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MARINE BIOLOGY

Bacterial and Primary Production in the Pelagic Zone of the Kara Sea

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Abstract—Data on the bacterial and primary production, which were obtained simultaneously for the same water samples, are presented for three regions of the Kara Sea. The samples were collected for the transect westwards of the Yamal Peninsula, along the St. Anna Trough, and the transect in Ob Bay. Direct counts of the DAPI-stained bacterial cells were performed. The bacterial production and grazing rates were determined using a direct method when metabolic inhibitors vancomycin and penicillin were added. The primary production rates were estimated using the ^{14}C method.

The average primary production was 112.6, 58.5, and 28.7 mg C m^{-2} day^{-1}, and the bacterial production was 12.8, 48.9, and 81.6 mg C m^{-2} day^{-1} along the Yamal Peninsula, the St. Anna Trough, and Ob Bay, respectively. The average bacterial carbon demand was 34.6, 134.5, and 220.4 mg C m^{-2} day^{-1} for these regions, respectively. The data obtained lead us to conclude that the phytoplankton-synthesized organic matter is generally insufficient to satisfy the bacterial carbon demand and may be completely assimilated via the heterotrophic processes in the marine ecosystems. Therefore, the bacterial activity and, consequently, the amount of the synthesized biomass (i.e., the production) both depend directly on the phytoplankton's condition and activity. We consider these relationships to be characteristics of the Kara Sea's biota.

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INTRODUCTION

The shallow Kara Sea is characterized by the dominance of the shelf areas and is greatly influenced by the river discharge among the other seas of the Russian sector of the Arctic Ocean. The vast shallow estuarine areas, together with the significant freshwater discharge of the Ob River, the Yenisei River, and other rivers, result in a specific environment for the bacterial and phytoplankton growth. In the spring and summer, the most intensive river discharge and solar warming up lead to stable water stratification, which, in turn, determines the processes of the allochtonous organic matter transformation. The organic matter that comes with the riverine influx cannot pass through the pycnocline and thus is consumed and transformed by the plankton organisms in the upper mixed water layer. Nevertheless, the income of the nutrients within the riverine waters does not become the main trigger of the autotrophic and heterotrophic processes in the Kara Sea. The dissolved organic matter (DOM) that penetrates to the Kara Sea with the river discharge is refractory to bacterial utilization and thus plays an insignificant role in the bacteria's metabolism [18]. Only 6 to 16% of the available DOM in the estuarine area is represented by the autochthonous organic components of plankton origin. That is why the bacterial growth and activity are limited there by its insufficiency [10].

A significant positive correlation exists for the phytoplankton abundance and the bacterial production, when the DOM's standing stock in the Kara Sea is limited. The autochtonous organic matter, which is used by the heterotrophic bacteria, is a major source of the carbon for them. The data on the daily carbon demand of the bacterioplankton is evidence that organic matter (OM) synthesized as the primary production is totally used by the heterotrophic processes in the Kara Sea [18].

All these conclusions were based on recalculations; no simultaneous direct experiments were performed until now. Data on the direct estimation of the bacterial production in the Kara Sea are totally absent. Only two publications include data on the bacterial activity, which was measured by the dark assimilation of labelled $^{14}CO_2$ [5] and the consumption of the labelled leucine [18]. The primary production in the Kara Sea was measured only once in 1993 [1]. That was the reason for the parallel experiments concerning the bacterial and primary production in the same environment during the 54th cruise of the R/V *Academik Mstislav Keldysh*.

MATERIALS AND METHODS

Studies of the bacterial abundance, biomass, and production, as well as the chlorophyll *a* (Chl *a*) con-

centration and the primary production, were performed on September 10–29, 2007, in three regions of the Kara Sea including (1) the transect westwards of the Yamal Peninsula (stations 4946, 4948, 4950, 4952, 4956, and 4960), (2) the transect along the St. Anna Trough (stations 4983 and 4986–4991), and (3) the transect along Ob Bay (stations 4993–5000). A map of the sampling sites, the stations' coordinates, and the dates and times of the sampling are presented in [9] of the current volume.

The water was sampled from 2–5 layers within the euphotic water layer, which lasted from 3 to 30 m, to obtain the data on the primary production, the Chl *a* concentration, and the Assimilation number (AN) or from 2–8 water layers from the surface to the bottom (11–555 m depths) for the microbiological studies using 5-l, 10-l, or 30-l Niskin bottles incorporated into a "Rosette" complex equipped with a CTD probe (Sea Bird Equipment, United States). The stations' location and the sampled water layers were distinguished after the analysis of the temperature, conductivity, and fluorescence obtained using a ship-towed Idronaut probe and a CTD probe SBE-19 Plus (Seabird Electronics) equipped with sensors of the fluorescence and the water turbidity. The critical depth of the euphotic layer was distinguished using illumination sensors for the photosynthetic activity radiation (PAR) (Li-190A and Li-192A, the Li-Cor Co., United States) and a Secchi disk. Near-bottom water samples were obtained at stations 4952, 4956, 4960, 4983, 4996, and 5000 using a Neimisto multicorer, and experiments on the bacterial production were performed later on.

Direct bacterial counts under a fluorescence microscope were performed to estimate the Bacterial abundance in the experiments on the bacterial production. The bacterial cells were stained with DAPI prior to the analysis [16]. Water samples 20 or 50 ml in volume were fixed using a pH-neutral formaldehyde solution (the final concentration was 1%) and were stored in polystyrene bottles. The stained samples were concentrated using a black nuclear filter with a 0.17 μm pore diameter (Dubna City Enterprise, Russia). The samples were analyzed using a LUMAM P-8 fluorescent microscope with 1375× magnification and using a Leica DM 5000B fluorescent microscope with 1000× magnification. At least 20 fields of the microscope were analyzed for each sample; the total amount of the counted cells was more than 200. Bacterial size was measured using an eyepiece micrometer or by means of the software ImageScopeColor; at least 20 cells were measured for each sample. The cell volume was recalculated as a sphere for the cocci or a cylinder for the rods. The bacterial biomass in carbon units was recalculated according to the cell volume as

$$\text{fgC cell}^{-1} = 133.754 \times V^{0.438},$$

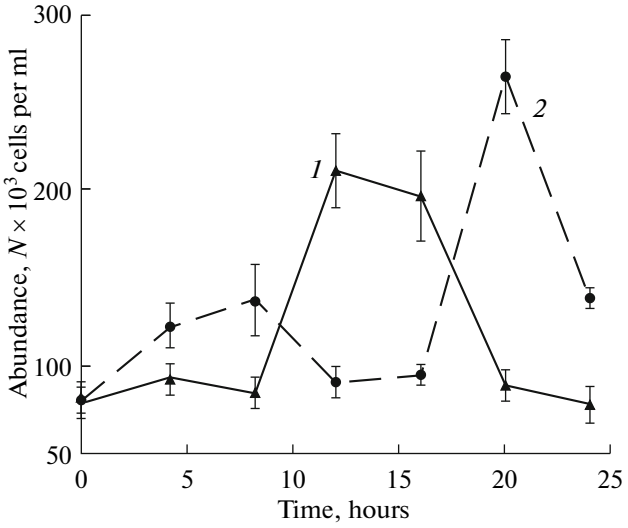
where fgC cell^{-1} is the carbon content per one cell, fg; and V is the cell volume, μm^3.

The bacterial production and the consumption of bacteria by the grazers were estimated using the method of [24] in a modification for the natural environment [26]. In contrast to the original method, we skipped the prefiltration of the water to exclude the mesozooplankton, taking into account its low abundance in the studied area, but the samples were controlled visually. Another reason for skipping the water filtration was to avoid increasing the extra organic matter, which may result after the destruction of the plankton organisms during the water's sieving. Finally, special slides were prepared to take into account the number of potential bacteria consumers and heterotrophic nano- and microplankton [11, 15, 20].

Immediately after the water samples were taken, they were poured onboard in 55-ml sterile transparent polystyrene bottles (Costar, Nunclon). The bottles were put into large-size mesh containers and were exposed for 24 hours in the deck aquarium (4.85 × 2.58 × 2.5 m, 31 m^3 in volume) with running subsurface seawater. The grazing on bacteria was estimated using the parallel exposition of the samples with and without antibiotics (benzylpenicillin, 1 mg l^{-1}; vancomycin, 200 mg l^{-1}), which stopped the bacterial growth but had no influence on the grazers [24]. At several stations, in the course of the experiment subsamples were taken every 6 h to estimate the daily dynamics of the bacterial production. After the experiment ended, the samples were fixed and treated as described before for the bacterial abundance samples. All the sample preparations were performed on the deck at an air temperature of +10°C and less, which was close to the temperature of the surface water layer.

When the bacterial production was estimated, special experiments were performed to assess the antibiotics' activity dynamics and their possible impact on the bacterial lysis, as well as to estimate the daily dynamics of the bacterial growth [26]. As a result, the bacterial production was calculated for a 12-h time period for the further recalculation for a 24-h time period taking into account the daily dynamics of the bacterial abundance (figure).

The estimation of the primary production was performed by means of the carbon isotope method [2]. A solution of $NaH^{14}CO_3$ was added to the 140-ml bottles in low-light-level conditions. The bottles were incubated using the light imitation method using neutral filters in the same aquarium where the bacterial bottles were exposed. The filter density depended on the natural light intensity observed for each sampling site. The light intensity of the photosynthetic activity radiation (PAR) was measured continuously during the day by means of a light sensor (Li-190A). After the incubation ended, the water was filtered through membrane filters (Vladipor (Russia)) with a 0.8 μm pore diameter under a <0.3 atm vacuum. The filters were rinsed using a 0.1 N HCl solution and filtered seawater and air dried. The filters' radioactivity was measured using a liquid scintillation counter (Rack-



Dynamics of the bacterial growth without (*1*) and with (*2*) antibiotics added for the surface water layer of the Kara Sea (station 5000).

Beta (LKB, Sweden)). The carbon concentration data necessary for the primary production estimation were kindly provided by P.N. Makkaveev (Institute of Oceanology, Russian Academy of Sciences). The concentration of Chl *a* was measured by fluorometry [17]. 0.5–1.0 l water samples were filtered through fibreglass filters (Whatman GF/F) under a <0.3 atm vacuum. The Chl *a* was extracted in 90% aqua acetone and incubated for 24 hours at +4°C. The fluorescence of the extracts was measured using a Trilogy fluorometer (Turner Designs, United States).

The average values of the studied parameters for the different areas were recalculated as the geometrical mean.

RESULTS

1. Bacterioplankton. The bacterial abundance ranged from 9.8 to 150 thousand cells per ml for the different stations and water layers of the transect along the Yamal Peninsula; the average was 36 thousand cells per ml (Table 1). The bacteria were mostly represented by solitary small cells, mainly cocci; we did not find aggregated bacterioplankton. The bacterial cell size ranged from 0.02 to 0.13 μm^3. The bacterial biomass along the Yamal transect varied from 0.11 to 7.51 mg C m^{-3}; the average was 1.38 mg C m^{-3}. The bacterial production (where possible) varied from –1.22 (i.e., the consumption of the bacteria exceeded their production) to 3.16 mg C m^{-3} day^{-1}; the average was 0.15 mg C m^{-3} day^{-1}. The integral daily bacterial production varied from 1.95 to 28.04 mg C m^{-2} day^{-1}; the average was 12.76 mg C m^{-2} day^{-1}. The specific growth rate, the P/B ratio, ranged from –0.9 to 0.66 day^{-1}.

The bacterial abundance along the St. Anna Trough transect varied greatly: from 6.8 to 370 thousand cells per ml for the different stations and water layers; the average was 24.4 thousand cells per ml (Table 1). As was observed for the Yamal transect, the bacteria were mainly represented by small solitary cocci, while aggregated bacterioplankton was not found at all. The bacterial cell size ranged from 0.03 to 0.18 μm^3. The bacterial biomass varied from 0.22 to 6.76 mg C m^{-3}; the average was 0.95 mg C m^{-3}. The bacterial production ranged from –1.75 to 2.72 mg C m^{-3} day^{-1}; the average for the whole water column was 0.21 mg C m^{-3} day^{-1}. The integral daily bacterial production varied from 15.7 to 442.8 mg C m^{-2} day^{-1}; the average was 48.9 mg C m^{-2} day^{-1}. The P/B ratio ranged from –0.66 to 1.5 day^{-1}.

The bacterial abundance ranged from 66 to 914 thousands cells ml^{-1} for the different stations and water layers for the transect along Ob Bay; the average was 424 thousand cells per ml (Table 1). Bacterial abundance in the brackish water environment (waters with salinity less than 5 psu) averaged 428 thousand cells per ml. The average bacterial abundance for the marine environment (waters with salinity of more than 8 psu) was 380 thousand cells per ml. The bacteria were mostly represented by solitary small cells, mainly cocci; aggregated bacterioplankton was not found at all. Detrital particles were quite abundant, but they were not colonized by the bacteria at all or slightly were. The bacterial cell size varied greatly for the different stations and water layers and might differ by

Table 1. Bacterioplankton characteristics in the studied areas in the Kara Sea

Studied site	$N_b \times 10^3$ cells per ml	B_b, mg C m^{-3}	P_b, mg C m^{-3} day^{-1}	P_b, mg C m^{-2} day^{-1}
Yamal Peninsula	9.8–150	0.11–7.51	–1.22–3.16	1.95–28.04
Average	36	1.38	0.15	12.76
St. Anna Trough	6.8–370	0.22–6.76	–1.75–2.72	15.7–442.8
Average	24.4	0.95	0.21	48.9
Ob Bay	66.4–914	0.39–41.58	0.03–6.02	66.15–96.5
Average	424	12.01	4.46	81.64

Note: Bacterial abundance ($N_b \times 10^3$ cells ml^{-1}), biomass (B_b, mg C m^{-3}) and production (P_b, mg C m^{-3} day^{-1}); integral daily bacterial production (P_b, mg C m^{-3} day^{-1}). Data spread and the average.

Table 2. The phytoplankton characteristics in the studied areas in the Kara Sea: the integral daily phytoplankton production ($P_{p,daily}$); the chlorophyll *a* concentration summarized (Chl *a*); and the assimilation number (AN). Data spread and average for the euphotic layer

Studied site	$P_{p,daily}$, mg C m^{-2} day^{-1}	$P_{p,daily}$ (average), mg C m^{-2} day^{-1}	Chl *a* (average), mg m^{-2}	AN (average), mg C mg^{-1} Chl a^{-1} h^{-1}
Yamal Peninsula	70.1–148	112.6	19.4	0.62
St. Anna Trough	44.1–89.2	58.5	9.8	0.46
Ob Bay	11.1–91	28.7	6.6	0.43

10 times or more. The maximal bacterial cell size in Ob Bay was 0.14 μm^3. Relatively big bacterial cells were registered for the southern (riverine) station. Downstream in the Ob River, their size did not exceed 0.08 μm^3.

The bacterial biomass along the Ob Bay transect varied from 0.39 to 41.58 mg C m^{-3}; the average was 12.01 mg C m^{-3}. The maximal values were registered for the southern (riverine) station, while the lowest ones, for the near bottom layers of the marine part of the transect.

The bacterial production (where possible) varied from 0.03 to 6.02 mg C m^{-3} day^{-1}; the average was 4.46 mg C m^{-3} day^{-1}. The integral daily bacterial production varied from 66.15 to 96.52 mg C m^{-2} day^{-1}; the average was 81.64 mg C m^{-2} day^{-1}. The specific growth rate, the P/B ratio, ranged from 0.07 to 1.55 day^{-1} and increased with the depth, while the minimal values were registered for the surface water layer.

2. Primary production. The maximal primary production (P_p) was observed for the surface water layer at most of the stations in the Kara Sea. The same was registered for the Chl *a* concentration for all three sampling areas: near the Yamal Peninsula, along the St. Anna Through, and in Ob Bay. The euphotic layer lasted down to the 25–30 m depth with the exception of the riverine station, where the water turbidity was extremely high and the photosynthetic layer occurred in the upper 0–3 m layer.

The primary production along the Yamal transect varied from 0.3 to 1.29 mg C m^{-3} h^{-1} in the surface water layer; the average was 0.87 mg C m^{-3} h^{-1}. In the euphotic layer, the integral AN, which usually characterizes the photosynthetic activity, ranged from 0.34 to 1.21 mg C mg^{-1} Chl a^{-1} h^{-1}; the average was 0.62 mg C mg^{-1} Chl a^{-1} h^{-1}. The integral daily P_p ranged from 70.1 to 148.0 mg C m^{-2} day^{-1}. The average Chl *a* concentration was 0.69 mg m^{-3} for this area of the Kara Sea.

Along the St. Anna Trough transect, the maximal values of the primary production were also registered for the surface water layer and varied from 0.18 to 1.63 mg C m^{-3} h^{-1}; the average was 0.43 mg C m^{-3} h^{-1}. The AN in the euphotic layer ranged from 0.22 to 0.94 mg C mg^{-1} Chl a^{-1} h^{-1}; the average was 0.46 mg C mg^{-1} Chl a^{-1} h^{-1}. The integral P_p values varied from station to station from 44.1 to 89.2 mg C m^{-2} day^{-1}; the average was 58.5 mg C m^{-2} day^{-1}. The average Chl *a* concentration in the euphotic layer of this area was 0.5 mg m^{-3}.

In Ob Bay, the primary production in the surface water layer varied from 1.02 to 3.98 mg C m^{-3} h^{-1}; the average was 1.57 mg C m^{-3} h^{-1}. The highest values of the surface P_p were registered for the southern (riverine) station. The AN in the euphotic layer ranged from 0.35 to 0.57 mg C mg^{-1} Chl a^{-1} h^{-1}; the average was 0.43 mg C mg^{-1} Chl a^{-1} h^{-1}. The integral P_p values varied from station to station from 11.1 to 91.0 mg C m^{-2} day^{-1}; the average was 28.7 mg C m^{-2} day^{-1}. The average Chl *a* concentration in the euphotic layer in Ob Bay was 1.6 mg m^{-3} at the end of September 2007.

The integral daily primary production in the euphotic layer varied for different areas of the Kara Sea from 11.1 to 148.0 mg C m^{-2} day^{-1} (Table 2). The waters along the Yamal transect may be characterized as the most productive area (112.6 mg C m^{-2} day^{-1} on average). The areas of the St. Anna Trough (58.5 mg C m^{-2} day^{-1} on average) and Ob Bay (28.7 mg C m^{-2} day^{-1} on average) were characterized by significantly lower primary production (half as large and four times less, respectively) compared to the Yamal transect waters. Regard must be paid to the wide range of the integral primary production in Ob Bay; it reached as much as 59.6 and 91.0 mg C m^{-2} day^{-1} in the riverine and marine parts of the transect (stations 4993 and 5000) and was only 11.0 mg C m^{-2} day^{-1} in the marginal filter area (stations 4996 and 4997).

DISCUSSION

Along the western coast of the Yamal Peninsula, the bacterial abundance observed in the end of September 2007 (the present study) is comparable to the values registered for the autumn period of 1993 [5]. In the area of the St. Anna trough (a single station) the same authors report values of bacterial abundance also close to that obtained in the current study. However according to the data of 2001 (also only a single station in the region) [18] bacterial abundance was significantly greater. These authors did not work in the Yamal Peninsula area.

Somehow, a significant dataset of the bacterioplankton characteristics in the Kara Sea exists only

for Ob Bay. When comparing the previously published and original data, the bacterial abundance in 2007 was 2–4 times higher than in August–October of 1993 [5] and 2.0–2.5 times lower than in August–September of 2001 [18]. We tend to link this phenomenon with interannual variability of the bacterioplankton abundance. The Chl *a* concentrations, which were registered simultaneously with the observations of the bacterial abundance, were lower in 2007 compared to 2001.

The average bacterial abundances for the marine waters (salinity of more than 8 psu) and the brackish waters (salinity of less than 5 psu) did not differ significantly, which might provide evidence of the secondary role of the salinity factor's influence on the bacterial growth, which is opposite to that of the phytoplankton, for which such a dependence is well-known [1]. Nevertheless, the inverse relationship of the bacterial activity and the water salinity is a characteristic of the Kara Sea waters [18].

Low and sometimes negative (the grazing on bacteria exceeds their production) values of the bacterial production were observed both in 2007 (Table 1) and in 1993 (four sites in different regions) in the Kara Sea. In 1993, some functional characteristic of the bacterioplankton was measured as the dark fixation of $^{14}CO_2$, which ranged from 0.3 to 1.44 mg C m^{-3} day^{-1} and sometimes was in the same range as the method's sensitivity [5]. The bacterial activity (production) measured by the ^{3}H-leucine in 2001 varied from 1.44 to 2.45 mg C m^{-3} day^{-1} along the St. Anna Trough and from 4.32 to 7.98 mg C m^{-3} day^{-1} in Ob Bay [18]. Data for the western coast of the Yamal Peninsula are totally absent for the year of 2001. Even taking into account the different methods used to measure the bacterioplankton production in 1993 and 2001, the same range of low values was obtained in 2007 when special experiments were established.

Meon and Amon [18] provided evidence of high correlation ($r = 0.78$) between the Chl *a* concentration and the bacterial production in the surface water layers in Ob Bay. We found a weaker relationship between these parameters ($r = 0.55$); however, regard must be paid to the inverse relationship ($r = -0.76$) between the specific growth rate and the Chl *a* concentration. Probably, the high microbial activity in the water corresponds to a lower Chl *a* concentration; i.e., the dying cells of autotrophic microalgae, which include chlorophyll, are rapidly utilized by bacteria. In the riverine and estuarine areas of the Kara Sea, the bacterial growth was especially limited by the concentration of organic autochthonous matter, which is mainly formed after the dying of the algae. A slight artificial increase of the organic compounds in the experimental chambers raises the bacterial production by 17–43%. The accessibility of the necessary substrates is the limiting factor for the bacterial growth. As was mentioned above, most of the organic matter transported from the rivers to the Kara Sea is represented by compounds that are not efficiently utilized by bacteria and thus play a minor role in the bacterial metabolism [18]. Less than 16% of the DOM in the riverine and estuarine waters is of plankton origin and can be used by bacteria [10].

The correlation between the Chl *a* concentration and the bacterial production along the Yamal Peninsula coast was slight and positive ($r = 0.54$), but no correlation was found for the Chl *a* concentration and the specific growth rate. The same recalculations resulted in no interrelationships between the similar parameters for the area of the St. Anna Trough.

We did not find any correlation between the bacterial and primary production for all the studied areas. First, a low number of sampling sites was analyzed; second, the activity of the bacterio- and phytoplankton may be limited by many other factors (not only the micronutrient concentration). The bacterioplankton growth may be limited by the low water temperature, which affects the bacterial growth in 40–45% of cases [14, 18]. Nevertheless, R.B. Rivkin and coauthors performed an analysis of 66 publications and found that the bacteria inhabiting cold waters (about +4°C) are well-adapted to this environment [22]. In turn, the low water clarity (especially in the estuarine areas), the long periods of unfavourable weather conditions, and the associated low phytoplankton metabolism are the main limiting factors of the primary production [1, 23].

The high primary production values along the Yamal Peninsula coast compared to the other studied areas were characterized by both higher Chl *a* concentrations and assimilation numbers (AN), which were approximately 1.5 times higher than those observed for Ob Bay (Table 2). The assimilation number is a characteristic of the photosynthetic activity of the phytoplankton. Regard must be paid to the significantly low average AN (0.49 mg C mg^{-1} Chl a^{-1} h^{-1}) for the whole Kara Sea, which may provide evidence of the phytoplankton bloom's end. Probably, the high level of the phaeophytine (about 30% of the total phytopigments) provides more evidence of the phytoplankton bloom falling. The same value range was observed for the Arctic waters by other authors [1, 25].

It is well know that bacteria are responsible for utilizing the organic matter in the water; they consume up to 40–60% of carbon produced by the phytoplankton [4, 12, 13, 19, etc.]. The accessibility of the autochtonous (phytoplankton) organic carbon is the limiting factor for the bacterial growth in the Kara Sea [18]. We can estimate the carbon demand for the bacterial growth using the well-known equation

$$D_b = P_b(1 - K_2)/K_2,$$

where D_b is the bacterial destruction or the bacterial carbon demand, and K_2 is the coefficient reflecting the bacterial growth efficiency, i.e. the part of consumed food used for growth. The K_2 coefficient for the Kara Sea waters is 0.27 [18], and $D_b = 2.7\ P_b$; thus, the bac-

Table 3. Production of phyto- and bacterioplankton in the studied areas in the Kara Sea: the average integral daily primary production of the phytoplankton in the euphotic layer ($P_{p,daily}$), and the bacterioplankton production (P_b) and the integral bacterial carbon demand (D_b) both recalculated for the whole water column

Studied site	$P_{p,daily}$, mg C m^{-2} day^{-1}	P_b, mg C m^{-2} day^{-1}	D_b, mg C m^{-2} day^{-1}
Yamal Peninsula	112.6	12.8	34.6
St. Anna Trough	58.5	48.9	134.5
Ob Bay	28.7	81.6	220.4

terial carbon demand for the studied areas of the sea differs (Table 3).

As proceeds from the original data, the primary production covers the bacterial carbon demand only for the Yamal Peninsula area, when P_b exceeds the D_b threefold. During our studies, this area appeared as the most productive region compared to the others (Table 2). The Chl *a* concentration, the elevated AN values, and the chlorophyll : phaeophytine ratio in the microalgae are altogether evidence of the lasting phytoplankton bloom in this area. The region is also characterized by the patchiness of the large diatom's spatial distribution [7]. The primary production along the St. Anna Through and the Ob Bay transects were half as much compared to the Yamal Peninsula area, and the bacterial carbon demand was 2.3–7.7 times higher than the primary production, respectively (Table 3). The extremely low microalgae biomass and abundance along the northern coast of Novaya Zemlya is also evidence of the phytoplankton bloom's end. In the estuary of the Ob River, the phytocenoses depended on the geographical position of the sampling sites, and the riverine (southern) stations were characterized as the most productive [8]. The bacterioplankton was also the most successful in the riverine waters, where the bacterial carbon demand was 642–1235 mg C m^{-2} day^{-1} in the freshwater areas (station 4993; the P/B ratio here varied from 0.39 to 0.75) compared to 230 mg C m^{-2} day^{-1} in the open sea waters (station 5000).

The data on the integral bacterial carbon demand for the estuarine and open sea areas [18] are close to the values obtained for the St. Anna Trough and the Ob Bay areas in the present study. However, the bacterial carbon demand along the Yamal Peninsula coast, where no studies took place in 2001, was 4 times lower compared to the open sea part. We argue that our results seem to be true, since the data on the bacterial and primary production were obtained simultaneously from parallel experiments performed for the same water samples. The data on the primary production cited in [18] were recalculated using the data obtained in 1993 [1] by Vedernikov and coauthors and have no connection with the expedition of 2001.

As proceeds from the experimentally assessed or recalculated values of the primary production in the Kara Sea [1, 3, 21, 23, and original data], the organic matter synthesized by the phytoplankton cannot meet the bacterial carbon demand; thus, the OM is totally utilized by the heterotrophic processes in the marine ecosystems of the sea. Therefore, the functional activity of the bacteria and their production (biomass growth) is affected by the activity and physiological status of the phytocenoses, which may be considered as characteristics of the Kara Sea.

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