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MARINE BIOLOGY

Seasonal Variation of the Satellite-Derived Phytoplankton Primary Production in the Kara Sea

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Abstract—Seasonal variation of the integrated primary production (IPP) and surface chlorophyll (Chl_0) in different regions of the Kara Sea was studied from satellite data obtained by the MODIS-Aqua colour scanner and averaged for 2003–2015. The minimum variation of Chl_0 concentration during the growing season (from April to October) was 1.5 times in southwestern region and 2 times in the northern region of the sea. It was found that the Chl_0 concentration increased slightly in all regions by the end of the growing season. The maximum IPP value recorded in June coincided with the peak level of photosynthetically active radiation (PAR) and maximum river discharge. The IPP value varied in a wider range compared with the Chl_0 concentration. The ratio of the maximum and minimum monthly average IPP values varied from 8.9 times in Southwestern region to 11.7 times in the Northern region of the sea. The average increase in the Chl_0 concentration was 1.7 times (from 0.78 mg/m^3 in April to 1.29 mg/m^3 in October). The IPP value varied by a factor of 10.7 (from 26 mg C/m^2 per day in October to 279 mg C/m^2 per day in June). The article also discusses the influence of water column stratification, the concentration of nutrients, the PAR level, and river discharge on the seasonal IPP dynamics in the Kara Sea.

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INTRODUCTION

Seasonal variations in the primary production (PP) are a key factor in the transformation of biomass and energy in food chains during the year [53]. Therefore, the seasonal dynamics of this parameter is the basic subject in trophodynamics studies. Another important subject is the impact of long-term changes on the integrated primary production (IPP) dynamics. For example, global climatic changes observed over the last decades must have influenced the patterns of seasonal dynamics of production parameters of phytoplankton [20, 33, 41, 44, 76]. In addition, the investigation of global and regional factors involved in these seasonal changes will help to determine the annual IPP values, which is one of the basic problems in ocean biogeochemistry [15, 18, 54, 78].

The developmental cycle of phytoplankton differs between latitudinal zones [29, 53, 55, 79, 80]. The main element of this cycle is phytoplankton bloom; the onset, duration and intensity of this process depend greatly on the trophic status of a waterbody [19, 28, 69]. Phytoplankton bloom in the pelagic zone of Arctic seas, which leads to an increased level of PP and biomass, starts when the ice cover melts after winter. This process is contributed by stable water column stratification and a sufficient amount of photosynthetically active radiation (PAR) and nutrients [24, 49, 67, 71, 73]. Phytoplankton bloom can start from April to September. In northern areas it usually starts closer to the end of the growing season than in the southern areas; its duration is usually within one month [81].

In addition to general trends typical of the Arctic region, each area seems to have a specific pattern of seasonal PP dynamics due to differences in the hydrological regimens. It can be assumed that changes in the production parameters of phytoplankton in the Kara Sea must depend greatly on the intense influence of continental, particularly, river discharge, and on the shallowness of this sea [22, 58].

Field studies of PP in the Kara Sea were performed from August to October [1, 2, 11, 12, 30]. Therefore, the production parameters of phytoplankton have not been measured throughout the entire growing season in the Kara Sea, which starts in April and ends in October (approximately 214 days). By now, studies on the seasonal dynamics of PP in the Kara Sea can only be based on satellite data due to bad climatic conditions in this area for the better part of the year, which make field studies impossible. Previously, satellite data have been used to study the seasonal dynamics of PP in this area in order to determine its annual rates [3, 4, 17, 46]. However, in these studies the IPP data were obtained using nonregionally adapted models or based on only concentration of chlorophyll *a*. Meanwhile, the models used in such studies can be improved by adjusting them

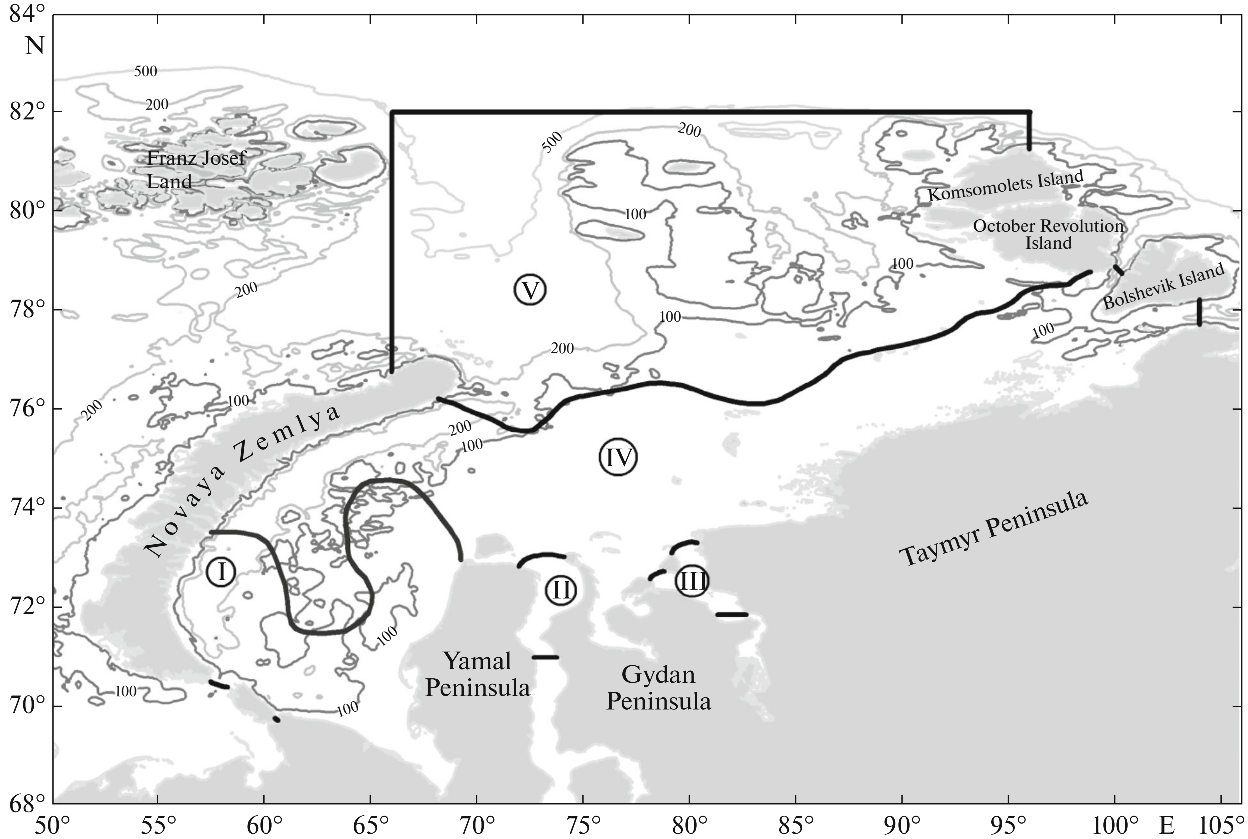

Fig. 1. Kara Sea sub-regions for measurement of seasonal changes in PP rate. I—Southwestern region, II—Ob estuary, III—Yenisei estuary, IV—River runoff region, V—Northern region. Boundaries of the Kara Sea are established according to [46]. The boundaries of the regions I, IV, and V are established according to average long-term annual location of 25 psu isohaline [30, 64] with modifications [8]. Northern boundaries of estuaries correspond to average long-term location of 10 psu isohaline [30]; southern boundaries approximately correspond to distribution of fresh waters.

to different regions and by including parameters for photoadaptation to PAR [48, 52].

The region-specific Kara Sea IPP and Chl algorithms were developed in recent studies [7, 10]; these algorithms can be used to determine the primary production based on satellite data. We also suggest that the most contrasting areas of the Kara Sea, such as the estuaries of the Ob and Yenisei and northern parts of the St. Anna and Voronin troughs, can have some other pattern and amplitude of the PP dynamics. Therefore, investigation of the seasonal IPP dynamics in these areas is of interest.

Thus, the aims of this study were as follows: (1) to describe the seasonal IPP and chlorophyll *a* variations in different areas of the Kara Sea using regional models and satellite data, and (2) to estimate the influence of abiotic factors on the seasonal IPP dynamics.

MATERIALS AND METHODS

Field data. The regional models of the IPP and Chl concentration were developed and verified using data sets obtained during expeditions to the Kara Sea from the end of August until the beginning of October [2, 7, 10–12, 30]. The values for these months were derived from field data obtained during the expeditions. The values for other months were derived from different databases created from the 1930s to 2016 [6, 16]. The integrated database was used to determine the values of seasonal changes in surface temperature (T_0), salinity (S_0), and concentrations of the main nutrients.

Kara Sea subregions. The boundaries of the Kara Sea were determined from the results of previous IPP studies in the Arctic region [46]. Based on the classification of water masses (WMs) described in [64] and zoning approaches for the Kara Sea [30], we divided the studied area into the following regions: the southwestern zone (I), the estuaries of the Ob (II) and Yenisei (III), the river runoff zone (IV), and the northern zone consisting of the St. Anna and Voronin troughs (V) (Fig. 1). The southern boundary of the river runoff zone coincided with the long-term average 25 psu isohaline [64] in surface waters, which was used in [30], was adjusted based on the location of a quasi-stationary freshwater lens near Novaya Zemlya [8].

Satellite data. We used the L2 level data obtained by the Moderate Resolution Imaging Spectroradiometer (MODIS- Aqua) from 2003 until 2015 presented on the website of the National Aeronautics and Space Administration (NASA) www.oceancolor.gsfc.nasa.gov/. The data were processing using the software developed at the Shirshov Institute of Oceanology, Russian Academy of Sciences [70]. The water-leaving reflectance $R_{rs}(\lambda_i)$ values were used to calculate the surface chlorophyll concentration (Chl_0) with an algorithm developed for the region [10].

The PAR values were derived as a standard product of the MODIS- Aqua [35]. As mentioned in this study, the model values of PAR were higher than the measured values. The analysis of PAR in the Kara Sea also showed the overestimation of the satellite values of this parameter. The average ratio of measured and satellite values was 0.64 ($N = 30$; $cv = 20\%$). Based on this ratio, we used this value as the correction coefficient for satellite PAR.

Files with temperature data (Optimum Interpolation Sea Surface Temperature, OI SST) with a spatial resolution of 0.25° × 0.25° averaged for each day were downloaded from ftp://ftp.solab.rshu.ru/data/allData/OISST-AVHRR-AMSR-V2. These files were created with data obtained by Advanced Very High Resolution Radiometer (AVHRR) deployed on the satellite of the National Oceanic and Atmospheric Administration (NOAA), as well as shipboard and weather buoys data [66].

The area covered by ice was calculated by software described in [70] using the primary data presented by the National Snow and Ice Data Center at ftp://sidads.colorado.edu/pub/DATASETS/NOAA/G02202_v2/north/daily [27].

Region-specific models of primary production and chlorophyll. We used the following coefficients in the regional-specific model of IPP in the Kara Sea [7]: (1) average values of the solar energy utilization coefficient for the area:

$$\psi = \mathrm{DAN_m}/I_0, \tag{1}$$

where $\mathrm{DAN_m}$ is the averaged daily assimilation number in the photosynthetic layer (mg C/mg Chl$a$) and I_0 is daily subsurface PAR (Ein/m^2) [34]; and (2) the coefficient of vertical distribution of Chl$a$:

$$k = \mathrm{Chl_{ph}}/\mathrm{Chl_0}, \tag{2}$$

where $\mathrm{Chl_{ph}}$ is the integrated concentration of Chl in photosynthetic layer and $\mathrm{Chl_0}$ is its surface concentration [21]. The geometric mean of $k \times \psi$ for the Kara Sea is 8.27 [7].

The input parameters are the $\mathrm{Chl_0}$ concentration and incident PAR (I_0). These parameters can be measured relatively easily in the field. Thus, the final equation based on Eqs. (1) and (2) and the $\mathrm{Chl_0}$ and I_0 values is

$$\mathrm{IPP} = 8.27 \times \mathrm{Chl_0} I_0. \tag{3}$$

The standard algorithm of the MODIS- Aqua overestimate of $\mathrm{Chl_0}$ concentration values in case II waters [47]. In order to avoid large bias of the IPP, we determined a regional-specific algorithm for calculating $\mathrm{Chl_0}$ [10], where the best correlation of predicted and measured values of Chl a concentrations ($R^2 = 0.47$; $N = 185$) was obtained using the ratio $R_{rs}(531)/R_{rs}(547)$:

$$\ln(\mathrm{Chl_0}) = -3.66\ln(R_{rs}(531)/R_{rs}(547)) + 0.116. \tag{4}$$

RESULTS

During the growing season (from April to October), the $\mathrm{Chl_0}$ concentration varied by a factor of 1.5 in the southwestern region and by a factor of 2 in the northern region. Meanwhile, the $\mathrm{Chl_0}$ concentration tended to increase in all areas of the Kara Sea by the end of the growing season (Table 1). The IPP values varied in a wider range. The ratio of the maximum to minimum monthly average rate of IPP changed by a factor of 8.9 in the southwestern region and by a factor of 11.7 in the northern region. In general, the $\mathrm{Chl_0}$ concentration in the Kara Sea in creased by a factor of 1.7: from 0.78 mg/m^3 in April to 1.29 mg/m^3 in October. The mean IPP value increased by a factor of 10.7: from 26 mg C/m^2 per day in April to 279 mg C/m^2 per day in October (Table 1).

The minimum monthly average values of $\mathrm{Chl_0}$ concentration were observed in the northern region in April (0.67 mg/m^3); the maximum values were observed in the Ob estuary in August (1.89 mg/m^3). The monthly average IPP values in the entire area of the Kara Sea increased beginning from April, reached a peak in June, and gradually decreased until the end of the growing season (Fig. 2). The maximum monthly average IPP values varied from 185 mg C/m^2 per day in northern areas to 471 mg C/m^2 per day in the Ob estuary (Table 1). The highest values were observed in southwestern and northern regions and in the Enisei estuary in June (Figs. 2a, 2c, 2e). The monthly average IPP values in the Ob estuary were the same (471 mg C/m^2 per day) in June and July (Fig. 2b); nearly the same values were observed in the river runoff region (Fig. 2d) in May, June, and July (Table 1).

Figure 3 shows the seasonal dynamics of PAR, surface water temperature (T_0), and the area of ice cover (S). The general pattern of changes in PAR and T_0 was similar in all areas. The maximum values of PAR were recorded in June, and the minimum ones were recorded in October. The temperature maximum shifted from the PAR maximum values. In all areas of the Kara Sea, the maximum temperature values were recorded in August, except for the Yenisei estuary, where it was a little higher in September. The area of ice cover decreased in all areas from April to September and then increased beginning from October (Fig. 3).

Table 1. Seasonal dynamics of IPP and chlorophyll concentration in different areas of the Kara Sea

Month	Area											
	Southwestern region		Ob estuary		Yenisei estuary		River runoff region		Northern region		Kara Sea	
	Chl_0	IPP	Chl_0	IPP	Chl_0	IPP	Chl_0	IPP	Chl_0	IPP	Chl_0	IPP
April	0.74	94	1.12	–	0.86	–	0.90	212	0.67	100	0.78	109
May	0.83	234	1.17	–	0.91	237	0.83	297	0.72	221	0.80	251
June	0.93	268	1.58	471	1.49	421	0.98	305	0.75	246	0.89	279
July	0.94	237	1.87	471	1.58	364	1.08	276	0.74	185	0.93	235
August	0.89	164	1.89	340	1.68	310	1.10	185	0.77	118	0.94	156
September	0.92	85	1.77	153	1.68	146	1.10	83	0.90	47	1.00	69
October	1.11	30	1.65	47	1.44	41	1.29	27	1.40	21	1.29	26

Note. We used average long-term (2003–2015) values of Chl *a* concentration in surface waters (Chl_0, mg/m^3) and integrated PP (IPP, mg C/m^2 per day).

DISCUSSION

The pattern of seasonal IPP dynamics in the Kara Sea, which was investigated with the use of satellite data obtained in 2003–2015, is generally similar to the dynamics of these parameters in other areas of the Arctic Ocean [24, 49, 67, 71, 73]. The dynamics of the production parameters is known to depend greatly on the processes of ice cover melting and changes in the PAR, the concentration of nutrients, and water column stratification [72]. Other factors in seas with river discharge include the flow of allochthonous nutrients, as well as suspended and dissolved organic matter (POM and DOM), which depend on the time of the spring thaw and its intensity [42, 51]. An analysis of different abiotic factors and their effects on the seasonal IPP dynamics in the Kara Sea is presented below.

As can be seen in Fig. 3, the majority of the Kara Sea is covered by ice from the end of October until the middle of April. Due to this and the large number of overcast days, satellite data cannot be obtained for most of the area in October and April. Therefore, the values of the production rate at the beginning and end of the growing season cannot be derived without extrapolation of available data to ice-free areas covered by clouds.

According to the classical concept of seasonal dynamics of production parameters in seas covered by first-year ice, the growing season in such areas starts soon after ice breakup, and phytoplankton bloom can be observed near the ice edge, in ice fractures, and glades [65 and references therein]. Phytoplankton bloom is initiated by water column stratification (caused by ice melting and the seasonal increase in temperature), elevated PAR, and high concentration of nutrients in surface waters after density convection in winter. Thus, the combination of favorable abiotic factors promotes the excess of phytoplankton biomass over respiratory losses, cell sinking, grazing, and DOM excretion [75].

The Kara Sea is influenced by intense river discharge, mainly from the Ob and Yenisei rivers [37, 38, 42, 51, 68], which results in a sharp pycnocline caused by the salinity gradient (the upper limit of the gradient lies at a depth of around 10 m) [8] and in the horizontal and vertical differentiation of the structural and functional parameters of plankton communities [5, 13, 14, 45, 57, 59]. In general, the stratification process in high-latitude seas is regulated rather by salinity than by temperature, in contrast to subtropical areas (α and β oceans, respectively) [23].

However, intense stratification of the water column has been observed in summer and autumn, i.e., by the end of the spring thaw and after it. It is unclear whether stratification of the Kara Sea is the same in other seasons, and if it is, how does it influence the flow of nutrients to euphotic zone before and during the phytoplankton bloom? According to the small amount of data on the seasonal dynamics T_0 and S_0 [16], presented in Fig. 4 and Table 2, the surface water layer remains desalinated during winter and spring; this layer is especially notable in the river runoff zone. These data can be evidence of salinity stratification during winter and spring. This, as well as the fact that almost the entire region is covered by ice in winter and early spring, i.e., there is no wind-driven mixing, has a negative effect on the flow of nutrients in the upper water layers. The presence of desalinated upper water layers in winter is due to long-term (2–4 years) accumulation of river discharge compared to other Arctic seas (the Chukchi and Beaufort seas) [56].

The seasonal dynamics of mean concentrations of nitrates (NO_3), phosphates (PO_4) and dissolved silicon (Si) is shown in Fig. 5. According to the averaged data from 1934 to 1983 [6], the concentration of NO_3 in summer and autumn tended to decrease compared

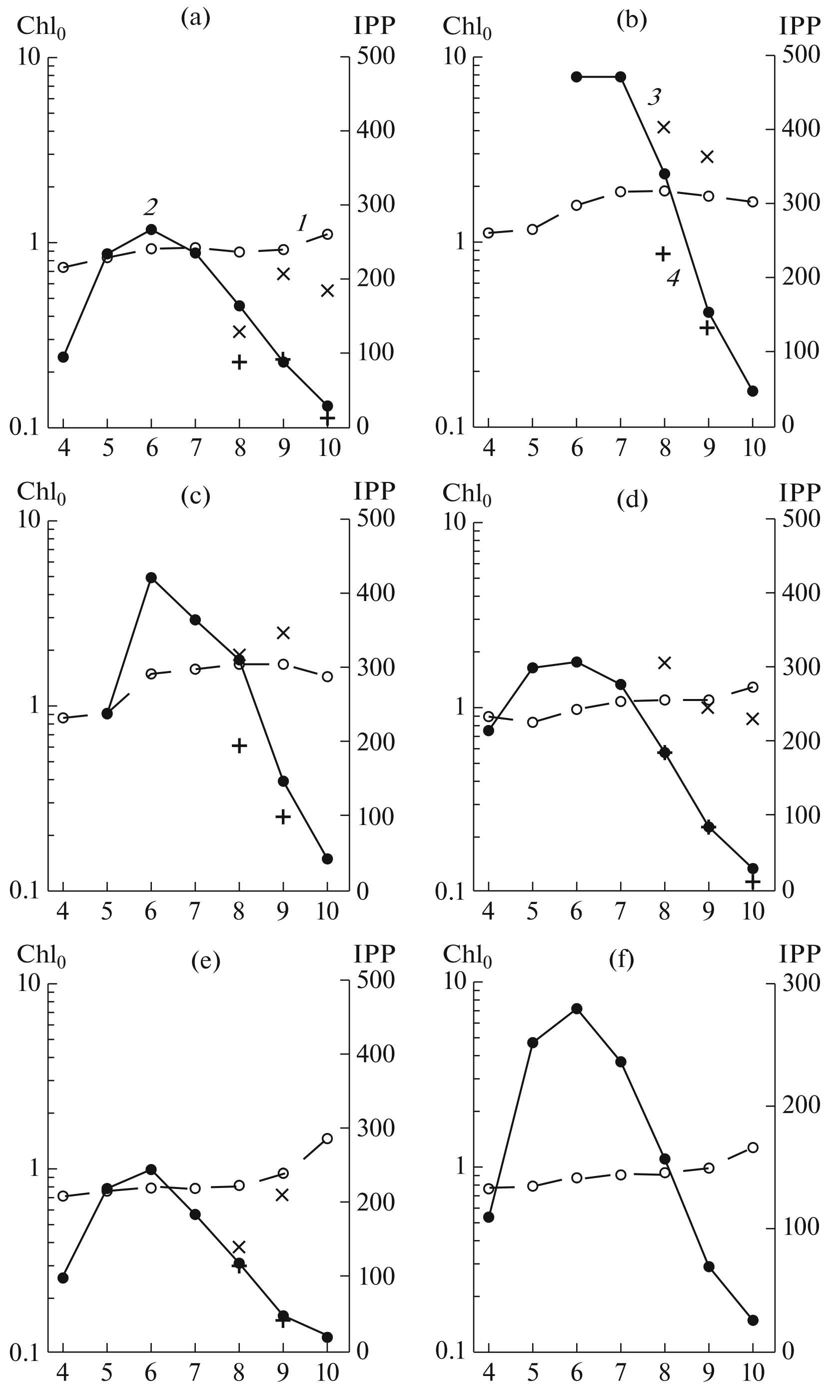

Fig. 2. Seasonal dynamics of chlorophyll concentration in surface waters (Chl$_0$, mg/m^3, *1*) and integrated PP (IPP, mg C/m^2 per day, *2*) in different regions of the Kara Sea according to data of MODIS- Aqua averaged for 2003–2015. Data of field measurements of Chl$_0$ (*3*) and IPP (*4*) are presented for same time period. (a) Southwestern region, (b) Ob estuary, (c) Yenisei estuary, (d) river runoff region, (e) northern region, (f) entire Kara Sea.

with winter and spring, while the concentrations of PO_4 and Si were almost constant during the year. Such dynamics of the level of nutrients was also observed in previous studies, which showed that this dynamics in the Kara Sea has a low amplitude [74]. Notably, the concentrations of nutrients in summer and autumn 1985–1993 and 2007–2016 are higher compared with values recorded during earlier studies (Table 3). Such elevation in the last few decades could have resulted from increased river discharge, which is one of the main sources of biogenic matter for the surface waters of the Kara Sea [60, 63].

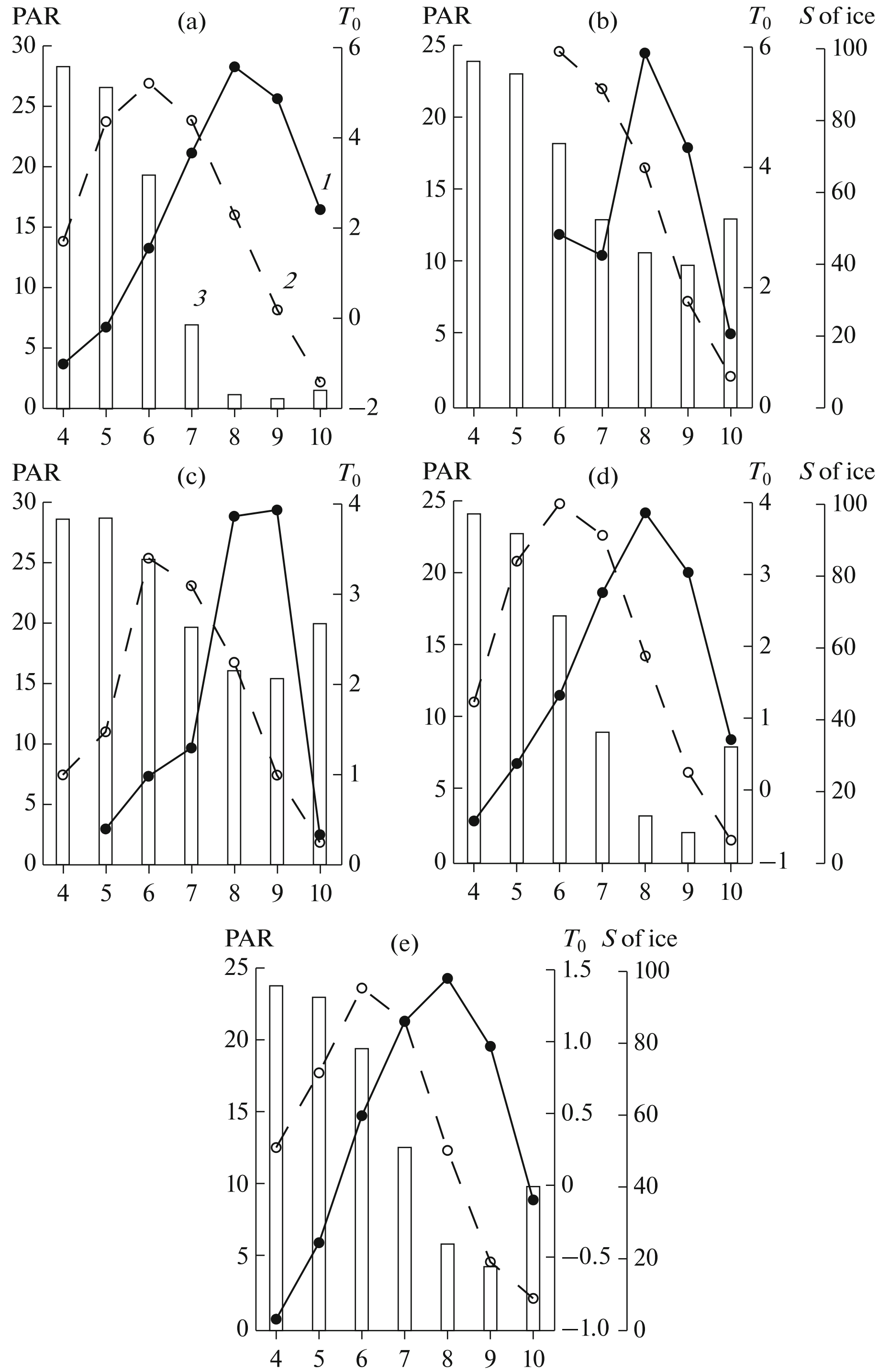

Fig. 3. Seasonal changes in (*1*) surface water temperature (T_0, °C), (*2*) photosynthetically active radiation (PAR, Ein/m^2 per day), and (*3*) ice-covered area (*S*, % of total area) in different parts of Kara Sea according to satellite data (see Materials and Methods). For legend, see Fig. 2.

According to the data in Fig. 5, the level of NO_3, PO_4, and Si in the surface layer at the beginning of years (from January until April) can exceed the limiting concentration values for phytoplankton growth (0.9, 0.5, and 2 μM for nitrates, phosphates, and dissolved silicon, respectively) [31, 36, 77]. Apparently, the limiting elements from May until October are nitrogen and phosphorus, while the concentration of dissolved silicon is excessive. The vertical distribution of NO_3 (Fig. 6) is characterized by a nitrocline of dif-

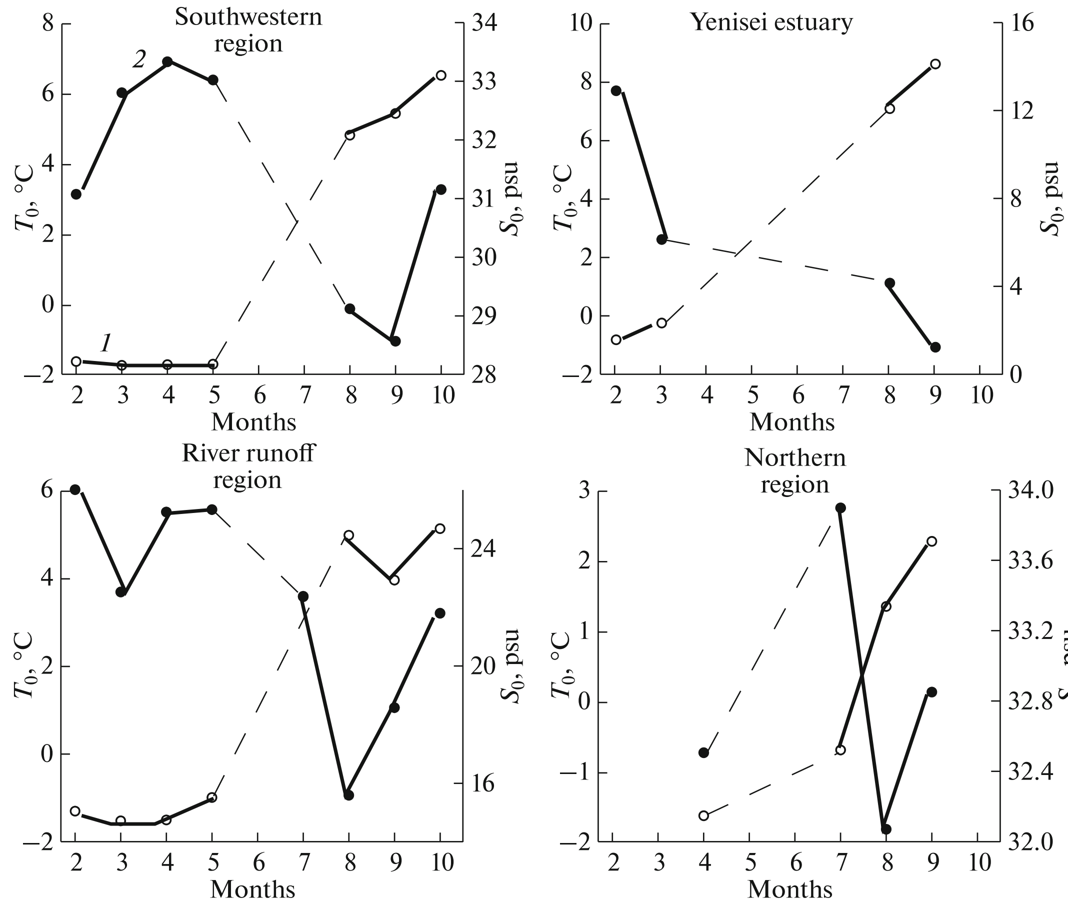

Fig. 4. Seasonal changes in (*1*) surface water temperature (T_0) and (*2*) salinity (S_0) in different regions of Kara Sea.

ferent degrees during all months of the year. The nitrogen concentration gradient has a wider range in summer and autumn than in winter and spring. Such an vertical NO_3 distribution pattern indicates that the flow of nutrients to the eutrophic zone in the winter season (from November until March) is limited by the low intensity of convection and wind-driven mixing due to the halocline and ice cover, which blocks the wind [58].

Thus, the usual enrichment of the euphotic zone by nutrients in autumn and winter, which induces development of phytoplankton in warmer seasons, is limited in the studied area. However, the concentrations of NO_3 and PO_4 in early spring have been elevated, especially over recent decades (Fig. 5). The accumulation of biogenic matter under ice at the beginning of the year can be explained by the fact that its consumption by algae decreases during the winter season, as well as by regeneration processes and river discharge. Such a mechanism has been observed in different areas of the Arctic Ocean [24, 25, 50]. According to data of previous studies, the flow of biogenic matter from the discharge of the Ob and Yenisei rivers in the winter season (from November until April) is higher than during the spring flood (from May until June) [42, 51]. The river discharge seems to have significant effect on the level of nutrients in the Kara Sea in all seasons. If we compare Figs. 2 and 7, we see that the maximum flow of nutrients corresponds to the maximum IPP rate. Thus, rivers have a contradictory influence on the productivity of the Kara Sea. On the one hand, river discharge limits the convectional flux of biogenic matter from below and decreases water transparency and the depth of the euphotic zone [30]. On the other hand, the flow of nutrients and organic matter, which are remineralized, although at different rates [26, 40, 43, 61, 62], partially compensates the lack of flux from lower layers. During the summer season, nutrients are consumed by phytoplankton and are included in recycling.

The mechanism described above indicates that the main source of nutrients for the PP in the Kara Sea is regeneration processes in the eutrophic zone. The types of PP based on nutrients of different origin can be described by the concept of new and regenerated production [32]. New production is based on nutrients (mainly nitrates) moving to the euthotic zone from lower layers. Regenerated production is based on ele-

Table 2. Statistical parameters of seasonal temperature and salinity dynamics in surface waters in different regions of the Kara Sea

Month	Southwestern region		Yenisei estuary		River runoff region		Northern region	
	T_0	S_0	T_0	S_0	T_0	S_0	T_0	S_0
February	$\frac{-1.59 \pm 0.07}{12}$	$\frac{31.07 \pm 1.12}{12}$	$\frac{-0.87 \pm 0.38}{5}$	$\frac{12.82 \pm 8.52}{5}$	$\frac{-1.31 \pm 0.12}{9}$	$\frac{25.99 \pm 2.52}{9}$	–	–
March	$\frac{-1.7 \pm 0.13}{11}$	$\frac{32.81 \pm 1.27}{11}$	–0.3	6.06	$\frac{-1.53 \pm 0.10}{4}$	$\frac{22.50 \pm 5.72}{4}$	–	–
April	$\frac{-1.68 \pm 0.14}{18}$	$\frac{33.33 \pm 0.66}{18}$	–	–	$\frac{-1.51 \pm 0.29}{13}$	$\frac{25.23 \pm 5.42}{13}$	$\frac{-1.61 \pm 0.14}{14}$	$\frac{32.50 \pm 1.92}{14}$
May	$\frac{-1.67 \pm 0.16}{6}$	$\frac{33.0 \pm 21.07}{6}$	–	–	$\frac{-1.00 \pm 0.28}{2}$	$\frac{25.31 \pm 0.66}{2}$	–	–
July	$\frac{3.57 \pm 2.94}{4}$	$\frac{22.34 \pm 6.38}{4}$	–	–	–	–	$\frac{-0.67 \pm 1.54}{40}$	$\frac{33.89 \pm 0.47}{40}$
August	$\frac{4.84 \pm 1.64}{7}$	$\frac{29.12 \pm 2.33}{7}$	$\frac{7.01 \pm 1.20}{6}$	$\frac{4.08 \pm 3.00}{6}$	$\frac{4.96 \pm 2.40}{10}$	$\frac{15.57 \pm 7.28}{10}$	$\frac{1.36 \pm 0.31}{12}$	$\frac{32.07 \pm 1.45}{12}$
September	$\frac{4.45 \pm 0.82}{12}$	$\frac{28.57 \pm 4.05}{12}$	$\frac{8.53 \pm 1.01}{5}$	$\frac{1.16 \pm 2.08}{5}$	$\frac{3.94 \pm 1.98}{23}$	$\frac{18.56 \pm 6.51}{23}$	$\frac{2.29 \pm 0.73}{11}$	$\frac{32.85 \pm 2.47}{11}$
October	$\frac{6.54 \pm 0.46}{6}$	$\frac{31.15 \pm 1.06}{6}$	–	–	$\frac{5.11 \pm 0.36}{2}$	$\frac{21.78 \pm 2.31}{2}$	–	–

T_0 is surface water temperature, °C; S_0 is surface water salinity, psu. Numerator contains arithmetic mean and standard deviation, and denominator contains number of measurements (averaging period: 1995–2014). Data on June 1995–2014 are unavailable.

Table 3. Minimum (min), maximum (max), and mean (M) values of concentrations of main nutrients in surface waters of the Kara Sea from July until October in different years

Years	Month	NO_3			PO_4			Si		
		min	max	M	min	max	M	min	max	M
1934–1983	July	0	0.8	0.22	0	1.14	0.17	0	47.0	5.0
	August	0	3.4	0.28	0	0.68	0.10	0	70.0	1.96
	September	0.03	1.70	0.65	0	1.0	0.16	0	90.0	9.53
	October	0.02	2.48	0.70	0.09	0.48	0.25	0	16.98	4.28
1985–1993	July	0	14.64	1.10	0.03	0.58	0.20	0.32	128.5	23.04
	August	0	13.71	1.03	0	1.14	0.18	0	124.6	28.2
	September	0	5.46	0.49	0.01	1.74	0.22	0.29	82.0	18.7
	October	–	–	–	–	–	–	–	–	–
2007–2015	July	–	–	–	–	–	–	–	–	–
	August	0	6.56	0.66	0.03	2.76	0.62	0.20	77.2	19.3
	September	0	6.04	0.71	2	2.57	0.23	0	113.6	19.97
	October	0.04	5.71	0.93	0.04	0.68	0.13	0.62	28.09	5.75

NO_3, PO_4, and Si are concentrations of nitrates, phosphates, and dissolved silicon, respectively (μM).

ments released during the mineralization of organic matter in the euthotic zone. The higher ratio of new and total (new + regenerated) PP (f- ratio) evidence the greater role of new biogenic matter in production processes in the euthotic zone. The proportion of new PP in communities with intense winter convection is usually higher than 50% ($f > 0.50$) [72]. Examples of such communities in the Arctic Ocean are areas with high annual IPP, such as the Barents Sea. In contrast, the proportion of regenerated PP is higher in oligotrophic waters. For example, the *f*-ratio in the Kara Sea is 0.24 [72], which is one of the lowest values in the Arctic

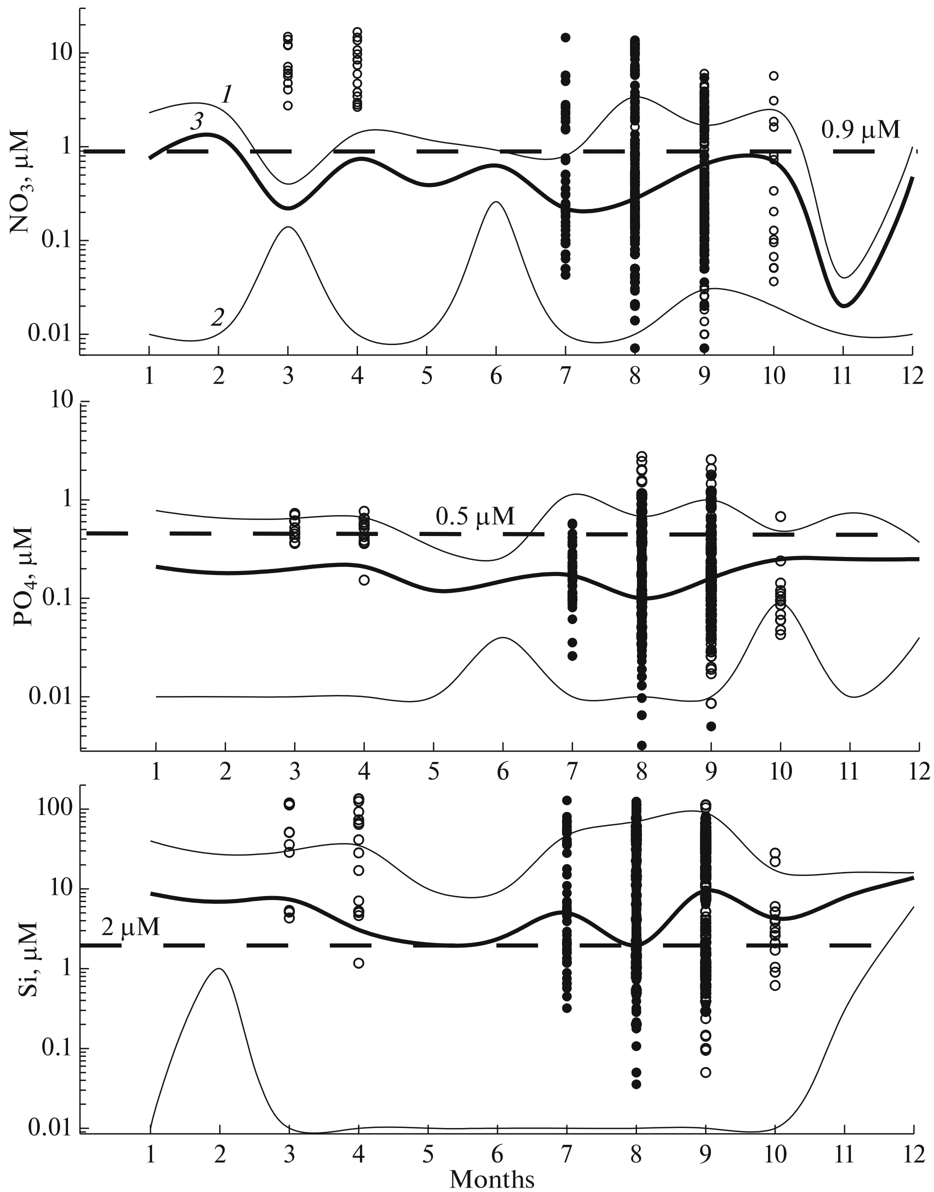

Fig. 5. Seasonal changes in concentration of nitrates (NO_3), phosphates (PO_4), and dissolved silicon (Si) in the Kara Sea: (*1*) maximum values, (*2*) minimum values, and (*3*) mean values for period from 1934 until 1983. Dark circles, data for period of 1985–1993. Light circles, data for period of 2007–2016. Horizontal dashed lines designate concentration values that limit phytoplankton growth.

Ocean [72]. Thus, the concept of new and regenerated production supports the described mechanism of nutrients flows in the upper layer of the Kara Sea.

If we compare Figs. 2 and 3, we see that the seasonal IPP dynamics is determined by annual changes in PAR. The results of model calculations are generally confirmed by IPP measurements (Fig. 2). The main regulating factor in the seasonal PP dynamics in high-altitude areas is light [72], while the level of nutrients has some effect on the process but does not induce it [39].

One of the features typical of the IPP dynamics and Chl_0 in the studied area is the discrepancy of the maximum values of these parameters during the year (Fig. 2). A small variation in the Chl *a* concentration in surface waters compared with IPP is also notable (Fig. 2). These findings confirm the results of previous studies, which showed that photophysiological parameters and PAR play an important role in the formation of IPP in the Kara Sea, while the biomass of phytoplankton has a smaller effect [30]. It should be noted that obtained pattern of the seasonal dynamics of Chl_0 can be partially affected by model calculation errors, since the regional algorithm overestimates its parameter with a low in situ concentration (<0.5 mg/m^3). Spatio-

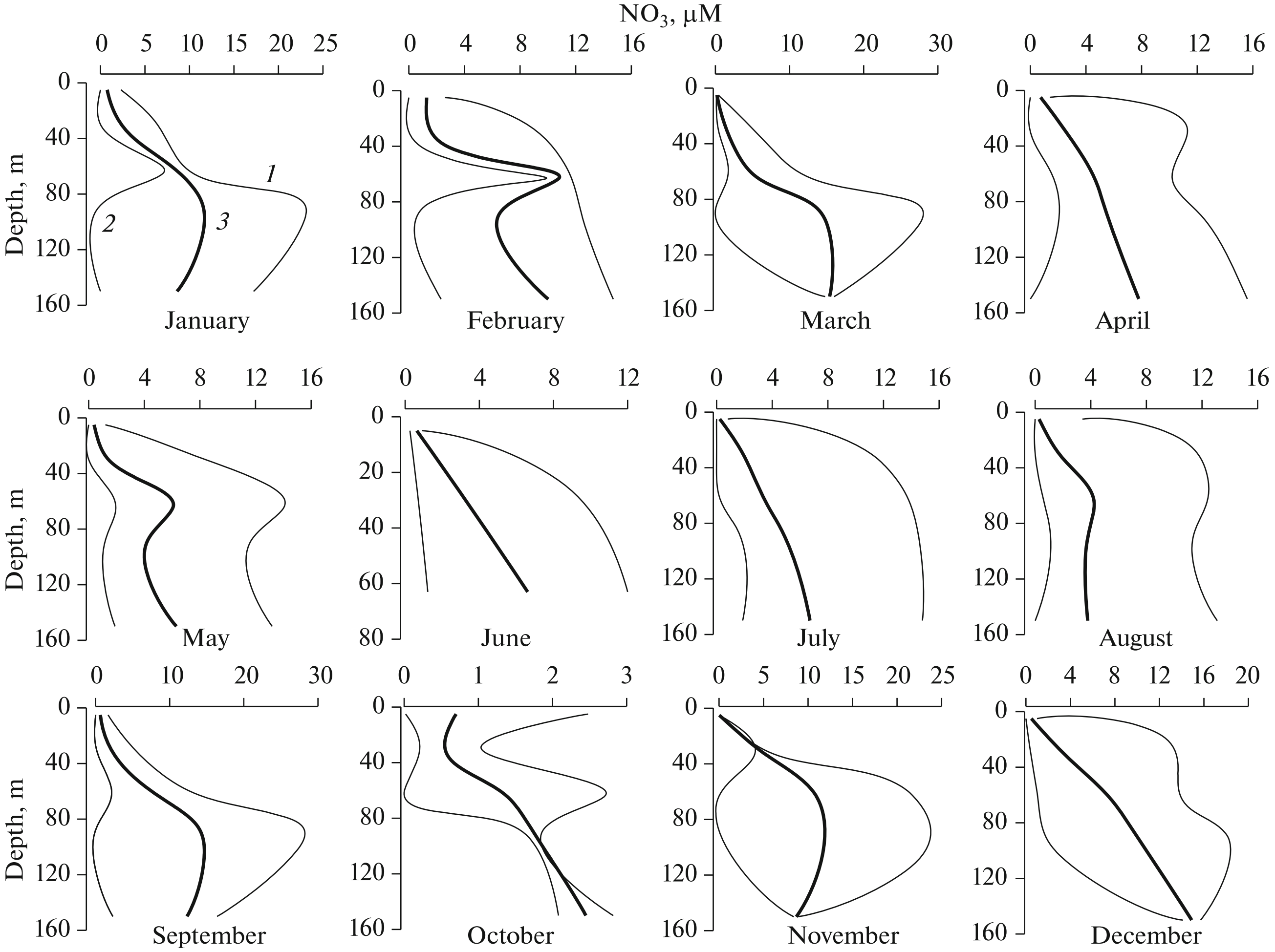

Fig. 6. Vertical distribution of nitrates (NO_3) in the Kara Sea in different months: (*1*) maximum values, (*2*) minimum values, and (*3*) mean values for period from 1934 until 1983.

temporal averaging can also affect the accuracy somewhat. Annual and spatial variability of the Chl_0 concentration can smooth the seasonal dynamics curve. It is also seen that the Chl_0 concentration tends to increase by the end of the growing season (Fig. 2). One possible cause of accumulation of phytoplankton in the Kara Sea during the year is a decrease in grazing intensity at the end of summer and in autumn.

According to Koblentz-Mishke and Vedernikov [9], the average monthly IPP values (<100 mg C/m^2 per day) in all studied areas of the Kara Sea indicate that the areas are oligotrophic at the beginning (April) and at the end (September, October) of the growing season. The mean values for all studied areas are generally consistent with this conclusion (the IPP values in April are close to 100 mg C/m^2 per day; Table 1). In the period from May until August, the Kara Sea is mesotrophic (the IPP rate is 100–500 mg C/m^2 per day). Remarkably, the maximum IPP values in June are relatively low (from 246 mg C/m^2 per day in the northern region to 471 mg C/m^2 per day in the Ob estuary; Table 1). Such a low IPP rate in the Kara Sea is due to all the abiotic factors that limit production processes (significant water column stratification, low amount of light, low temperature, and low concentration of nutrients, primarily nitrogen and phosphorus) [2, 30]. Apparently, the nutrients from the river discharge cannot compensate the low inflow of elements from deeper layers caused by winter convection. The rivers that empty into the Arctic Ocean have low concentrations of minerals compared with other rivers of the World [58].

It should also be noted that the values of the IPP rate were obtained from satellite data, which are available in cases when the sky is cloud-free. Therefore, high PAR values recorded on sunny days are extrapolated to areas and time periods with lower values (due to cloud cover) and then used for model calculations. Thus, the values of the IPP rate in this work can be

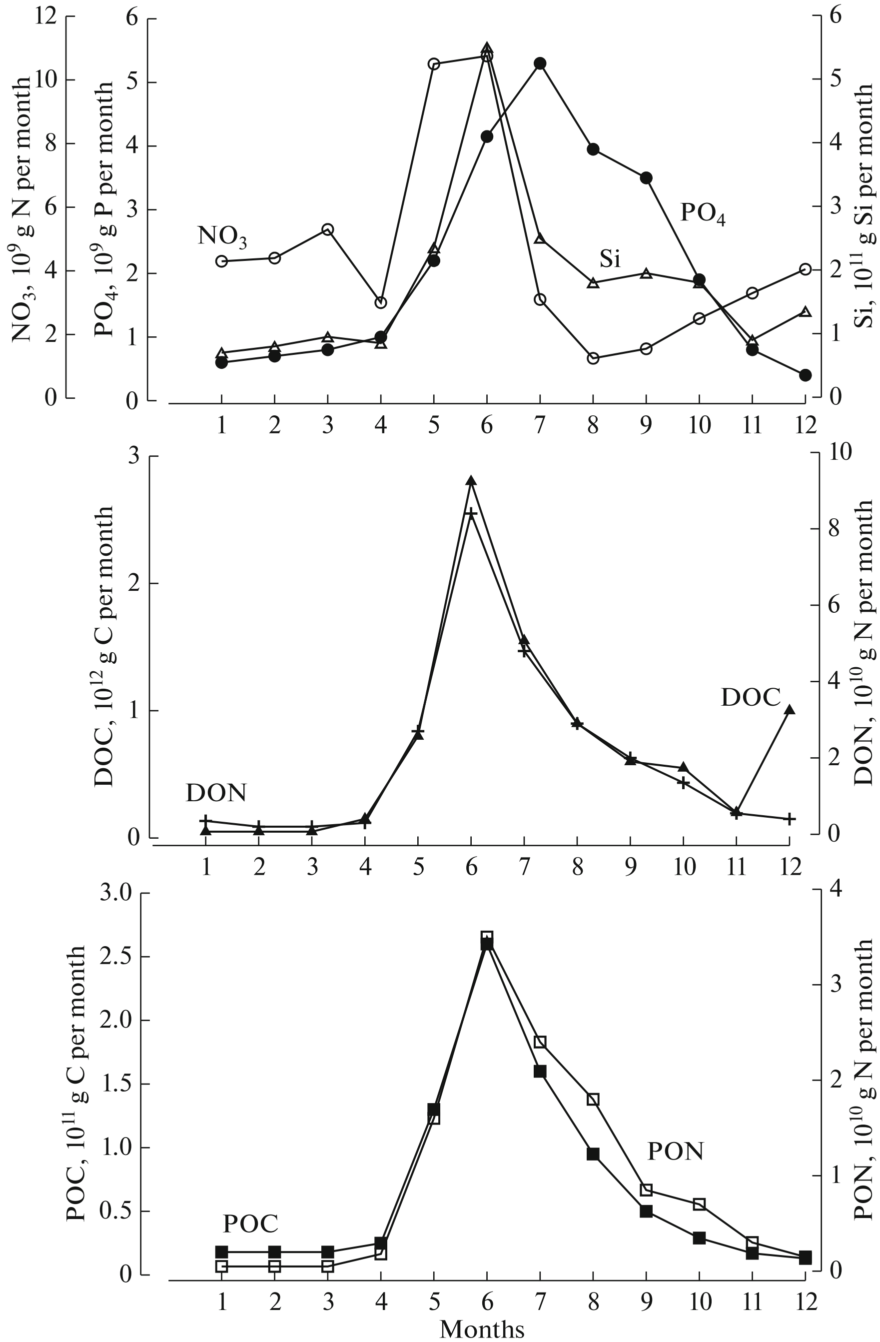

Fig. 7. Seasonal dynamics of flow of nitrates (NO_3), phosphates (PO_4), dissolved silicon (Si), dissolved organic nitrogen (DON), dissolved organic carbon (DOC), suspended organic nitrogen (PON), and suspended organic carbon (POC) from Ob and Yenisei rivers to the Kara Sea [51 with some modifications].

considered as “cloud-free sky PP,” which overestimates the true IPP values in the Kara Sea.

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