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Primary Producers of the Barents Sea

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1. Introduction

1.1 Morphologic features of the relief, hydrologic regime and types of water masses

Studies of patterns of production processes in marine arctic ecosystems have a long history. Over the last decades this branch of hydrobiology has been demonstrating a significant increase in research activity. The main driven factor here is rational use of biological resources increasing year by year. In this respect, the Barents Sea has always been among bodies of water experiencing intensive exploitation of their living resources: fish, invertebrates and marine mammals. Issues of both sustainable exploitation of fish and other living resources and their conservation and restoration need more profound and thorough ecological research in areas subject to heavy exploitation by man. Studies of production processes in the ocean have gained particular importance in the last years of the XX century in the light of a significant increase in man-caused pressure on marine ecosystems, including those in the Arctic and Northern Basin of the World Ocean.

The Barents Sea is fairly considered the most productive body of water among Arctic shelf seas. Duration of the primary production cycle determined for different areas of the Barents Sea enables the annual primary production of this water body to be estimated as equal to 33 tonnes C/km²/yr (tonnes of carbon per square kilometer per year), or 562 tonnes (wet weight) per square km per year. Such high productivity is possible on the one hand due to a full range of pelagic and bottom floral communities, phytocoenoses (macrophytes, microphytobenthos, phytoplankton, and cryoflora), and on the other hand due to specific conditions of flow and transformation of biogenic elements (Makarevich & Druzhkova, 2010).

Oceanographically, the Barents Sea is a unique natural body of water with complicated geomorphology and hydrology. The pelagic zone of the Barents Sea presents an aggregation of water masses, each with its specific type of a pelagic ecosystem. The Barents Sea lies at the junction of the Arctic and Atlantic Oceans, therefore it contains two major types of waters, Arctic and Atlantic water masses. Their interconnections form the general system of anticyclonic macrocirculation when arctic waters dominate in the north and waters of the Atlantic Ocean origin prevail in the south. The zone of contact between these two water masses called the Polar Front presents a natural structural border which divides not only two types of waters and mixing regimes but also two basic types of pelagic communities, arctic and subarctic, and two classes of their annual production cycles.

The latter, however, by no means are single formations. Geographical position of the Barents Sea determines its complicated hydrodynamic structure and the system of constant currents which form circulations of a smaller scale (although some of them can occupy large areas, for instance the basin of a so-called Pechora Sea, the south-eastern Barents Sea). In coastal areas, such factors as river and glacial run-off, tidal events, high isolation of inlets and bays, etc. can produce specific abiotic conditions in smaller water areas and therefore relatively independent assemblages of primary producers. However, each of them possesses features characteristic of one of the two aforementioned types, i.e. arctic or subarctic.

Parallel to this, all pelagic ecosystems of the Barents Sea shelf area can bathymetrically be divided into two groups: 1) ecosystems of the open shelf, and 2) coastal ecosystems, which in their turn also greatly differ in the course of annual cycles of autotrophic organisms and processes of the primary production of organic matter. Besides, complicated seabed relief of the Barents Sea includes such forms as deepwater troughs (in the northern and north-eastern Barents Sea). However, they do not present separate biotopes for primary producers as the major representatives of the latter, phytoplanktonic organisms, mainly inhabit the upper 50-meter layer of the water column with single individuals living lower than 100 meters. Other primary producers, microphytobenthos and macrophytes, do not live at great depths at all.

All the traits of the Barents Sea geomorphology and water dynamics described above do not have direct impacts on assemblages of autotrophic organisms but are determinative for the factors that directly affect their structure and functioning, first of all the thermal regime. The degree of heat uptake and recoil differs among water areas. Thus, the non-freezing part of the Barents Sea does not freeze exactly due to compensation of the heat lost from the surface by the heat advected with the Atlantic Ocean waters (Kudlo, 1970). However, the temporal structure of consecutive changes of hydrological parameters, mainly the parameters of water temperature, is common for all areas of the Barents Sea. This temporal structure presents a series of periods changing each other through the year, which are called hydrological seasons. The hydrologic spring starts with the beginning of the thermocline and the formation of positive heat exchange between the sea and atmosphere and usually lasts about one and a half month (April – May). Summer is characterized by distinct stratification (June – July) and lasts 2.5 – 3.5 months. Autumn (September) as opposite to spring starts with the formation of the negative heat budget and simultaneous destruction of temperature stratification and lasts 1.5 – 3 months. The hydrologic winter is characterized by complete homogeneity of waters and vertical distribution of major hydrological and hydrochemical parameters. This is the longest season in the Barents Sea which lasts 5 to 6.5 months.

The annual production cycle forms according to the same principles as the hydrologic one, i.e. it consists of stages characterized by particular biologic parameters. In pelagic ecosystems, the basis for such division is the structure of the succession cycle of the phytoplankton cell abundance, the major primary producer. The range and consecutiveness of succession stages in different pelagic ecosystems are mostly common, although some stages may drop out. However, the terms of the beginning and duration of each stage differ greatly across ecosystems (table 1).

Stage of the hydrologic cycle	Phytoplankton succession stages				
	Shelf ecosystems of the open sea		Coastal ecosystems		
	Subarctic	Arctic	Subarctic	Arctic	Estuarine
Winter	Dormant stage	Dormant stage; cryoflora bloom	Dormant stage	Dormant stage; cryoflora bloom	Dormant stage; cryoflora bloom
Winter-spring transition period	Spring succession cycle	Early spring succession cycle	Early spring succession cycle	Spring succession cycle	Early spring succession cycle
Spring	Balanced stage	Late spring succession cycle	Late spring succession cycle	Balanced stage	Late spring succession cycle*
Spring-summer transition period		Balanced stage	Early summer succession cycle*		Balanced stage
Summer			Balanced stage		
Summer-autumn transition period	Autumnal succession cycle*	Phytocoenosis degradation stage	Autumnal succession cycle	Phytocoenosis degradation stage	Phytocoenosis degradation stage
Autumn	Phytocoenosis degradation stage	Phytocoenosis degradation stage; cryoflora bloom	Phytocoenosis degradation stage	Phytocoenosis degradation stage; cryoflora bloom	Phytocoenosis degradation stage; cryoflora bloom
Autumn-winter transition period			Early winter nannoplankton maximum		

* – facultative stage of the cycle

Table 1. Annual cycle of the phytoplankton cell abundance in different ecosystems of the Barents Sea.

The thermal regime is also one of the major factors determining a specific structure of the annual cycle of pelagic algal cenoses in coastal ecosystems and high total productivity of the latter: increased water temperature throughout the year determines higher speed of biochemical reactions, and production and decomposition of organic matter. Still other factors also play a significant role. Little depths allow other organisms beside phytoplankton, such as macrophytes and microphytobenthos, to vegetate actively. Smaller volumes of seawater, tidal events and wind mixing intensify exchange processes. Freshwater runoff supplies primary producers with biogenic elements.

Thus, the Barents Sea evidently occupies a special place among arctic seas due to a range of specific natural conditions. The unique geographic position, large extent of the water area both in longitudinal and latitudinal directions, and abundance of shallow coastal zones result in extraordinary high diversity of abiotic environmental factors. This high diversity determines the composition of biota, including assemblages of primary producers, and patterns of all biologic processes, mainly the structure of the annual production cycle.

1.2 Zoning of the Barents Sea water area according to the oceanologic structure of its pelagic zone

All the aforementioned features of the distribution of abiotic parameters enable the Barents Sea water area to be divided into four distinct zones (excluding estuaries), each with its peculiar type of the pelagic ecosystem (fig. 1). These types are characterized first of all by the seasonal course of phytoplankton cell abundance, the main primary producer, and correspondence of its succession stages to phases of the annual hydrological cycle (table 1).

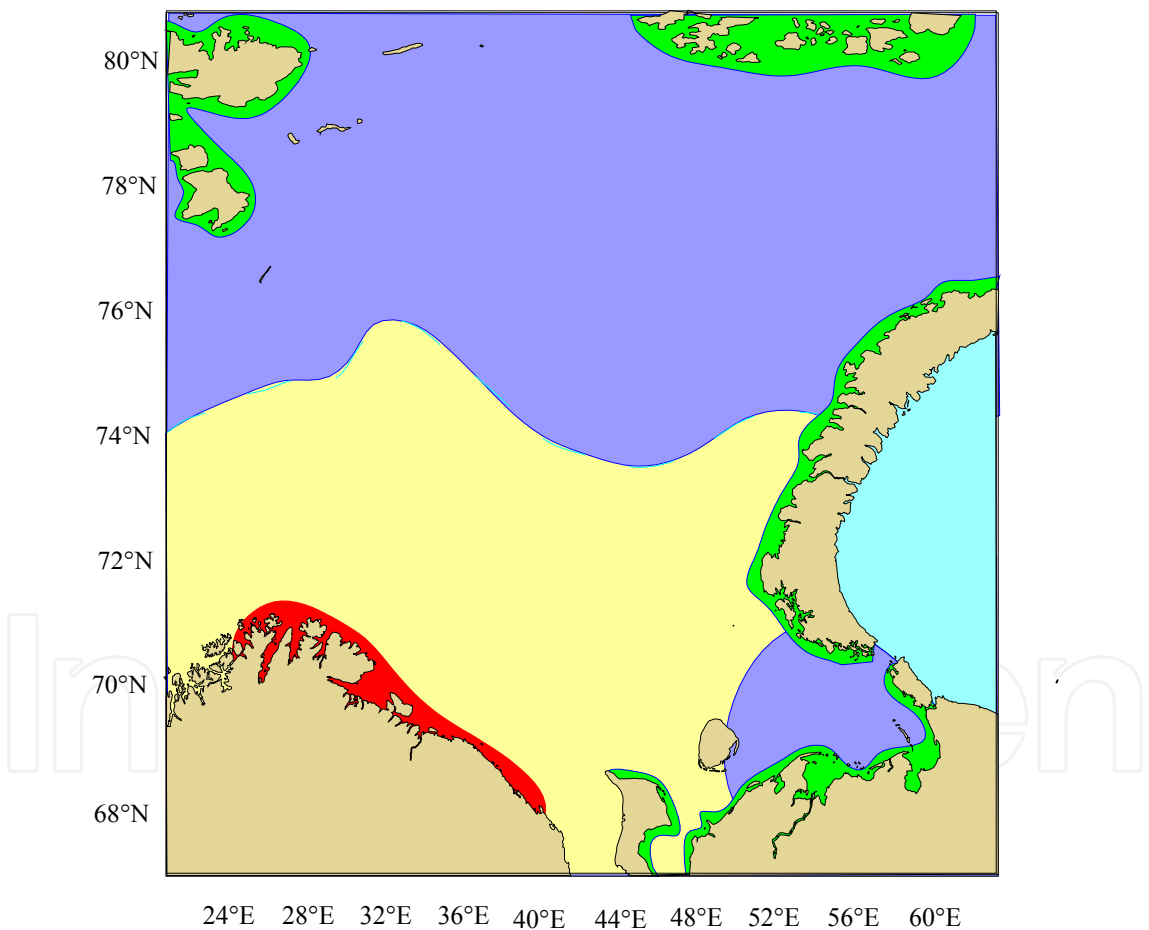


Fig. 1. Pelagic ecosystems of the Barents Sea. Legend: – subarctic shelf, – arctic shelf, – subarctic coastal ecosystems, – arctic coastal ecosystems

Shelf pelagic ecosystems of the open sea are spatially the most common type in the Barents Sea. The biotope area of these ecosystems is limited by shelf edge fronts on the side of the high seas and by systems of shallow fronts of different types on the side of coasts. The

formation of the seasonal pycnocline in the warm period of the year is the most universal feature of the structural organization of the water column in the shelf zone (Bouden, 1988). At the same time subarctic and arctic areas have principle differences in the way of forming the seasonal stratification. The thermal stratification is characteristic of the subarctic shelf. The water column of the arctic shelf is stratified mainly due to freshening of the upper layer as a result of the sea ice cover melt.

In fact, the whole open area of the Barents Sea subarctic shelf is occupied by waters of the Atlantic Ocean origin, which determines the homogeneity of the taxonomic and temporal structure of microphytoplankton assemblages. As mentioned above, the temporal structure of the hydrologic cycle in this area (as in other areas free of seasonal ice cover) is determined by regimes of warming of the sea surface.

2. Pelagic ecosystems of the outer shelf zone

Shelf pelagic ecosystems of the open sea are spatially the most common type in the Barents Sea. The biotope area of these ecosystems is limited by shelf edge fronts on the side of the high seas and by systems of shallow fronts of different types on the side of coasts. The formation of the seasonal pycnocline in the warm period of the year is the most universal feature of the structural organization of the water column in the shelf zone (Bouden, 1988). At the same time subarctic and arctic areas have principle differences in the way of forming the seasonal stratification. The thermal stratification is characteristic of the subarctic shelf. The water column of the arctic shelf is stratified mainly due to desalination of the upper layer as a result of ice cover melt.

2.1 Subarctic shelf

In fact, the whole open area of the Barents Sea subarctic shelf is occupied by waters of the Atlantic Ocean origin, which determines the homogeneity of the taxonomic and temporal structure of microphytoplankton assemblages. As mentioned above, the temporal structure of the hydrologic cycle in this area (as in other areas free of seasonal ice cover) is determined by regimes of warming of the sea surface.

The annual hydrological cycle of the open subarctic shelf presents the most basic type typical of the whole moderate zone (table 1).

The biologic spring begins in March when quantitative characteristics of the phytocenosis stably increase, mainly at the expense of intensive growth of the diatomic complex. In May, diatoms form the first vernal maximum of microphytoplankton bloom when not only quantitative parameters but also species diversity of planktonic community reach their maximum annual values (more than 1 mil cells per liter in numbers and more than 1 mg/l in biomass) (fig. 2A).

This period lasts 2 – 3 weeks. Almost all the phytoplankton of the subarctic shelf area is presented in this period by arcto-boreal neritic forms. The composition of the phytoplankton here consists mainly of dominant species of colonial diatoms of the genus *Thalassiosira* (*T. angulata*, *T. antarctica*, *T. cf. gravida*, *T. hyalina*, *T. nordenskiöldii*), genus *Nitzschia* (*N. arctica*, *N. cylindrus*, *N. grunowii*), genus *Navicula* (*N. granii*, *N. pelagica*, *N. vanhoeffenii*) and genus *Chaetoceros* (*C. cinctus*, *C. curvius*, *C. debilis*, *C. diadema*, *C. fragilis*, *C. furcellatus*, *C. holsaticus*, *C. socialis* and other species), and the flagellate species *Phaeocystis pouchetii*.

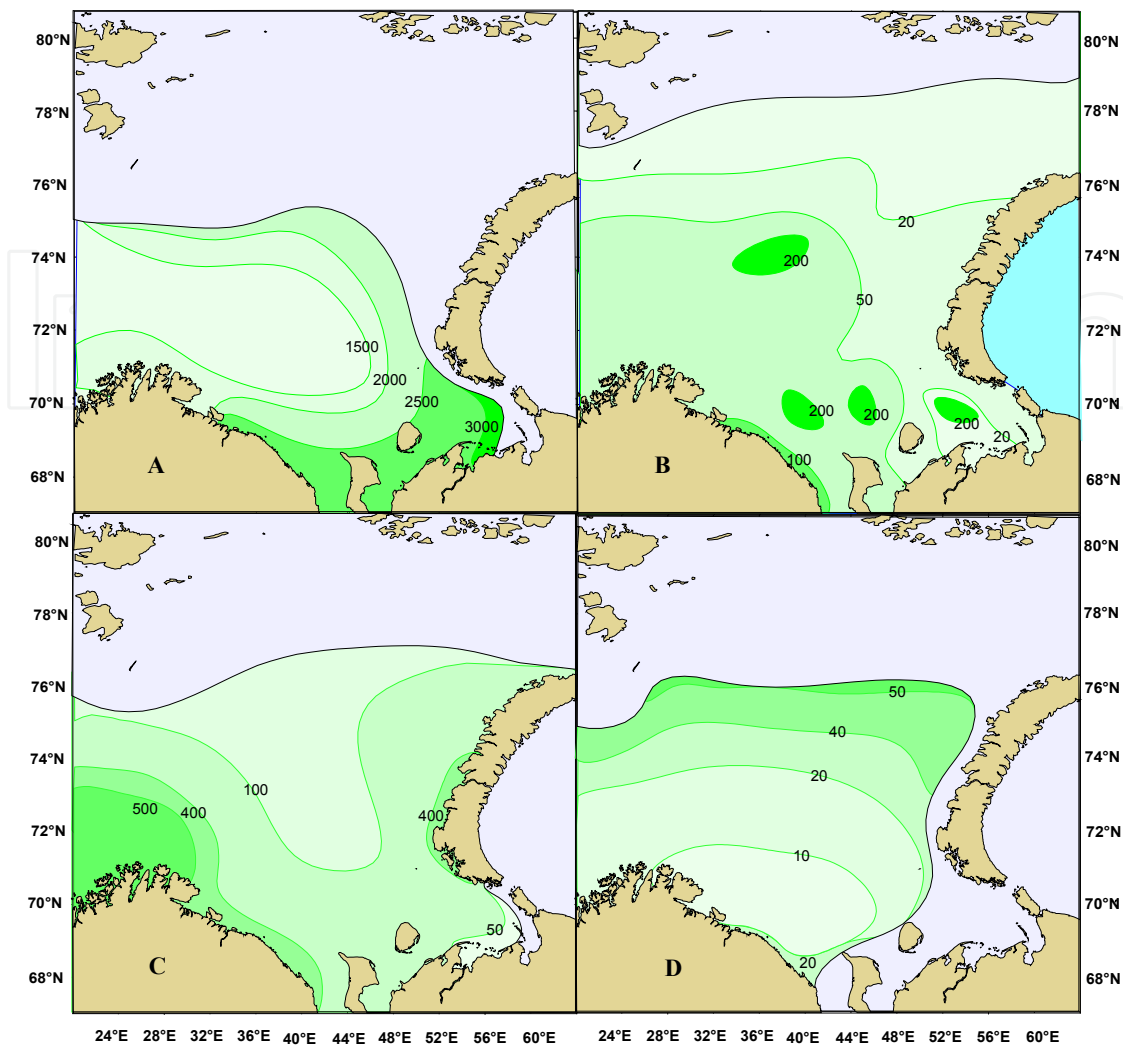


Fig. 2. Distribution of microphytoplankton biomass ($\mu\text{g/l}$) in the Barents Sea. A – spring, B – summer, C – autumn, D – winter

At the end of May/beginning of June the primary production activity of pelagic algae rapidly decreases and vertical redistribution of phytoplankton biomass occurs. The dominant position in upper layers is occupied by flagellate species (mainly Cryptophyceae, Prymnesiophyceae, Chrysophyceae and Dinophyta, sometimes Prasinophyceae and Raphidophyceae). Diatomic algae sink to the pycnocline forming the phytoplankton subsurface maximum at the end of the vernal period.

Rapid depletion of contents of biogenic elements in the upper layer and the trophic activity of zooplankton lead to the formation of the summer balanced stage of phytoplankton annual cycle when abundance and biomass of planktonic algae remain stable (fig. 2B). Populations of autotrophic flagellates of different taxa (Dinophyta, Chrysophyceae and Prymnesiophyceae) start playing a dominant role within microalgae assemblages. This structural condition of the Barents Sea outer shelf pelagic ecosystem remains until the early autumn period (until August). In September, a distinct autumnal maximum of the phytoplankton biomass presented by large dinoflagellates (mainly *Ceratium* spp.) forms in the south-western Barents Sea (fig. 2C).

Then, numbers and biomass of the microphytoplankton community gradually decrease reaching their winter values by the beginning of November. Spatial distribution of quantitative parameters of planktonic algae is quite homogeneous, which is determined by substantial taxonomic homogeneity of the pelagic phytocenosis on the whole water area. Transition to the winter stage in the shelf pelagic zone occurs during the autumn-winter transition period (presumably the second decade of November – first decade of December). The hibernal stage of dormancy lasts from November until February. Maximum desintegrity of the phytoplankton community is a distinctive feature of this period. This stage is characterized by low values of both quantitative parameters (fig. 2D) and species diversity of the pelagic algal cenosis. Its background forms at this stage are represented mostly by *Protoperdinium* species.

Thus, total duration of the active vegetation period of planktonic microalgae of the subarctic pelagic zone lasts approximately 8 months. The course of the seasonal dynamics of phytocenoses as a whole is characterized by a rapid increase in numbers and biomass of organisms, vernal maximum and a consequent decrease. Then these values increase again as the summer species complex starts forming, first of all due to increased inflow of warm Atlantic waters entering the Barents Sea from the west and rich in biogenic matter. After that levels of microalgae constantly decrease and the dormant stage begins.

2.2 Arctic shelf

The Barents Sea arctic shelf can spatially be subdivided into two main zones: (1) deep-water outer shelf zone (northern Barents Sea beyond the Polar Front) and (2) shallow nearshore shelf zone (Kanin–Kolguev shallow area and Pechora Sea) (fig. 1).

Deep-water outer shelf zone. The hydrological year in the ice-covered arctic pelagic zone begins with the formation of ice edge zones (table 1, fig. 2D). These zones are formed by a complex of microalgae, in which early spring neritic diatoms and some colonial flagellates, such as *Phaeocystis pouchetii* and *Dinobryon balticum*, occupy the dominant position (Hansen et al., 1990).

As the ice cover melts it desalinates the upper layer of water causing stratification of the water column. In such a stratified state the water column of the arctic pelagic zone remains during the open sea period until the beginning of active vertical autumn-winter mixing. As a result, in the summer period (fig. 2C) after the end of the spring bloom, microalgae biomass is redistributed vertically, with its subsurface maximum in the pycnocline zone formed mainly at the expense of *Phaeocystis pouchetii* and *Thalassiosira* spp.

As farther north to higher latitudes, the autumnal maximum gradually drops out from the annual cycle structure of the algal cenosis and the seasonal curve of the microphytoplankton abundance acquires single-peak character.

Shallow nearshore shelf zone. The main feature of the south-eastern Barents Sea (Pechora Sea) is its shallowness. Due to this the whole water column in the cold period of the year presents the hibernal mixed layer surface to bottom. During this period, pennate diatoms dominate within the phytoplanktonic community. *Coscinodiscus cf. stellaris*, *Amphiprora kjellmanii*, *Cylindrotheca closterium*, *Gyrosigma fasciola*, *Navicula/Plagiotropis* spp., *Nitzschia grunowii* and *Pleurosigma stuxbergii* are the most common floristic elements. It should be

noted that at this stage the biomass of this complex is formed mainly by single non-colonial algae. The only exclusion is *N. grunowii* that plays a rather insignificant role in quantitative respect being the constant component of the flora. The phytoplankton succession cycle in the Pechora Sea begins in March with activation of populations of early-spring neritic diatoms typical for the ice-edge bloom (*N. grunowii*, *Achnanthes taeniata*, *Thalassiosira* spp., *Chaetoceros* spp.). Abundance levels of pelagic phytocenosis reach their maximum annual values by April (fig. 2A). In the warm period of the year, a distinct mosaic structure of water masses and heterochrony of the seasonal development of microphytoplankton hamper the analysis of spatial and temporal structure of the pelagic community. Numbers of autotrophs may reach in summer 200 000 – 300 000 cells per liter with a biomass of 150 – 200 µg/l (fig. 2B). The dominant position is occupied by Bacillariophyta algae, species of the genera *Nitzschia* and *Skeletonema*, and by large dinoflagellates. During the autumnal degradation of the algal cenosis, numbers of microalgae vary within 500 – 3 000 cells per liter with a biomass of 2 – 50 µg/l (fig. 2C). The main contribution into the structure of the community in this period belongs to centric diatomic algae *Paralia sulcata*.

The runoff of the Pechora River is undoubtedly the most important factor affecting phytoplankton abundance. In the summer period (June – July), levels of phosphates and dissolved silicon in Pechora Bay are an order of magnitude higher than those in the open part of the Pechora Sea. Apparently, constant inflow of biogenic matter into the bay with good mixing of water masses due to a relative shallowness of the basin ensures a high level of primary production of pelagic microalgae. The generated organic matter is only half utilized within Pechora Bay. The rest of it is carried out into the Pechora Sea where it is assimilated within the water area of local circulation that occupies the central part of the sea. As a result, the open part of the Pechora Sea also demonstrates high values of phytoplankton abundance.

3. Coastal ecosystems

3.1 Microphytoplankton annual succession cycle

3.1.1 Subarctic coastal ecosystems

As a whole the annual cycle of microphytoplankton of the coastal pelagic zone is much more complicated compared to that of the outer shelf zone. Thus, in subarctic coastal ecosystems two maximums of microphytoplankton cell abundance occur at the end of winter and in spring, i.e. the early-spring one and the late-spring one. Besides, the summer phase of balanced numerical abundance, which comes after the formation of the seasonal stratification, also begins with the early-spring maximum and ends with the autumnal one. As farther to the north-east, early-summer and autumn cycles become occasional and form only in certain years (Druzhkov et al., 1997b) (table 1).

The spring activity of phytoplankton (second decade of March) begins when early-spring diatomic forms, *Thalassiosira hyalina*, *T. cf. gravida*, *Navicula pelagica*, *N. septentrionalis*, *Nitzschia grunowii* and *Amphora hyperborea*, appear in coastal pelagic waters. Numbers of cells in this period are little and vary within several dozens to several hundreds of cells per liter (Larionov, 1997). The first spring maximum of phytoplankton cell abundance, the most universal ecological event in the coastal zone, occurs in the middle of April and is formed by

early-spring neritic arcto-boreal diatomic genera *Thalassiosira*, *Chaetoceros*, *Navicula* and *Nitzschia*. Phytoplankton numerical abundance reaches its maximum which remains within several days. During the early-spring bloom, numbers of phytoplankton vary within several hundreds of thousands to two million cells in a liter with a biomass of 1 to 3 mg/l. The core of the community is concentrated in this period in the upper ten-meter layer. This first maximum of phytoplankton cell abundance is formed by species *Thalassiosira* cf. *gravida*, *T. nordenskiöldii*, *Chaetoceros socialis*, *C. furcellatus* and *Navicula vanhoeffenii*.

The second spring maximum (end of May – beginning of June) is associated with the continental runoff and varies from year to year in terms of the beginning, numbers, and taxonomic composition depending on the terms of the continental runoff maximum. In most cases, it repeats the first spring maximum, probably with reduced number of dominants. However in years when volumes of the continental runoff are the lowest, the species *Phaeocystis pouchetii* dominates in the bloom with highest registered levels of cell numbers and biomass of 8 mil cells/l and 1.7 mg/l, respectively (Druzhkov, Makarevich, 1999). Spatially, the wave of the spring bloom starts from the Cape of Svyatoy Nos and spreads to the west.

In the summer period (end of June – end of August) the role of dinophyte microalgae increases in the phytoplanktonic community. At the same time cosmopolite forms take the place of arcto-boreal ones, while panthalassic and oceanic algae take the place of neritic species. It should be noted that the summer phase of the balanced cell abundance is the most variable. All possible ecological scenarios can be combined into two main types: 1) summer abundance minimum of the community consisting of small pennate diatoms and unarmored (naked) dinophlagellates and 2) formation of one succession cycle at the end of July with a subsequent decrease in activity until the end of the summer period. In this case the early-summer maximum is as a rule monospecific as it forms at the expense of a mass bloom of a single planktonic species *Skeletonema costatum*, which accounts for more than 80 % of phytoplankton biomass in this period.

Autumnal succession cycle (from the middle of September till the beginning of October) is casual and usually associated with the appearance of spring diatomic forms in the pelagic zone (Druzhkov et al., 1997b; Kuznetsov et al., 1996). Diatomic algae of the genus *Chaetoceros* and dinophyte algae of genera *Ceratium*, *Dinophysis* and *Protoperidinium* dominate in the pelagic zone in this period. Numbers of cells are less than 2 000 per liter with a biomass of less than 5 µg/l.

During the whole winter period (middle of November – middle of March) the phytoplankton community rests in dormancy. In the pelagic zone, it mostly consists of large oceanic dinophyte algae of the cosmopolite and arcto-boreal origin. The concentrations vary within several cells to dozens of cells per liter. Species *Ceratium longipes*, *C. tripos*, *Dinophysis norvegica* and *Protoperidinium depressum* form the basis of the dominant complex.

3.1.2 Arctic coastal ecosystems

The main feature of arctic nearshore ecosystems of the open type is the seasonal occurrence of fast shore ice. As in pelagic ecosystems of the outer shelf zone, the whole seasonal

dynamics of the development of coastal phytoplanktonic ecosystems (especially in case of polar archipelagos where the role of the continental runoff is insignificant) is fully determined by the seasonal dynamics of the ice cover.

Apart from subarctic coastal ecosystems, in coastal waters of the so-called Pechora Sea (southeastern Barents Sea), the early-summer and autumnal succession cycles completely drop out from the structure of the annual cycle of the floral cenosis. The hydrologic year in the Pechora Sea begins at the end of February when populations of neritic diatoms become active. The early-spring cycle, as in the outer shelf zone, transforms into the ice-edge bloom, though in this case it occurs near the edge of the fast shore ice but not the pack ice. In March the coastal algal community of the Pechora Sea enters the initial stages of the spring bloom and in some areas is characterized by intensive growth (with a two- and threefold increase in biomass, up to 500 µg/l) of populations of early-spring colonial forms of centric diatoms. By April, levels of the phytoplankton cell numbers and biomass reach their maximum annual values of more than 500 000 cells per liter and more than 2 mg per liter, respectively. Diatomic algae belonging to genera *Thalassiosira*, *Chaetoceros*, *Navicula* and *Pleurosigma* as before remain dominant species. The late-spring bloom in this body of water forms somewhat later (in June) when the continental runoff reaches its maximum volumes (Grönlund et al., 1996, 1997; Druzhkov et al., 1997a; Kuznetsov et al., 1997).

In coastal zones of arctic archipelagos, the phytoplankton active vegetation period is even shorter (less than three months) and the annual succession cycle of phytoplankton cell abundance actually lacks the early-spring, late-spring and autumnal stages. Single studies in coastal waters off the Franz Josef Land Archipelago enable an assumption to be made that the ice-edge bloom does not occur here at all. Intensive ice melting during the April – June period, simultaneous inflow of fresh melt water from glaciers and snowfields, and wind-induced and wave-induced mixing of water must have negative effects on populations of pelagic microalgae. The spring stage of the algal community (June – August) gradually passes into the summer one (August – September) after which the degradation stage begins. Taxonomic composition of the community, according to field observations made in August, was quite unvaried and consisted mostly of diatomic algae of the genus *Chaetoceros* and dinoflagellate algae of the genus *Protoperdinium*. However, at the same time the numerical abundance maximum was made by the species *Dinobryon balticum* while the biomass was mostly made by large-sized forms *C. decipiens* and *P. ovatum*. In whole, the values of these parameters were quite low and varied within 3 500–89 700 cells per liter and 28.0–40.2 µg/l, respectively. Representatives of microphytobenthos, namely pennate diatoms of genera *Navicula*, *Pleurosigma* and some other, have many times been found in the pelagic zone together with typically planktonic organisms (especially in shallow areas and areas exposed to impact of the ice melt). Production of the pelagic floristic cenosis, according to samples taken in the upper layer of the water column at different sites of the Franz Josef Land coastal waters, made up on average 20.2 µgC/m³/day varying within 16.1–50.4 µgC/m³ during the day (Kuznetsov & Shoshina, 2003). At the same time, when this parameter was calculated for 1 m² with the use of the equation created for this very region (Bul'yon, 1985), an average value of 113.4 µgC/m³/day was obtained which is consistent with the data for the same period in the subarctic coastal zone (along the Eastern Murman Coast, Kola Peninsula).

3.1.3 Estuarine ecosystems

In typical cases, the main dynamic characteristics of microphytoplankton in boreal and arctic estuarine ecosystems with the constant stratification are close to those of outer shelf ecosystems with the exclusion that the stratification here is driven by the continental runoff but not by thermal factors (Svendsen, 1986). It should be noted that due to intensive eutrophication of continental waters, the inflow of biogenic elements into estuaries loses its cyclic manner and therefore the whole warm period of the year is characterized by a single large spring-summer-autumn maximum with an unexpressed structure of peaks.

Kola Inlet is a typical example of an estuarine ecosystem in the Barents Sea. The activity of primary producers in Kola Inlet can remain at a rather high level even during the whole period of the polar night. Although the abundance of phytoplankton cells at this time demonstrates a clear decrease in December and the beginning of January, still the concentration of phytoplankton reaches a value of 10^3 - 10^4 cells per liter, i.e. 1-2 orders higher than in nearshore marine ecosystems (Druzhkov et al., 1997b). Which is the most important here is that the phytoplankton community at this time mostly consists of autotrophic organisms: diatomic algae, and chlorophyll-bearing flagellates. Apparently, the reason of such a phenomenon is that biologic processes in the warm period of the year are more intensive in estuarine zones constantly exposed to freshwater runoff from large rivers, the Tuloma River in the case of Kola Inlet. This enables algae to accumulate a considerable production potential.

The spring development of phytoplankton in Kola Inlet begins in March and is characterized by the complete dominance of diatomic algae. The bloom peak occurs in the second half of April with cell numbers of up to 1 mil cells per liter and a biomass of 1.5 mg per liter and is represented by three diatomic species: *Thalassiosira cf. gravis*, *T. nordenskiöldii* and *Chaetoceros socialis*. During May, the abundance and biomass decrease down to 100 000-200 000 cells per liter and 300-400 $\mu\text{g/l}$, respectively. At the same time the structure of the algal coenosis changes as new species appear, mainly dinophyte algae, and the community demonstrates the greatest species diversity. This transition period ends by July when the pelagic phytocoenosis enters the summer phase of its succession cycle with cell numbers of 3 000-4 000 cells per liter and a biomass of 30-40 $\mu\text{g/l}$ (Makarevich, 2007). Shares of diatomic algae (mainly species of the genus *Chaetoceros*) and dinoflagellate algae are much alike in the community. Shares of golden, green, and euglena algae are much lesser. The latter however are capable of forming sites of a mass bloom with an increase in cell abundance 3 to 4 orders of magnitude but only in separate local nearshore areas of Kola Inlet (Trofimova, 2009). In September, the autumnal stage of the algal coenosis succession cycle begins when species with mixotrophic and heterotrophic feeding types start dominating in the pelagic zone. At this time, a distinct dominance of oceanic forms, mostly dinophyte species, is observed in the phytoplankton community. In whole, the change of the spring phase by the summer one and of the summer phase by the autumnal one happens by means of the inflow of a microalgae complex of the Atlantic Ocean origin into Kola Inlet with marine coastal waters. The winter succession stage is characterized by a decrease in activity of phytocenosis: quantitative parameters demonstrate the lowest values of the whole annual cycle (Makarevich, 2007).

A similar but somewhat different picture is observed in Pechora Bay covered with ice a considerable part of the year. Apparently, due to little depths and the active hydrodynamic regime in this body of water, which homogenizes the density structure of the pelagic biotope surface to bottom, the phytoplankton bloom does not occur in the form of shaped "classic" ice-edge spots as ice melts, but develops in the whole water column in areas becoming free of ice as it breaks up and is carried out to the open part of the sea. A distinct spring maximum does not form in Pechora Bay. After the spring bloom the estuarine ecosystem passes into the balanced cell abundance stage (table 1). The beginning of the intensive numerical growth of microalgae in the mouth of the Bay falls onto the end of April and the first decade of May. Centric diatoms of genera *Thalassiosira* and *Chaetoceros*, the pennate algae *Nitzschia grunowii*, and the golden algae *Phaeocystis pouchetii* completely dominate in the community at this time. The maximum registered phytoplankton numbers in this body of water is 1.4 mil cells per liter with a biomass of 2.7 mg/l (Makarevich, 2007). It should be noted that a rapid increase of these values in Pechora Bay may happen not only due to the intensive cell fission, but also owing to the incoming of the microalgae hibernating in bottom sediments, which is typical for shallow estuarine zones (McQuid, Hobson, 1995).

The summer season in Pechora Bay begins in June when diatomic algae *Aulacoseira granulata*, *Asterionella formosa*, *Skeletonema costatum*, *Chaetoceros wighamii* and *C. constrictus* still dominate in the pelagic algal coenosis. In July the composition of the community slightly changes as diatomic algae *C. compressus*, *Paralia sulcata* and *Rhizosolenia setigera* appear in the dominant complex. Dinoflagellates of the genus *Protoperdinium* and the golden algae *Dinobryon balticum* start playing a significant role. In whole, concentration and biomass levels of phytoplankton during summer vary within a rather wide range, 120 000 to 850 000 cells per liter and 200 to 1 100 µg per liter, respectively (Makarevich, 2007). At the end of August the pelagic algal coenosis of Pechora Bay enters the autumnal stage. During this stage, quantitative parameters of numerical abundance and biomass decrease to several tens of thousands of cells per liter and tens of micrograms per liter, respectively. The species diversity is characterized by the complete dominance of a single species of microalgae and these dominant species are different at different sites of the water body. Among such dominant species are *Paralia sulcata*, *Asterionella formosa*, *A. kariana* and *Nitzschia seriata*. At the same time over the whole water area, particularly in the mouth of the bay, the largest part in the quantitative structure of the algal coenosis belongs to dinophyte algae.

Like in the outer shelf zone, as farther north, the autumnal cycle gradually drops out from the succession structure. In arctic stratified estuaries covered with ice large part of the year (which spring phytoplankton and cryoflora are unfortunately very poorly studied), there is probably only one succession cycle, the spring one, which follows the cryoflora bloom.

In the coastal pelagic zone of outlet glaciers of the Novaya Zemlya Archipelago there is the most simple type of the seasonal succession of the arctic coastal phytoplankton with the only maximum in the structure of the annual cycle, the spring one (ice-edge bloom) (Druzhkov et al., 1997b). Thus, there are only three stages in the vegetation season of microalgal communities, i.e. fast ice cryoflora bloom, the spring maximum, and the balanced cell abundance stage. The similar situation is obviously happens in the coastal waters of the

Svalbard Archipelago (Węslawski et al., 1988, 1991). In high arctic latitudes, an extreme variant of the annual cycle of pelagic algae is possible, with the development of the ice-associated flora only.

It should be noted once again that the sub-ice bloom described above is registered in coastal areas directly close to estuarine zones and is not observed in open parts of water bodies. However, analyzing data of planktonic studies at the central part of the Barents Sea basin and in coastal waters off the Novaya Zemlya Archipelago we can suppose the existence of such a phenomenon there. Already in May, in that area near the ice edge, there are phytocoenoses at different stages of the vernal bloom. In June almost the whole eastern part of the Barents Sea contains the summer complex of pelagic microalgae. This suggests the rapid development of the succession cycle, which can obviously be explained by a short vegetation period of phytoplankton in the area free of ice during only a short period of the year. It should be mentioned that this factor causes different specific manifestations at different areas of the arctic basin. In high latitudes, single stages simply drop out from the succession cycle. In the eastern Barents Sea, microalgae belonging to different seasonal complexes are registered simultaneously in the pelagic zone, i.e. one stage of the succession clashes with another. In the region described, especially near the shores of the Novaya Zemlya Archipelago, where environmental conditions enable autotrophic organisms to function over a longer period of time, a phenomenon called *sinking of bloom* is observed when communities of phytoplankton at earlier stages of the seasonal succession occur in deeper layers of the water column (Larionov, 1995).

However, both qualitative and quantitative compositions of phytocoenoses in this region distinctly differ from those in the aforementioned coastal and near-estuarine zones. Although the latter also do not remain long under the condition of open water, communities of microalgae in these zones are characterized by much greater species diversity and high quantitative parameters. At the same time, pelagic algal assemblages of the eastern Barents Sea rarely include more than ten species, and the biomass (less than 1 mg/l) is formed mostly by a single species, the diatomic alga *Thalassiosira antarctica*. The summer complex is also characterized by low quantitative values and is often formed by only several representatives of dinophyte algae: large-sized species of the genus *Protoperidinium*, and sometimes by Chrysophyceae and Cryptophyceae organisms. In the southern and western Barents Sea, such a state more likely corresponds to the autumnal stage of the succession of the algal coenosis.

3.2 Nanophytoplankton annual succession cycle

The conceptual scheme of the annual succession cycle of nanophytoplanktonic algae (unicellular organisms 2-20 μm in size belonging to different taxonomic groups) forms like that of the microphytoplankton, i.e. in correspondence with the stages of the seasonal dynamics of the hydrophysical structure and with the stages of the microphytoplankton succession cycle (Druzhkov et al., 1997b) and the stages of the production cycle of northern seas (Fyodorov, 1987; Fyodorov et al., 1988; Smirnov et al., 1989). The graph of the annual course of biomass of both size groups of algae in the Barents Sea coastal zone (fig. 3) suggests distinct correlation between them and at the same time definite autonomy of the nanoplanktonic component of the pelagic algal cenosis.

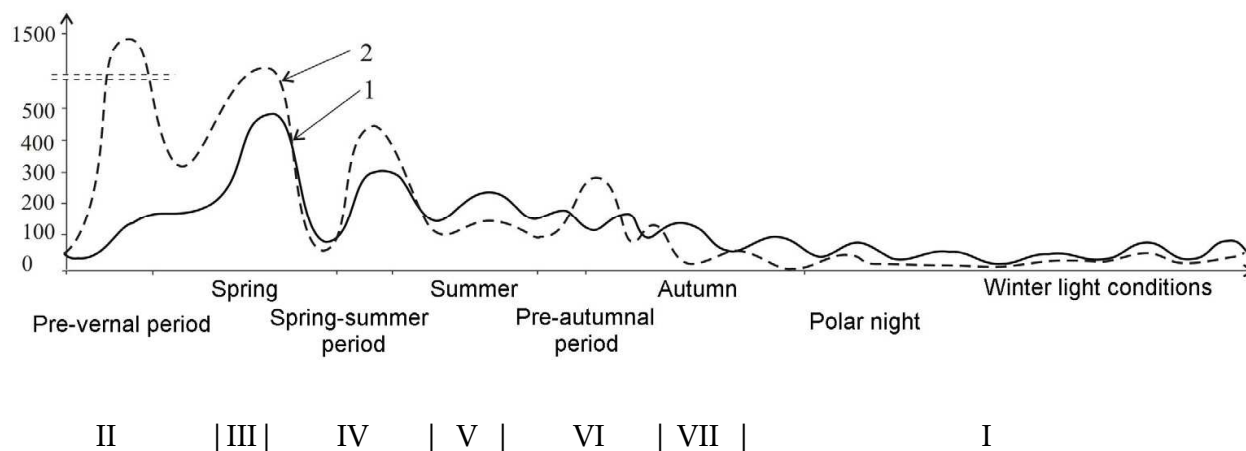


Fig. 3. Major dynamic trends (polynomial smoothing) of biomass ($\mu\text{g/l}$) change of nanophytoplankton (1) and microphytoplankton (2) in the pelagic zone of the Central Murman Coast (Kola Peninsula) in different seasons (averaged data over 6 years of observations). Roman numerals stand for the stages of the annual succession cycle (see in the text)

The annual cycle of the nanoplanktonic community includes the following periods.

- I The winter minimum stage. The winter season in the Subarctic (the longest stage of the annual cycle) can be divided into two stages: the period of the polar night (December – January) and the following period of the winter light regime (February – March). In general, the annual minimum of the phytocoenosis falls on the winter season which is characterized by the absolute dominance of nanophytoplankton in the coastal pelagic zone. During the polar night, the biomass of organisms of this group rapidly decreases and their size structure grows smaller. Rapid cooling of the water column and increased turbulent activity act as the main ecosystem regulators determining the dynamics of this community during the period of the polar night. In the second half of winter, processes of accumulation of winter supplies of biogenic matter no longer occur in the pelagic zone. The role of the main regulator passes to light, which causes the development of the primary production processes in the coastal ecosystem at the expense of nanoalgae populations dominating at this time.
- II Spring activation stage. In the pre-vernal period, the early spring succession cycle of microphytoplankton starts developing in the coastal pelagic zone under conditions of the light optimum, relative stabilization of the coastal water column, maximum levels of biogenic elements, and maximum screening from negative influence of the ultraviolet. Evident activation of nanophytoplankton still does not enable it to occupy the leading position. Perhaps, this fact can first of all be explained not by competitive interactions with microphytoplankton, but by restrictive influence of distinct turbulence, low temperatures, and microzooplankton predation pressure.

- III Spring maximum stage. During this period which is characterized by rapid warming of coastal waters and maximum levels of the continental runoff, the second succession cycle of the pelagic algal coenosis forms in the coastal pelagic zone. In contrast to the previous stage, at this one maximums of biomass of microphytoplankton and nanophytoplankton develops simultaneously (synchronically). Besides, nanoalgae make a substantial contribution into primary production processes.
- IV Early summer maximum stage. The biomass maximum in the spring-summer transition period, like in the previous one, also forms synchronically in both assemblages. The primary production activity of the phytocoenosis is very high at this stage. Intensive photosynthesis is accompanied by rapid transformation of biogenic elements into dissolved and shaped organic matter. Apparently, this is the very period of the annual cycle that ends the primary synthesis phase. Then the pelagic ecosystem enters the mixed synthesis stage which is characterized by the balance of primary production and heterotrophic processes and a complicated hierarchical system of redistribution of organic matter within heterotrophic components of planktonic biota.
- V Balanced cell abundance stage. Development of the nanophytoplanktonic community at this stage is possible according to two scenarios. The first one is a rather long period of balanced cell abundance (thus in 1989 this phase lasted through the whole summer and summer-autumn periods). During this period, quantitative parameters of the phytocoenosis, which is characterized by the absolute dominance of nanoalgae, change in an oscillatory manner. These oscillations, on the one hand, can be explained by competitive interactions between microphytoplankton and nanophytoplankton assemblages. On the other hand, they can be caused by intensive predation pressure from microzooplankton and mesozooplankton assemblages, which demonstrate the highest numerical abundance at that time. The period of balanced abundance is characterized by a distinct decline in photosynthetic activity of the coastal phytocoenosis, decreased reproductive rates of pelagic algae and/or substantially increased predation pressure from phytoplankton-eating organisms, and by intensive accumulation of organic substances in the fraction of suspended matter. Ultraviolet radiation being at its maximum during this period can have a substantial effect on the structure of algal coenosis. Thereupon, nanoplanktonic flagellates, more resistant to negative impact of this factor, account for the major part of the community. Processes of recycling prevail in the hydrochemical regime of the pelagic zone at this stage. A great role in these processes by all appearances belongs to nanoplanktonic algae actively consuming dissolved organic forms of biogenic elements. Afterwards, in the early autumnal period, the inflow of shelf waters rich in biogenic matter into the pelagic zone turns the nanophytoplanktonic community out of the balanced state and stimulates a new burst of its primary production activity, i.e. the formation of the autumnal maximum. At the same time, the nanofraction of the phytocoenosis keeps functioning in an oscillatory regime with a general trend to gradual attenuation of activity. The other scenario of the summer development of the nanophytoplanktonic community is the formation of a distinct maximum. In coastal waters of the Central Murman Coast (Kola Peninsula) such a scenario occurs in years with decreased hydrodynamic activity of coastal waters (like for instance in 1987). At this period, nanoalgae demonstrate both high photosynthetic and heterotrophic activities taking part in processes of the secondary synthesis of organic matter and recycling of biogenic elements.

- VI Activity attenuation stage. In the autumnal period, both nanophytoplankton and microphytoplankton assemblages undergo a gradual decrease in abundance progressing in an oscillatory manner. Parallel to this runs the process of disintegration of the phytocoenosis floristic structure developing on the background of rapid cooling of coastal waters and increased hydrodynamic activity. Mass decay of pelagic algae stimulates processes of re-mineralization of dead organic matter in the coastal zone and accumulation of biogenic elements in mineral fractions. This is the very period when the main winter structural trend in the development of the nanophytoplanktonic community takes shape, i.e. nanophytoplanktonic algae gradually grow smaller in size. The main factors regulating the community structure at this period are likely the light regime and hydrodynamic (turbulent) activity of the pelagic biotope.
- VII Pre-hibernal maximum stage. At the end of November and the beginning of December, in the Barents Sea coastal zone, there is a distinct increase in activity of phytoplanktonic community, which in this autumn-winter transition period mostly consists of nanophytoplankton. Although in subarctic latitudes, when the polar night is drawing near, extremely low levels of solar radiation in the pelagic zone hamper an evident manifestation of this phase. It's hard to tell by now what structural transformations in the coastal biotope cause this late outburst of activity of the nanophytoplanktonic community. Determining this stage and describing its ecologic characteristics is the task for future studies.

3.3 The role of other groups of primary producers in the coastal zone

3.3.1 Cryoflora

As it was mentioned before, a substantial contribution into primary production processes in the Barents Sea area covered with pack ice belongs to the cryoflora. An average annual production of sea-ice algal community per day makes up to 30 mgC/m²/day, within which phytoplankton accounts for 18 mgC/m²/day and 12 mg C/m²/day is the share of the cryoflora (Gosselin et al., 1997). Thus, if the ice cover area and the duration of daylight hours are taken into account, the primary production of the cryoflora can be estimated at 3 mil tons of carbon, i.e. about 5 % of the whole primary production of the Barents Sea pelagic zone.

However, results of studies in arctic coastal zones carried out over the last twenty years enable the conclusion to be made that the major part of this volume is produced by algae of the fast ice biotope. In August, the primary production of the cryoflora off the Franz Josef Land Archipelago made up 42.7 mgC/m²/day (Kuznetsov et al., 1994). Moreover, samples were made already at the heterotrophic stage of the ice-associated algal community succession when the respiration exceeded the photosynthesis level more than two orders of magnitude. A supposition can be made that during the spring exponential growth of sea-ice microalgae abundance, this value may be an order higher. Optimal light regime for the vegetation of the cryoflora remains in these latitudes within four months (from May till August). During this time the Barents Sea ice breaks up and the area of the ice cover decreases reaching the minimal values. Thus, the production of Barents Sea ice algae may make up to 6-8 gC/m²/year (Kuznetsov & Shoshina, 2003).

3.3.2 Macrophyte algae

The main difference between processes of the primary organic matter synthesis in coastal ecosystems of the Barents Sea and those in outer deep-water shelf areas is that the major producers of organic matter in coastal areas are not pelagic algal communities but macrophytes with annual production of ca. 630 000 tons in wet weight which is equal to ca. 66 000 tons of organic carbon per year. Calculated for a unit of area of Barents Sea coastal regions, the phytobenthos production makes up 1.2-2.3 kgC/m²/year, i.e. it can exceed the production of phytoplankton an order of magnitude (Romankevich & Vetrov, 2001).

The littoral zone of the Eastern Murman Coast (Kola Peninsula) is the habitat for macrophytes belonging to three major taxonomic groups: brown, red, and green algae. Each group numbers a dozen of species; still the most common are *Laminaria saccharina*, *Palmaria palmata* and *Ulvaria obscura*. During the polar night (from the beginning of December till the third decade of January) vital functions of algae is characterized only by respiration processes. In a month after the end of the polar night, the speed of the photosynthesis starts exceeding the consumption of oxygen. The vegetation period lasts eight months a year. Reduction of photosynthesis to the respiration level falls on the end of September. After that destruction processes prevail in the bottom phytocoenosis.

According to experimental studies made in bays of the Eastern Murman Coast (Kola Peninsula) over the last years, the production of brown algae averaged to 0.98 mgC/g/day (wet weight) with a range of 0.32 to 1.74 mgC/g/day (wet weight). The same average value for the green algae was slightly higher, 1.18 mgC/g/day (wet weight), and for the red algae still higher, 1.65 mgC/g/day (wet weight). Ranges of these values were also higher, 0.31-2.24 and 0.53-3.18 mgC/g/day (wet weight), respectively (Kuznetsov & Shoshina, 2003). However, it should be taken into account that brown algae absolutely dominate the macrophyte community in this area. The species *Laminaria saccharina* can account for 85-99 % of the total biomass (Propp, 1971). Having an average biomass of 8 kg/m² laminaria algae can make a pure production equal to 1 500 gC/m²/year (Kuznetsov & Shoshina, 2003).

As for arctic coastal ecosystems, available data of single studies off the Franz Josef Land Archipelago enable the production potential of these areas to be assessed very approximately. Taxonomic composition of bottom assemblages here is several times poorer than in the southern Barents Sea and mostly consists of different species. Among species typical for bays of the Eastern Murman Coast (Kola Inlet) only brown algae *Laminaria saccharina*, *Alaria esculenta*, and *Pilayella littoralis* are found here. The production of brown algae compared to coastal waters of the southern Barents Sea is 26 % lower and the production of green algae is 42 % lower. Respiration levels differ even more greatly, 58 % and 83 % lower for brown and green algae, respectively (Kuznetsov & Shoshina, 2003). That gives reason to suppose that the main factor determining the differences observed is low water temperature that to a greater extent affects the intensity of respiration of macrophytes than the process of photosynthesis.

3.3.3 Microphytobenthos

Microphytobenthic organisms also play an important role in coastal ecosystems though they somewhat yield to phytoplankton in productive capacity. The total annual biomass of the

Barents Sea microphytobenthos makes up 0.35 mil tons with the annual production of 5.3 mil tons of carbon (Vetrov & Romankevich, 2004).

In the littoral and upper sublittoral zones of the Eastern Murman Coast (Kola Peninsula), the flora of soft grounds is represented solely by diatomic algae. The dominant position in the community belongs to pennate diatoms which remain in bottom biocoenoses throughout the year (Bondarchuk & Kuznetsov, 1988). An assumption can be made that in the winter period when the photosynthesis is hampered by the absence of light, pennate diatoms turn to mixotrophic and heterotrophic types of feeding. The taxonomic list of organisms of this community includes, according to data of different studies, 65-70 species and forms of bottom diatoms (Korotkevich, 1960; Kuznetsov & Shoshina, 2003). In April and May, during the vernal bloom of phytoplankton, and in autumn at the end of the vegetation period of pelagic microalgae, samples of benthos contain typical planktonic species.

The beginning of active development of microphytobenthos in coastal waters of the southern Barents Sea occurs in April while the end falls on September or October. Studies carried out in different areas of the southern Barents Sea coastal waters showed a rather wide range of values of the bottom flora production, 80 to 500 mgC/m²/day. Levels of the primary production were measured in areas with different depths. The maximum values were registered in shallow water (with depths less than 5 meters) and averaged 16.4 mgC/m² over the period from April till September with a range of 0.1 to 50.6 mgC/m²/hour. According to calculations, taken in whole over the given period of time, this value exceeds the production of phytoplankton in the water column almost three orders of magnitude. At a depth of 10 m this value averaged 15.0 mgC/m²/hour (which is 1.2 times lower than the production level of pelagic algae) and at a depth of 17 m it made up 9.9 mgC/m²/hour on average (40 % of the phytoplankton production in the water column) (Kuznetsov & Shoshina, 2003).

Studies of microphytobenthos off the Franz Josef Land Archipelago are also of great interest. These studies showed that during the period of open water (from June till September) the community of bottom microalgae remains in the active photosynthesis stage and the level of photosynthesis to a considerable degree depends on depth. In shallow water at depths less than 5 m, where small grounded hummocks, icebergs, and fast shore ice have destructive impacts on biotopes, levels of the primary production are very low. The maximum levels are observed at depths of 7-20 m, at greater depths levels of photosynthesis sharply decrease (Kuznetsov & Shoshina, 2003). The values of the primary production of microphytobenthos here make up on average 40 to 65 mgC/m²/day, with values of 170 to 235 mgC/m² registered in a single small area where fast shore ice is subject to destruction accompanied by the inflow of allochthonous organic matter into bottom sediments.

To sum it up, the following conclusions can be made. An analysis of calculation data well enables the contribution of coastal ecosystems of the Barents Sea into the total production balance of this water body to be estimated. The area of coastal waters is less than 3 % of the whole area of the Barents Sea. Still it accounts for 9-33 % (14 % on average) of the total organic matter in this body of water. Even more significant are differences between the productivity of coastal waters and waters of the deep-water outer shelf zone calculated for a unit of area. Calculations show that the productivity of coastal waters is 3 to 12 times higher and makes up 253 tons of carbon per square km a year versus 21.1-77 tons in the deep-water

outer shelf zone. The productivity of shallow waters (with depths from 0 to 10 meters) makes up 1 222 tons of carbon per square km a year, which is 16 to 58 times higher of the corresponding values for the deep-water outer shelf zone.

4. Planktonic assemblages associated with the sea ice

4.1 Ice-edge bloom of pelagic microalgae

In previous chapters we described the so-called *ice-edge phytoplankton bloom* as the first stage of the annual cycle of Barents Sea pelagic algal assemblages or the main stage of the primary production formation in the pelagic zone of arctic coastal ecosystems (see above). In truth, this phenomenon has already been known for a hundred of years and was first recorded in reports of polar expeditions as long as the beginning of the XX century. Still it continues provoking interest among specialists. By all appearances, first researchers were very much amazed just by the fact of rapid growth of microalgae abundance in cold high latitudes right near the ice edge while in southward warmer open waters it was not observed. Ever since hydrobiologists have been discussing the connection between the impetus of the phytoplankton bloom and processes of the sea ice melt.

The most complete review of hypotheses on this issue proposed in the first quarter of the XX century was made by P. Shirshov (1937). Shirshov described all possible mechanisms of direct influence of sea ice melt on microalgae abundance growth including freshening of the upper water layer, inflow of nutrients from the ice surface with melt water, and even increased levels of carbonates and tri-hydrolic molecules reported in publications of that time. Using many examples Shirshov shows the impossibility to give a comprehensive explanation of how these factors, taken either separately or in combination, can stimulate the beginning of the spring bloom. P. Shirshov (1937) believes that the only factor able to act as a trigger is light or rather an increase in insolation as the sea ice melts. This point of view for a long time occupied the dominant position in hydrobiology although it was in a simplified manner treated as if it asserted that the state of the ice cover has no effect on the behavior of production processes in the pelagic zone. This idea has been many times criticized. It was pointed out that in the Barents Sea, which never completely freezes, an increase in insolation cannot serve as a comprehensive explanation of the abundance growth of phytoplankton just near the ice edge. In high arctic latitudes this increase in insolation is insignificant while in open waters of the southern Barents Sea, where the level of the solar radiation rapidly increases as the polar night comes to an end, such a rapid bloom as near the ice edge is not observed. This is why the appearance of a new concept was quite expected. The authors of this new concept took notice of one more phenomenon driven by the sea ice melt, namely the density jump caused by the freshening of sea water and separating the upper homogeneous water layer. Norwegian oceanologist H.U. Sverdrup (Sverdrup, 1953) introduced the notion of a so-called critical depth. According to Sverdrup's Critical Depth Hypothesis, when the lower boundary of the mixed homogenous layer locates below the critical depth, the bloom is impossible because the organic matter decomposing in the water column below this compensation level exceeds the organic matter produced by the photosynthesis in the layer above the compensation depth.

This concept was then developed and many times confirmed by other researchers when they observed the phytoplankton bloom in different areas of the Barents Sea (Rey et al.,

1987; Skjoldal et al., 1987; and other). Nowadays most biologists adhere to this concept though it is not able to explain, in particular, the fact of the bloom outburst both in coastal waters with little depths, where the whole water column locates above the critical depth, and in outer areas never being freshened. Thus, the question remains open and needs further discussion. The ice-edge phytoplankton bloom, an important stage in the succession cycle of Barents Sea primary producers, still needs thorough research.

4.2 Phytoplanktonic assemblages in water areas entirely covered with the sea ice

Among different aspects of influence of the sea ice on the development of primary producers in the Barents Sea pelagic zone, one more thing needs thorough attention. For a long period of studying arctic pelagic ecosystems, the winter season has always been considered a dormant stage when all vital processes in phytoplankton populations come to a stop. Only at the end of the 1970s, a rapid burst of studies on pelagic unicellular organisms with the heterotrophic type of feeding revealed inconsistency of orthodox opinions explaining processes of the organic matter re-mineralization solely by the activity of bacterioplankton. In truth, a complicated system of the heterotrophic metabolism functions in the pelagic zone in winter. This system includes different groups of mixotrophic and heterotrophic organisms belonging to several divisions and categories of microalgae and heterotrophic flagellates, which form the basis of the winter algal coenosis.

Results of studies carried out over the last decades in winter and at the beginning of spring in coastal arctic areas from nuclear powered ice-breakers are of particular interest in this respect. These studies show that over a large area, from the Kanin-Kolguev Shoal to the southern coast of the Pechora Sea (southeastern Barents Sea), the activation of production processes starts during the polar night already under the complete sea ice cover. Although the most part of studies was carried out in the Pechora Polynia, the biologic activity of the community cannot be explained solely by the occurrence of an open water area of the pelagic zone. Observations made at the same period of time in the Eastern Novaya Zemlya Polynia located approximately at the same latitude and thus having similar light conditions did not prove even the slightest signs of the spring awakening of phytoplankton populations (Makarevich & Druzhkova, 2010).

An analysis of the taxonomic structure and quantitative parameters of the community revealed that in the first half of February the core of the community consists of flagellates including unarmored (naked) forms. The composition of this group was almost homogeneous over the whole water area while the diatomic complex demonstrated diversity though yielding to the dynophyte complex in biomass. At the end of February, the seasonal state of pelagic floral assemblages in the Pechora Sea (southeastern Barents Sea) can be characterized as a stage of the primary activation of diatomic populations. Pennate forms dominate the community at this stage. Moreover, mostly single non-colonial algae account for the most part of the biomass. The most typical representatives of the flora at this stage are *Coscinodiscus cf. stellaris*, *Amphiprora kjellmanii*, *Cylindrotheca closterium*, *Gyrosigma fasciola*, *Navicula/Plagiotropis* spp. and *Pleurosigma stuxbergii*. In March, the community comes into the initial stage of the spring bloom and at some sites demonstrates a rapid growth of abundance of early-spring diatomic populations. As typical for arctic pelagic ecosystems at the beginning of the bloom, the increase of biomass happens mostly at the expense of species of the genus *Thalassiosira*: namely *T. antarctica*, *T. cf. gravida*, *T. hispida* and *T. hyalina*.

Thus, the sequence of initial stages of the phytoplanktonic community succession system in the Pechora Sea coastal zone corrected according to the latest data, first of all data on the active development process of microalgae under the sea ice, looks as follows (Makarevich & Druzhkova, 2010). I) winter stage (the first and the second decades of February): heterotrophic processing of organic matter, II) early spring stage: 1) activation of the early spring diatomic complex (from the third decade of February till the first decade of March): beginning of photosynthesis processes, 2) rapid growth of biomass of early spring diatomic algae (the second and the third decades of March): exponential growth of abundance.

5. Spatial and temporal dynamics of the primary production in the Barents Sea

In general, in the Barents Sea, zones of increased productivity correspond to seats of the phytoplankton bloom, i.e. to near-shore areas, ice edge zones, and streams of permanent currents of the Atlantic Ocean origin. The analysis of the spatial distribution of chlorophyll-*a* confirms this regularity. Thus in April 1985, in the southeastern Barents Sea, maximum concentrations of chlorophyll-*a* were registered in the coastal zone (21.8 mg/m²) and the ice edge zone (19.6 mg/m²) while in the central part of the area lower levels of chlorophyll-*a* were observed with an even distribution of this parameter. In the western Barents Sea the same year in April, chlorophyll-*a* levels varied from 6.2 mg/m² to 34.6 mg/m² with local maximums confined to streams of permanent currents of the Atlantic Ocean origin, namely the Central Branch of the Nordkapp Current (17 mg/m²), the Murman Current (34.6 mg/m²), and the Coastal Murman Current (28.1 mg/m²) (Savinov & Bobrov, 1990).

Maximum levels of the primary production in the Barents Sea were registered over seabed elevations (Murman, Finnmarken, and Nordkinn Shoals), in the coastal zone, and in areas where waters of the Atlantic Ocean origin mix with Barents Sea waters (Bobrov, 1985).

As it was mentioned before, the beginning and duration of the phytoplankton vegetation cycle in different latitudinal zones of the Barents Sea in temporal aspect depend first of all on ice conditions, i.e. the duration of the active vegetation season shortens from 8-9 months in the southern Barents Sea to 2-3 months in its northern part. Simultaneous occurrence of phytoplankton assemblages, being at different succession stages, in the pelagic zone determines the formation of seasonal heterogeneities of the primary production distribution. At the same time, areas with increased productivity confined to frontal zones do not have seasonal character and are connected to upward water movement along the frontal surface.

Despite sufficient knowledge on the Barents Sea compared to other arctic seas, there are no reliable estimates of the annual primary production of the Barents Sea phytoplankton. The situation is hampered by a mixed hydrological structure and a diversity of seasonal changes of the productivity of various Barents Sea areas. As a result, estimates of the Barents Sea total production made by various researchers greatly differ. In a number of publications (Romankevich et al., 1982; Danyushevskaya et al., 1990) estimates of the primary production are much the same, 77 to 80 mil tons of organic carbon per year, while other publications suggest higher values of the Barents Sea total production, 100 to 150 mil tons of C_{org} per year (Matishov & Drobysheva, 1994).

Based on the generalization of published data and the use of the existing notions of the typical seasonal course of the primary production, P. Makarevich (2007) makes the reconstruction of this parameter for the Barents Sea ecosystem (fig. 4). Over the period of 1964 to 2002 this parameter varied in a range of 23 $\text{gC}_{\text{org}}/\text{m}^2/\text{year}$ (1970) to 69 $\text{gC}_{\text{org}}/\text{m}^2/\text{year}$ (2002) with an average value of 44 $\text{gC}_{\text{org}}/\text{m}^2/\text{year}$, which well correlates with the estimate made in the last review (Romankevich & Vetrov, 2001): 44.5 $\text{gC}_{\text{org}}/\text{m}^2$.

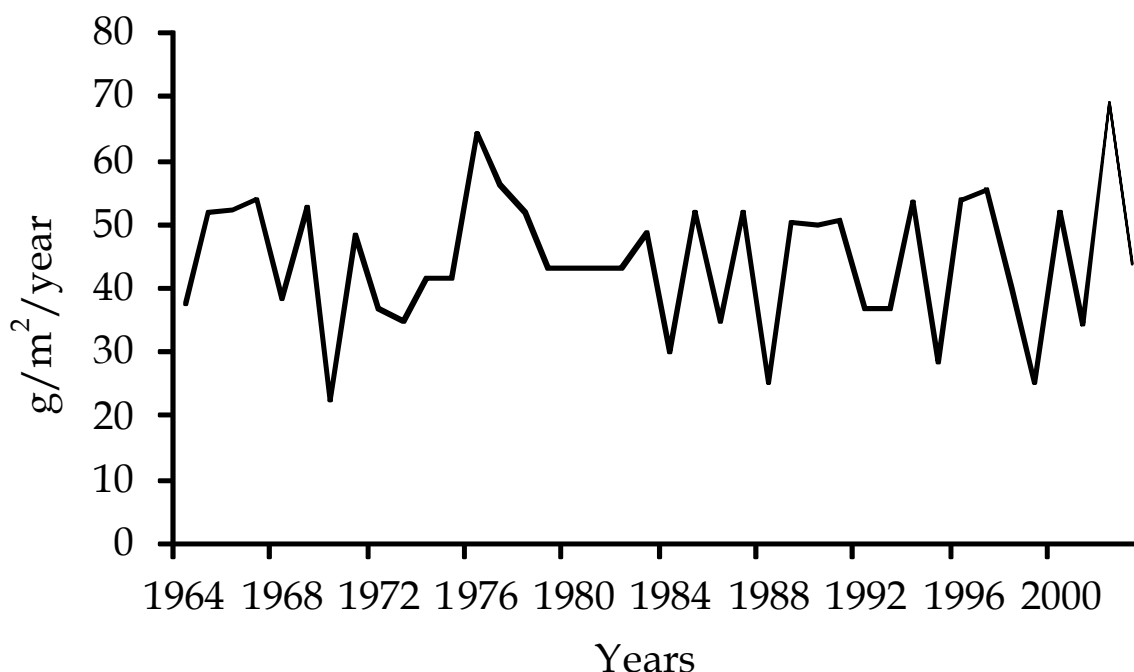


Fig. 4. Dynamics of the annual primary production in the Barents Sea over the period of 1964-2000 (reconstruction)

It is evident that both values and the character of the primary production distribution in the Barents Sea greatly differ across seasons. At the same time, there is distinct interrelation between spatial and temporal variability of this parameter, i.e. its seasonal dynamics appears similar in areas with a definite type of water masses. Thus, in waters of the Atlantic Ocean origin, in the outermost southwestern Barents Sea, the maximum of the specific primary production falls on the end of May and the beginning of June (2.5-3 mil tons per month); in July this value decreases (0.5 mil tons/month) while in August the second peak of productivity is observed (1.3 mil tons per month). The variations established are obviously determined first of all by changes in the zooplankton community, as the predation of zooplankton on phytoplankton in warm waters of the Atlantic Ocean origin is the main regulator of abundance in pelagic algal assemblages.

In the arctic zone occupying the whole northern part of the Barents Sea, the only primary production maximum registered (1.2 mil tons per month) is determined by the aforementioned ice-edge bloom, which starts in June during the intensive ice melt and lasts through the whole warm period in a narrow stripe of water along the retreating edge of the ice cover. Besides, an area with increased productivity is registered off the southern coasts of the Franz Josef Land Archipelago where prevailing summer winds push the sea ice off the

coast and release a space of open water occupied by an actively vegetating phytoplankton complex. A similar picture is observed in the southeastern Barents sea (often called the Pechora Sea), the zone of the maximum continental runoff. The period of high productivity here also relates to the sea ice melt and falls on June – September (0.8-1.3 mil tons per month), however the bloom is not confined only to the ice edge and occupies a larger water area.

The central part of the Barents Sea, from the Murman Coast to the Novaya Zemlya Archipelago, contains waters of mixed origin and therefore is characterized by a more complicated hydrological regime, which affects the course of seasonal change of productivity. Maximum values of the specific primary production are observed in April and make up 6.5 mil tons per month. Then in May a short recession period begins with a level of the specific primary production of 1.5 mil tons per month. This period is replaced in summer months by the period of a stable increase of the specific primary production level up to 5 mil tons per month. The main factor affecting the dynamics of the primary production in this water area is the concentration of biogenic elements in the water column. Usually registered in September, the autumn maximum (ca. 4 mil tons per month) forms in the southern coastal area of the water body and is determined by the activation of the spring phytoplankton when water is enriched with biogenic elements mainly due to the wind mixing and its temperature decreases.

According to Vinogradov et al. (2000), the total primary production of the Barents Sea calculated with the use of remote sensing data and average values for the defined ranges of the chlorophyll contents in surface waters of arctic seas (for the period from April till September) makes up 38.4 mil tons C_{org} per year. When the values for the months characterized by a continuous cloudiness are corrected, the annual production makes up 55 mil tons C_{org} per year. The level of the average annual primary production in the Barents Sea calculated in that way appears rather little, 0.12 gC_{org}/day (compared to 0.45 gC_{org}/day for the World Ocean). According to existing classifications, the Barents Sea corresponds to mesotrophic water bodies by the level of biological productivity: 0.1-0.5 gC_{org}/day (Romankevich & Vetrov, 2001).

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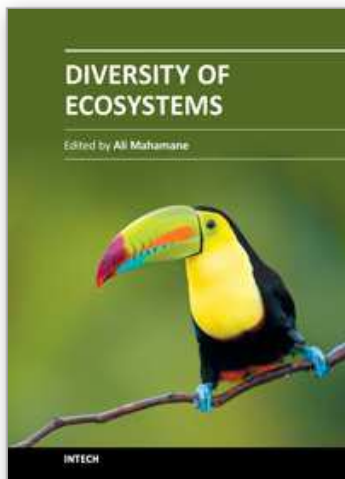
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Diversity of Ecosystems

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The ecosystems present a great diversity worldwide and use various functionalities according to ecologic regions. In this new context of variability and climatic changes, these ecosystems undergo notable modifications amplified by domestic uses of which it was subjected to. Indeed the ecosystems render diverse services to humanity from their composition and structure but the tolerable levels are unknown. The preservation of these ecosystemic services needs a clear understanding of their complexity. The role of research is not only to characterise the ecosystems but also to clearly define the tolerable usage levels. Their characterisation proves to be important not only for the local populations that use it but also for the conservation of biodiversity. Hence, the measurement, management and protection of ecosystems need innovative and diverse methods. For all these reasons, the aim of this book is to bring out a general view on the function of ecosystems, modelling, sampling strategies, invading species, the response of organisms to modifications, the carbon dynamics, the mathematical models and theories that can be applied in diverse conditions.

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