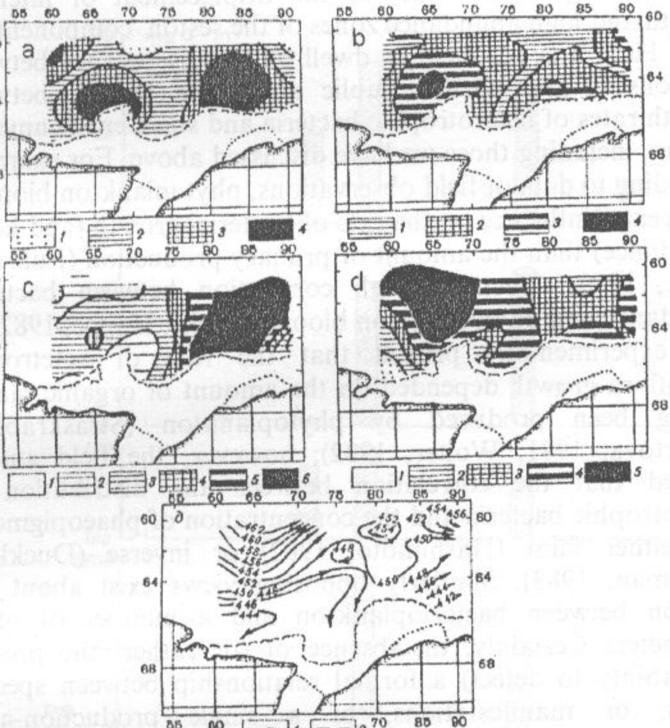

Fig. 34. The distribution of bacterial production (a), primary production (b), phytoplankton biomass (c), POM (d) in photic layer, the near-surface geostrophic currents (e) at the Commonwealth Sea (January 1980).

a: 1 - < 50; 2 – 50-70; 3 – 70-100; 4 - > 100 mg C·m^{-2}·d^{-1};

b: 1 - < 100; 2 – 100-200; 3 – 200-300; 4 - > 300 mg C·m^{-2}·d^{-1};

c: 1 - < 300; 2 – 300-600; 3 – 600-900; 4 – 900-1200; 5 – 1200-1500; 6 - > 1500 mg C·m^{-2};

d: 1 - < 75; 2 – 75-100; 3 – 100-125; 4 – 125-150; 5 - > 150 g· m^{-2} (dry weight);

e: 1 – streamlines, 2 – ice-edge.

proceeded accordingly, maximums generated by different trophic groups showed no marked spatial shifts. In February 1981 we registered events of the displacement of intensive growth and high abundance zones of the seston components.

Here it is pertinent to dwell on the discrepancy between opinions of the learned public about the linkage between growth rates of heterotrophic bacteria and some environmental factors, including those we have discussed above. For example, according to data of field observations, phytoplankton biomass has greater influence on the rate of bacterial growth (and hence abundance) than the amount of primary production (Fuhrman et al., 1980). There is high correlation between bacterial abundance and phytoplankton bloom (Gocke, Hoppe, 1982). It was experimentally proved that the rate of hetetrophic microflora growth depended on the amount of organic matter having been produced by phytoplankton (Straskrabova, Desortova, 1981; Wolter, 1982); however, the field studies showed that the correlation between the distribution of heterotrophic bacteria and the concentration of phaeopigments was either faint (Hashimoto, 1982) or inverse (Ducklow, Kirchman, 1983). Similarly opposing views exist about the relation between bacterioplankton and a number of other parameters. Certainly, the absence of (or rather the present incapability to detect) a formal relationship between specific events, or manifestations, of a single production-and-destruction process should be explained by the fragmentary and protracted character of the field observations. Usually, the observations were conducted at different stages of the production-destruction process that eventuated in the discord; or the observations took place simultaneously with the spatial transfer of seston components - in this case the researcher meets with a variety of possible patterns of the distribution of the individual components dependent on the velocity and the regime of transfer.

Being subject to seasonal fluctuations (Fig. 35), quantitative characteristics of bacterioplankton reach their peak by the end of growing season.

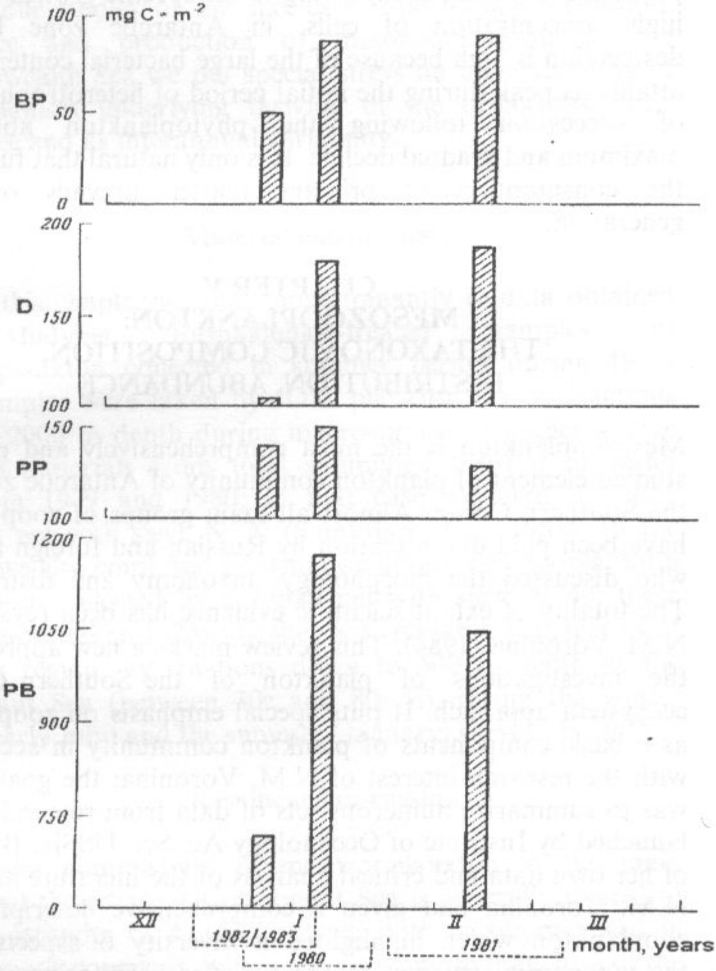

Fig. 35. Changes of the average estimates of bacterial daily production (BP) and destruction (D), daily primary production (PP) and phytoplankton biomass (PB) in photic water layer at the Commonwealth Sea during summer season of 1980, 1981 and 1982-1983.

Unlike in the tropical or temperate zones of the ocean at which bacteria play extremely important role in destruction processes (Sorokin, 1982) owing to the specific growth rate and high concentration of cells, in Antarctic zone bacterial destruction is high because of the large bacterial content which attains its peak during the initial period of heterotrophic phase of succession following the phytoplankton abundance maximum and gradual decline. It is only natural that further on the consumption of primary matter prevails over the generation.

CHAPTER V
MESOZOOPLANKTON: THE TAXONOMIC COMPOSITION, DISTRIBUTION, ABUNDANCE

Mesozooplankton is the most comprehensively and minutely studied element of plankton community of Antarctic zone and the Southern Ocean. Almost all main groups of zooplankters have been paid due attention by Russian and foreign authors, who discussed the morphology, taxonomy and distribution. The totality of extant scientific evidence has been reviewed by N.M. Voronina (1984). This review marks a new approach to the investigations of plankton of the Southern Ocean – ecosystem approach. It puts special emphasis on zooplankton as a basic components of plankton community in accordance with the research interest of N.M. Voronina; the goal she set was to summarize numerous sets of data from research cruises launched by Institute of Oceanology Ac. Sci. USSR. By means of her own data and critical analysis of the literature available, N.M. Voronina had given a comprehensive description of zooplankton which highlighted a diversity of aspects – from the taxonomic structure to the function main components of the zooplankton perform in communities of the Southern Ocean. The book tells about the current knowledge having been gained about the subject and may serve a reliable basis for advancing towards better understanding of the general rules and regularities, the region-specific features of zooplankton growth and production.

In our studies of the species composition, distribution, abundance and production of mesozooplankton at the Commonwealth Sea we put special stress on understanding of the mechanism underlying thriving of the organisms, their abundance and its interannual variability.

Material and methods

In this chapter we refer predominantly to data obtained from studying formaldehide-treated samples of mesozooplankton collected in summer period during 1977-1984. Samples were taken by JOM plankton net by fractions down to 2000 m depth during macrosurveys. Another source were the materials from total sampling of 0-100 m water column in 1979 and 1980; in that case we used a Juday plankton net with sieve N 70 (Samyshev et al. 1983). In the analysis we also employed information about mesozooplankton having been collected by a Juday net with sieve N 49; these samples were taken following the same research scenario as at the main region, by fractions down to 500 m depth at the Cosmonaut Sea (between 30° and 80° E) during the winter (June – early July) and the summer (January) surveys in 1973.

Results and discussion

The species composition of mesozooplankton in the main region and the adjacent Cosmonaut Sea is generally typical of the high latitudes of Antarctic zone. Both in summer and in winter among copepods, which generated more than 70% of the total biomass and contributed as huge share as 80-99% to the total abundance, 4 species – *Calanoides acutus*, *Calanus propinquus*, *Rhincalanus gigas* and *Metridia gerlachei* – dominated the biomass (Table 13). Therefore, the distribution

Table 13

The species composition and biomass of the mesozooplankton prevailing in 0-500 m water layer in winter and in summer

Species	June – July 1973,		January 1978		February 1978	
	between 30° and 60° E		between 60° and 75° E			
	mg · m^{-3}	%	mg · m^{-3}	%	mg · m^{-3}	%
Calanoides acutus	1.2	6.3	8.2	9.3	7.0	9.7
Calanus propinquus	0.4	2.1	1.7	1.9	1.8	2.5
Rhincalanus gigas	7.4	38.9	33.6	38.4	50.7	70.4
Metridia gerlachei	1.6	8.4	3.5	3.9	3.6	5.0
Other	8.4	47.3	41.0	46.5	8.9	12.4
Total:	19.0	100.0	88.0	100.0	72.0	100.0

of total mesozooplankton biomass in summer as well as seasonal and interannual fluctuations of the abundance depended primarily on the quantitative characteristics of these taxa. Other prevalent copepods were *Ctenocalanus vanus*, *Microcalanus pygmaeus*, and *Scolecithricella glacialis* (Calanoida); *Oithona similis*, *Oncea curvata* and *Microsetella norvegica* (Cyclopoida). Along with the small, large forms - *Pareuchaeta antarctica*, *Haloptilus oxycephalus*, *Heterorhabdus austrinus* – also played significant part in the mesozooplankton: despite their relatively small numbers, they collectively generated up to 10-20% of total mesozooplankton biomass. Other taxa, though very diverse, were of minor importance.

During winter depression period, the zooplankton was composed predominantly (over 90%) of senior age groups. This was clearly manifested in the age structure of populations of mass interzonal species. Taking into account the numbers of particular species and difference between their quantitative characteristics in different water layers, the shift in the cycles of all the four mass taxa may be regarded as an aftereffect of summer succession processes. In the upper 0-100 m layer relative abundance of *C. acutus* and *Rh. gigas* is negligible (Table 14); in deeper water their numbers are almost an orderof magnitude larger (cf. Tables 13 and 14), predominantly owing to copepodite stages III – IV (*C. acutus*) and copepodite stages II – III (*Rh. gigas*) (Table 15). Noteworthy distinctions were also found between relative numbers of other stages: in *C. acutus* copepodites I and VI were almost absent, copepodites II were few; in *Rh. gigas* relatively large amounts of senior copepodite stages were found in the depth, especially in 200-500 m layer, while the rest of stages were numerically minor in upper water layer. Relative abundance of *C. propinquus* measured in the 0-100 m layer was 20 times and of *M. gerlachei* 200 times as large as that of the two species discussed above; in deeper water the relative abundance decreased more than twice. From the noticed aftereffects it follows that by the beginning of autumn *C. acutus* unlike the rest of the species had completed its reproduction. The shift in the cycles of *C. propinquus* and *Rh. gigas* which developed after the cycle of *C. acutus* manifested itself as larger relative numbers of junior copepodites: in *C. propinquus* it was higher than in *C. acutus*, and in *Rh. gigas* higher than in *C. propinquus*. The fact that the populations of the two species included all age groups – from copepodites I to VI (in some water layers the latter, which were undoubtedly from the last year generation, contributed as considerable share as 15-24%) points out that because of short summer some part of these populations did not spawn. Apparently, this is one of key factors which determine the abundance of the population in the region. The age structure (copepodite stages I - V) and the relatively high total abundance of *M. gerlachei* population indicate that the final stage of reproduction of this copepod is

Table 14

The basic species of mesozooplankton in 0-100 m layer between 30° and 60° E (June – July 1973)

Species	Numbers %	Biomass (for the copepods) %
Calanoides acutus	0.01	0.64
Calanus propinquus	0.20	5.40
Rhincalanus gigas	0.01	4.48
Metridia gerlachei	2.06	17.20
Ctenocalanus vanus	18.48	22.27
Microcalanus pigmaeus	12.44	8.11
Spinocalanus abissalis	0.03	0.04
Scolecithricella glacialis	0.37	0.97
Pareuchaeta antarctica	0.03	3.14
Heterorhabdus austrinus	0.04	1.18
Haloptilus oxicephalus	0.08	2.38
Oithona similis	51.64	39.40
O. frigida	0.73	0.64
Oncaea conifera	0.08	0.12
O. curvata	3.43	0.50
Polychaeta (larvae)	0.16	-
Euphausicea	0.39	-
Varia	6.13	-
Total:	100.00	100.00

Table 15

The age structure of the prevailing copepod populations in June – July 1973[*]

Sampling depth, m		0-25	25-50	50-100	100-200	200-500
Calanoides acutus	I	0	0	0	0	0
	II	0	3	7	0	2
	III	30	4	48	2	14
	IV	30	88	18	87	39
	V	40	5	27	10	45
	VI	0	0	0	1	0
Calanus propinquus	I	2	1	0	0	0
	II	19	5	8	11	0
	III	37	59	23	52	0
	IV	15	15	18	7	48
	V	24	15	37	15	52
	VI	3	5	14	15	0
Rhincalanus gigas	I	1	4	1	2	0
	II	80	52	32	25	11
	III	16	30	66	63	36
	IV	0	0	0.7	4	11
	V	0	6	0.1	3	18
	VI	3	8	0.9	3	24
Metridia gerlachei	I	0	46	17	26	20
	II	4	9	5	30	40
	III	6	13	16	33	9
	IV	42	4	36	0	24
	V	47	27	23	6	4
	VI	1	1	3	5	3

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[*] According to E.V. Budnichenko (1983)

even more prolonged than in the other three species. Another evidence that *C. propinquus* and *M. gerlachei* do not cease reproducing in winter is the presence of their eggs and nauplii (Budnichenko, 1983). In the northern part of the region the findings were especially multiple amounting to 1600 ind · m^{-3} and more in 0-100 m water layer; in the southern part their abundance was an order of magnitude less. As the result of the low numbers of the discussed interzonal copepods and the deeper location of their populations, in winter in the upper 0-100 m water layer the small forms with relatively high numbers – primarily *Ctenocalanus vanus* and *Oithona similis* – played the leading role. Together with *Microcalanus pygmeus*, another prevailing species, they had been generating 82% of the total mesozooplankton abundance and 62% of the total biomass.

Though the mesozooplankton numbers within the 0-100 m water layer was as high as 736 ind · m^{-3}, its biomass was estimated 25 mg · m^{-3}. The increase of relative numbers of the interzonal copepods with the increase of depth does not lead to enlargement of total mesozooplankton abundance in 0-500 m layer; the biomass of mesozooplankton is 19 mg · m^{-3} that is even less than for the 0-100 m layer, i.e. the small forms contribute substantial share in the biomass.

As the summer comes, the interzonal copepods float up to the surface and reproduce so intensively that this has effect on the composition and abundance of mesozooplankton almost throughout the entire water depth. Let us examine data of the two consecutive surveys conducted in January and in February 1978 in order to comprehend the result of change in the composition of summer mesozooplankton.

As Table 13 demonstrates, in January the four interzonal species composed over 53% of the biomass of mesozooplankton in 0-500 m layer, in February the collective share increased to 87%. In both cases, *Rh. gigas* and *C. acutus* dominated the biomass. The portion generated by the former had increased 1.5 times and that by the latter slightly decreased from January to February; the corresponding ratio between their biomass was 4 : 1 in January, and 7 : 1 in February. *C. propinquus* and *M. gerlachei* were of minor importance during the summer and displayed the tendency towards insignificant increase from January to February. In general, in comparison with the winter, the abundance of mesozooplankton in the favourable years rose more than two times by the mid-summer owing to mass interzonal species, and the biomass more than four times. For example, in January 1973 mesozooplankton numbers and biomass in 0-100 m water layer of the Cosmonaut Sea made up 154 ind · m^{-3} and 94 mg · m^{-3}, correspondingly, while in June – July 1973 736 ind · m^{-3} and 25 mg · m^{-3}, correspondingly. At the main region the biomass of summer mesozooplankton in 0-100 m layer was about 120 mg · m^{-3} in the favourable years.

In the summer, quantitative ratios of the mass copepod species changed usually in conformity with their asynchronous life cycles. There were, however, some features which might be caused by short summer and therefore be characteristic of high latitudes in general; they may also be associated with the uneven distribution of the abundant copepod species and primarily their wintering stock. The uneven distribution was related to different reproductive success of the four species and displacement of their cycles on the time scale. At last, there were features induced by the special regional environment, by spatial and temporal variability of the environmental conditions.

Studying of the catches brought by Juday plankton net (sieve N 70) in January 1980 and in February 1979 has shown that in the beginning of summer intensive reproduction took place in small copepods (*Ctenocalanus vanus, Microcalanus pygmaeus, Oithona similis*) and some time after in larger species named above (Samyshev et al., 1983). In the mid-summer relative numbers of the small copepods' eggs and nauplii sharply dropped and the part of junior copepodites increased. Increase of the relative numbers of *Oncaea spp.* was characterisic of the period from January to February. Naturally, the share contributed to total mesozooplankton biomass by these small copepods was considerably less than that by large copepods floating up to the surface for spawning.

It follows from the distribution of maximums of the abundance of different age classes and from the ratios between age classes in different copepods that during January – February 1978 the acsent and reproduction of the mass species had been displaced on time scale. In most cases, spatial incoherence between maximums of the abundance of these species was also noticed. Neither *C. acutus*, which the first of the copepods began floating up and spawning, nor *Rh. gigas* did not have time sufficient for the entire wintering stock to have floated up to the surface for reproduction. By late summer considerable portion of the populations, especially the population of *Rh. gigas*, had found themselves plunged in deep water. The sparsity of different developmental stages of *C. propinquus* in the sea surface and of the adult copepods in the depth may, apparently, be due to the same reason. The reproduction term of *M. gerlachei* was also out of schedule; the peak was registered later than in the other three species. Like in other copepods, a part of the winter stock of the population was found at surprisingly large depths in the second half of the summer. This, probably, explains why some part of the populations of *Rh. gigas* and *M. gerlachei* had been reproducing until late autumn (as it was at the Cosmonaut Sea in June – July 1973).

Thus, the limited growing season at the high latitudinal zone is among factors which hamper the reproduction of mass species, especially those in which the ascent to the surface and the reproduction take place in the late summer. The asynchronous cycles and the spatial discord between abundance maximums of different species during the spring – summer floating up to the surface predetermine the uneven chances for reproduction success. In some species the peaks of abundance concentrate in the system of stationary gyres in coastal zone or in the zone of Antarctic divergence rich in phytoplankton. In other species maximums located outside those zones (Fig. 36) had been transferred by the currents to the north, in waters relatively poor in phytoplankton, that lessenned reproductive success of the populations. Possible negative effects of such a transport on the Antarctic forms were discussed in N.M. Voronina (1984). It is reasonable to suggest that efficient reproduction and the resulting overall abundance of mesozooplankton should depend, firstly, on how distinct is the system of water circulation on the time and space scale, and, secondly, on the portion of reproducing zooplankton which would reach the field of stationary gyres after the ascent to the surface. The validity of these assumptions had been proved by data about the total mesozooplankton abundance measured over the region for several years (Fig. 37). The elicited interannual variability of the abundance of mesozooplankton has much in common with the variability of phytoplankton numbers (see Chapter II). Simultaneously, the tendency towards mesozooplankton abundance reduction during those years and especially in 1980, 1981 and 1984 allows to associate this phenomenon with interannual fluctuations of quantitative characteristics of the population of krill (Chapter I).

Analysis of the compared data permits to interpret the specific nature of the relations forthe particular components of plankton – phytoplankton, mesozooplankton and krill. The abundance of phytoplankton, or mesozooplankton, or krill depends on one factor – the turbulence of the regional field of currents. The mechanisms of this relationship has been described for phytoplankton (Chapter II) and for krill (Chapter I).

Distinctions between the curves describing the interannual variability of the abundance of phytoplankton and krill are determined by different rates of the organisms response to favourable environment; in its turn, the response is determined by the duration of life cycles. The position of mesozooplankters is between phytoplankton and krill. Having shorter life cycle in comparison with krill, mesozooplankton usually rapidly responds to favourable nutritive conditions

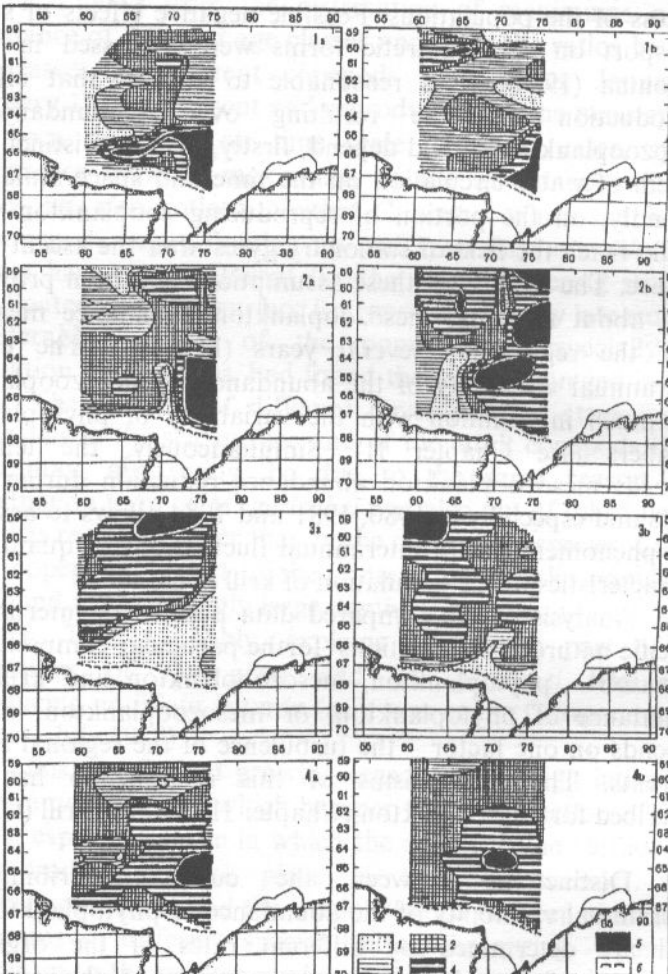

Fig. 36. The distribution of the biomass (mg · m^{-2}) of the prevailing copepods in 0-500 m water layer in January (left) and in February (right) 1978, 6 – ice edge.

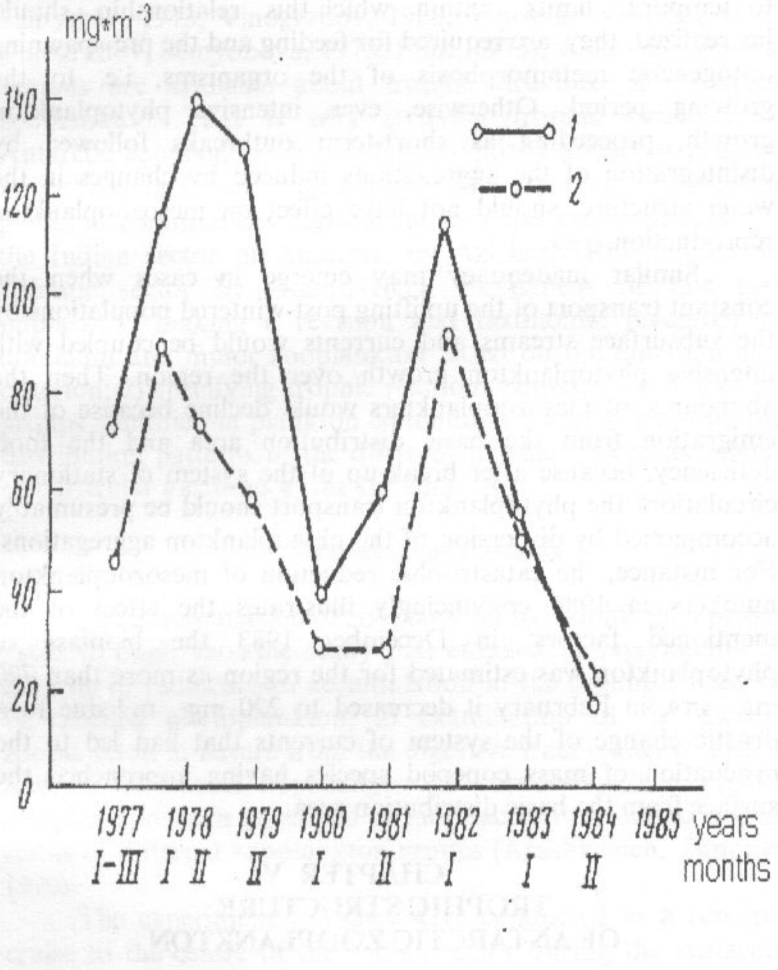

Fig. 37. The interannual variability of mesozooplankton biomass at the main region (1 – 0-100 m and 2 – 0-500 m water layer).

appearing for a season; therefore, interannual fluctuations of the abundance of mesozooplankters display more distinct coherence with fluctuations of phytoplankton abundance. As to temporal limits within which this relationship should be realized, they are required for feeding and the pre-spawning ontogenetic metamorphosis of the organisms, i.e. to the growing period. Otherwise, even intensive phytoplankton growth, proceeding as short-term outbreaks followed by disintegration of the aggregations induced by changes in the water structure, should not have effect on mesozooplankton reproduction.

Similar inadequacy may emerge in cases when the constant transport of the uplifting post-wintered populations by the subsurface streams and currents would be coupled with intensive phytoplankton growth over the region. Then the abundance of mesozooplankters would decline because of the emigration from the basic distribution area and the food deficiency, because after break-up of the system of stationary circulations the phytoplankton transport should be presumably accompanied by dispersion of the phytoplankton aggregations. For instance, the catastrophic reduction of mesozooplankton numbers in 1984 convincingly illustrates the effect of the mentioned factors: in December 1983 the biomass of phytoplankton was estimated for the region as more than 700 mg $\cdot$ m^{-3}, in February it decreased to 220 mg $\cdot$ m^{-3} due to a drastic change of the system of currents that had led to the evacuation of mass copepod species having approached the surface from the basic distribution area.

CHAPTER VI
TROPHIC STRUCTURE OF ANTARCTIC ZOOPLANKTON

It is impossible to gain understanding of functional roles played by different groups of organisms constituting zooplankton without knowledge of trophic structure of the zooplankton. Zooplankton of the temperate and tropical zones has been studied thoroughly and in detail (Geinrich, 1963; Arashkevich, 1969; 1970; Timonin, 1969; 1973; Samyshev, 1973; Vinogradov, 1980; Vinogradov et al., 1977; Vinogradov, Semyonova, 1975; Flint, 1975), while only general notions are available about trophic structure of Antarctic zooplankton. That is why studying trophic structure of Antarctic zooplankton had been recognized a task of primary importance in Soviet investigations of the structure of Antarctic plankton communities carried out by expeditions launched to the Indian sector of Antarctic by AzCherNIRO and to the Atlantic sector by AtlantNIRO. Fulfillment of this task implied: 1) making a revision and taxonomic inventory of dominant and minor zooplankton based on the nutrition as a criterion; 2) specifying trophic relations between the functional groups identified in plankton communities; and 3) pointing out distribution patterns of the different trophic groups as related to particular locations at the Indian sector.

Material and methods

The differentiation of zooplankton by trophic groups was made through versatile study that entailed 1) experiments on the rate of radiocarbon accumulation in the organisms fed on ^{14}C-labelled phytoplankton; 2) examination of the diet of zooplankton in nature from the digestive tract contents; and 3) revision of buccal appendages (in copepods). The applied complex approach permitted to more accurately define trophic status of different zooplankton groups (Arashkevich, Timonin, 1970).

The experimental studies were conducted in a research cruise to the centre of the Indian sector during the Antarctic summer 1982-1983. The experimental technique was as that described in Arashkevich (1970) and Chmyr and Zagorodnyaya (1981). In order to have got sufficient quantity of zooplankton, samples were collected by modified Juday plankton net at the sites where high concentrations of the organisms had been noticed during a survey (usually in 0-100-m water layer). In target sampling of euphausiids a fishing trawl was used. Monospecific cultures of phytoplankton (*Monochrysis sp.* and *Gymnodinium lanskoi* with mean cellular volume of 80 and 620 ɼm, correspondingly, and the specific radioactivity of $16.5 \cdot 10^{-6}$ mg C · imp^{-1}) were used in the experiments. The temperature of sea water in 3-l laboratory bottles was identical to that in the natural environment (+1.0 - +3.0° C). After acclimation to the experimental conditions, the zooplankton had been fed for 10-12 hours on ^{14}C labelled cultured phytoplankton. The initial concentration of the phytoplankton culture brought into the experimental flasks reached 5.0 mg · l^{-1} that was an order of magnitude higher than in the natural environment but corresponded to natural phytoplankton biomass from the overgrowth sites. Similarly higher in comparison with natural was the concentration of organisms of different trophic classes placed into the flasks. The organisms kept feeding on the traced forage for 24 hours; after that they were rinsed and put into the sea water with non-labelled phytoplankton for 3-5 h[*] (the concentrations of the studied zooplankton and nutrients were identical to those maintained under the experimental feeding on ^{14}C-labelled phytoplankton). Then the animals were fixed with formaldehyde, sorted into taxonomic and size-age groupings, and the dosage of radioactivity they had received was measured. The zooplankton was divided into three basic trophic groupings – phytophagous, euryphagous and predators – on the basic of the specific radioactivity (radioactivity to unit body weight ratio). Altogether 35 experiments had been conducted with representatives of 39 taxonomic groupings. Each of the experiments was performed in triplicate.

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[*] Tentatively determined at the given water temperature maximum time required for the mass mesozooplankton species to have the food digested and excreted was about 3 h and for the macrozooplankters 5 h.

From results of the repeated experiments means of the specific radioactivity were computed for animals of the same species and with identical body weight.

The contents of the digestive tract had been studied in 23 taxa (in the mass copepods the study implied division by age groups – copepodites). The method applied was as that described in Samyshev (1971). 20 samples had been collected from 0-100 m water layer at the sites of the Indian sector of Antarctic which differed in the abundance of phytoplankton; 1500 copepods had been dissected.

Buccal appendages were examined in 20 copepod species.

Proceeding from the analysis of digestive tract contents and the peculiar structure of buccal appendages, more detailed differentiation of the copepods was proposed according to the nutrition and with the involvement of the experimental data; the examined zooplankters were divided into functional groupings as it had been done by Vinogradova et al. (1979). In reconstructing the scenario of the food relations, phytoplankton from the Indian sector was divided into dimensional-functional groups; data from the earlier studies (Samyshev et al., 1983 a) were used in making the classification based on a 0.5-logarithm alteration of cell's weight (these are the limits in which the content of carbon determining the production capacity of cell changes insignificantly (Strathmann, 1967). The identified functional groupings underlay the matrix of the substance flux through plankton community which highlights the main food relations and takes into account changes in the food spectrum of consumers in the ontogenesis.

In studying the distribution patterns of zooplankters referred to different trophic groupings net samplings were made during the oceanological surveys to the Indian sector of Antarctic (between 60° S and the ice-edge in the south; in particular, two surveys were conducted between 30 and 60° E in January – February and in June 1973, two more between 60 and 90° E in January and in February – March 1978, and also in February 1979 and in December 1982 – January 1983). Samples of zooplankton were collected with the modified Juday

(JOM) net with the entrance diameter 80 cm, and capron sieve N 49. Stations were situated with the step of 1° latitude and 5° longitude. Spatial distribution of the trophic groupings of zooplankton was studied from the samples collected in 0-100-m sea-water layer during the years of the observations; vertical distribution from samples taken from the standard series of depths down to 2000 m, i.e. 0-25, 25-50, 50-100, 100-200, 200-500, 500-1000, 1000-2000 m, in 1978.

Valuable reference material were the maps of subsurface geostrophic currents having been drawn from the surveys dated 1973 (Khimitsa, 1976) and those earlier unpublished which were owing to the courtesy of V.A. Lednichenko (the surveys of 1979 and 1982-1983) and N.A. Ryabchikova (the surveys of 1978).

Results and discussion

Data of the experimental studies allow to tentatively differentiate three groups of zooplankters based on the specific radioactivity level (Fig. 38). According to experimental conditions, the group with high specific radioactivity may incorporate potentially phytophagous zooplankters. The following equation approximates the relationship between specific radioactivity and the weight of organism:

$$R/W = 57.5 \cdot W^{-0.84}\ , \qquad (a)$$

where R is specific radioactivity (imp·min^{-1}·ind^{-1}) and W is the body weight (mg fresh weight).

The group with low specific radioactivity combines potential predators in which the relationship between specific radioactivity and the weight is weak:

$$R/W = 0.07 \cdot W^{-0.24}\ . \qquad (b)$$

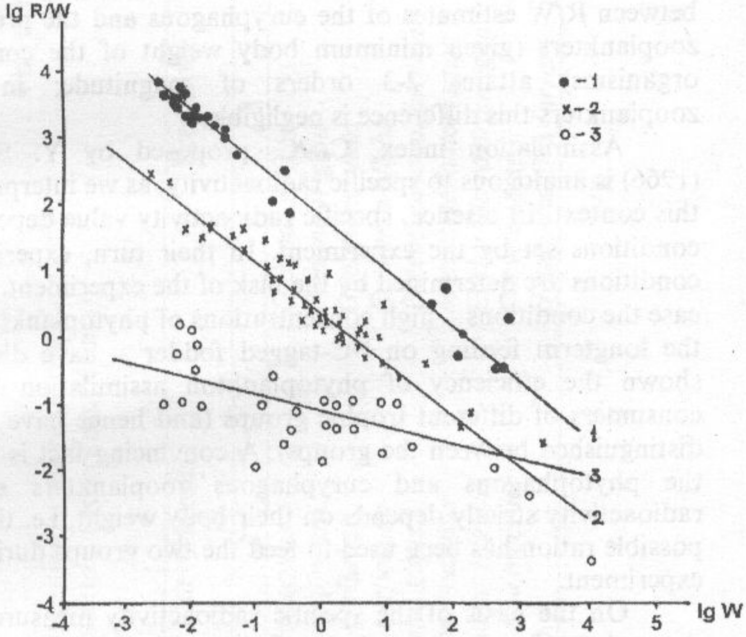

Fig. 38. Specific radioactivity values in the zooplankters of different groups (**1**- phytophagous, **2** – curyphagous, **3** – predators).

The third – intermediate – group are potential euryphagous zooplankters in which the relationship looks as follows:

$$R/W = 2.51 \cdot W^{-0.79}. \qquad (c)$$

Dispersion analysis has shown that by the values of specific radioactivity the phytophagous organisms differ from the euryphagous and the predatory with the level of significance 0.05. The fact that the factors in the equations (a) and (c) are numerically comparable allows to compare between the specific radioactivity of phytophagous and euryphagous zooplankters within the entire range of the body weight estimates. The comparison points out that the former have the radioactivity more than 20 times as high as the latter. The largest difference between R/W estimates of the euryphagous and the predatory zooplankters (given minimum body weight of the compared organisms) attains 2-3 orders of magnitude; in large zooplankters this difference is negligible.

Assimilation index, C_{ass}/C, proposed by Y. Sorokin (1966) is analogous to specific radioactivity, as we interpret it in this context. In essence, specific radioactivity value depends on conditions set by the experiment. In their turn, experimental conditions are determined by the task of the experiment. In our case the conditions – high concentrations of phytoplankton and the longterm feeding on ^{14}C-tagged fodder – have distinctly shown the efficiency of phytoplankton assimilation by the consumers of different trophic groups (and hence have clearly distinguished between the groups). A convincing fact is that in the phytophagous and euryphagous zooplankters specific radioactivity strictly depends on their body weight, i.e. the best possible ration has been used to feed the two groups during the experiment.

On the basis of the specific radioactivity measurements the variety of taxa under the study have been divided into the main trophic groups (Table 16).

As for the totality of the species, for individuals of a particular species there is an inverse relationship between specific radioactivity estimate and body weight (and hence the age) (Figs. 39, 40) that reflects the relationship between the amount of food consumed and the weight of the organism and convincingly indicates the correctness of the division into trophic groups according to the experimental data. Equations describing these relations are similar to the given above. Analysis of intestinal contents of the zooplankters has shown that the spectrum of food items consumed was very wide. Almost all mass representatives – both plants and animals – identified at handling of the fixed phyto- and zooplankton samples had been found well-preserved in the guts owing to specific structural elements which ensured the preservation. As

Table 16

The species composition of the basic trophic groups of zooplankton (experimental data)

Phytophagous	Euryphagous	Predators
1	2	3
Clausocalanus laticeps	*Calanoides acutus*	*Oithona similis*
Clausocalanus arcuicornis	*Calanus propinquus*	*Oithona frigida*
Scaphocalanus brevicornis	*Metridia gerlachei*	*Oncaea curvata*
Spinocalanus magnus	*Metridia curticauda*	*Euchaeta biloba*
Spinocalanus antarcticus	*Rhincalanus gigas*	*Pareuchaeta antarctica*
Ctenocalanus venus	*Rhincalanus nasutus*	*Microsetella norvegica*
Stephus longipes	*Onchocalanus frigidus*	*Euchirella rostramagna*
Microcalanus pygmaeus	*Thysanoessa macrura*	*Corycaeus sp.*
Drepanopsis pacificus	*Salpae sp.*	*Heterorhabdus farrani*

1	2	3
Nauplii Copepoda *Euphausia superba*	*Larvae salpae spp* *Hyperiidae* *Scolecithrix pollaris* *Spongiobranchoea australis* *Clione antarctica* *Tomopteris carpenteri* *Gastropoda*	*Gaidius tenuispinus* *Chaetognatha*

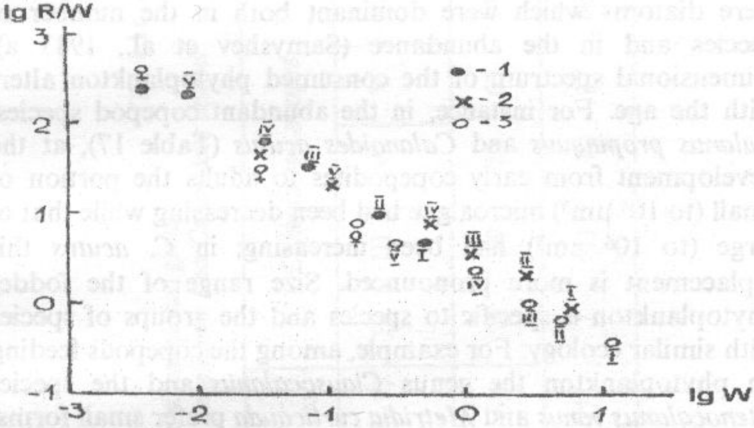

Fig. 39. Changes of the specific radioactivity in copepodites of the mass euryphagous species, *Metridia gerlachei* (1), *Calanus propinquus* (2) and *Rhincalanus gigas* (3). R- imp · min-1 · ind-1; W – mg wet weight.

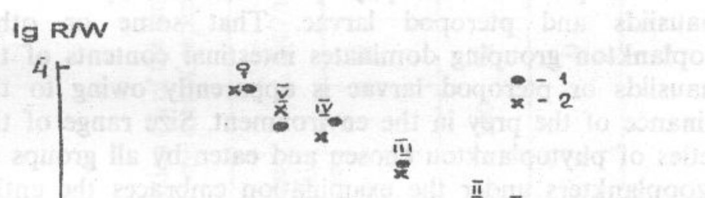

Fig. 40. Changes of the specific radioactivity in copepodites of the mass phytophagous species, *Clausocalanus laticeps* (1) and *Ctenocalanus vanus* (2).
R- imp · min-1 · ind-1; W – mg wet weight.

it might be expected, forms which dominated the food spectrum were those which dominated the natural environment. In the phytoplankton grazed by the zooplankters the prevailing item were diatoms which were dominant both in the number of species and in the abundance (Samyshev et al., 1983 a). Dimensional spectrum of the consumed phytoplankton alters with the age. For instance, in the abundant copepod species, *Calanus propinquus* and *Calanoides acutus* (Table 17), at the development from early copepodites to adults the portion of small (to 10^4 µm^3) microalgae had been decreasing while that of large (to 10^6 µm^3) had been increasing; in *C. acutus* this replacement is more pronounced. Size range of the fodder phytoplankton is specific to species and the groups of species with similar ecology. For example, among the copepods feeding on phytoplankton the genus *Clausocalanus* and the species *Ctenocalanus vanus* and *Metridia curticauda* prefer small forms, while *Metridia gerlachei* and *Calanus propinquus* larger forms, and *Calanoides acutus* and *Rhincalanus gigas* the largest available (Fig. 41). The smallest (about 10^3 µm^3) of the phytoplankton were found in intestinal contents of nauplii from different trophic groupings. Especially broad is the dimensional spectrum of the phytoplankton eaten by dominant euphausiids and pteropod larvae. That some or other phytoplankton grouping dominates intestinal contents of the euphausiids or pteropod larvae is apparently owing to the dominance of the prey in the environment. Size range of the varieties of phytoplankton chosen and eaten by all groups of the zooplankters under the examination embraces the entire size spectrum of phytoplankton. Therefore it is reasonable to state that phytoplankton is exploited by the array of the consumers in full.

The spectrum of prey is wide and similar for the majority of the examined euryphagous and predatory zooplankters. Basic constituents of the animal food are junior copepodites of the large copepods and copepodites and adults of the small copepods. Less frequent were found nauplii and senior copepodites of the large size species, except for chaetognaths

Table 17

The portion (% of the numbers) of different dimensional groups of phytoplankton in the diet of copepodites of *Calanus propinquus* and *Calanoides acutus*

Species and the developmental stage / Cell volume, μm^3	*Calanus propinquus*						*Calanoides acutus*				
	I	II	III	IV	V	VI	II	III	IV	V	VI
$10^2 - 10^4$	100	91	85	76	76	63	99	89	88	63	14
$10^4 - 10^6$	-	9	15	24	24	37	1	11	12	37	86

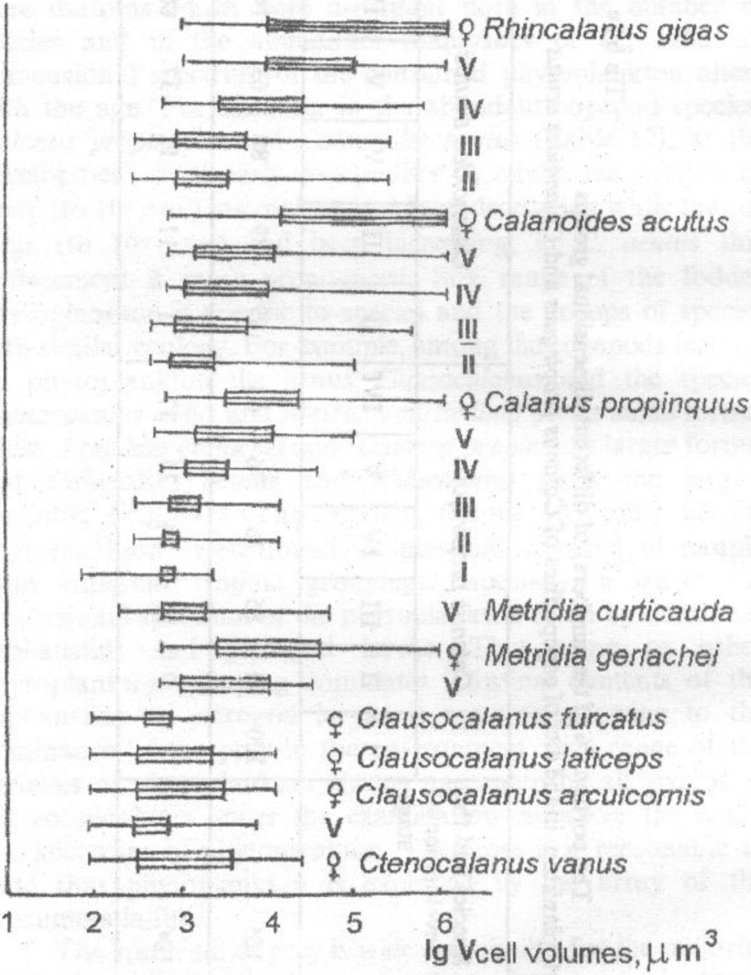

Fig. 41. The size spectrum of phytoplankton consumed by some mass copepods at different developmental stages. Shaded segments are for the dimensional range of phytoplankton species dominating the food pellet.

which can, depending on their length, eat almost all of the studied zooplankters. For many of the species a relatively large food fraction were tintinnian infusorians. Along with the structural remnants in the intestinal tract of the examined zooplankters different amounts of an amorphous substance of plant or animal origin and detritus were also found.

The portion of the basic food components in the intestinal contents differs depending on the developmental stage and the trophic group (Table 18). As Table 18 demonstrates, the contents of guts in small copepods is predominantly phytoplankton. In the large mass euryphagous *Calanoidae* the share of vegetable food is overwhelming (85-95%) in junior copepodites and decreases with age to 30-50%; accordingly, the portion of animal food has been increasing from several per cent in early copepodites to 40-60% in the adults. *Euphausia superba*, the most abundant of the zooplankters, which is capable of assimilating vegetable food like phytophagous organisms, had the intestinal content composed by more than 30% of animal food. Such predators as senior copepodites of *Oithona*, *Oncaea* and *Microsetella spp.* had their intestines filled with predominantly (over 90%) animal food.

Proceeding from the known composition of the gut contents and the structure of buccal appendages, the copepods which form the cone of Antarctic zooplankton divide into five trophic groupings: the euryphagous and the predatory zooplankters have two distinctly different groupings each.

The first group unites fine filter-feeders feeding on small (< 20 μm) phytoplankton, small protozoans and particles of detritus. A characteristic feature of these organisms are long polytrichous setae of their buccal appendages (Fig. 42). Similarly, setaceous have some setae at the inner edge and at the distal end of the maxillae I (Mx I), maxillae II (Mx II) and maxillipedes (Mxp). Proximal and median setulae on the Mx I are covered with the filamentous spiculae more densely than distal ones. The inter-filament distance is about 5 rm on the median setulae (Table 19). Obtuse and multi-apex denticles on the manducatory edge of Md are situated close to each other.

Table 18

The share (%) of the main food items in intestinal contents of zooplankters

NN	Zooplankters	Sex, copepodite stage	Food items			
			Microalgae	Animal food	Amorphous substance	Detritus
1	2	3	4	5	6	7
1	*Clausocalanus furcatus*	♀	97	-	+	3
2	*Clausocalanus laticeps*	♀	95	-	+	5
3	*Clausocalanus arcuicornis*	♀	93	-	+	7
		V	100	-	+	-
4	*Ctenocalanus vanus*	♀	98	-	+	2
		V	96	-	+	4
5	*Calanus propinquus*	♀	45	50	+	5
		V	45	45	+	10
		IV	60	35	+	5
		III	88	12	+	-
		II	80	18	+	2
		I	98	2	+	-
6	*Calanoides acutus*	♀	56	37	+	7
		V	54	46	+	-
		IV	59	37	+	4
		III	60	40	+	-
		II	80	15	+	5
7	*Metridia curticauda*	♀	35	50	+	15
		V	51	44	+	5
		IV	64	30	+	6
8	*Metridia gerlachei*	♀	30	64	+	6,
		V	70	25	+	5
		IV	76	17	+	7
		III	80	16	+	4
9	*Pleuromamma robusta*	♀	30	60	+	10

1	2	3	4	5	6	7
10	*Scolecithrix sp.*	♀	39	61	+	-
11	*Microsetella rosea*	♀	2	-	98	-
12	*Rhincalanus gigas*	♀	50	45	+	4
		V	40	32	+	28
		IV	44	50	+	6
		III	48	43	+	9
		II	66	34	+	-
13	*Haloptilus ocellatus*	♀	2	84	+	14
14	*Oithona similis*	♀	-	-	98	2
15	*Oncaea curvata*	♀	1	4	95	-
16	*Euchaeta biloba*	♀	7	93	+	10
17	*Pareucheata (barbata (?))*	♀	3	97	+	10
18	*Euphausia superba*	♀	60	33	+	7
19	*Polychaeta (Tomopteris (?))*	-	56	41	+	3
20	*Salpae*	-	54	46	+	-
21	*Hyperiidae*	-	19	66	+	15
22	*Clione antarctica*	-	64	36	+	-
23	*Limacina helicina*	-	48	37	+	15

The second group are coarse filter-feeders which feed on large (> 20 µm) microalgae and small animals. Mouth appendages of this group (Fig. 43) are typical of the filter-feeders and differ from those of the first group by less plumage on filtering appendages (the distance between the bristles on median setulae Mx II is from 12 to 15 µm) and distinct diastema – the clearance between ventral and central denticles on the manducatory plate Md which facilitates retaining of large microalgal cells torn up at feeding.

The third group embraces mixed-feeders which filter small food particles or capture larger food such as microalgal cells and small prey. Crustaceans of this group have their Mx II and Mxp setae armoured with strong short spicules (Fig. 44).

Table 19

The bristles of the setae on Mx II of copepods from different trophic groups

NN	Species	The distance (µm) between bristles on the setae		
		proximal	median	distal
1.	*Ctenocalanus vanus*	0,4	0,81	1,21 (1,62)
2.	*Stephus longipes*	0,81	1,62	2,43
3.	*Drepanopsis pectinatus*	1,62-2,43	3,24	4,05-4,86
4.	*Clausocalanus laticeps*	3,24	4,05	13,8
5.	*Clausocalanus arcuicornis*	3,6	4,8	10,8
6.	*Calanoides acutus*	4,0	6,5	12-13
7.	*Calanus simillimus*	8-10	12-13	15-18
8.	*Calanus propinquus*	8	11	17-18
9.	*Metridia gerlachei*	10	12-14	18-22
10.	*Pareuchaeta antarctica*	10	12-14	18
11.	*Rhincalanus gigas*	12	12,2	13
12.	*Lucicutia macrocera*	12	14,5	18-22
13.	*Euchaeta antarctica*	13,5	20,5	22
14.	*Pleuromammaa antarctica*	15	15	33
15.	*Haloptilus ocellatus*	8,3	14,1	16,6
16.	*Heterorhabdus farranii*	3-4	-	-
17.	*Racovitzanus antarcticus*	saber-like setae		
18.	*Candacia falcifera*	bears closely-set spicules		
19.	*Oithona similis*	the distance between the spicules is		
		1.4	2.7	3.3
20.	*Oncaea conifera*	the distance between them is 2.8		

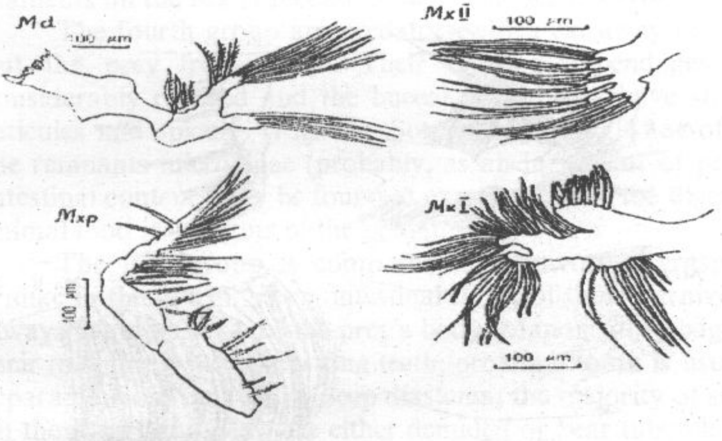

Fig. 42. Buccal appendages of *Ctenocalanus vanus*:
Md – mandible;
Mx I – maxilla I;
Mx II – maxilla II;
Mxp – maxillipede.

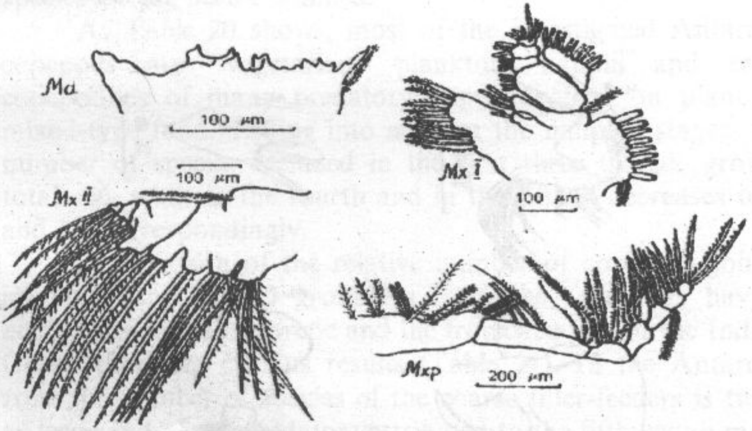

Fig. 43. Buccal appendages of *Calanoides acutus*:
Md – mandible;
Mx I – maxilla I; Mx II – maxilla II;
Mxp – maxillipede.

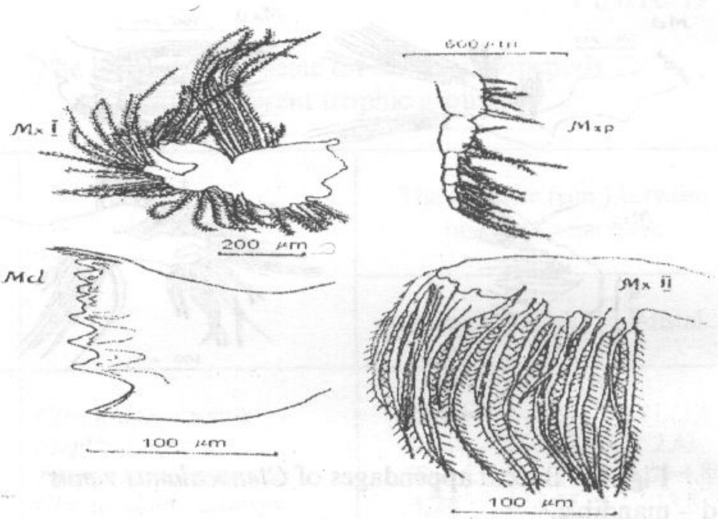

Fig. 44. Buccal appendages of *Metridia gerlachei*; (see Figs. 42, 43 for the abbreviations).

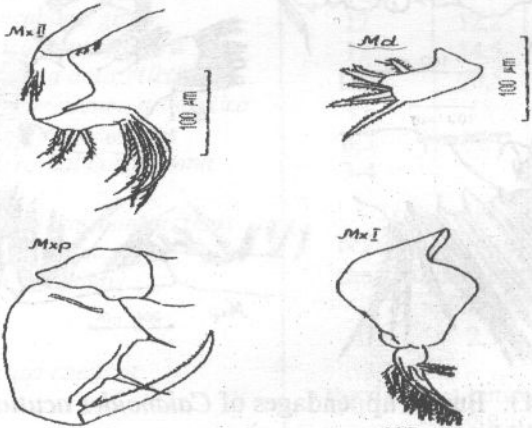

Fig. 45. Buccal appendages of *Oncaea conifera*: (see Figs. 42, 43 for the abbreviations).

The span between the Mx II spicules is similar to that between filaments on the Mx II median setule of the second group.

The fourth group are predators which eat away or suck out the prey from inside. Their filtering appendages are considerably reduced and the buccal appendages have strong seticules and spicules (Fig. 45). Sometimes, though not often, the remnants microalgae (probably, as an ingredient of prey's intestinal content) may be found at examination of the digested animal food in the guts of the predators.

The fifth group is composed of carnivorous graspers. Unlike in the fourth group, intestinal filling of those carnivores always contains parts of the prey's body. Manducatory edge of their mandibule has sharp long teeth; proximal tooth is usually separated from the rest by deep diastema; the majority of setae on the Mx II and Mxp are either denuded or bear tubercles or spicules instead of filaments; manducatory edge of the Mx I internal lobe is armoured with spikes (Fig. 46).

A number of minor copepod species which were out of focus of the applied methods, were placed into a particular trophic group by analogy with the taxonomically neighbouring species having been examined.

As Table 20 shows, most of the investigated Antarctic copepods are "vegetarian" plankton, nauplii and early copepodites of many predatory copepods feed on plant or mixed-type food. Taking into account the nauplial stages, the number of species included in the first three trophic groups totals 46, while in the fourth and in the fifth it decreases to 9 and 12, correspondingly.

Comparison of the relative number of copepods joined into different trophic groupings from the samplings having been made in the Antarctic and the tropical zones of the Indian Ocean produces curious results (Table 21). In the Antarctic zone the number of species of the coarse filter-feeders is twice as large and of the predators attributed to the fifth group more than twice as large as in the tropical zone; however, the relative species number of the fine filter feeders (without nauplii), euryphagous and sucking predators is, correspondingly, 20, 30

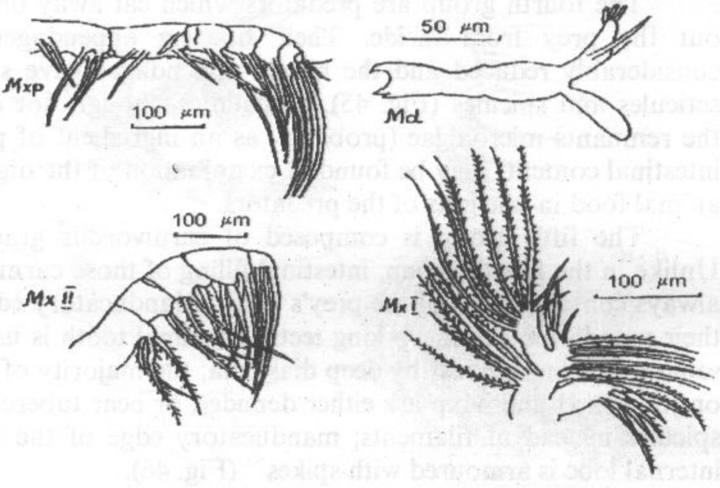

Fig. 46. Buccal appendages of Haloptilus ocellatus: (the abbreviations as in Figs. 42-45).

and 40% less than in the tropical waters. The two zones have identical collective (IVth + Vth groups) number of the predatory zooplankters.

The preponderance of phytoplankton-eating species and the adherence to plant food found in early developmental stages of traditionally predatory *Cyclopoida* (e.g. *Oncaea* and *spp.*) are a specific manifestation of the existing structure of eutrophic pelagic ecosystem of Antarctic with the unbalanced food relations among the living elements and their production cycles.

At reconstructing the food relations of Antarctic plankton communities the entire dimensional range of microalgae was divided into 11 groupings (Table 22).

The dimensional-functional differentiation of the zooplankton is based on the differentiation of varieties (forms) of the major trophic groupings in which the food relations and the dominance of a particular species (or several species) was

Table 20

Main trophic groups composition of copepods in the Indian sector of Antarctic

I-st group	II-nd group	III-rd group
1. Calanus acutus (I – II)	1. Calanoides acutus (III – IV)	1. Calanoides acutus (V – VI)
2. Calanus propinquus (I – II)	2. Calanus propinquus (III – IV)	2. Calanus propinquus (V –VI)
3. Calanus simillimus (I – II)	3. Calanus simillimus (III – IV)	3. Calanus simillimus (V – VI)
4. Ctenocalanus vanus (I – VI)	4. Rhincalanus gigas (I – II)	4. Rhincalanus gigas (III – VI)
5. Spinocalanus abyssalis (I – VI)	5. Scaphocalanus brevicornis (I–VI)	5. Eucalanus aquus (I – VI)
6. Spinocalanus magnus (I – VI)	6. Scaphocalanus subbrevicornis (I – VI)	6. Onchocalanus magnus (I – VI)
7. Microcalanus pygmaeus (I – VI)	7. Racovitzanus antarcticus (I – VI)	7. Cornucalanus robusta (I –VI)
8. Clausocalanus laticeps (I – VI)	8. Metridia gerlachei (I –III)	8. Cornucalanus magnus (I – VI)
9. Calocalanus teleremis (I – VI)	9. Metridia curticauda (I –III)	9. Metridia curticauda (IV – VI)

10. Minocalanus ramphitera (I – VI)	10. Metridia lucens (I – III)	10. Metridia gerlachei (IV – VI)
11. Scolecithricella glacialis (I – VI)	11. Pleuromamma robusta (I – II)	11. Metridia lucens (IV-VI)
12. Stephus longipes (I – VI)	12. Drepanopsis frigidus (I – VI)	12. Pleuromamma robusta (III – VI)
13. Nauplii Copepoda (I – VI)	13. Temorites brevis (I – VI)	13. Lucicutia ovalis (I – VI)
	14. Oncaea curvata (I –II)	14. Lucicutia frigida (I – VI)
	15. Oncaea conifera (I – II)	15. Lucicutia grandis (I – VI)
	16. Oncaea notopus (I – II)	
	17. Oithona frigida (I – II)	
	18. Oithona similis (I – II)	
IV-th group	**V-th group**	
1. Oncaea curvata (III – VI)	1. Pareuchaeta antarctica (I – VI)	
2. Oncaea conifera (III – VI)	2. Pareuchaeta farrani (I – VI)	
3. Oncaea notopus (III – VI)	3. Pareuchaeta rasa (I – VI)	
4. Oithona frigida (III – VI)	4. Pareuchaeta biloba (I – VI)	

5. Oithona similis (III – VI)	5. Heterorhabdus farrani (I – VI)	
6. Monstrilla spp. (I – VI)	6. Heterorhabdus austrinus (I – VI)	
7. Marmonilla spp (I – VI)	7. Haloptilus oxicephalus (I – VI)	
8. Microsetella norvegica (I – VI)	8. Gaidius tenuispinus (I – VI)	
9. Harpacticus spp	9. Gaidius affinis (I – VI)	
	10. Euaugaptilus sp. (I – VI)	
	11. Euchirella sp.	
	12. Candacia parafalcifera (I – VI)	

NOTE: Roman numerals mark copepodite stages of crustaceans.

Table 21

The relative number of copepod species in the plankton trophic groups from the Antarctic and the tropical* zone of the Indian Ocean

Trophic group	Relative number of copepod species (%)		Antarctic / tropical species ratio
	Antarctic zone	tropical zone	
I	18	23	0.8
II	28	14	2.0
III	22	31	0.7
IV	14	24	0.6
V	18	8	2.3

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* Computations for the tropical zone were made based on the data from Timonin, 1973

Table 22

The division of phytoplankton into groups
by size and function

Grouping NN	Cell volume, ŕm^3
I	50-100
II	100-500
III	500-1000
IV	1000-2000
V	2000-3000
VI	3000-5000
VII	5000-10000
VIII	10000-20000
IX	20000-50000
X	50000-100000
XI	100000-1000000

taken into account. The rest of zooplankton was divided into groups according to taxonomic status, size and specific food relations. 16 dimensional-functional groups have been distinguished altogether (Table 23).

Table 24, having been compiled from the results of the Antarctic phyto- and zooplankton differentiation, points out that nutritive spectrum of the zooplankton forms increases naturally and drastically with increase of the individuals length which corresponds to the number of the group. Dimensional-functional groups of phytoplankton are almost fully consumed approximately the entire spectrum - by the zooplankton referred to the I – IV groups. The rest of the prey spectrum is grazed by the spectrum of the coarse filter-feeders and euryphagous zooplankters. This leads to relatively even and complete phytoplankton eating-away by the heterotrophs. Euryphagous and predatory zooplankters also consume most of the phytoplankton. In the studied plankton communities only chaetognaths do not have natural enemies. In the diet of

Table 23

The division of zooplankton into groups
by size and function

Group NN	Dominant forms
1	Nauplii phytophagous
2	Nauplii euryphagous
3	Nauplii predatory
4	Junior copepodites (I-III) of the small copepods (*Microcalanus, Ctenocalanus, Clausocalanus*)
5	Senior copepodites (IV-VI) of the small copepods (*Microcalanus, Ctenocalanus, Clausocalanus*)
6	Appendicularia
7	*Scolecithricella* sp., cop. I-III
8	*Oithona* spp, cop. I-II, *Oncaea* spp. Cop. I-II
9	*Calanus* spp. cop. I-III, *Scolecithricella* spp, cop. III-IV , *Metridia* spp., cop. I-III
10	*Calanus* sp., cop. IV-VI, *Metridia* spp, cop. IVϑVI, *Rhincalanus gigas*, cop. I-II
11	*Rhincalanus gigas*, cop. III-IV
12	*Euphausiacea*
13	*Polychaeta* (larvae)
14	*Oithona* spp, cop. III-IV, *Oncaea* spp., cop. III-VI
15	*Pareuchaeta* spp, cop. I-IV
16	*Chaetognatha*

the predatory and euryphagous zooplannkters early developmental stages make up significant part; cannibalism may also take place.

Assessing the qualitative aspect of matter flux from the food relations in the Antarctic plankton communities, one should be aware of two notable features: 1) the absence of narrow specialization in the consumers that facilitates and diversifies predator-prey food relations in the environment, and

Table 24

Metric table of the food relations in planktonic community of the Southern Ocean

Functional groups	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1	+	+	+																									
2	+	+	+																									
3	+	+	+																									
4	+	+	+	+	+	+	+																					
5	+	+	+	+	+	+	+	+	+	+																		
6	+	+	+	+	+	+	+																					
7		+	+	+	+	+	+	+	+	+																		
8	+	+	+	+	+	+	+						+		+	+	+	+	+									
9	+	+	+	+	+	+	+	+	+	+				+														
10	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+							
11		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+							
12		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+				
13		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+				

Table 24 (continued on page 188)

Functional groups	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
14													+	+	+	+	+	+	+	+	+							
15													+	+	+	+	+	+	+	+	+	+	+	+				
16													+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	

Note: arrows are for the food relations in ontogenesis

2) the potentiality to widen functional significance for all the community components. Realization of this potentiality strongly depends on the quantitative aspect, i.e. quantitative characteristics of the involved components.

A characteristic feature of the trophic structure of Antarctic zooplankton (in particular copepods) is the steady leadership of the first three trophic groups, for which phytoplankton is the major food item, in upper 100-m seawater layer (Table 25). The collective share the three groups contribute to total zooplankton biomass amounts to 70-90% and more. Correspondingly, the portion generated by predators is estimated from less than 10% to 30%. The ratios evaluated in particular trophic groups vary far greater, sometimes an order of magnitude. Fluctuations in "vegetarian" to predatory zooplankton ratio and in the ratio between particular trophic groupings of zooplankters are determined by seasonal condition of the community and by vertical migrations undertaken by interzonal forms.

It is evident from Table 25 that in winter the full-grown community from upper 100-m layer (30 – 60° E) maintains relatively low quantitative level in all the trophic groups; the natural results is the relatively high portion of minor phytoplankton forms and predators. As summer comes and abundant interzonal plankton rise to the surface and begin reproducing, the trophic structure changes. Surveys conducted at the region in different months of different years registered phases of this transformation. As the result of the early-summer ascent and intensive reproduction of the mass species of *Calanoida* (*Calanus acutus, C. propinquus, Rhincalanus gigas*),the II and III trophic groups dominated the plankton (the survey dated December 1982 – January 1983, 60-85° E). From the mid- to late summer about 80% of the biomass are owing to senior copepodites of the III group (February 1979, 60-80° E and January – February 1973, 30-55° E). The contribution owing to other trophic groups is insignificant; the collective share generated by predators is about 10%. During the two surveys conducted in 1978 between 60 and 75° E, along

T a b l e 25

The biomass and percentage of copepods from the five trophic groups, and the overall mesozooplankton biomass in 0-100-m layer of the Indian sector of Antarctic

Location	Year, month(s)	Biomass, mg · m^{-3} / percentage ratio in copepods of different trophic groups						Overall mesozooplankton biomass, mg · m^{-3}
		I	II	III	IV	V	Total	
1	2	3	4	5	6	7	8	9
30-55° E	1973, I-II	$\frac{6}{7.0}$	$\frac{2}{2.5}$	$\frac{69}{82.0}$	$\frac{5}{6.0}$	$\frac{2}{2.5}$	$\frac{84}{100}$	94
30-60° E	1973	$\frac{4}{19.0}$	$\frac{1}{5.0}$	$\frac{11}{52.0}$	$\frac{4}{19.0}$	$\frac{1}{5.0}$	$\frac{21}{100}$	29
60-75° E	1978, I	$\frac{11.6}{11.8}$	$\frac{8}{8.2}$	$\frac{62}{63.3}$	$\frac{16}{16.3}$	$\frac{0.4}{0.4}$	$\frac{98}{100}$	115

1	2	3	4	5	6	7	8	9
60-75° E	1978, II	$\frac{25}{18.0}$	$\frac{17}{12.3}$	$\frac{63}{45.7}$	$\frac{22}{16.0}$	$\frac{11}{8.0}$	$\frac{138}{100}$	138
60-80° E	1979, II	$\frac{3}{3.0}$	$\frac{9}{9.0}$	$\frac{81}{79.0}$	$\frac{3}{3.0}$	$\frac{6}{6.0}$	$\frac{102}{100}$	133
60-85° E	1982, XII, 1983, I	$\frac{0.7}{2.0}$	$\frac{18}{41.0}$	$\frac{20}{45.0}$	$\frac{1.3}{3.0}$	$\frac{4}{9.0}$	$\frac{44}{100}$	54

with the "usual" mass species of *Calanoida* also abundant were some representatives of the I and IV trophic groups (*Ctenocalanus vanus* and *Oithona similis* and *O. frigida*, respectively), which yielded, correspondingly, 12-18 and 16% of the biomass.

In the end of the summer 1978, predatory zooplankters of the II group appeared in relatively large quantities in the upper sea-water layer; the collective biomass by predators of the IV and V groups made up 24% of total copepod biomass.

Dominating the upper 100-m water layer in summer and in winter, the III trophic group has a profound effect on the scenario of local zooplankton distribution (Figs. 47-52).

The heterogeneous hydrological field and its irregular variability account for the extraordinary uneven, irregularly altering mosaic-like distribution of zooplankton at the investigated areas of the ocean. Therefore, the relation between the currents and the pattern of distribution differed depended on particular case. Sometimes there was distinct relationship between accumulation of the aggregations and strong anticyclonic water circulation (Fig. 48, the central site between 62° S and 55° E; Fig. 49, AII, BII; Fig. 50, A2, the localities at 60° S, 63° S and 60° E, 65° S and 70° E; Fig. 49 BIV; Fig. 50 C, the site at 66° S and 65° E). In other cases the aggregations concentrated amidst cyclonic circulations (Fig. 49 A1, B1; Fig. 50 A1; the sites at 64° S and 70° E, 66° S and 75° E; Fig. 49 AIII; Fig. 50 B, the locality in Prudz Bay, 67-68° S and 75° E) or at their periphery (Fig. 47, the zone stretching along 64-62° S; Fig. 49 AIII, BIII; Fig. 50 B, the zone along 64-63° S between 65-80° E).

During summer, the main body of zooplankton gathers in upper water layers, the vertical distribution of the trophic groupings looks very heterogeneous (Fig. 51). Such distribution is most typical of the III trophic group and may be explained by dense local swarms of mass interzonal species of *Calanoida* occupying the surface (0 – 50 m) or subsurface (50 –100 m). Measured in the core of those swarms, which are usually by 70-100% composed of one of the abundant species (*Calanus*

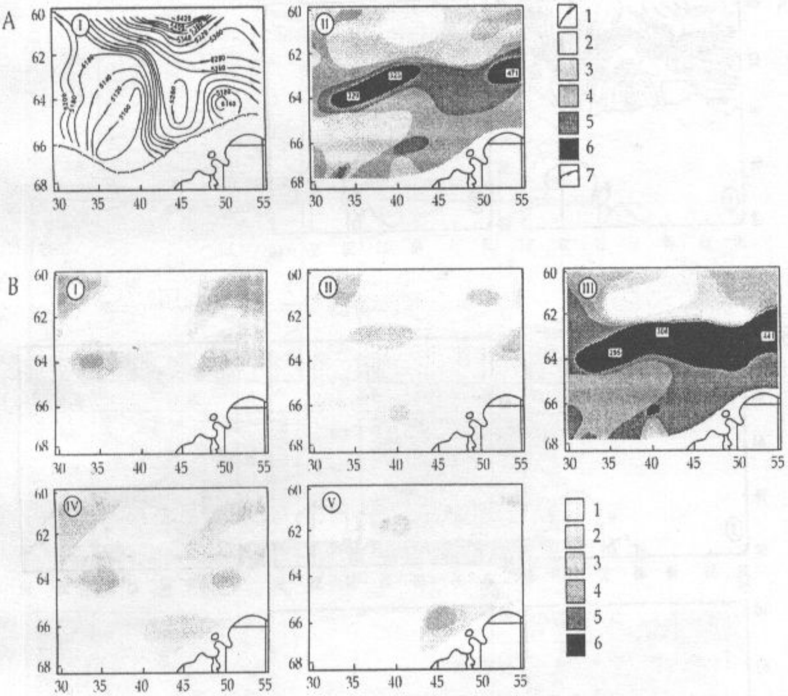

Fig. 47. **A**. The geostrophic currents[•] on the sea surface (**I**) and the distribution of mesozooplankton biomass (**II**) in 0-100-m water layer of the western Indian sector of Antarctic (January – February 1973):

1 – isolines of the currents;

2 - < 10; **3** – 10-50; **4** – 50-100; **5**- 100-200; **6** - > 200 mg m^{-3} .

B. The distribution of mesozooplankton biomass (I – V trophic groups) in the 0-100-m water layer:

1 – 0-5; **2** – 5-10; **3** – 10-25; **4** – 25-50; **5** – 50-100; **6** - >100 mg m^{-3}; 7 – the ice edge.

[•] Cited from V.A. Khimitsa, 1976.

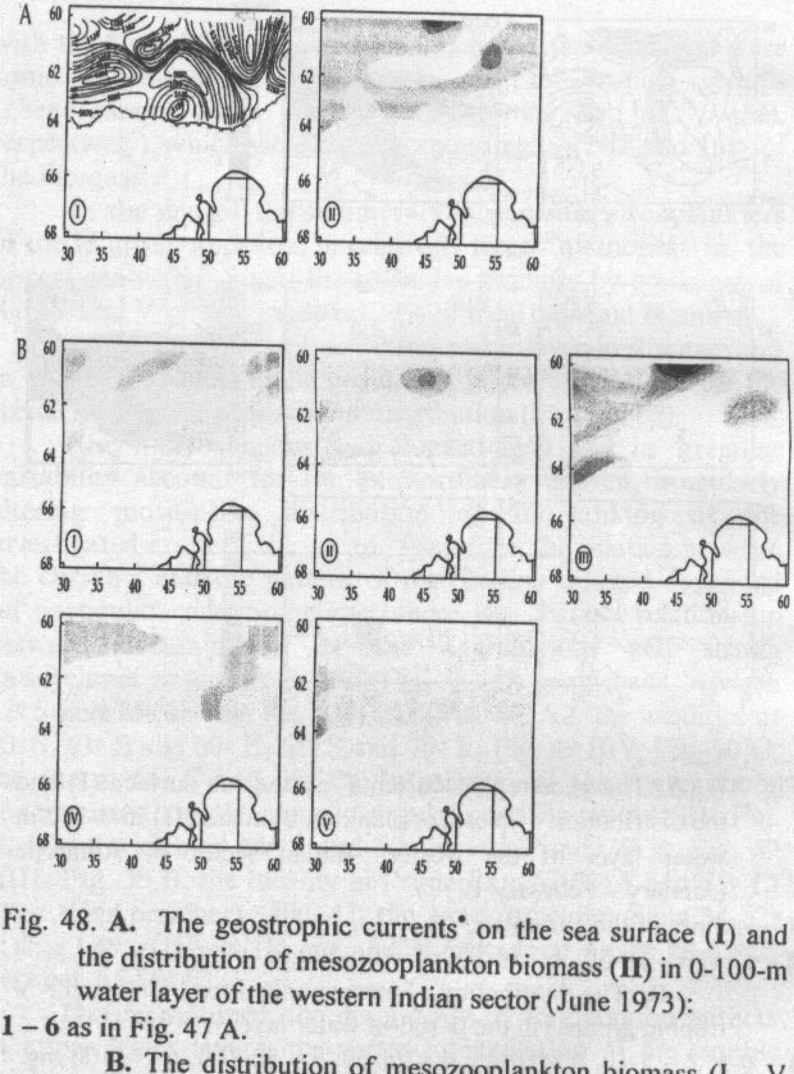

Fig. 48. **A.** The geostrophic currents* on the sea surface (**I**) and the distribution of mesozooplankton biomass (**II**) in 0-100-m water layer of the western Indian sector (June 1973):

1 – 6 as in Fig. 47 A.

B. The distribution of mesozooplankton biomass (I – V trophic groups) in the 0-100-m water layer:

1 – 7 as in Fig. 47 B.

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*Cited from V.A. Khimitsa, 1976.

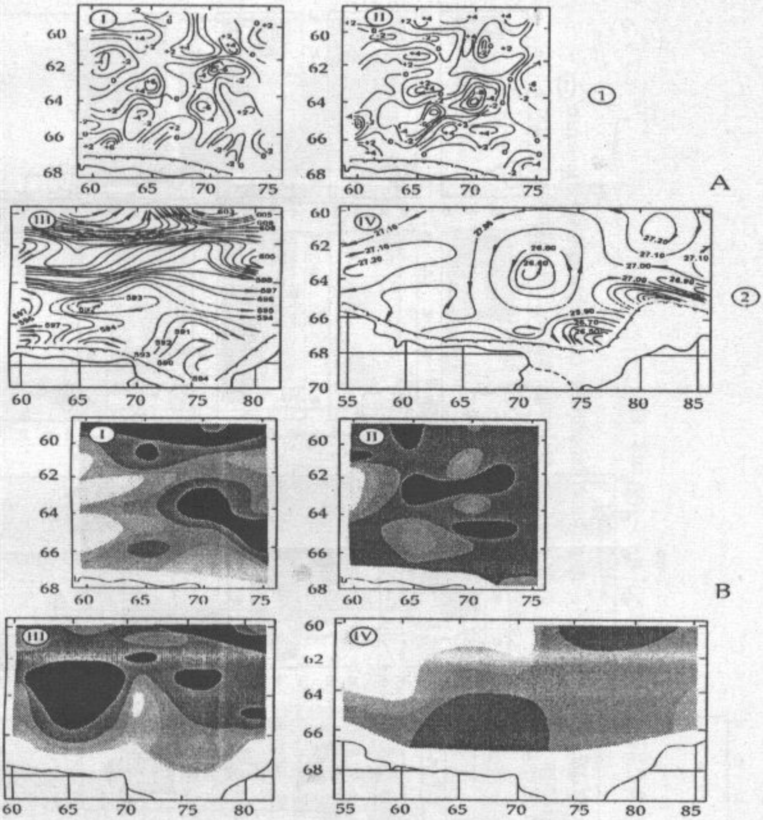

Fig. 49. **A. 1.** The turbulence of the field of geostrophic currents (rot $\pm \xi \cdot 10^{-7}$ s^{-1}; “+” = anticyclone; “- “ - cyclone) according to N.A. Ryabchikova (December 1977) (**I**) and February – March 1978 (**II**). 2. The geostrophic currents on the sea surface at the central Indian sector of Antarctic in February 1979 (**III**) and in January 1983 (**IV**) according to V.A. Lednichenko.

B. The distribution of mesozooplankton biomass in 0-100-m water layer (see Fig. 49.**A.1, 2**. for the dates and Fig. 47 **A, B** for the signs).

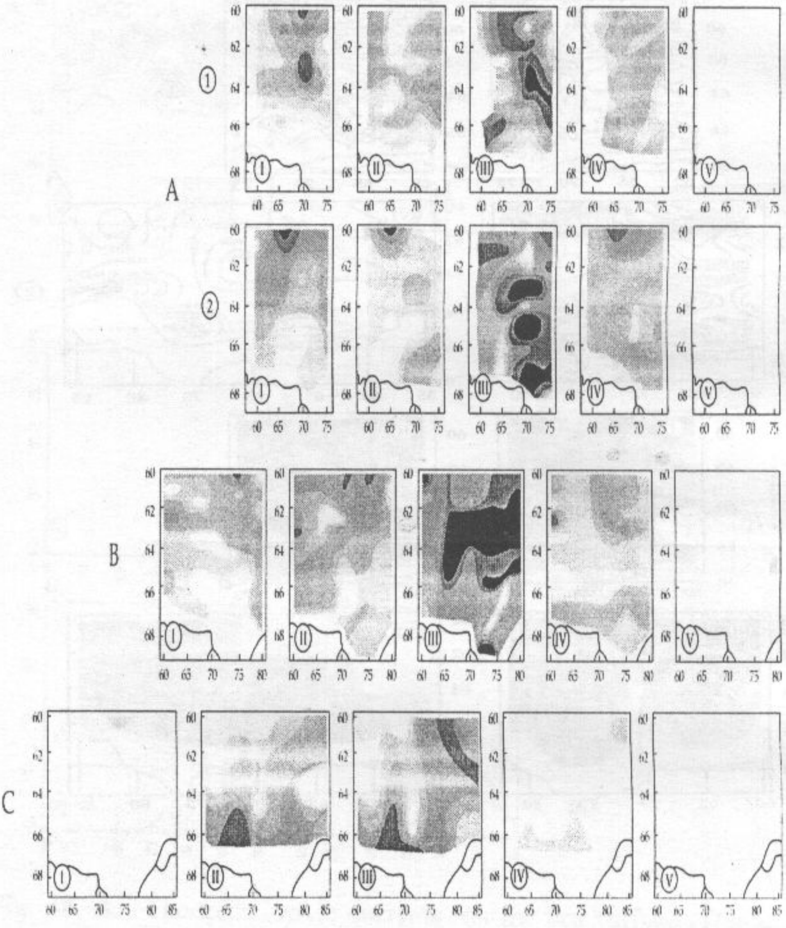

Fig. 50. The distribution of the biomass of copepods (I – V trophic groupings) in 0-100-m water layer in the central part of the Indian sector in December 1977 (**A 1**), February – March 1978 (**A 2**), February 1979 (**B**) and in January 1983 (**C**).
(See Figs. 47 **B** for the signs).

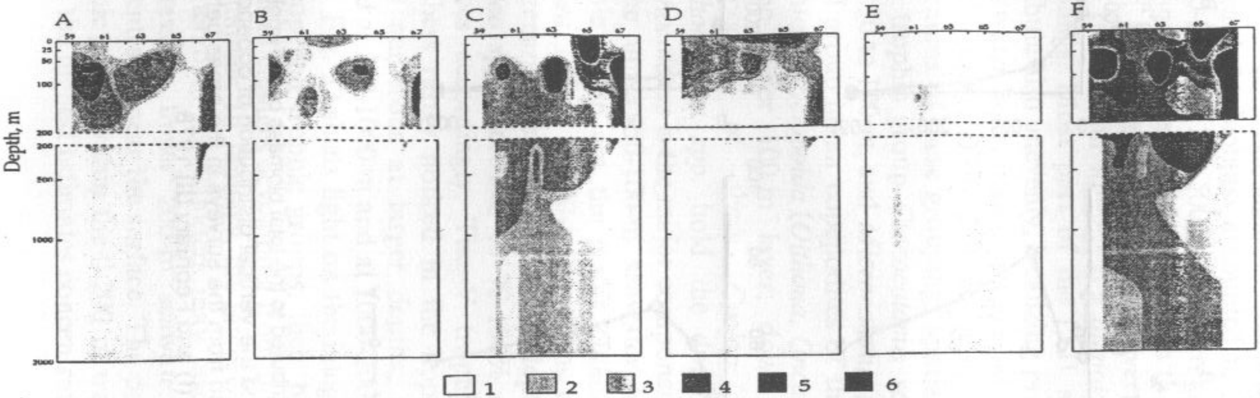

Fig. 51. The distribution of the biomass generated by copepods of different trophic groupings in the section along 70° E (February 1978): **A, B, C, D, E** are the I to V-th trophic groupings, correspondingly; **F** – the totality of copepods.

Biomass: **1** – 0-5; **2** – 5-10; **3** – 10-25; **4** – 25-50; **5** – 50-100; **6** - > 100 mg m^{-3}.

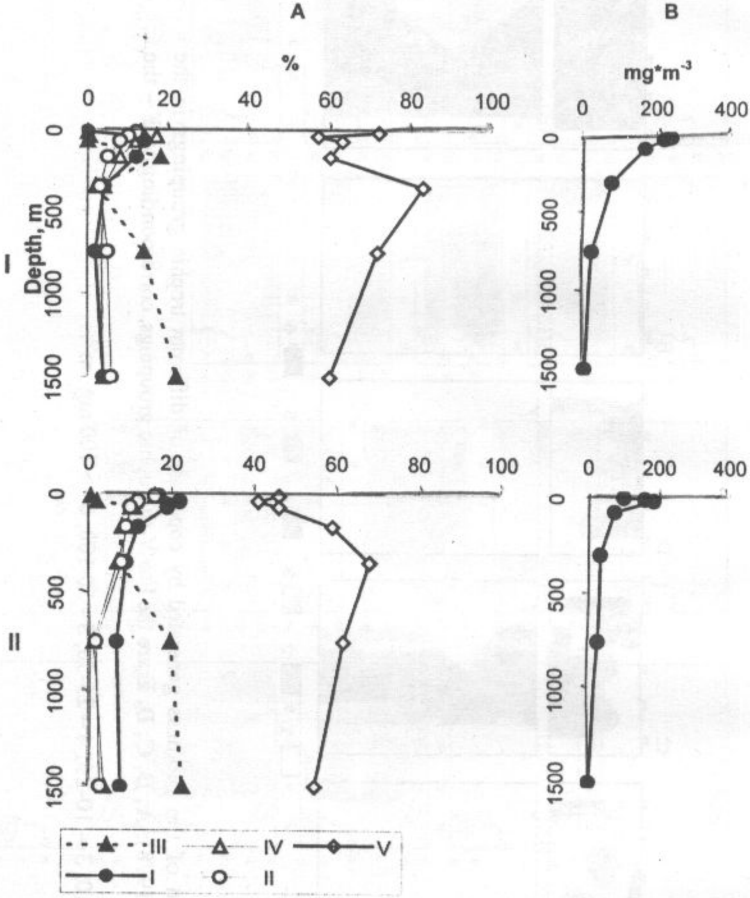

Fig. 52. The share (%) contributed to the total biomass by the trophic groups (I to V) (A) and the vertical distribution of copepods biomass (B) averaged from the surveys in the areas between 60-75o E in January (I) and February (II) 1978.

acutus, C. propinquus, Rhincalanus gigas, Metridia gerlachei),the biomass amounted to 300-700 mg · m^{-3}. Deeper, at 100-200 and 200-500 m the aggregation density was an order of magnitude less; at greater depth the measured estimates were about 10 mg · m^{-3}, not more. Nevertheless, even in the depth, some of the four abundant *Calanoida* dominated each of the samplings. Most part of the I, II and IV trophic groupings distribute also unevenly, localizing predominantly in upper 100-m seawater layer; occasionally, relatively small swarms may be found from 100 to 200 m depth. As a rule, quantitative maximums of these groupings spatially overlap each other. In the I trophic group *Ctenocalanus vanus* dominates the depth from 50 to 100 m, and *Microcalanus pygmaeus* deeper water. In the II group junior copepodites of the mass *Calanoida* and the predatory *Cyclopoida* (*Oithona, Oncaea*) are the most abundant in the upper 100-m layer; down to 500-m depth junior copepodites of these *Cyclopoida*, or *Calanoida*, or *Scaphocalanus spp.* hold the dominance; deeper the genus *Scaphocalanus* is the major component of this trophic grouping. In the upper 50-100-m seawater layer 70-100% of the IV trophic group are the genus *Oithona*, the rest is the genus *Oncaea*. Down to 500-m depth the disproportion between the two genera is levelling, at larger depth the relative numbers of *Oncaea spp.* increases to 70-100% and that of *Oithona spp.* reduces accordingly. The V trophic grouping includes few members rarely noticed in the upper 50-m layer; they were more numerous at larger depths, their small swarms were found at 500-1000 m and at 1000-2000 m.

Fig. 52 sheds light on the integral vertical distribution of the copepod trophic groups, their biomass and also on some trends of changes developing from the first half to the middle of the summer. In January, the intensive ascent and reproduction of interzonal zooplankters may lead to accumulation of the biomass in upper 200-m seawater layer, with maximums concentrated near the surface. The portion generated by the III trophic group within the 0-200 m water column makes up 58-72%, the highest estimates concentrate in the upper 25-m layer.

The contributions owing to the I, II and IV groups differ only insignificantly and, reaching a peak within the upper 50 m, they decrease at larger depths.

The percentage of the V trophic group found in the upper 100-m water layer was evaluated as about 1%, but within the 100-200 water column their share grew to 10-15%. Below, with the increase of depth and the reduction of total copepod biomass the III trophic group quantitatively varied from 60-85%, slightly rising in the 200-500 m depth and decreasing in deeper sea water. Minimum of the collectively taken I, II and IV groups has been measured at 200 to 500 m depth and maintained in deeper water. The portion of predators of the V group was growing with increasing depth and reached maximum at 1000-2000 m. In February, the first manifestations of the quantitative decline were noticed as the reduction of the III trophic group in the upper 100-m layer (1.5 times as less as in January). However, the rest of the identified trophic groups displayed a slight increase that month. Total copepod biomass maximum had dislocated to 50-100 m depth. Below the 100-m depth mark total copepod biomass and the quantitative ratio of the trophic groupings did not conspicuously differ from those in January.

The array of the facts and investigation results adds clarity to understanding of the trophic structure of Antarctic zooplankton. The trophic structure has some features inherent to communities with unbalanced food relations inhabiting highly productive local zones. The combination of two contradictory features – the potentially wide food spectrum of the individual community components and the diversity of the identified dimensional-functional groups – predetermines the possibility of optimal realization of food relations in the plankton communities, i.e. those directed to the most efficient utilization of the forage by the consumers. In fact, this possibility finds its top realization only between phytoplankton and first-order consumers, that is, apparently, owing to the short-term growing period and the scarcity of faunistic diversity. It is noteworthy that in the subsurface (to 100 m) and in deeper (200-500 m) sea water the predatory fraction of community does not substantially enlarge even in winter at the peak of the development; "vegetarian" plankton remains dominant during this season as during the growing period. Among the predatory varieties the most wide-spread and numerous are small forms of the IV trophic group; their seasonal and interannual fluctuations influence predominantly this trophic level. Large predators are only of local significance.

CHAPTER VII

MICROZOOPLANKTON (INFUSORIANS): TAXONOMIC COMPOSITION, DISTRIBUTION, ABUNDANCE

The importance of microheterotrophic organisms, primarily infusorians and zooflagellates, in transforming nutrients in the food chains has been demonstrated for planktonic communities of the tropical and temperate ocean zones (Sorokin, 1975, 1979, 1982 a,b; Tumantseva, 1980). Less clear is the situation with the communities in Antarctic. The shortage of literature about Antarctic microzooplankton species composition and abundance roots in slight knowledge of the subject and in technical difficulties – microscopic studies of the protozoans are not an easy task because contact with the solid surface (glass) destroys these fragile organisms. The majority of early studies dealt with qualitative composition of the Antarctic protozoans (Hentschel, 1936; Balech, 1958; Balech, El-Sayed, 1965; Hasle, 1969). Data on quantitative characteristics of Antarctic microheterotrophs appeared relatively recently (Tumantseva, 1978, 1982; Mamayeva, 1984) owing to the investigations having been carried out in the Pacific sector of Antarctic. We did not find any scientific evidence which would shed light on the abundance of protozoans in other sectors, and this makes the topic under the study even more interesting and significant.

It was found that small infusorians (*Oligotricha, Holotricha*), several species of the genus *Strombidium* and tintinnians dominate Antarctic protozoan plankton

(Tumantseva, 1978; Mamayeva, 1984). Infusorians were most plentiful in the zones of Antarctic convergence and Antarctic divergence. As N.I. Tumantseva wrote, the biomass measured in the Antarctic convergence zone sometimes was more than 100 mg $\cdot$ m^{-3}; in the Antarctic divergence zone the corresponding estimate, according to N.V. Mamayeva, had been as high as 5 g $\cdot$ m^{-2}. In both cases the greatest abundance of protozoans was in upper 10-25-m water layer. High concentrations of the protozoans were associated with the abundance of phytoplankton (Mamayeva, 1984). Average biomass of protozoan plankton in Antarctic waters of the South-West Pacific was evaluated as 136 mg C $\cdot$ m^{-2} for the layer 0-75 m that exceeded the corresponding average (84 mg C $\cdot$ m^{-2}) for Subantarctic waters (Tumantseva, 1982). According to the calculations by Tumantseva, infusorian production in Subantarctic makes up 10-32% of the collective production by phyto- and bacterioplankton.

Evidences given above, though not numerous, point out that in Antarctic waters microheterotrophs may play very important role. Proceeding from this, we endeavoured to assess the significance of microheterotrophic organisms for plankton community of the two insufficiently explored sectors of Antarctic.

Materials and methods

In doing this research we used materials of the synchronous cruises organized by AzCherNIRO and AtlantNIRO to the main region of our studies (60° – 80° E) and to the Atlantic sector (between 30° and 60° E)* in 1983-1984, and the data obtained from samplings at the basic region during the season of 1984-1985.

Samples of microzooplankton were taken during the complex oceanological surveys by 6-and 7-l plastic water bottles from depths receiving 100, 50, 25, 10 and 1% light, from the traditional series of depths (0, 10, 25, 50 and 100 m) and in

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* Materials from the Atlantic sector of Antarctic have been collected, handled and processed by V.A. Sushin and E.Z. Samyshev.

several cases from 200, 500, 1000 and 2000 m. Species identification and quantitative counts of the microheterotrophs (infusorians) were made in fresh (non-fixed with formaldehyde) samples with the employment of penal-shaped chamber (Sorokin, 1980).

Results and discussion

In the season of 1983-1984 infusorians identified for the two regions were mostly the genus Strombidium and tintinnians, *Cymatocylis spp.* and *Epiplocylis spp.* dominated the latter.

The length of the naked infusorians varied from 10 to 150 µm and of the tintinnians from 50 to 250 µm. Size structure of infusorians was different if compared between the different water areas of Antarctic. The most distinctly this phenomenon was manifested at the Atlantic sector of Antarctic. In the Weddell Sea, *Ciliata* found in the sea water coming from the south were predominantly small (20-30 µm) (Fig. 53 A). On the contrary, in neritic water of the Antarctic Peninsula large (40-50 µm and more) forms prevailed (Fig. 53 B). At the confluence of the two water masses (Secondary Frontal Zone – SFZ) the small and the large forms presented almost in equal portions (Fig. 53 C). The curve representing size classes of infusorians from the Antarctic Circumpolar Current (ACC) has two peaks, like that referring to SFZ, but they are closer to the left end of the diagram (Fig. 53 D).

It is noteworthy that in December size structure of the infusorians from the main region, in which the dominance of small forms was evident, was almost the same as in the Weddell Sea (Fig. 53 E); in February even smaller forms took over the leadership (Fig. 53 F). This similarity may be explained by the same latitudinal position of the two sea-water areas.

In the explored areas of the ocean infusorians distributed very unevenly because of the heterogeneous water structure, different water productivity and the phases of plankton

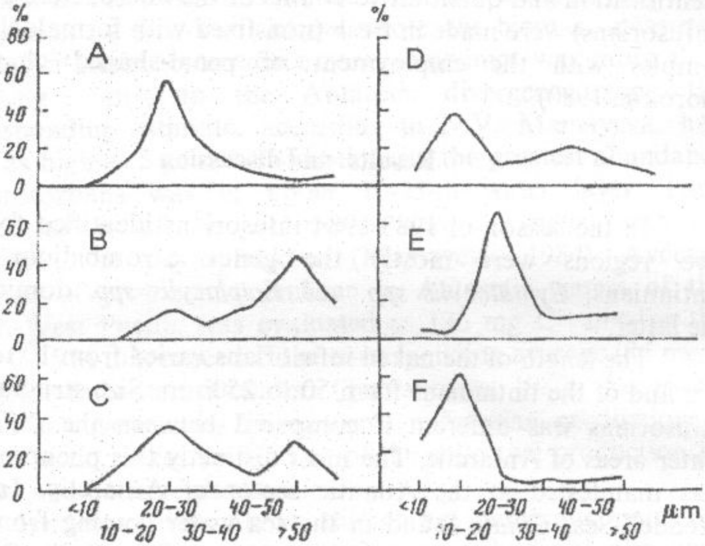

Fig. 53. The size structure of infusorians during the season of 1983-1984.
A – the Weddell Sea; B – the shelf of the Antarctic Peninsula; C – Secondary Frontal Zone (SFZ); D – Antarctic Circumpolar Current (ACC); E – the Commonwealth Sea, December 1983; F – the Commonwealth Sea, February 1984.

community succession shifted both on the temporal and on the spatial scale. There was distinct relationship between the position of infusorian concentration maximums and the depth of seasonal pycnocline (Fig. 54, 55); this relationship manifested itself also at the study of other plankton components at the Commonwealth Sea. Usually, the majority of ciliates concentrated in upper 10-25-m water layer. Deeper position of the maximums, similar to those of phytoplankton (Chapter II), was noticed either in the coastal zone as associated with shelf water downwelling, or in the north where water stratification was less distinct and thermocline might go

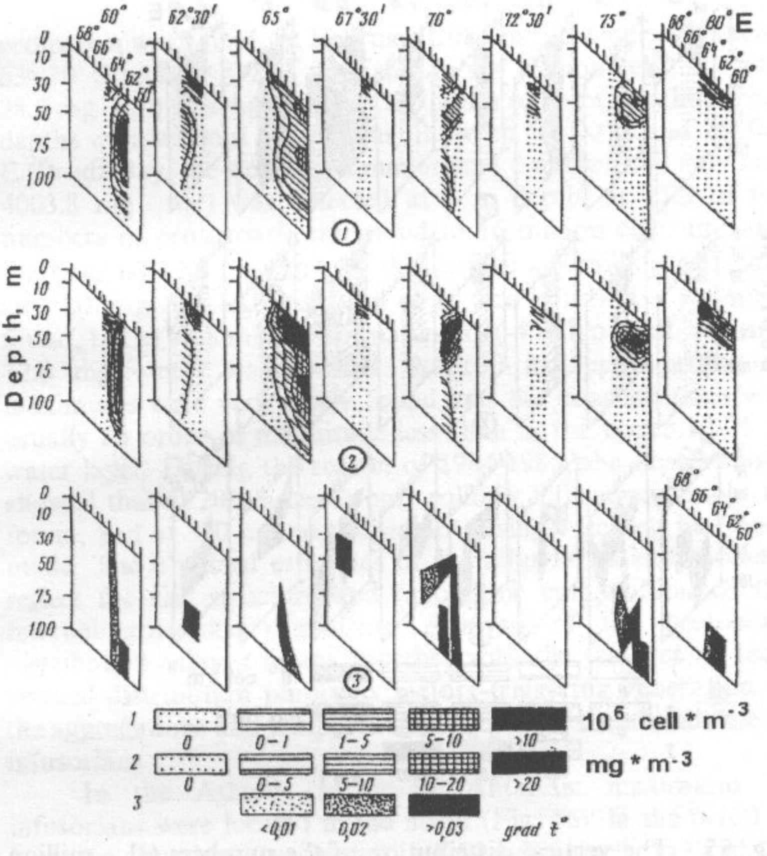

Fig. 54. The vertical distribution of the numbers (1 – million cell · m⁻³) and biomass (2 – mg · m⁻³) of infusorians and the position of seasonal thermocline (3 – t°) based on the meridional sections in the Commonwealth Sea (December 1983).

to depth. Protozoan concentration maximums were clearly stratified and situated in narrow water layers; as a result they were usually registered only at one depth, or sometimes at two neighbouring depths from which samples were collected. For

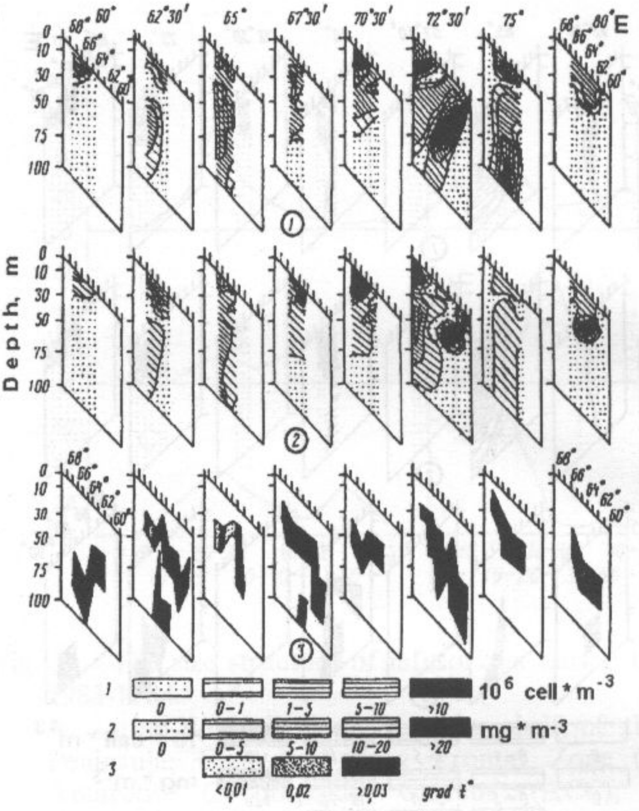

Fig. 55. The vertical distribution of the numbers (1 – million cell · m^{-3}) and biomass (2 – mg · m^{-3}) of infusorians and the position of seasonal thermocline (3 – t°) based on the meridional sections in the Commonwealth Sea (February 1984).

instance, in December 1983, at the sea-water area lying between 63° 40' S and 62° 30' E infusorian maximums (the abundance 16 million cell · m^{-3} and the biomass 28.8 mg · m^{-3}) concentrated in the surface (0 m); at 9 m depth the corresponding estimates were 4 times as less, and at 17 m and deeper not a single protozoan was found. In February 1984 in the waters between 63° 30' S and 75° 00' E a maximum (24 million cell · m^{-3} and 28.8 mg · m^{-3}) was registered at the depth of 23 m, neighbouring depths were without protozoans. Between 68° 00' S and 75° 00' E (Prudz Bay, the ice-edge) a maximum (6 million cell · m^{-3} and 4003.8 mg · m^{-3}) was detected at 6 m depth, at 11.5 m the numbers of protozoans amounted to 16 million cell · m^{-3} and the biomass 12.8 mg · m^{-3}; at the surface - 10million cell · m^{-3} and 4.0 mg · m^{-3}. At the depth of 19.4 m infusorians were not found, but at 38.8 m another maximum (4 million cell · m^{-3} and 12.8 mg · m^{-3}) was located. At 100 m depth protozoan maximums were very rarely found and the concentration was usually an order of magnitude less than in the upper 10-25 m water layer. During the season of 1984-1985, the observations showed that at 200 m depth only solitary infusorians might be found, and at 500 m and deeper not a single finding had been made. The obtained estimates of the abundance and biomass reflect the size structure and taxonomic composition of the microheterotrophic organisms. Analysis of the protozoan distribution of protozoans together with the features of their vertical distribution pinpoints factors triggering generation of the aggregations and temporal fluctuations of the abundance of infusorians.

In the Atlantic sector of Antarctic maximums of infusorians were located in the north (Fig. 56): in the 0-100 m layer the abundance amounted to 1.64 million cell · m^{-3} and the biomass to 77 mg · m^{-3} (compare with 11.4 mg · m^{-3} – the mean infusorian biomass for the region in 0-100-m water layer). Minimums – the numbers of 25 000 million cell · m^{-3} and the biomass of 25 mg · m^{-3} – were found at water areas most strongly affected by the sea-water masses transferred from the Weddell Sea. East from 40° W, where the Secondary Frontal Zone was disintegrated and dispersed, the abundance and the biomass of ciliates were relatively high – about 0.5 million cell · m^{-3} and 45 mg · m^{-3}, correspondingly.

In December and in February the concentration of infusorians over the Commonwealth Sea was 1.5 times larger than in the Atlantic sector, in the photic layer average estimates

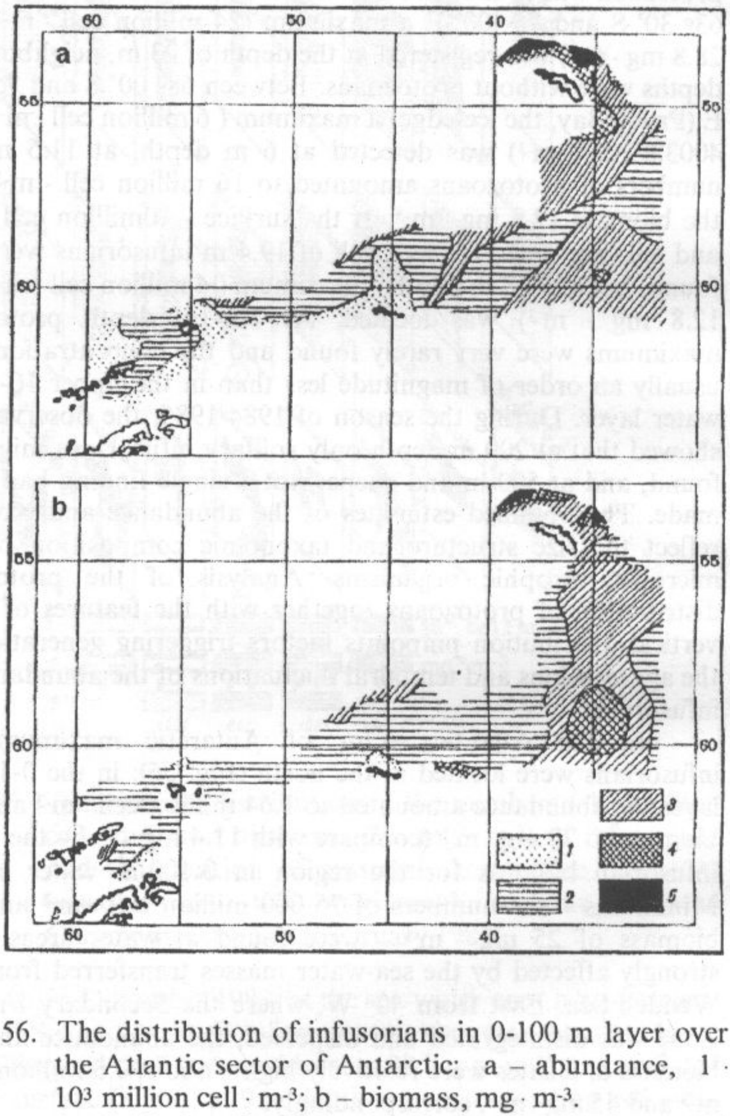

Fig. 56. The distribution of infusorians in 0-100 m layer over the Atlantic sector of Antarctic: a – abundance, 1 · 10^3 million cell · m^{-3}; b – biomass, mg · m^{-3}.
1 : 0-10, 2 : 10-25, 3 : 25-50; 4 : 50-100, 5 : > 100 thousand cell · m^{-3} (mg · m^{-3}).

in these mounts were 18.3 and 16.2 mg · m-3, correspondingly. Unlike in the Atlantic sector, there was better coherence between the quantitative distribution and primary production of infusorians and the bacterioplankton production in the area (Figs. 57, 58). The coincidence between the maximums generated by the community components is indicative of relatively stable water dynamics in the locations where deeply indented ice edge and coastline had been formed under the influence of topogenic factor. Manifestations of the topogenic effect were noticed in February at the Commonwealth Sea area when the retreat of sea ice towards the continent began; the infusorian biomass was as high as 300 mg · m-3 during that period. Maximums of infusorian concentration detected in December near the ice-edge both in the Commonwealth Sea and around the islands in the Atlantic sector were, most probably, owing to the same effect. Comparison of infusorian abundance measured in December and in February at a particular area of the Commonwealth Sea clearly reveals seasonal changes: the early summer estimate of 18.3 mg · m-3 dropped to 1.2 mg · m-3 in the mid-summer (February). Relatively high phyto- and bacterioplankton production generated in the zones of minimum infusorian numbers in February suggests that the seasonal changes should be strongly influenced by water transfer.

In February 1985 the quantitative characteristics of microzooplankton in the Commonwealth Sea were generally higher than in February 1984. In 0-100 m water layer the average abundance of microzooplankton was 0.9 million cell · m-3, with the range of estimates from 0.1 to 3.5 million cell · m-3, and the average biomass 41 mg · m-3, with the range from 0.0 to 175.0 mg · m-3. The distribution of protozoans over the area (Fig. 59) followed the same pattern: maximums of microzooplankton abundance had been concentrated predominantly in the coastal or near-ice zones, and maximums of the biomass also in the zone of Antarctic divergence; they overlapped the maximums of net seston (mostly phytoplankton and detritus). It is noteworthy that this coherence manifests itself more distinctly at comparing the distribution of

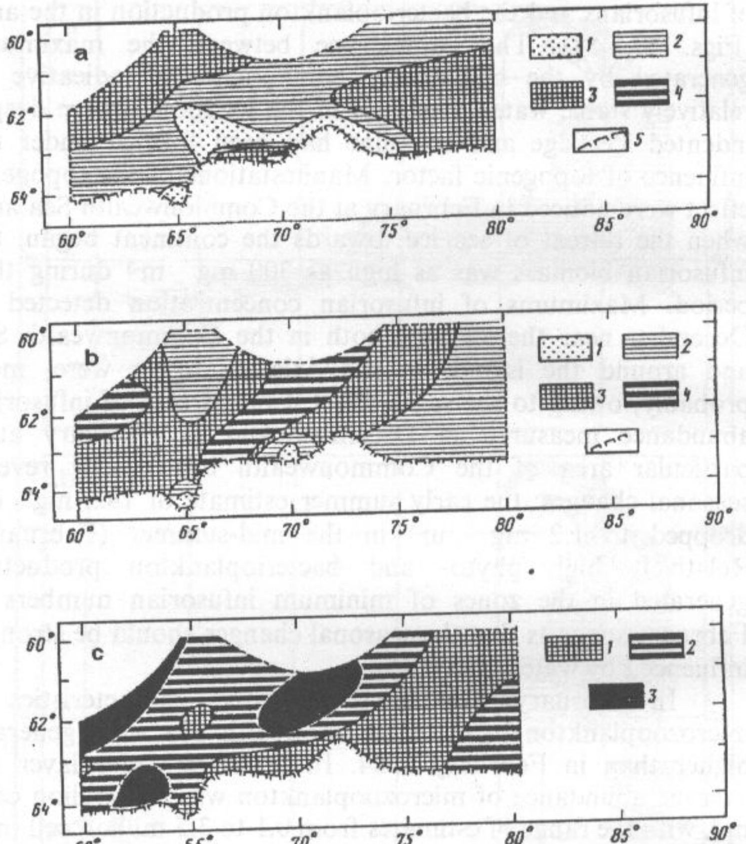

Fig. 57. The infusorian abundance distribution (a), bacterioplankton production (b) and primary production (c) in photic water layer at the Commonwealth Sea (December 1983):
a : 1 – 0-1; 2 – 1-10; 3 – 10-100; 4 - > 100 mg · m-3; 5 – the ice-edge;
b : 1 - < 15; 2 – 15-30; 3 30-50; 4 50-100 mg C · m-2 · d-1;
c : 1 – 50-100; 2 – 100-150; 3 - > 150 mg C · m-2 · d-1.

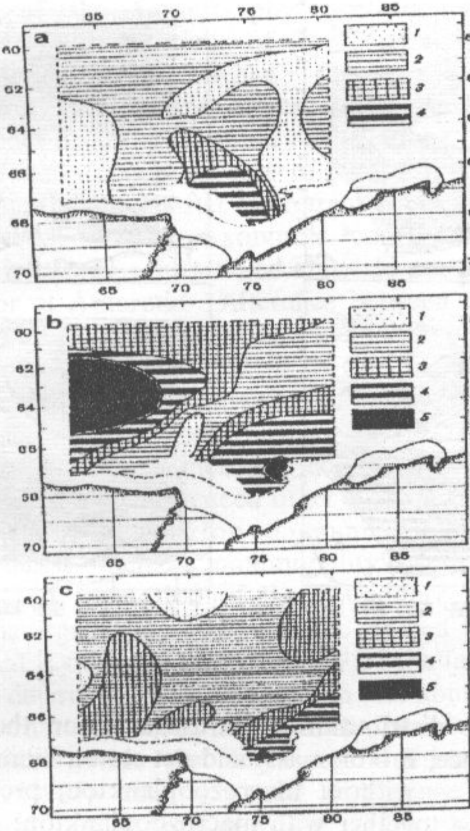

Fig. 58. The distribution of infusorians (a), bacterioplankton production (b) and primary production (c) in photic layer of the Commonwealth Sea (February 1984):

a : 1 – 0-1; 2 – 1-10; 3 – 10-100; 4 - > 100 mg · m^{-3}; 5 – the ice-edge;

b: 1 - < 15; 2 – 15-30; 3 – 30-50; 4 – 50-100; 5 - > 100 mg C · $m^{-2} \cdot d^{-1}$;

c : 1 - < 25; 2 – 25-50; 3 – 50-100; 4 – 100-150; 5 - > 150 mg C · $m^{-2} \cdot d^{-1}$.

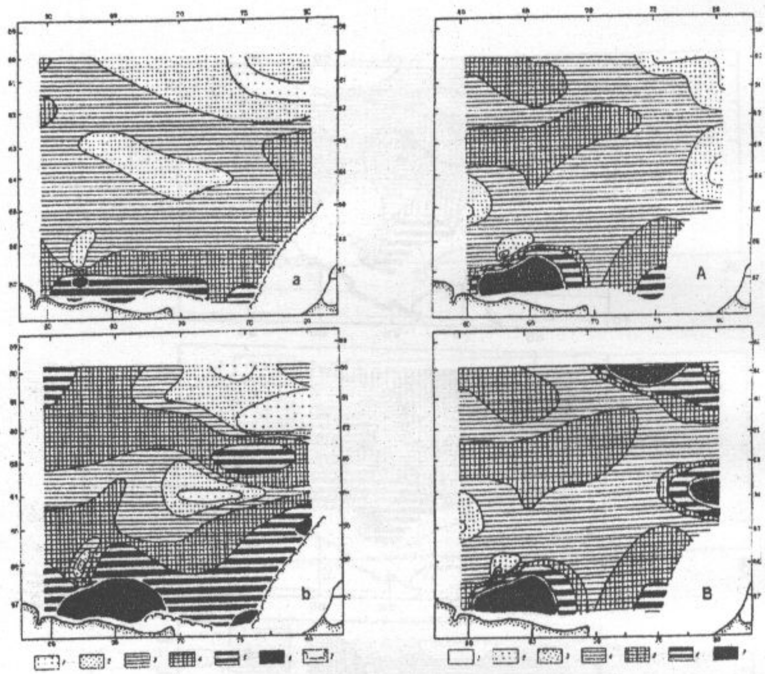

Fig. 59. The distribution of infusorians (on the left, A – abundance, B – biomass) and net seston biomass (on the right, A – without macrozooplankton, predominantly krill; B – together with macrozooplankton) in 0-100 m layer of the Commonwealth Sea.

Infusorians: abundance (million cell $\cdot$ m^{-3}) :

1 - < 0.15; 2 – 0.15-0.5; 3 – 0.5-1.0; 4 – 1.0-2.0; 5 – 2.0-3.0; 6 - > 100; 7 – the ice-edge;

biomass (mg $\cdot$ m^{-3}):

1 - < 5; 2 – 5-10; 3 – 10-20; 4 – 20-50; 5 – 50-100; 6 - > 100; 7 – the ice-edge.

Net seston biomass (mg $\cdot$ m^{-3}):

1 - < 50; 2 – 50-100; 3 – 100-200; 4 – 200-500; 5 – 500-1000; 6 – 1000-2000; 7 - >2000.

microzooplankton with the distribution of net seston excluding macrozooplankton. Certainly, microheterotrophic growth during the phase of community succession coming after the period of the highest phytoplankton abundance is accompanied by formation of the aggregations of the microheterotrophs only when there are long-lasting phytoplankton aggregations either in the sheltered coastal (near-ice) zones or at the stationary circulations. This explains, in particular, the drastic decrease of protozoan abundance in open waters of the region after the retreat of sea ice in February 1984 and 1985. In the taxonomic composition and size structure of infusorians the studied areas do not differ from the Pacific sector of Antarctic. Difference between the regions in the abundance of infusorians is due to specific combination of factors during the observations; in its turn, each combination of factors depends on the environment, water productivity, the phase of community succession and so on. The difference between local environmental conditions during our investigation had also influenced other plankters and therefore the "age" of the entire plankton community (see Chapter IX).

Neverheless, there is commonality of the patterns of distribution and generation of the abundance maximums in heterotrophic organisms inherent to the studied water areas of Antarctic that is owing to commonality of the factors we have indicated as determining the distribution and abundance. In the quantitative characteristics of infusorians the investigated areas are comparable with the highly productive Bering Sea (Mamayeva, 1983), the equatorial divergence zone of the Pacific Ocean (Tumantseva, Sorokin, 1975), the open ocean zone of the Peruvian upwelling (Tumantseva, 1980) in which the functional significance of protozoans in planktonic communities is very high. These evidences permit to suggest that microheterotrophs should be an essential and functionally meaningful component of the communities of plankton in Antarctic.

CHAPTER VIII
SUSPENDED ORGANIC MATTER: THE CONTENT, DISTRIBUTION AND GENERATION RATE

Taking into account the extant discord among the experts about the term, we find it essential to explain that we understand suspended organic matter (SOM) as the organic constituent part of total particulate matter (TPM), which in our case is fine seston fraction separated from coarse of seston fraction by means of the sieve N 68 with the mesh 76 μm. In our case SOM consists predominantly of the organic matter produced by phyto-, bacterio- and microzooplankton and detritus. The preponderance of the organic matter of detritus over plankton fraction of seston is an acknowledged fact. The portion of organic detritus in SOM depends on water productivity; in the sea water it is as high as 80-99% and more (Sushchenya, 1961; Sushchenya, Finenko, 1966; Samyshev, 1968). Blooming phytoplankton may account for almost 100% of the biogenic fraction of suspended organic matter (Finenko, 1971).

Though the basic component of ecosystem (Odum, De la Cruz, 1963), detritus is still the least studied of the components. The explanation roots primarily in the lack of simple and reliable methods for detritus collection and quantification. Any of the presently used methods has faults that makes comparison of data obtained by different methods a hard task to cope with. For instance, seston content in mesotrophic lake Naroch, which had been determined in samples obtained through separation in a supercentrifuge, was underestimated by 50% in comparison with the content having been determined by gravimetric method (Ostapenya, 1979). The content of C_{org} in SOM collected in the Atlantic Ocean through setting onto compact glass powder layer was 3-4 times as large as that determined in post-separation samples (in both cases C_{org} was measured employing modified Knoppe method); similarly, the content of microorganic particles larger than 1 μm, which were retained by membrane filters with the pore size 0.4 – 1 μm even discarding the filter-clogging fraction less than 1 μm, was far greater than the content of organic matter determined from C_{org} by chemical analysis of the filtered simples (Yemelyanov, Romankevich, 1979). The elicited distinctions associated with the inadequate counting of the microscopic organic particles, which are, probably, the main component of detritus, raise serious doubts about the current notions about intensive conversion of the detritus to solution especially in Antarctic sea water, where the cold environment and the scarcity of bacterial coating (over 80% of the bacteria do not form aggregations and do not adhere to the detritus) hamper this process (Wiebe, Pomeroy, 1972) (cit.: A.P. Ostapenya, 1979). Certainly, for the most part this organic substance is biochemically stable suspended fraction of plankton humus (Skopintsev, 1961). There is a number of scientific evidences of the reduction of dead plankton transformation rate at low ambient temperature. It follows from the experiments that the loss of organic fraction in the substance of dead plankton made up 66% at 20° C for a month and 77% of the initial substance during the following 5.5 months (Skopintsev, 1979), while at the temperature of 8° C the rate of this process decreased two times (Bikbulatova et al., 1979). Studies in waters of the tropical zone have shown that unstable organic matter in upper water layer was decomposed in 1.5 day at 30° C; in the depth (1500 and 3000 m), where the temperature keeps at 2 – 3°C, this process takes from 27 to 150 days (Finenko, 1971; Finenko, Ostapenya, 1971). The authors arrived to a conclusion that even at great depths the content of oxidized organic matter should be substantial. High content of easily hydrolyzed substances (C_{org} 25.9-34% carbohydrate fraction of C_{org} 67.9 – 75.8%) in the bottom sediment of Kerguelen Archipelago (Spiridonov, Tribrat, 1977) also implies that the organic matter sinking to the sea floor at the depth of 250 m and more should be incompletely transformed. These examples prove the validity of the hypothesis about the low-rate transformation of detritus in Antarctic and about a larger than at low latitudes easily oxidized fraction of SOM.

Usually, studies of SOM in Antarctic waters were the matter of geology. In the Indian sector of Antarctic researches of this sort had been conducted within the framework of the International Geophisical Year (IGY) programme during 1957-1959 (Lisitsyn, 1960, 1964). Organic fraction was studied by means of chemical analysis of samples got through separation. The content of organic carbon in the suspension was 8.67% on the average, varying from 0.4 to 18.84%; converted to ash-free organic matter the corresponding estimates were 17.34% and 0.8-37.8% (Lisitsyn, 1964). In the early 1980-s we had learnt through dry burning of suspension collected on membrane filters (Samyshev, 1983 b) that SOM fraction in the suspension from the Indian sector was usually 3-4 times larger than that; accordingly higher were also SOM concentrations. The drawbacks of research technique which probably underlie this difference have been discussed before. Besides, fluctuations of the abundance of plankton registered during the years of the studies might also add to the discrepancy. During our studies we found that the amount of SOM considerably changed over the summer season. Therefore, discarding the seasonal aspect inevitably leads to the incorrect deductions at comparing the relevant data.

The richness of the descending SOM flux in waters above the Antarctic shelf has been proved in experiments with the employment of detritus samplers set at 5 and 25 m depths (Mutsuda Osamu et al., 1987) and also at 100 and 200 m (Karl et al., 1987). The experiments by Mutsuda have unveiled seasonal dynamics of the composition and those by Karl the intensity of SOM supply to the sea bottom.

Material and methods

The body of materials was collected during the macroscale surveys in March 1977[*], January 1980, February

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[*] In 1977 the suspended matter was collected along 75° E only.

1981, December 1982 – January 1983 and in February 1985. In 1977 the study of SOM was based on the particulate matter settled onto Synpore membrane filters N 2 with the pore size of 2.5 μm coated with barium sulphate. Further SOM content was determined directly on the preliminary weighed Synpore filters N 4 with 0.82 μm pores; the samples were taken from usual series of depths – 0, 10, 25, 50 and 100 m – in 1980-1981, 1982-1983; in 1985 the sampling was made also at 200 and 500 m depths, and in 1982-1983 and in 1985 at 1000 and 2000 m in the sections along 75° E. In 1980, 1981, 1982-1983 at the stations intended for studying primary production, bacterio- and microzooplankton samples of the sea water for particulate matter separation were taken in the photic layer from depths which corresponded to 100, 50, 25, 10 and 1% light on the sea surface; additionally, samples were collected from 100-m depth. On barium sulphate coated filters SOM was studied by iodine oxidation method (Karzinkin, Tarkovskaya, 1962), and on the membrane filters by the method of dry burning at 900° C in a muffle oven. The weight of suspension was tentatively determined as the difference between initial and final weight of the filter, and the amount of SOM as the difference between the weight of suspension and the weight of ash remained after the sample had burnt up. Control tests did not elicit ash residue worthy of taking into account in the corresponding calculations. The array of weighings was made using a pair of laboratory scales with the precision of 0.1 mg.

Results and discussion

Inasmuch as in March 1977 SOM was studied from the samples settled on barium sulphate-coated filters, the resulting data are considered separately. From Fig. 60 it is evident that SOM content having been measured at different sites of the 100-m water layer varied broadly from 0.6 to 4.1 mg · l^{-1}, making up 1.54 mg · l^{-1} (dry organic matter) on the average for the meridional section. The distribution displayed features having been elicited for the phyto- and zooplankton;

maximums concentrated above thermocline, in the divergence zone (63° S) and in the northern part of the section they were

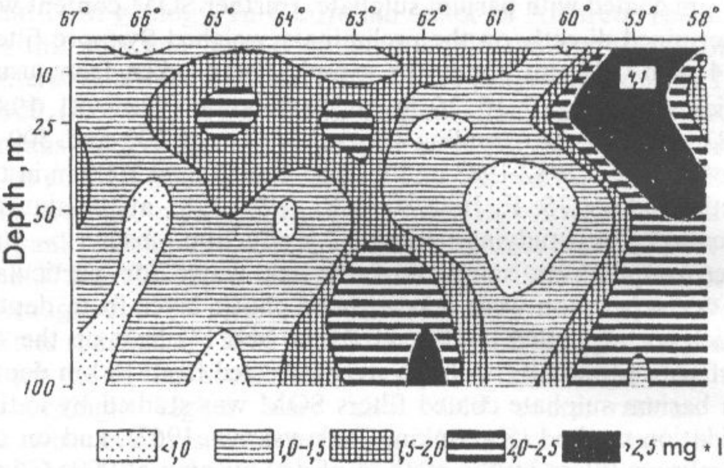

Fig. 60. The distribution of SOM (mg · l^{-1} dry organic matter) in the meridional section along 75° E, 11 – 17 March 1977.

found down to 100 m depth. At the same time, there was no distinct coherence between the distribution of SOM produced by phyto- and zooplankton. Taking into account the technique applied for collecting SOM in 1977, which entailed the possibility of dissolved and colloid organic matter sorption by the particles of barium sulphate (Romankevich, Lyutsarev, 1980), it was reasonable to expect the related overestimation of SOM content. However, results obtained later through different methods are comparable with those dated March 1977.

Extreme estimates of SOM content determined in 1980 – 1983 and 1985 by dry burning method differed sometimes more than an order of magnitude; the corresponding averages, were comparable on the one hand, the distinctions between them were linked with the term of the observations, on the other hand, that logically associates with the seasonal course of production-destruction processes in the pelagic zone. The closest coherence has been acknowledged for the series of data compared between 1980, 1981 and 1982-1983; during these years no anomalies had been noticed in the growth of the plankton components (primarily phytoplankton), therefore SOM concentrations measured in different months can be considered as having been obtained in different periods of the same summer season.

In December 1982 – January 1983 (the surveys of 20 December – 14 January), i.e. in the beginning of growing season, the average SOM content for 0-100-m water layer in the region was 1.4 mg (dry organic substance), varying at some stations from 0.4 to 5.2 mg · l^{-1}; the share of SOM in TPM had been evaluated as 64% on the average, varying between the stations from 33 to 88% (Fig. 61,3).

In January 1980 (the survey of 1 – 26 January), in the middle of the growing period, the amount of SOM in 0-100 m layer had slightly increased to the average of 1.95 mg · l^{-1}, the range of between-station fluctuations had narrowed to 1.1 – 3.6 mg · l^{-1}, the percentage of SOM in TPM varied from 30 to 90%, with the average 46% (Fig. 61,1).

In February – March 1981 (1 February – 7 March) at the late growing season, SOM concentration increased more than three times compared with the beginning of the season and amounted to 4.29 mg · l^{-1} on the average for the water layer 0-100 m, its values varied from 1.9 to 6.2 mg · l^{-1} between the stations; the percentage of SOM in TPM had been estimated 64% (average), varying from 50 to 76% (Fig. 61,2).

The observations which had been made in different years and covered the full season showed that SOM and TPM had been conspicuously increasing over the region.

The content of SOM measured from 5 to 22 February 1985 was relatively high. Its averages for 0-100-m and 0-500-m water layers approximated 1.7 mg · l^{-1}; the range of fluctuations between the stations was 0.3 – 3.5 mg · l^{-1} for the 0-100-m layer and 0.4 – 2.3 mg · l^{-1} for the 0-500-m layer. The portion of SOM in TPM had been 37% on the average (from 29 to 81%

depending on the site) in the 0-100 m water layer, and 60% and 35-80%, correspondingly, in the 0-500-m layer (Fig. 62).

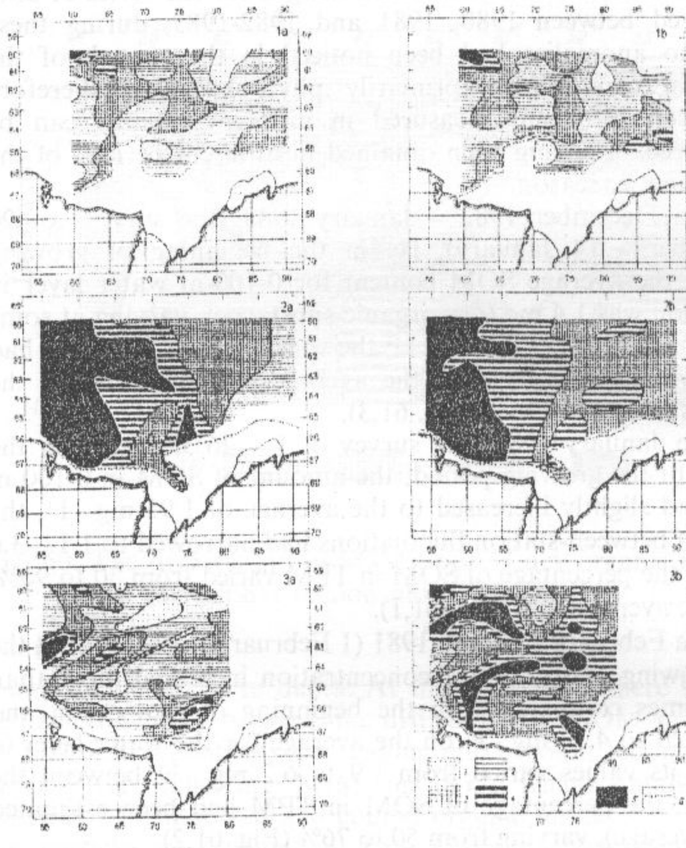

Fig. 61. The distribution of SOM (mg · l^{-1} dry organic matter) [left] and SOM percentage in the total particulate matter [right] in 0-100-m water layer (January 1980 – 1; February 1981 – 2; December 1982 – January 1983 – 3).

1 a – 3 a: 1 - <1.5; 2 – 1.5-2; 3 – 2.0-2.5; 4 – 2.5-3.0; 5 - >3.0; 6 – ice-edge

1 b – 3 b: 1 - <40; 2 – 40-50; 3 – 50-60; 4 – 60-70; 5 - >70; 6 – ice edge.

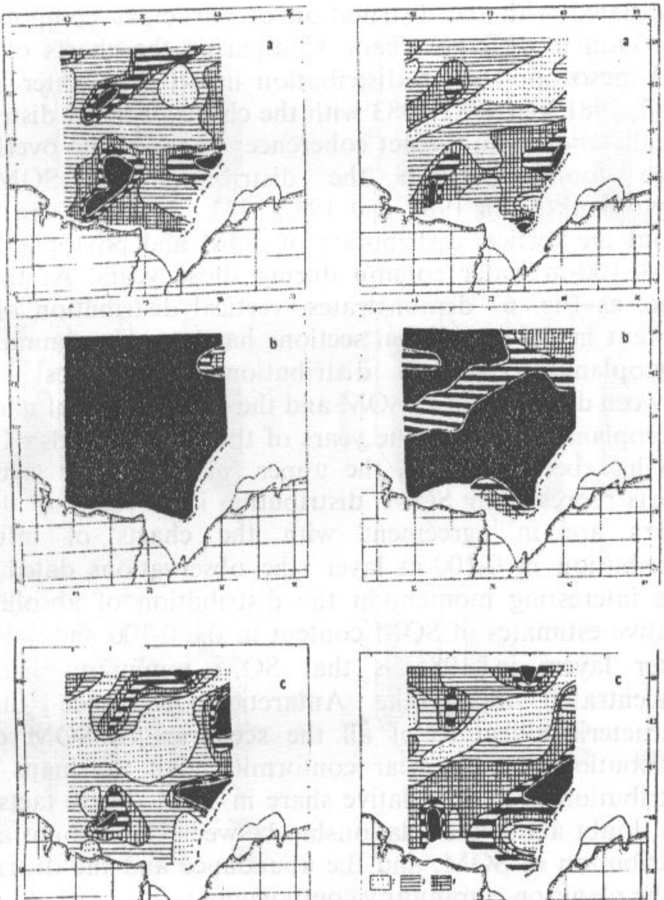

Fig. 62. The distribution of SOM (a, mg · l-1 dry matter), TPM (b, mg · l-1 dry weight) and SOM percentage in TPM in 0-100-m (left) and in 0-500-m (right) water layers, February 1985. Designation marks as in Fig. 61.

The mosaic pattern of SOM distribution persisted at the region over the years of the observations and was associated with the distribution of particular components of plankton in different years. Comparing the charts of phyto- and mesozooplankton distribution in 0-100-m water layer in 1980, 1981 and 1982-1983 with the charts of SOM distribution usually shows no distinct coherence; traces of the overlapping were found between the distribution of SOM and phytoplankton in 1981 and 1982-1983. The same can be said about the vertical distribution of SOM and phytoplankton in the 0-100-m water column during those years. At the same time, as Fig. 63 demonstrates, vertical distribution of SOM content in the meridional sections has many in common with phytoplankton vertical distribution. The closest relation between distribution of SOM and the components of nano- and microplankton during the years of the study (see also Chapter IV) had been found in the upper (photic) water layer. The charts representing SOM distribution in 0-100 and 0-500 m layers are in agreement with the charts of infusorian distribution in 0-100-m layer (the observations dated 1985). The interesting moment in the distribution of absolute and relative estimates of SOM content in the 0-100 and 0-500 m – water layers in 1985 is that SOM minimums had been concentrated along the Antarctic Divergence Line. A characteristic feature of all the scenarios of SOM content distribution is their clear conformity with the maps of the distribution of SOM relative share in TPM. These facts dispel any doubt about the relationship between the amount and the distribution of SOM, and the abundance and the distribution of the plankton community components.

Different degree to which the maximums of SOM content overlapped plankton abundance maximums may more or less exactly indicate the "age", i.e. the conversion phase of the substance. The high level of SOM content is determined by high content of humus fractions in the sea water; the humus constituent has remarkably high biochemical stability and therefore sustains high background concentration. SOM maximums, or trace maximums which are maximums

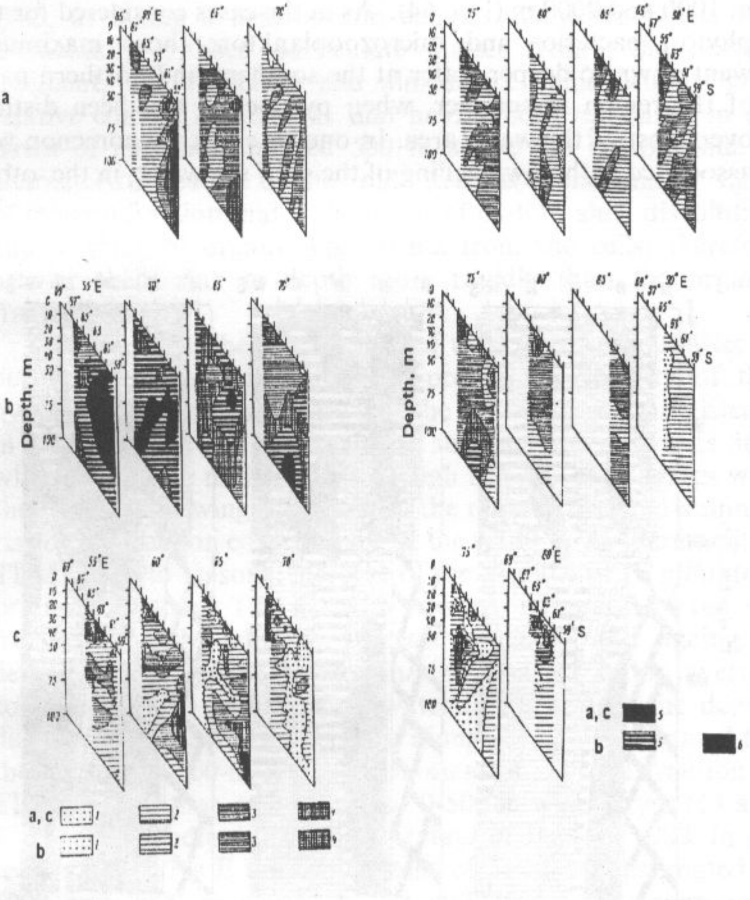

Fig. 63. Vertical distribution of SOM (mg · l^{-1} dry organic matter) in the meridional sections in January 1980 (a), February 1981 (b) and December 1982 – January 1983 (c).

a, c: 1 - < 1.0; 2 – 1.0-2.0; 3 – 2.0-3.0; 4 – 3.0-4.0; 5 - > 4.0;

b: 1 - < 2.0; 2 – 2.0-3.0; 3 – 3.0-4.0; 4 – 4.0-5.0; 5 – 5.0-6.0; 6 - >6.0.

inherited from plankters, usually persist for a long time, not disintegrating in water column: they were registered as deep as at 1000 and 2000 m (Fig. 64). As in the cases considered for the phyto-, bacterio- and microzooplankton, those maximums went down to deeper water at the southern and northern parts of the region in summer, when pycnocline had been distinct over most of the water area. In one case this phenomenon was associated with downwelling of the shelf sea water, in the other

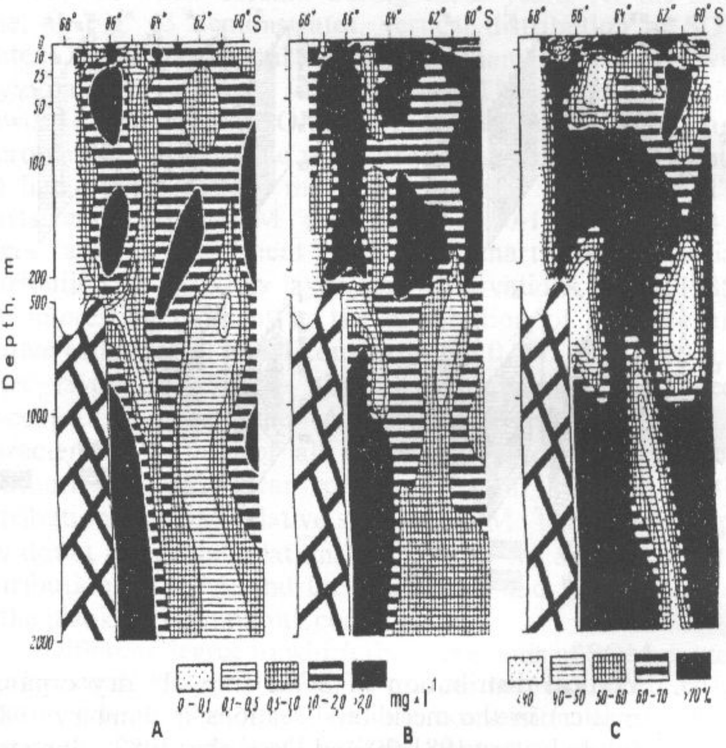

Fig. 64. Vertical distribution of SOM (A), TPM (B) and SOM and TPM relative estimates (C) in the meridional sections.

case with sinking and disintergating of pycnocline. On the shelf those maximums might approach sea bottom: in February 1985, at taking a near-bottom sample the water bottle had accidentally grabbed particulate matter from the bottom sediment; this substance had almost the same (about 60%) relative content of SOM as that having been measured in the patch of maximum located 500 m above the bottom site. A characteristic feature of the "old" detritus is the smaller share of mineral fraction that is the result of diatom shell dissolution and washing of organic ingredients from the cells; therefore heavier shells sink to depth more rapidly than the organic fraction.

Changes in the ash fraction of total particulate matter as dependent on season and depth proved the validity of this hypothesis. Average estimate of the ash content registered in the beginning and in the end of summer was as low as 36% while that in the mid-summer as high as 54%, that agrees with the seasonal growing dynamics at the region. The mid-summer rise of ash fraction content may be the result of an increment in TPM owing to seasonal increase of the abundance of plankton, primarily diatoms. The tendency towards reduction of the ash fraction in TPM with the increase of depth and ageing of detritus is clearly seen at examination of ash fraction average content in 0-100 and 0-500-m water layers and of the depth-dependent changes in the sections along 75° E. Computed for the regional 0-100-m layer, the content of mineral fraction in TPM was 1.5 time as large as for 0-500-m water layer (63 and 40%, correspondingly). In the first days of January 1983, in the section along 75° E the ash content of TPM was estimated at 1000 and 2000 m depths as 22 and 30%, correspondingly, varying from 5 to 47% and from 5 to 100%, respectively; average concentration of SOM was similar (1.5 $mg \cdot l^{-1}$, fluctuating from 0 to 4.3 $mg \cdot l^{-1}$) at the two depths. In mid-February 1985, the repeated measurements had demonstrated that averages of the ash fraction were 55 and 40%, varying from 16 to 99% and from 13 to 61%, at 1000- and 2000-m depths, correspondingly; the average content of SOM made up 1.0 and 1.5 $mg \cdot l^{-1}$, with fluctuations from 0 to 2.0 $mg \cdot l^{-1}$ and from 0.5 to 2.0 mg·l^{-1}, at the 1000 and 2000 m depths, correspondingly.

The values given before point out that SOM content is subject to considerable interannual variation. Relevant estimates obtained at the season of 1983-1984, were 3-4 times less than those measured during the same months in different years; this decrease is in concord with the above-stated concept of the intensive seasonal transport of growing plankton into the open ocean by streams composing the currents. This allows to associate the amount of SOM with plankton abundance in the region, and to stress the significance of dynamic factors (namely, the development of the system of stationary circulations fostering seston accumulation) for the replenishment of SOM. The knowledge gained about SOM concentration in different periods of summer season from the observations of 1980 – 1983 permits to tentatively compute the rate of SOM replenishment and to roughly approximate the production generated by phytoplankton – the basic source of the organic matter. Here a series of essential assumptions should be made. Firstly, for the time spans (13, 36 and 60 days) distinguished within the season the suspended organic matter should be replenished through the supply from phytoplankton and heterotrophic organisms (e.g. bacteria, protozoans, meso- and macrozooplankton). Secondly, the major share in the ash fraction of TPM should be contributed by diatoms in which the content of ash amounts to 60% (Serenkov, Barachkov, 1955); ash content of the heterotrophs is an order of magnitude less (Samyshev, 1970) and therefore may be ignored. Thirdly, living fraction in SOM is as negligible as 2-3% and therefore can also be neglected. Fourthly, the loss of mineral fractions goes at the rate which is similar between all seston components.

Computations have been done for two time spans of the season term, data from comparable neighbouring pairs of surveys were used (Table 26). SOM estimates are expressed as the quantity of carbon; the estimates are rough because of the tentative character of calculations.

The following example illustrates the order of computations referring to the first pair of the surveys.

Table 26

Tentative evaluation of summer SOM replenishment in upper 0-100-m water layer of the Commonwealth Sea

Paired survey NNo	Survey term	Time span, d	SOM content, 10^3 mg C $\cdot$ m^{-2}	Ash fraction, %	Average ash content in SOM, %	Average ash content of diatoms, %	SOM replenishment, mg C $\cdot$ m^{-2} $\cdot$ d^{-1}		
							total	including the contribution of	
								diatoms	heterotrophs
I	1. 20.XII. 1982 – 14.I. 1983 2. 1-26. I. 1980	13	70 92.5	36 54	45	60	1730	1300	430
II	1. 1-26. I. 1980 2. 1.II – 7.III. 1981	36	92.5 214.5	54 36	45	60	3380	2530	850

- Overall replenishment of SOM for 13 days is: $(92.5 - 70) \cdot 10^3\ mg\ C \cdot m^{-2} = 22.5 \cdot 10^3\ mg\ C \cdot m^{-2}$.
- A one-day replenishment is: $22.5 \cdot 10^3\ mg\ C \cdot m^{-2} / 13\ d = 1730\ mg\ C \cdot m^{-2} / d^{-1}$.
- With the average ash content of the suspension equal 45% (the average for the beginning and the end of observation term), the share supplied in SOM replenishment by phytoplankton is 75% and by heterotrophs 25%, i.e. *1300 and 430* $mg\ C \cdot m^{-2} / d^{-1}$, correspondingly.

It is evident that even without assimilated portion of the phytoplankton having been consumed by heterotrophic organisms* the SOM replenishment estimates are substantially higher than the measured primary production estimates but conform to the results obtained about the primary production employing the model (Chapter III). These reasons permit to look upon the estimates discussed as approximating actual.

The results obtained are remarkable for the large heterotrophic contribution to SOM. However, firstly, in studying microzooplankton we did not take into account such group of plankton protozoans as zooflagellates, which are also very abundant and play in the communities the part not the less significant than infusorians (Sorokin, 1979); secondly, the considerable summer input of animal organic substances to SOM is the natural result of molting of crustaceans and of the mortality of post-spawned meso- and macrozooplankters. Finally, some overestimation of the heterotrophic contribution may be related to underestimation of diatoms as the result of the earlier assumption about the low-rate reduction of ash content in dead phytoplankton cells.

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* proceeding from the tentative computation, maximally possible assimilation values (assuming that all heterotrophs under the examination fed on phytoplankton only) were about 15-25% of absolute values of the SOM replenishment owing to phytoplankton.

Antarctic sea water is rich in SOM that is determined by its generous production during the growing season and slow transformation rate. An important way of the Antarctic SOM realization is through the intensive growth of benthic fauna based on the principle of inheritance (Romankevich, 1971). Indeed, high abundance is characteristic of Antarctic benthic fauna (Koltun, 1969). In the uppermost (to 50-m depth) sublittoral water layer benthic biomass amounts to 2-3 kg $\cdot$ m^{-2}; for the rest of the shelf zone down to 500-m depth its average estimates are also high (450 – 500 g $\cdot$ m^{-2}), that exceeds the biomass of benthic organisms measured at comparable depths over the World Ocean. Large biomass of bottom fauna is the result of combined efforts of seston-eaters, e.g. sponges, bryozoans and ascidians, which supply over 60% to total benthic biomass. Deeper, to 1000-m mark, the biomass of benthos decreases to estimates measured at other areas of the World Ocean. Another way of the surplus organic matter realization is through its transport into tropical ocean water (Sorokin, 1971).

CHAPTER IX

FUNCTIONAL SIGNIFICANCE OF THE MAJOR PLANKTON COMPONENTS

This chapter tells about functional significance of the investigated components of Antarctic plankton community may it be in a broad outline.

Data available from the literature underlie our computations of balance equilibrium elements of the rations of the examined micro- and mesoheterotrophs. The method applied in evaluating the assimilation and the metabolic expenditure of bacteria was presented in Chapter IV. Infusorian metabolic expenditure was estimated by means of the equation given in T.V. Khlebovich (1974), proceeding from the cell volumes having been measured with the reference to temperature amendment by Vant-Hoff equation with the coefficient Q_{10} equal 2.25 (Vinberg, 1983). Based on the results obtained, the ration and growth increment of infusorians have been computed ,with the involvement of K_1 and K_2 coefficients assumed, according to T.V. Khlebovich (1979), to be 0.35 and 0.44 , correspondingly. Elements of the substance balance for mesozooplankters (predominantly copepods) were calculated from their ration having been admitted after E.G. Arashkevich (1978) as 10% of the biomass of the organisms, and coefficients K_1 and K_2 as 0.25 and 0.35, correspondingly (Sorokin, 1975). In the computations of the krill balance estimates the ratios obtained in the experiments were employed (Chapter I). All the estimates were converted into carbon content; in particular, phytoplankton composed mostly of diatoms (as it was in our case) and having the caloric content 2.5 cal $\cdot$ mg^{-1} dry weight and 12% moisture (Petipa 1981) contains 3% of carbon; the content of carbon in bacteria (wet weight) was evaluated as 10% (Troitsky, Sorokin, 1967). The dry suspended organic matter (SOM) incorporates 50% carbon (Skopintsev, 1950). For all zooplankton groups balance estimates were computed assuming that caloric content of their wet weight was 1.0 cal $\cdot$ mg^{-1} (Ostapenya, 1968; Shushkina et al., 1984) and carbon caloric content equivalent 10 cal $\cdot$ mg C^{-1} (Vinberg, 1960; Platt, Irwin, 1973).

Let us first have a glance at the results of the balance estimate computations referring to the components of plankton which had been got from the summer surveys at the Commonwealth Sea and the Atlantic sector of Antarctic (Table 27). Distinctions in the condition of plankton community characteristic of the two regions have been discussed in Chapter IV. Integrally, these distinctions agree with the values of maturity indices calculated according to M.E. Vinogradov and E.A. Shushkina (1983) as $Q = D / PP$, where D is overall heterotrophic destruction and PP – primary production. Taking into account probable underestimation of the primary production, the earlier deductions about the condition of the community at the number of areas based on the criterion suggested by the two authors are only partially, or relatively, applicable to our case.

In December, in the Commonwealth Sea and at the adjoining seawater areas Q = - 0.03 (equilibrium state of the community), in February Q = + 0.64 (advanced community); in February – March at the Atlantic sector of Antarctic Q = - 0.33 (young community). The distinctions noticed in the community condition and in the abundance of plankton community components at the different regions (Chapter VII) permit to compare these components for their functional significance as dependent on situation.

Table 27 points out that despite the distinctions, a feature common to the communities of the two regions is that bacteria and infusorians perform the leading role in heterotrophic transformation of the matter flux. In the Commonwealth Sea and around, in December bacteria accounted for more than 60% and in February for more than 70% of balance ration ingredients including total heterotrophic destruction. At the Atlantic sector of Antarctic the involvement of bacteria was even greater: over 90% of the total heterotrophic destruction was owing to bacteria. Judging from bacterial production measurements, the explanation to this phenomenon roots in the huge abundance of bacteria over the Atlantic sector that, in its turn, is associated with high quantitative characteristics of local phytoplankton (estimates of the phytoplankton production measured at the Atlantic sector were 6-20 times as large as those of the Commonwealth Sea area). At the same time, infusorian biomass and total metabolic expenditure were also higher (17 and 13%, correspondingly) at the Commonwealth Sea compared with the Atlantic sector. Knowing that in the years with less intensive than during 1983-1984 the growing plankton transport with the currents the biomass of infusorians in the Commonwealth Sea may increase several times (e.g., during 1984 - 1985 the biomass was more than 2.5 times larger than during the season of 1983-1984, Chapter IV), and also that we did not include zooflagellates which often have biomass comparable with or exceeding that yielded by infusorians (Sorokin, 1979) in the array of microheterotrophic organisms under the study, it is reasonable to acknowledge the superior importance of protozoans for Antarctic plankton

Table 27

Balance estimates of the main plankton trophic groups in the Commonwealth Sea and the Atlantic sector of Antarctic (B - biomass, mg C · m^{-3} ; P – production; A –assimilation; C – ration; R – metabolic expenditure, mg C · m^{-3} · d^{-1})

Trophic group	B	P	P/B	A	C	R
Commonwealth Sea, photic layer, December 1983						
Phytoplankton	-	2.80	-	-	-	-
Bacterioplankton	-	0.81	-	2.53	2.53	1.72
Infusorians	1.83	0.36	0.20	0.82	1.03	0.46
Mesozooplankton•	1.80	0.04	0.02	0.14	0.18	0.10
Krill	53.80	0.16	0.003	0.50	0.62	0.34
Commonwealth Sea, photic layer, February 1984						
Phytoplankton	-	0.71	-	-	-	-
Bacterioplankton	-	1.09	-	3.41	3.41	2.32
Infusorians	1.62	0.32	0.20	0.73	0.91	0.41
Mesozooplankton•	1.25	0.02	0.02	0.08	0.12	0.06
Krill	51.70	0.15	0.003	0.48	0.60	0.33
Atlantic sector of Antarctic, 0-100 m water layer, February – March 1984						
Phytoplankton	-	18.00	-	-	-	-
Bacterioplankton	-	3.65	-	11.41	11.41	7.76
Infusorians	1.14	0.19	0.20	0.45	0.70	0.26
Mesozooplankton•	6.00	0.12	0.02	0.48	0.60	0.36
Krill	17.35	0.06	0.0033	0.19	0.22	0.13

• Predominantly phytophagous mesozooplankton community in comparison with the communities of other highly productive areas of the ocean (Tumantseva, 1980; Sorokin, 1982 a, b). Though the abundance of krill at the Commonwealth Sea area was relatively large, only 11-12% of the total production, assimilation and metabolic expenditure of heterotrophs were owing to the krill. In the Atlantic sector of Antarctic, where the measured numbers of krill was three times as less as that at the Commonwealth Sea, the corresponding parameters had been approximated 1.5%. The inadequately low estimates were evidently due to the relatively larger bacterioplankton fraction at the Atlantic sector. Finally, despite the considerable difference in the mesozooplankton abundance noticed between the two regions (depending on the observation time the corresponding estimates were from 3.3 to 4 times higher in the Atlantic sector of Antarctic) relative share of these heterotrophic organisms was insignificant in both cases: at the Commonwealth Sea it was 3-3.5% in December and 1.3-2% in February, and at the Atlantic sector it was 3-4%.

Similar results had been obtained from the observations conducted at the Commonwealth Sea area and from the surveys of 1980-1982/1983 (Table 28). In the early austral summer (December 1982 – January 1983, Q = 0.18; equilibrium community), when the bacterial biomass was comparable with the biomass of mesozooplankton, ration balance estimates made up 51-56% of the corresponding overall estimates for the heterotrophic totality. By the mid-summer (January 1980; Q = 0.18) and in the second half of the summer (February – March 1981; Q = 0.24), when the biomass of bacteria had been correspondingly two and three times as large as that of mesozooplankton, the studied parameters had increased to 78-80% on the average. In infusorians the corresponding estimates had been 5 to 10 times as less. Generally, in the early summer the collective microheterotrophic fraction accounted for about 60% and in the mid- and late summer for about 85% of total heterotrophic destruction. The contribution of phytophagousmesozooplankters was evaluated as 10-12%. In the season of 1982-1983 the share of krill, which was so abundant that had generated over 81% of total biomass, made

T a b l e 28

Quantitative characteristics of the basic examined seston components for 0-100 layer in the Commonwealth Sea (B, P, A, C, R, mg C · m^{-2} as in Table 27)

Seston components	B	P	P/B	A	C	R
20 December 1982 – 14 January 1983						
Phytoplankton	720	136	0.19	-	-	-
Bacterioplankton	440	50	0.11	156	156	106
Infusorians	75	15	0.20	34	43	19
Mesozooplankton:						
phytophagous	450	11	0.02	33	45	22
predatory	100	2	0.02	7	10	5
Krill	4700	16	0.0033	50	60	34
SOM content	70 * 10^3	-	-	-	-	-
1 – 26 January 1980						
Phytoplankton	1170	150	0.13	-	-	-
Bacterioplankton	850	85	0.10	265	265	180
Infusorians	90	18	0.20	41	51	23
Mesozooplankton:						
phytophagous	280	7	0.02	20	28	13
predatory	80	2	0.02	6	8	4
Krill	1200	4	0.0033	13	15	9
SOM content	92.5 * 10^3	-	-	-	-	-
1 February – 7 March 1981						
Phytoplankton	1050	140	0.13	-	-	-
Bacterioplankton	880	88	0.10	275	275	187
Infusorians	76	15	0.20	34	43	19
Mesozooplankton:						
phytophagous	460	11	0.02	38	46	22
predatory	120	3	0.02	9	12	6
Krill	1500	5	0.0033	16	19	11
SOM content	214.5 * 10^3	-	-	-	-	-

up about 17% of the total balance estimates; with less (49%) total relative biomass the percentage dropped to about 4%. The part taken by predatory zooplankton in the Antarctic community was as negligible as 2-3% of the total heterotrophic balance estimates.

Thus, much of the heterotrophic destruction of the matter going in the upper 100-m (photic) seawater layer of Antarctic is owing to bacterioplankton and other microheterotrophic organisms. Knowing about uneven distribution of all the components of plankton community, it is logical to suggest that the importance of individual plankton components should strongly vary depending on particular locality. Of similarly local significance should also be macroplankters (e.g. salps, coelenterates) ignored in making this research as too negligible, though capable of forming dense local aggregations, constituent part of the plankton.

In point of both theory and practice it is interesting to compare total consumption of the phytoplankton production by the examined heterotrophs and the scope of the phytoplankton production. This implies several assumptions, namely: among the heterotrophic organisms "vegetarian" mesozooplankton and krill are the major consumers of phytoplankton. Other food items of their diet are discarded here. In the diet of infusorians microalgae are of minor importance; these microheterotrophs feed on minute phytoplankton forms composing approximately 20% of total phytoplankton biomass (see Chapter II). Taking into account the comparability of the regional phyto- and bacterioplankton biomass and the rich detritus supply, the basic food of Antarctic protozoans (Lessard, Rivkin, 1986), it may be hypothesized that in the ration of infusorians the phytoplankton ingredient makes up 20%, not more. Correlating the measured primary production estimates with total consumption of the discussed phytophagous organisms leads to a curious deduction: for the Commonwealth Sea thiscorrelation was usually over 1.0 (e.g., 1.2 during the season of 1982-1983, 2.8 in January 1980 and 1.9 in February – March 1981), later, in December 1983 it was 2.3 and in February 1984 it decreased to 0.72; for the Atlantic sector, estimated in February --March 1984 it was as high as 17.6. In other words, in the majority of cases the phytophagous forms had been receiving sufficient food supply. Depending on the abundance, either mesozooplankters or the krill took on the leadership in the consumption of phytoplankton. At the Commonwealth Sea area phytophagous production and the measured primary production percentage ratios (ecological efficiency value) approximated the "norm" (10-15%) (Voronina, 1984) in January 1980, February - March 1981 and in December 1983; during the season of 1982-1983 and in February 1984 primary production deficiency was assessed as 100 and 300%, respectively. In the Atlantic sector of Antarctica the measured primary production had been generated in excess - an order of magnitude larger than food demands of the phytophagous plankters.

In Chapter III it has been stressed that actual primary production in the region had been considerably greater than the measured one. A number of computations and deductions provide indirect evidence to this statement. In particular, over the years of the investigation (1980-1983), when oceanographic conditions at the Commonwealth Sea varied insignificantly, mean microalgal biomass kept high in different months of the austral summer and even slightly increased by the mid-summer, regardless of quantitative changes in the components constituting seston. Daily phytoplankton P/B coefficients also varied in a narrow range from 0.19 to 0.13. Such a situation is hardly compatible with the regional SOM richness and intensive replenishment and the abundance of bacterial life (with the correspondingly high balance ration estimates): the bacterial biomass even in the early summer amounting to 60% of the microalgal biomass, the production of bacteria reached 40% of the measured primary production, with the later increase to 56 and 63%. For an equilibrium plankton community in the south-eastern Pacific (Vinogradov, Shushkina, 1983) daily P/B coefficient of the phytoplankton is about 1.0. In our case, though it is difficult to admit that at the peak of the summer growing season the Antarctic community maintains the state of equilibrium, actual primary production should be 5-7 times as large as measured, corresponding at least to the microalgal biomass level (ca. 700-1000 mg C · m^{-2} · d^{-1} for the full season). These values are an order of magnitude similar of the estimates of the primary production having been calculated for the years under the consideration and differ only 1.5-2 times from the average (1500 mg C · m^{-2} · d^{-1}). Then the factual correlation between the primary production, on the one hand, and the food demands and production of phytophagous plankton, on the other hand, should be accordingly different, i.e. at least 5 to 7 times higher. Elementary computations point out that even when the registered krill concentration and phytophagous mesozooplankton biomass were maximum (100 g · m^{-2} and 120 g · m^{-3} , correspondingly, for 0-100-m water layer), the regional food supply was sufficient to satisfy the demands of these phytophagous organisms. Overall demand for microalgal production having been calculated from the production of these consumers, given the above-stated concentration and assuming ecological efficiency equal 10%, made up 680 mg C · m^{-2} · d^{-1} , and that from their ration about 250 mg C · m^{-2} · d^{-1} . In both cases, these estimates distribute equally between the krill and mesozooplankters. Results of our computations prove that the direct count data are reliable for the krill and also that the discussed estimates fluctuate regardless of the nutritive base and that the dynamic factors (the currents owing to which the crustaceans are evacuated from the breeding area and from the core of the distribution area) play the key role in those fluctuations.

In summer, when microalgae are especially abundant, the limiting factor for the meso- and macroplankters is obviously due to temporal and spatial incoherence of their maximums. In the winter, detritus is usually the food held in reserve. However, the generally short growing period is among the essential factors which determine the character of the Antarctic community. In this context the point of special interest is the entire combination of factors influencing the abundance of krill and mesozooplankters, primarily copepods. Abundance of the krill is owing to a number of adaptive properties inherent in these organisms; of special value is their well-developed food adaptation (euryphagous nutrition, a diversity of feeding patterns, the adaptation to long-term – for several months – fasting (New Findings on Krill, 1984), high fecundity – the absolute value is from 3 to 25.8 thousand eggs per individual (International symposium on the biology of the krill *Euphausia superba*, 1983), the relatively less in comparison with short-cycle forms amplitude of seasonal variation in adult part of the population that is explained by some features of the life cycle. The richness of forms of Antarctic mesozooplankters is limited by the short growing period that is especially distinctly manifested in species with shifted developmental cycle, drastic (an order of magnitude large) seasonal fluctuations of population numbers due to the short life-cycle of its members, the poorer than in krill plasticity of feeding patterns and the narrow (by the prey size) food spectrum (Samyshev et al., 1986; Hopkins, 1987) and also the less fecundity: its relative value in copepods as compared to other small crustaceans was the least, estimated as 7.9% female body weight (Sazhina, 1975) and the absolute value in the Antarctic environment is limited, probably, by the short growing term.

CONCLUSIONS

The complex studies in the typical Antarctic region have highlighted characteristics of Antarctic krill and the overall planktonic community.

Repeated observations on the distribution of eggs and larvae of the krill and studies of the intactness of the eggs depending on depth (down to 2000 m) proved the unacceptability of the concept of the “rise with the development” to the life cycle of the krill. Though spawning of the euphausiids may take place at any site of the distribution area, survivors will thrive only in shallow coastal zone.

Adult portion of krill population displays an uneven aggregated distribution pattern that may be explained by activity of the organisms (e.g. gathering in swarms, migrations for favourable environment and forage) and by water dynamics which may have direct (the accumulative effect of gyres) and indirect (nutrient-dependent abundance of phytoplankton) impact on the population. The combination of positive factors which stimulate persistent krill superswarms is most probable in coastal (marginal ice) zones and in the vicinity of isles where topogenic factor provides stationary gyral system.

The Coastal Antarctic Current and the system of circulations in the Subantarctic and adjacent seas are the base of the distribution area of Antarctic krill; special orographic hydrological conditions account for the appearance of the circulation system.

As direct counts show, krill abundance and density in the investigated region are subject to interannual variations associated with degree of euphausiid expatriation which in its turn depends on the altering intensity of the along-meridian water transfer induced by atmospheric events. At a part of the study area where all observations conducted crossed, extreme estimates of the biomass and stock of krill differed 7 times, being 100 and 15 $g \cdot m^{-2}$ and 68 and 100 million tones, correspondingly. Krill biomass averaged for several years for a water area about 1 million km^2 was about 40 $g \cdot m^{-2}$.

Experimental estimates of krill's balanced ration depend on body weight of the euphausiids and may be approximated with power equations. Resulting values of the diet and its components in the Antarctic krill are lower in comparison with those citied by some other authors. The overestimated metabolic parameters and therefore overestimated ration of the krill are due to methodic errors, e.g. insufficient acclimation of euphausiids to experimental conditions. Annual P/B coefficient of the krill population was estimated as 1.0 based on experimental data.

Data on the krill population well agree with those about the structure of planktonic community in the distribution area. The explanation lies in the commonality of causes, primarily oceanographic factors, which determine structural and functional characteristics of main components of the community.

A dozen of diatoms whose geographic origin is different prevail in as rich taxonomic composition of Antarctic phytoplankton as 210 species. The portion of mass species varies with season and year to year. The phytoplankton succession tends to continual recruitment through a recurrence to early stage in response to unstable water structure. Extensive phytoplankton growth in Antarctic zone is owing to a favourable combination of related factors - shallow seasonal pycnocline, the development of stationary circulations (accumulative effect) and the intensive vertical water mixing above the pycnocline. These factors are most pronounced in the coastal (marginal ice) zone and the Antarctic divergence zone; therefore, productivity of these water areas may be estimated as identical. Interannual variations in phytoplankton biomass are as enormous as over 300% for the investigated region and are associated with fluctuations in the above mentioned factors.

Underestimation of phytoplankton production which takes place with the employment of radiocarbon bottle method is the result of non-authentical samplings under the extant procedure of collecting material with uneven or patchy distribution, asynchronous succession and short-term outbreaks of phytoplankton. According to calculations with the employment of a mathematical model, actual primary production in the region under the study was evaluated in years of moderate phytoplankton production as ca. 1.5 g C $m^{-2} \cdot d^{-1}$ during the vegetation period, or ca.160 g $C{\cdot}m^{-2} \cdot year^{-1}$. These results are in conformity with tentative estimates for the suspended organic matter replenishment and structural and functional parameters of some plankton components.

Cocci dominate Antarctic bacterioplankton. Bacterial concentrations may attain considerable values comparable with mesozooplankton biomass (up to 90 $mg{\cdot}m^{-3}$) that explains importance of bacteria for maintaining heterotrophic transformation of the organic matter.

Like in other productive waters of the World Ocean, the major part of Antarctic microzooplankton are infusorians - predominantly tintinnids and some species of the genus *Strombidium*.

Distribution patterns and development of microheterothrophic organisms (bacteria and infusorians) are linked with distribution patterns and the succession phase of the community.

During certain periods of time in mesozooplankton of Antarctic waters along with the three known large copepod species the portion of small forms may substantially increase. The record of different size and age groups of zooplankton has contributed to better understanding of the succession of spawning peaks in mass species.

Mesozooplankton abundance considerably fluctuates from year to year. Like in the case of krill, this may be caused by a varying intensity of expatriation of the organisms with water flows in the ocean surface.

The trophic structure of mesozooplankton embraces the five main groups among which the "vegetarian" plankton forms prevail. The combination of the wide food spectrum of the individual community components and the large diversity of the identified dimensional-functional groups predetermines the possibility of optimal realization of food relations in plankton community.

The Antarctic plankton display major features of communities with unbalanced trophic relations. In upper water layer only minor part of the primary production undergoes destruction. The total heterotrophic destruction, depending on the succession phase and the abundance of main constituent parts, is owing to bacteria (50-75%), infusorians (11-23%), phytophagous mesozooplankton (4-12%), krill (5-17%) and predatory zooplankters (about 2-3%).

The major (70-75%) portion of the primary production not utilized in the upper layer sinks to deeper water.

Some researchers erroneously explain limitation to krill stock by insufficient level of phytoplankton production. In fact, however, the production is high enough; krill abundance is much more dependent on the expatriation events than on the food supply.

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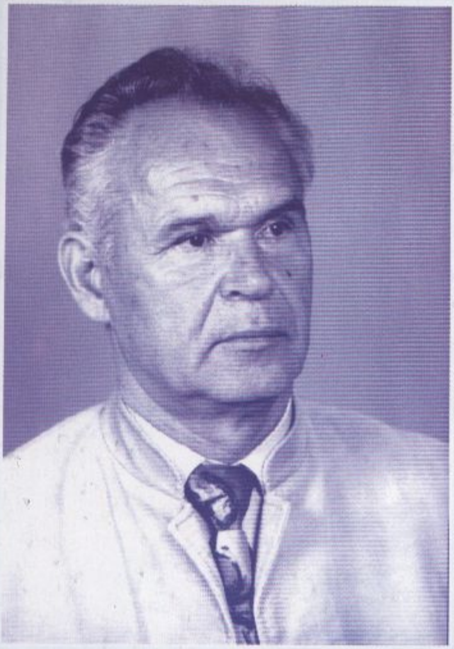
ERRATA

for the book of **E.Z. Samyshev**

"Antarctic krill and the structure of planktonic community in its distribution area "

Position:	**It is printed:**	**It is necessary read:**
Page 115, Fig. 28	Fig. 28. Average phytoplankton biomass .... and 1981 (C).	Fig. 28. Average phytoplankton biomass ... . and 1981 (C). 2: 1 - <100; 2-100-500; 3-500-1000; 4-1000-2000; 5 - > 2000 mg m^{-3}.
Page 152, Table 14	*Oithona similis* 51.64 39.40 *O. frigida* 0.73 0.64 *Oncaea conifera* 0.08 0.12 *O. curvata* 3.43 0.50 *O. frigida* 0.73 0.64 *Oncaea conifera* 0.08 0.12 *O.curvata* 3.43 0.50	*Oithona similis* 51.64 39.40 *O. frigida* 0.73 0.64 *Oncaea conifera* 0.08 0.12 *O. curvata* 3.43 0.50
Page 158, Fig. 36	Fig. 36. The distribution of the biomass .... 1978, 6 – ice edge.	Fig. 36. The distribution of the biomass ......1978. 1 – *C. acutus*; 2 – *C. propinquus*; 3 – *Rh. gigas*; 4 – *M. gerlachei*. 1 – 0; 2 – 0-100; 3 – 100-1000; 4 – 1000-10000; 5 - >10000; 6 – ice edge.
Page 187, Table 24	There is the XII-th functional group.	There is the unnecessary column. The XII-th functional group is superfluous. XI and 16 functional groups are selected only.



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Research interests focus on ecology, trophic dynamics and functional significance of marine ecosystem components, biological principles underlying fishing and mariculture. Scientific publications number more than 120. Prof. Samyshev is known as an organizer and a participant of many research cruises to different areas of the World Ocean, prior importance are the expeditions launched to conduct versatile investigations of Antarctic ecosystem.

Head of Department of Functioning of Marine Ecosystems, Institute of Biology of the Southern Seas (IBSS) National Academy of Sciences of Ukraine, Prof. Samyshev is also the scientific supervisor and executive officer of the BIORESOURCES Project performed within the framework of the Ukrainian National Research Programme for Antarctic. More information is given in the Twenty Second Edition (1992) of Dictionary of International Biography, published by International Biographical Centre, Cambridge, England.