

Structure and Productivity of the Phytocenosis in the Southwestern Kara Sea in Early Spring

S. A. Mosharov^{a, b, *}, A. F. Sazhin^a, E. I. Druzhkova^c, and P. V. Khlebopashev^a

^a*Shirshov Institute of Oceanology, Russian Academy of Sciences, Moscow, 117997 Russia*

^b*Bauman Moscow State Technical University, Moscow, 105055 Russia*

^c*Murmansk Marine Biological Institute, Kola Scientific Center, Murmansk, 183010 Russia*

**e-mail: mosharov@ocean.ru*

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Abstract—Results of plankton biota studies in the southwestern Kara are presented. The spatial distribution of hydrochemical and hydrophysical parameters related to structural and functional characteristics of phytoplankton in the surface water is considered. The chlorophyll *a* concentration varied in the surface layer of the Kara Sea from 0.08 to 3.22 mg m⁻³ (mean value 0.62 mg m⁻³). Primary production varied from 0 to 1.92 mg C m⁻³ day⁻¹ (the mean value of 0.42 mg C m⁻³ day⁻¹) in the ice-covered water areas and was greater by a factor of four, ranging from 1.01 to 3.46 mg C m⁻³ day⁻¹ (the mean value of 1.79 mg C m⁻³ day⁻¹) in ice-free areas. In this case, the total algal biomass varied from 0.8 to 110.7 mg C m⁻³ (mean value 10.6 mg C m⁻³). It is shown that in the study period, waters from the western Kara Sea were more productive than the estuarine water areas of the Ob and Yenisei rivers. The activity of phototrophic phytoplankton in river waters was almost completely absent. It is established that the contents of nutrients and iron were higher than the threshold for limitation of phytoplankton development. The experiments showed that the production activity of phototrophic algae is restrained by light deficit beneath the ice.

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INTRODUCTION

The almost complete lack of information on the state of the phytocenosis in the Kara Sea in early spring makes it impossible to reconstruct the entire cycle of the plankton community in this part of the Arctic shelf and consequently to obtain true estimates of its productivity. All studies of functional activity of phytoplankton, including experiments on measuring primary production in the Kara Sea from 1993 to 2016, were performed only in the summer–fall period [1, 2, 8, 11, 15]. Unfortunately, long-term studies of the quantity, biomass, and species composition of phytoplankton in 1996–2006 in the Ob–Yenisei shallow-water zone covered only part of the early spring period [7, 29]. To obtain information on the structure and functioning of the phytocenosis in the southwestern Kara Sea in early spring, expeditionary research was conducted on board the icebreaker *Norilsk Nickel* on March 29–April 8, 2016.

MATERIALS AND METHODS

As the vessel moved, samples of water to determine the temperature; salinity; concentrations of silicon, nitrates, and phosphates; analyze biological parameters, as well as for experimental works, were collected from the surface layer of the Kara Sea with a plastic

bucket at 27 stations from the Karskiye Vorota Strait to the estuary of the Yenisei River and back. The general information on the results of the expedition is presented in [12]. The sea surface along the route of the vessel was covered by ice 30–50 cm thick; however, there were also areas of open water (Table 1). During the studies, ice-free water areas were found in the Kara Strait (station 27) and further to the east, to the western coast of the Yamal Peninsula (stations 22, 23, 25, 26). The concentrations of phytoplankton, chlorophyll *a* (chl *a*) and primary production were estimated at 19 stations: 1–5, 7, 8, 14, 16, and 18–27 (Fig. 1).

The concentrations of nutrients were determined according to the procedures generally accepted in oceanological practice and most suitable for sea and river waters [13]. The iron content in seawater (stations 3, 20, and 24) was calculated at the Analytical Center of Moscow State University by inductively-coupled plasma atomic-emission spectrometry [16, 25].

To take into account pico-, nano- and microphytoplankton, as well as to determine their trophic status, 20 mL of a sample was stained by fluorochrome primulin, fixed with 3.6% glutaric dialdehyde solution, and deposited on black nuclear filters with a 0.4- μ m pore diameter [20, 23, 24] using our own modification of the procedure [37]. Right after being made, the preparations were frozen until treatment under stationary

Table 1. Production characteristics of phytoplankton in Kara Sea surface layer in March–April 2016

Station, no.	PP ₀ , mg C m ⁻³ day ⁻¹	Chl ₀ , mg m ⁻³	AN, mg C mg ⁻¹ chl ⁻¹ h ⁻¹	Pheo, %	State of sea surface
1	0.48	0.318	0.13	44	Ice
2	0.60	0.724	0.07	1	Ice
3	0.58	3.223	0.02	1	Ice
4	0	0.158	0.00	54	Ice
7	0.13	0.328	0.03	60	Ice
18	0	0.334	0.00	34	Ice
19	0.1	0.108	0.08	62	Ice
21	1.92	2.651	0.06	37	Ice
22	1.19	0.141	0.70	52	Open water
23	1.5	0.216	0.58	43	Open water
24	0	0.267	0	39	Ice
25	1.01	0.251	0.33	26	Open water
26	3.46	0.58	0.50	8	Open water
27	80.77	9.483	0.71	1	Open water

PP₀, surface primary production; chl₀, chl *a* concentrations in surface layer; AN, assimilation number; Pheo, pheophytin share in total quantity of chl *a* and pheophytin.

conditions using a luminescence Leica DM 5000 microscope at $\times 200$ – 1000 magnification. Small numerous forms were taken into account in 50–100 fields of vision; the rest, during complete examination of the preparation. Duplicate samples with a volume of 500 mL and also fixed by 3.6% glutaric dialdehyde solution were treated in Nozhotte chambers (volume 0.045 mL). The samples were preliminarily concentrated with excess water removed through a tube covered by a 5×5 - μm nylon mesh. The sample concentrate was examined completely under a light Carl Zeiss Axio Imager D1 microscope at $\times 400$ magnification. The volume of cells was calculated based on the corresponding stereometric figures. The algal biomass was recalculated to carbon equivalent according to their volumes [31].

The intensity of surface irradiation was measured using an LI-190SA incident radiation sensor (LI-COR) in the PAR range. The measurement results were integrated in the LI1400 block over 5-min intervals (mole photon m⁻²) during the whole day. Later on, as the primary production was being determined, these indices were used to calculate the integer value of incident radiation both for the exposure time of the experimental vials and for the whole daytime period for a particular date.

The rate of primary production was calculated experimentally by the radiocarbon method [4]. The NaH¹⁴CO₃ solution was placed in 50-mL vials containing water samples. The vials were exposed by imitated light and temperature conditions in a laboratory incubator with adjustable LED lighting [5, 10]. The incubation temperature, which conformed to the temperature at the sampling point, was maintained with a

laboratory HAILEA-100 chiller and an EHEIM pump for water pumping. The irradiance level was assigned for each vial by the adjusted value of direct current flowing through an LED [10]. Since the ice cover in the study area was not solid (there were frequent segments of open water with different areas), each sample was exposed at two irradiance values at its collection point: under open water conditions (250 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) and under ice conditions (20 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) [13, 36].

The chl *a* concentration was measured fluorometrically [25]. The 0.5–1 L water samples were filtered through Whatman GF/F glass microfiber filters at ≤ 0.3 atm. Then, the filters were placed in a 90% acetone solution and exposed to darkness at +4°C for 24 h. Next, the fluorescence of extracts was determined with a MEGA-25 fluorimeter (Moscow State University, Russia). The fluorimeter was calibrated using the standard chl *a* solution (Sigma).

The fluorescence parameters of chl *a* were also determined with a MEGA-25 PAM-fluorimeter. Measurement of the ratio of chlorophyll fluorescence intensity under exciting light that saturates photosynthesis (maximum yield of fluorescence, F_m) and during weak flashes of exciting light (minimum yield of fluorescence, F_o) for phytoplankton exposed to darkness makes it possible to determine the efficiency of primary photosynthesis processes (F_v/F_m) by the formula $F_v/F_m = (F_m - F_o)/F_m$ [27]. The relative variable fluorescence F_v/F_m is the maximum quantum yield of photosystem II, which serves as a measure of the potential photosynthetic capacity of phytoplankton. The fluorescence parameters of the photosyn-

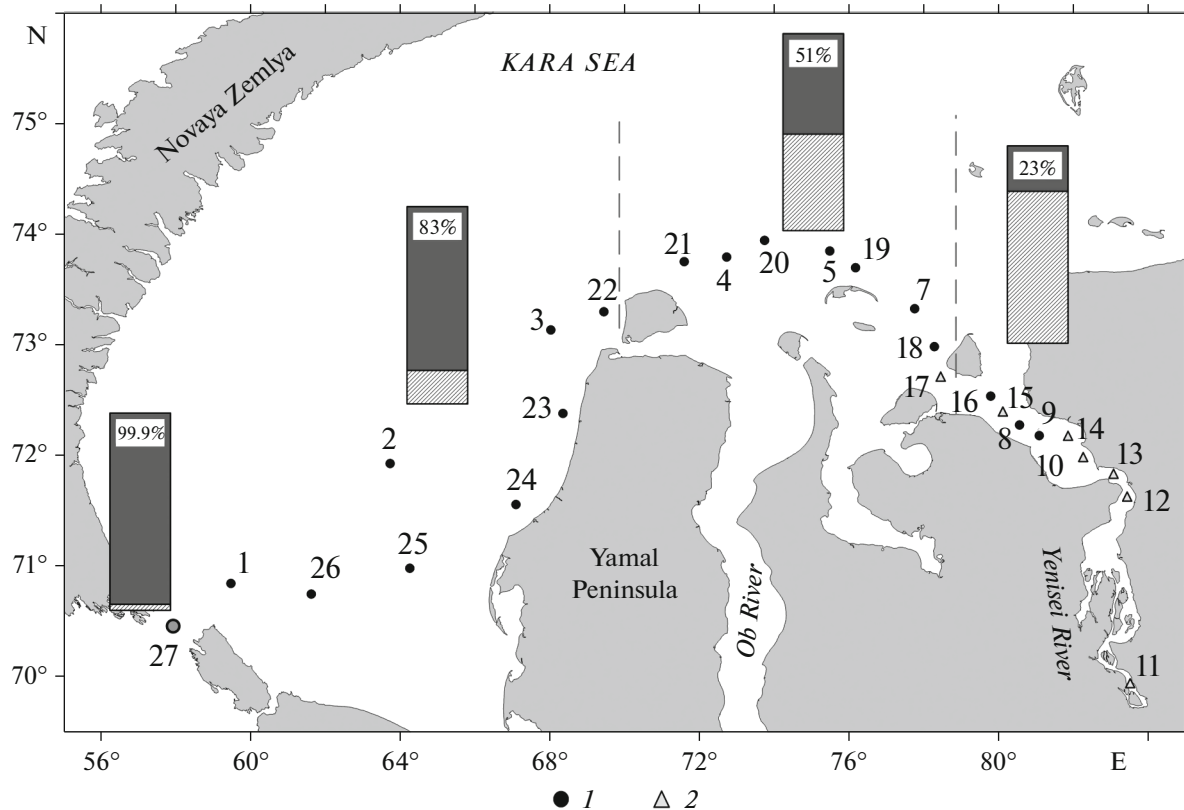


Fig. 1. Map of sampling area in three areas of southwestern Kara Sea (March–April 2016, vessel *Norilsk Nickel*), and mean values of share (%) of phototrophic (shaded) and heterotrophic (cross-hatched) algae in phytoplankton biomass in three areas of the southwestern part of the Kara Sea (boundaries of areas where averaging was performed are shown by dashed line): 1, stations where samples were collected to determine hydrophysical and hydrochemical parameters and to analyze structural and functional characteristics of phytoplankton; 2, stations where samples were collected to determine hydrophysical and hydrochemical parameters.

thetic system of phytoplankton F_0 and F_v/F_m were measured in samples exposed to darkness for 1 h.

To evaluate the current state of phytoplankton and its adaptation to light, the light curves method was used, according to which the effective quantum yield of photosystem II (Φ_{PSII}) is measured as a function of irradiance [18, 34]. A phytoplankton sample was divided into five subsamples, and each of them was exposed to different irradiance levels (0–500 $\mu\text{mole photon m}^{-2} \text{s}^{-1}$), after which parameters F_t and F'_m were recorded; their ratio $\Phi_{PSII} = (F'_m - F_t)/F'_m$ expresses the photochemical efficiency of photosynthesis II of cells under natural irradiance. Using the values of the effective quantum yield (Φ_{PSII}) and the corresponding values of irradiance (E), the values of the relative of electron transport rate were calculated ($rETR = \Phi_{PSII}E \times 0.5$) [8, 27]. The plot of the rETR dependence on irradiance (light curve) was used to determine the maximum potential photosynthetic activity ($rETR_{max}$) and the corresponding optimal irradiance value (E_k) reflecting the level of light adaptation of phytoplankton. The $rETR_{max}$ value makes it

possible to quantitatively estimate the maximum possible rate of solar energy conversion to cellular chemical energy, which ensures organic matter biosynthesis processes by phytoplankton.

RESULTS

The range of variations in all hydrophysical and hydrochemical parameters in the southwestern Kara Sea in late March–early April 2016 is given in [12]. Figure 2 shows the distributions of temperature, salinity, concentration, silicon, phosphates, and nitrates in the surface layer.

Most of the stations (19 of 27) are located in the sea zone (from station 27 in the west to station 16 in the east) with a salinity from 24.3 to 35.4 PSU (mean value 31.4 ± 2.8 PSU) and temperature from -1.31 to -1.94°C (mean value $-1.71 \pm 0.20^\circ\text{C}$). Four stations (stations 8, 9, 10, and 15) are found in the freshened estuary of the Yenisei River with salinity ranging from 2.6 to 14.8 PSU (mean value 7.14 ± 5.5 PSU) and temperature of -0.11 to -0.80°C . The next four stations (stations 11–14) are located in the Yenisei River with a salinity of 0.1–1.8 PSU (mean value 0.9 ± 0.7 PSU)

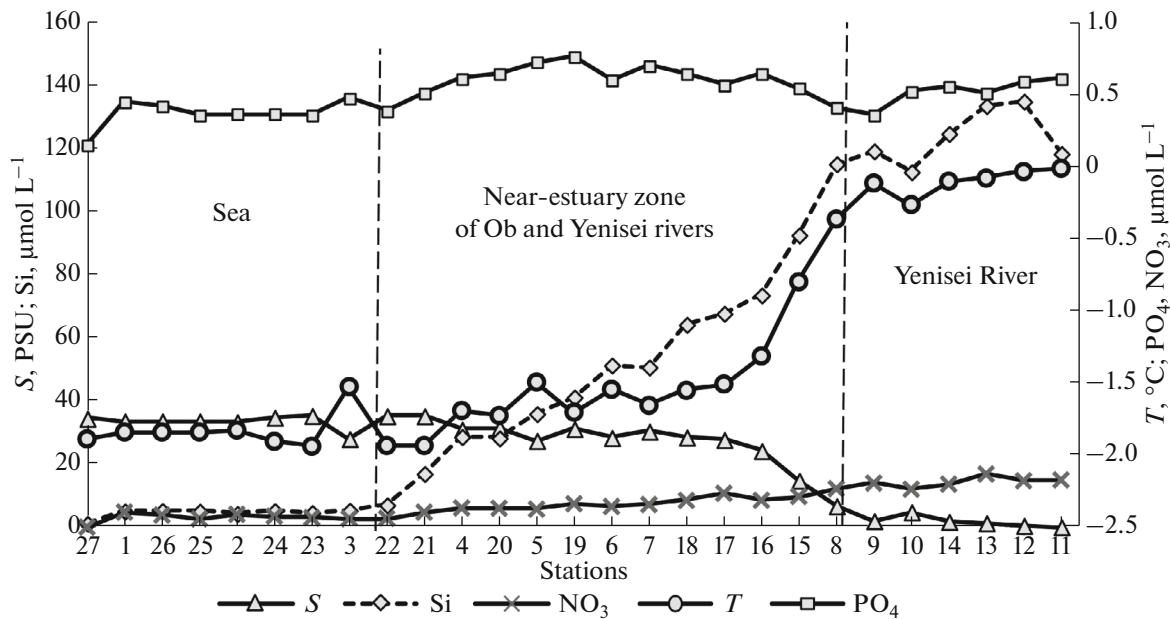


Fig. 2. Distribution of temperature (T , °C), salinity (S , PSU), silicate concentration (Si , $\mu\text{mol L}^{-1}$), phosphates (PO_4 , $\mu\text{mol L}^{-1}$), and nitrates (NO_3 , $\mu\text{mol L}^{-1}$).

and temperature from -0.01 to -0.10°C (mean value $-0.05 \pm 0.04^\circ\text{C}$).

The silicon concentration in waters west of the Yamal Peninsula varied from 1.17 to $7.08 \mu\text{mol L}^{-1}$. It considerably increased near the estuaries of the Ob and Yenisei Rivers (28.74 – $73.66 \mu\text{mol L}^{-1}$) and in river waters (92.73 – $135.13 \mu\text{mol L}^{-1}$). The content of nitrates in all studied regions was very low (0 – $0.12 \mu\text{mol L}^{-1}$). The concentrations of nitrates in waters west of the Yamal Peninsula varied from 2.65 to $4.78 \mu\text{mol L}^{-1}$ and, similarly to silicon, increased near estuaries (5.69 – $10.75 \mu\text{mol L}^{-1}$) and in river waters themselves (9.74 – $16.84 \mu\text{mol L}^{-1}$). The concentration of phosphates varied from 0.36 to $0.77 \mu\text{mol L}^{-1}$, almost not differing by regions.

In the area of the Kara Gates Strait (station 27), the contents of phosphates and silicon were the lowest (1.17 and $0.15 \mu\text{mol L}^{-1}$, respectively), and there were no nitrites or nitrates at all.

In the surface layer of the Kara Sea, the chl a concentration varied from 0.08 to 3.22 mg m^{-3} , 0.62 mg m^{-3} on average (Table 1). In the area of the Karskiye Vorota Strait, the chl a concentration increased by more than an order of magnitude. In seawater, the average share of pheophytin was 41% of the total chlorophyll and pheophytin (the variation range was 1–73%). In the estuary zone of the Yenisei River (stations 8, 9), the share of pheophytin reached 97% at very low chl a concentrations (0.12 – $0.22.0 \text{ mg m}^{-3}$). The maximum chl a values were determined at stations 3, 21, and 27; they exceeded the values at the rest of the stations by an order of magnitude.

The mean value of primary production was $0.42 \text{ mg C m}^{-3} \text{ day}^{-1}$ (with variation from 0 to $1.92 \text{ mg C m}^{-3} \text{ day}^{-1}$) in ice-covered water areas and was greater by a factor of 4: $1.79 \text{ mg C m}^{-3} \text{ day}^{-1}$ (with variation from 1.01 to $3.46 \text{ mg C m}^{-3} \text{ day}^{-1}$) in ice-free areas (Table 1). The exception was the area of the Karskiye Vorota Strait (station 27), where the level of primary production increased by more than a factor of 25. The primary production decreased in ice-free water areas (stations 22, 23, 25, 26, and 27) from station 27 to station 25 and further varied insignificantly at stations 22 and 23. In this case, the assimilation number (AN, the chlorophyll-specific primary production) varied by a factor of 2. The share of pheophytin monotonically increased at these stations, indicating a gradual decrease in potential chl a activity. In ice-covered water areas, the maximum value of primary production was determined in surface waters at station 21 in near the estuary of the Ob River. Here, at the closest station 4, the primary production had a zero value at very low chl a concentrations. In the western Kara Sea (stations 1–3), the subglacial primary production was higher than in the other studied regions covered with ice (0.48 – $0.60 \text{ mg C m}^{-3} \text{ day}^{-1}$). The share of pheophytin dropped to the minimum (about 1%) at stations 2 and 3, and high values (over 50%) were reached in the zone near the estuary of the Ob and Yenisei Rivers.

In the study period, solar irradiation (in the PAR range) varied on the sea surface from 9.44 to $14.62 \text{ mol photons m}^{-2} \text{ day}^{-1}$, amounting to $12.12 \pm 2.43 \text{ mol photons m}^{-2} \text{ day}^{-1}$ on average.

The value of relative variable fluorescence (F_v/F_m) was at a level of 0.50 ± 0.01 (variation range of 0.32–0.63) at all stations in the sea and estuary zones (except for station 4) and at two stations of the river zone (stations 15, 16). Considering that the highest possible value of this dimensionless value is 0.8 [38], it is evident that the potential photosynthetic activity of phytoplankton in the Kara Sea was rather high in late March–early April 2016. At station 4 in the estuary zone and in the river water, chlorophyll fluorescence was zero. The level of optimal irradiance (E_k), showing light adaptation of phytoplankton, varied from 53 to 264 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$. Irradiance under the ice was estimated at a level of 20 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$. It is evident that despite the ice cover, the phytoplankton had adapted to a high level of irradiance corresponding to ice-free water conditions.

In the study period, the phytoplankton quantity in the surface waters of the southwestern Kara Sea varied significantly between stations: 85–1054 cells mL^{-1} , 350 cells mL^{-1} on average. The total algal biomass varied from 0.8 to 110.7 mg C m^{-3} with an average value of 10.6 mg C m^{-3} .

The Karskiye Vorota Strait area (station 27) differed from the other water areas not only in the high level of primary production, but also in a very large quantity (2463 cells mL^{-1}) and biomass (458 mg C m^{-3}) of phytoplankton, which is the maximum value obtained in this period of the year. The base of the phytocenosis here was formed by several *Thalassiosira* species dominated by *T. hyalina*, as well as *Fossula arctica* and *F. glacialis*. A considerable contribution to the biomass and production of autotrophic phytoplankton was made by cells of *Phaeocystis pouchetii* as part of the colonies (26 mg C m^{-3} without taking the matrix into account). In this case, the colony size was 8550 L^{-1} with an average diameter of 130 μm . The role of heterotrophic algae was negligibly small in this area (96 cells mL^{-1} or 1.75 mg C m^{-3}), i.e., the quantity of autotrophic phytoplankton here was almost 100% (Fig. 1).

All data on the numbers, biomass, and species composition of phytoplankton can be divided into three groups: stations with a high developmental level of autotrophic algae (stations 3 and 27); stations where the phytoplankton numbers is not large, but autotrophic organisms are in the majority (stations 1, 2, 4, 5, 18, 21, 23–26); and stations dominated by a heterotrophic component among algae (stations 7, 8, 14, 16, 19, 20, and 22).

In the western part of the studied water area, autotrophic algae were the most abundant at all stations. Their numbers varied from 52 to 556 cells mL^{-1} , and the biomass varied within 1.35–11.53 mg C m^{-3} , while the numbers and biomass of heterotrophic algae was 14–185 cells mL^{-1} and 0.31–1.27 mg C m^{-3} , respectively. Biomass of autotrophic algae increased to

108 mg C m^{-3} at station 3 due to *Fossula arctica* and biomass of heterotrophic algae increased insignificantly (2.93 mg C m^{-3}). The average shares of the phototrophic and heterotrophic algae in the phytoplankton biomass in the western part of the studied area were 94 and 6%, respectively (Fig. 1). The autotrophic algae were dominated by *Fragilariopsis oceanica*, *F. cylindrus*, *Thalassiosira* spp., *Rhodomonas salina*, *Dicrateria inornata*, *Pauliella taeniata*, *Nitzschia frigida*, and *Entomoneis palludosa*, which were likely to fall migrate to the water from the lower ice surface, as well as *Thalassionema nitzschioides*.

Heterotrophic algae were the most abundant in the estuarial zones of the Ob and Yenisei at all stations (4, 5, 7, 18, 19, 20, and 21); their concentration was (66–639 cells mL^{-1}). The autotrophic algae numbers were in the range 20–150 cells mL^{-1} . The heterotrophic phytoplankton dominated (by biomass) only at two stations (7, 20). At the stations 4, 19 the biomass of autotrophic and heterotrophic algae were approximately equal. At stations 5, 18, and 21, the biomass of autotrophic phytoplankton was higher. In general, in the estuarial zones of the Ob and Yenisei, the variation of autotrophic algae biomass was 0.62–11.33 mg C m^{-3} , and heterotrophic algae biomass was 0.55–3.92 mg C m^{-3} , with mean values of 4.04 and 1.79 mg C m^{-3} , respectively. The average ratios of biomasses were 69 and 31% for autotrophic and heterotrophic phytoplankton, respectively (Fig. 1). Among the autotrophs, flagellate *Taleaulax acuta* was dominant; *Navicula* spp., *Melosira arctica*, and *Pyramimonas marina* were also widespread.

In the river zone of the Yenisei, 1.5–2 μm autotrophic *Synechocystis* sp. and *Nannochloris atomus* were the most abundant phytoplankton at stations 8 and 14. Their numbers were 201–867 cells mL^{-1} . The heterotrophs numbers at these stations were 66–188 cells mL^{-1} . However, the heterotrophic algae dominated by biomass with 0.49–1.06 mg C m^{-3} , and the biomass of autotrophic phytoplankton was 0.31–1.03 mg C m^{-3} .

At station 16, heterotrophic phytoplankton dominated by numbers and biomass (145 cells mL^{-1} and 2.16 mg C m^{-3} , with a concentration of phototrophs of 19 cells mL^{-1} or 0.54 mg C m^{-3} , respectively). The average share of phototrophic and heterotrophic algae in the phytoplankton biomass in the Yenisei River zone were 34 and 66%, respectively (Fig. 1). In the river water, 1.5–3 μm flagellates dominated among heterotrophs.

DISCUSSION

Our data show that during the studies, the irradiance level (9.44–14.62 $\text{mol photons m}^{-2} \text{day}^{-1}$) was quite sufficient for the normal development of phytoplankton and was not limiting on the open water. The

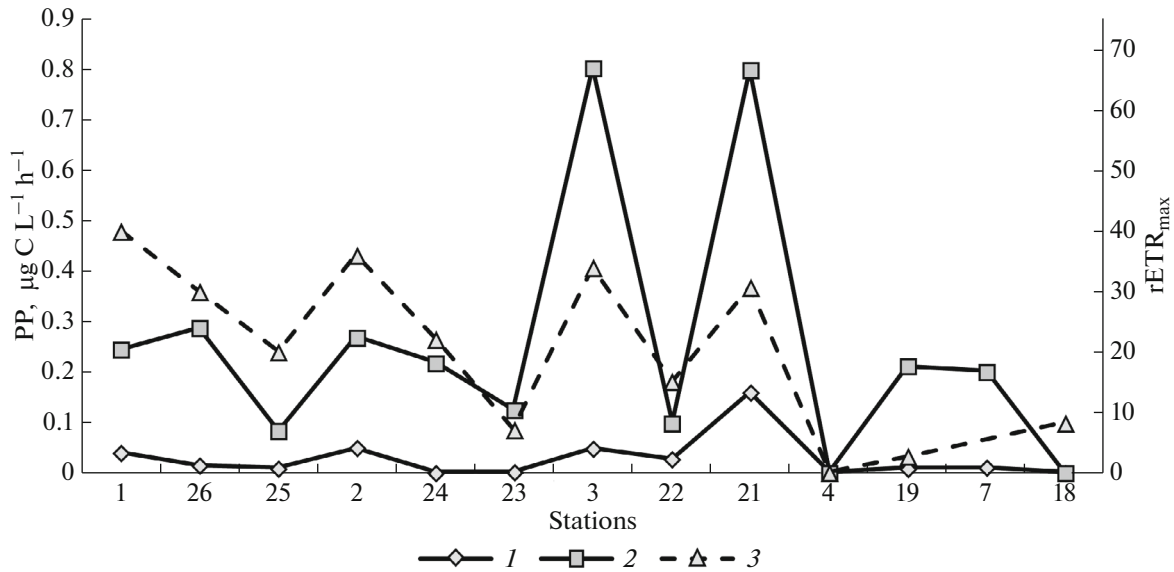


Fig. 3. Primary production (PP) under different light conditions. 1, PP value at irradiance of $20 \mu\text{mol photon m}^{-2} \text{s}^{-1}$ (beneath ice); 2, PP value at irradiance of $250 \mu\text{mol photon m}^{-2} \text{s}^{-1}$ (open water); 3, potential activity of primary photosynthesis processes at optimal irradiance (rETR_{max}).

daily average values of short-time solar activity ($222 \mu\text{mol photons m}^{-2} \text{s}^{-1}$) were much higher than the minimum necessary irradiance level for photosynthesis ($3\text{--}6 \mu\text{mol photons m}^{-2} \text{s}^{-1}$) [35]. According to the unique data, in the late-summer period (in September), the irradiance level in the Kara Sea was considerably lower, $4.0 \text{ mol photons m}^{-2} \text{day}^{-1}$ on average [11].

The values of relative variable fluorescence (F_v/F_m) at almost all stations were found at a level of $0.4\text{--}0.6$, which characterized very high quantum yield of phytoplankton photosystem II, i.e., potential activity of primary (light) photosynthetic processes. This indicates that at the end of March–early April, phytoplankton in the southwestern Kara Sea was in a physiologically active state even at a relatively low light conditions under ice.

As stated above, during the experimental determination of primary production, the light conditions were set at each station so that they imitated both natural under-ice irradiance ($20 \mu\text{mol photons m}^{-2} \text{s}^{-1}$) [13, 36] and open water conditions ($250 \mu\text{mol photons m}^{-2} \text{s}^{-1}$). This was done to determine the level of light needs for phytoplankton. The experimental results showed that at most of the stations covered by ice during the studies, primary production would increase by a factor of 12 on average in the ice-free waters (at a higher irradiance level) (Fig. 3). This agrees quite well with the above physiologically active state of phytoplankton in terms of the quantum yield of photosystem II (F_v/F_m). In addition, Fig. 3 shows that the rETR_{max} values reflecting the potential activity of primary photosynthetic processes at optimal irradiance correlated highly with the primary production values under similar irradiance. Note that the optimal irradiance determined by the light curves

for primary photosynthetic processes in phytoplankton taken from under-ice water almost coincided with the level of actual irradiance on open water. It is apparent that in this period, the phytoplankton of the southern Kara Sea, being primarily beneath ice, was nevertheless potentially ready to use light energy more actively and to form primary production at both levels of the primary and secondary stages of photosynthesis. This means that during study, the primary production was limited by a low irradiance due to dense ice cover. Although the southwestern Kara Sea is usually covered with ice for 8–9 months, the wind causes the formation of ragged polynyas, which are stable areas of ice-free water among the drifting ice bounded from the south by a floe [6]. We demonstrated that the primary production was greater by a factor of 4 exactly in ice-free water areas than in the ice-covered one. In addition, the periodic increase in irradiance in the case of polynyas or open water segments due to wind action in this area can result in higher values of under-ice primary production compared to other sea areas. In this case, the potential activity of primary photosynthetic processes with optimal irradiance (rETR_{max}) was maximum at stations 1–3.

At all stations in the Kara Sea, the phosphate (P), total inorganic nitrogen (N), and silicate (Si) concentrations in the surface layer was higher than the limiting level. At low temperature, the limiting levels for primary production of the major nutrients are $0.5 \mu\text{mol L}^{-1}$, $2 \mu\text{mol L}^{-1}$, and $2 \mu\text{mol L}^{-1}$ for P, N and Si, respectively [3, 22]. Thus, the nutrient concentrations in surface waters could not be a factor limiting the development of phytoplankton in the sea and estuary biotopes late March–early April.

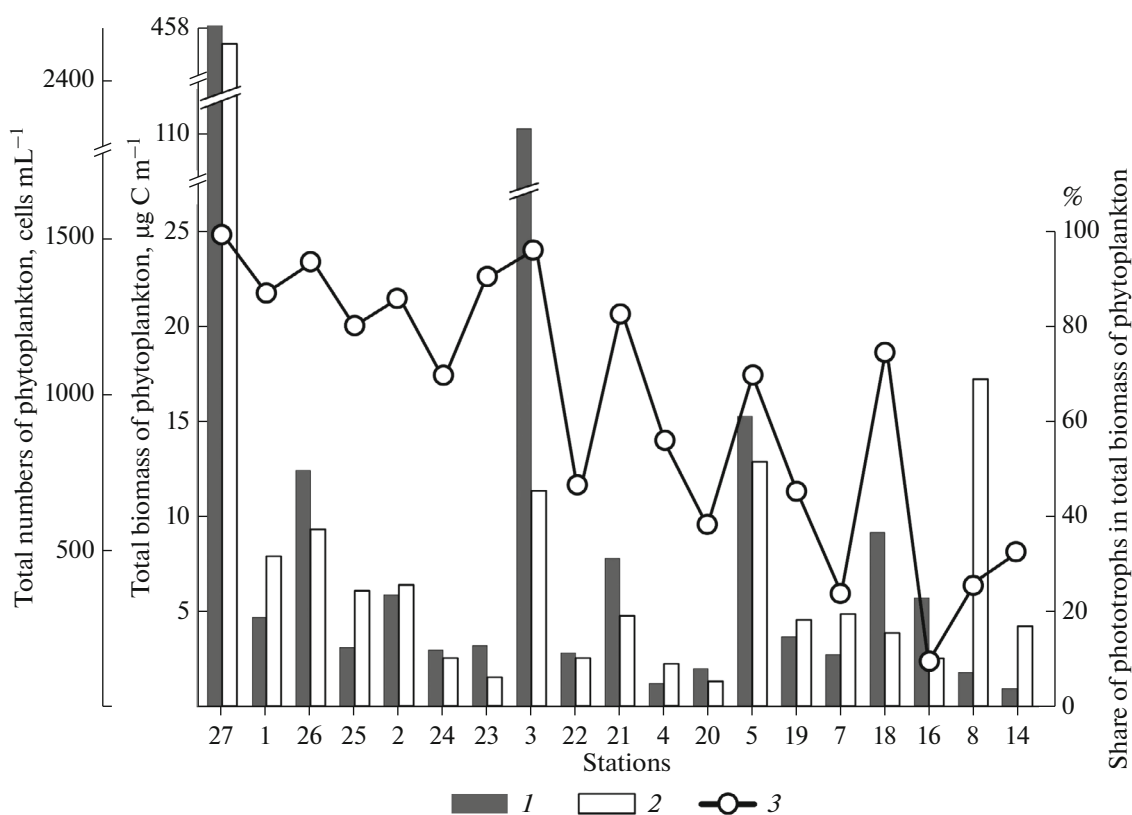


Fig. 4. (1) Total numbers and (2) total biomass of phytoplankton and relative contribution of phototrophic algae to (3) total phytoplankton biomass in southwestern Kara Sea in March–April 2016.

Silicate concentrations were low (less than $7 \mu\text{mol L}^{-1}$) in the southwestern Kara Sea with a salinity greater than 33 PSU, that is in the absence of the influence of river runoff. In the near-estuary zone opposite the estuaries of the Ob and Yenisei rivers with a slightly decreasing salinity (27–31 PSU), the silicate concentrations increased to 28–67 $\mu\text{mol L}^{-1}$, which was caused by the influence of river waters. The river zone was characterized by very high silicate concentrations (higher than $115 \mu\text{mol L}^{-1}$) and almost fresh water.

Among the potentially limiting chemical elements, N and Fe are acknowledged to play a key role in limiting oceanic primary production [21, 30]. The role of Fe as a limiting element has been well studied in waters with a high nutrient content and low chlorophyll concentration in the subtropical North Atlantic [32].

In our study, we verified the hypothesis on the potential Fe limitation of primary production in the southwestern Kara Sea in spring. The Fe concentrations in surface waters at stations with high and low levels of phytoecenotic development (station 3, 20, and 24) were 40–50 $\mu\text{g L}^{-1}$. The previous studies of the influence exerted by Fe additives on the function of phytoplankton activity showed that the limiting Fe concentrations in different oceanic areas and for a different state of phytoplankton were in range 0.022–

$0.112 \mu\text{g L}^{-1}$ [17, 19, 28]. It is evident that in our case, Fe compounds did not limit phytoplankton development.

In winter, the under-ice water temperature in the the open sea area is usually -1.8 to -1.5°C or it decreases even more down to freezing for a given salinity [6]. According to our data, the temperature of surface water corresponded exactly to the freezing temperature, which also does not promote the primary production.

The major cause for the different occurrence of hydrophysical and biogeochemical processes determining the conditions for the development and functioning of phytoplankton communities in the Kara Sea is a non-uniform influence of river runoff on areas at different distances from the Ob and Yenisei estuaries [33]. The surface salinity and dissolved silicate concentrations coming in with fresh waters can be used to determine the degree of river runoff influence on this sea area. Thus, these indices can be used to zone the studied water area: the sea zone, the estuary zone of the Ob and Yenisei, and the river zone of the Yenisei (Fig. 4).

Phytoplankton was represented by phototrophic forms in most of the studied areas of the Kara Sea. However, examination of variations in the ratio of phototrophic and heterotrophic algae in phytoplankton showed a distinct trend toward a decrease in the share of autotrophic organisms from the Karskiye

Vorota Strait to the Yenisei (Fig. 4). The zoning of the studied water area into the sea zone, the estuary zone of the Ob and Yenisei, and the river zone of the Yenisei reveals even more interesting tendencies.

Phytoplankton from the sea (southwestern) zone is represented mostly by phototrophic algae with an average share of 94% (Fig. 1), which varied insignificantly (70–99%). The mean value of primary production in this area was $1.1 \text{ mg C m}^{-3} \text{ day}^{-1}$ and the average concentration of chl *a* was 0.393 mg m^{-3} .

In the near-estuary zone, the ratio of phototrophic and heterotrophic algae varied very strongly at the stations (the share of phototrophs was 23–82%), reflecting high dynamics and spatial variability of the medium in the area of mixing of river and sea waters. Here, primary production also varied at the stations, but the values were very low (up to zero). The exception was station 21, where the primary production in the surface layer beneath the ice reached relatively high values, which was likely determined by very high chl *a* concentrations. In this zone, the mean value of primary production was $0.43 \text{ mg C m}^{-3} \text{ day}^{-1}$ and the average chl *a* concentrations was 0.602 mg m^{-3} .

The river zone was dominated by heterotrophic algae: their share was 55–80%. The concentration of chl *a*, as well as the total phytoplankton biomass, was extremely low here, and the share of pheophytin was 97%. Chl *a* fluorescence was almost absent. In this zone, the average chl *a* concentration was 0.015 mg m^{-3} . All this indicates the rather low effect of phototrophic phytoplankton in river waters and its complete inactivation during this period. The typical summer–fall dominant species *Aulacoseira* spp. was absent even in samples.

In contrast to early spring, there is an opposite pattern in the late summer and fall periods: compared to sea areas, river waters and the near-estuary zone of the Ob and Yenisei Rivers are characterized by the most abundant diatomic phytoplankton, represented primarily by *Aulacoseira* spp., as well as large values of biomass, chl *a*, and primary production [9, 11, 15, 29].

Station 27, which is located in the area of the Karskiye Vorota Strait, i.e., under the great influence of Barents Sea waters, greatly differed from the other stations in the adjacent area of the Kara Sea. At this station, the phytoplankton biomass exceeded the same averaged index for the Kara Sea stations by almost a factor of 40. The share of phototrophic algae was almost 100% of the total phytoplankton biomass; both dinophyte and haptophyte algae showed a high level of development. The chl *a* concentrations increased by almost a factor of 10 with an almost complete absence of pheophytin. Primary production at this station was greater by a factor 100 than at the other Kara Sea stations; in this case, the concentrations of major nutrients approached zero values. The values of optimal irradiance E_k and $rETR_{max}$ were also higher (by factors of 2 and 3, respectively).

It is evident that in the southwestern Kara Sea in late March–early April, phytoplankton is already active and has a high potential photosynthetic capacity that is restrained by light deficit beneath ice. In this case, neither nutrients nor iron are limiting factors. At the same time, at the boundary with the neighboring Barents Sea, there are optimal conditions for the active growth and functioning of phytoplankton up until its bloom. A distinctive characteristic of this area was the complete absence of ice cover in this period, which created favorable light conditions for the active development of phytoplankton. In the Karskiye Vorota Strait, against the background of an intense diatomic algae bloom, a *Phaeocystis pouchetii* bloom developed, which was recorded in the Kara Sea and adjacent areas of the Barents Sea for the first time. The size of colonies reveals that the *Phaeocystis pouchetii* bloom has not yet reached its maximum. Now we can only state that we still know little about the triggering mechanisms of intense functioning of particular algal groups in the Kara Sea. According to an oral report made by the participants of the vessel *Norilsk Nickel* cruise in February of the same year, marine phytoplankton started to develop as early as the end of February at the lower ice edge. The algae are also likely to develop in subglacial water, patchily, and this considerably depends on the concentration of the ice cover restraining penetration of light.

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