ISSN 0001-4370, Oceanology, 2015, Vol. 55, No. 4, pp. 535–546. © Pleiades Publishing, Inc., 2015.
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MARINE BIOLOGY

Evaluation of the Influence of Abiotic and Biotic Factors on Primary Production in the Kara Sea in Autumn

A. B. Demidov, S. A. Mosharov, and P. N. Makkaveev
Shirshov Institute of Oceanology, Russian Academy of Sciences, ul. Krasikova 23, Moscow, 117218 Russia
e-mail: demspa@rambler.ru
Received October 3, 2012

Abstract—A regression analysis of the parameters of primary production versus environmental factors was performed on the basis of data of three complex expeditions performed in the Kara Sea in September to October 1993, 2007, and 2011. The analysis of the dependence of the depth-integrated primary production (PP_{int}) on the value of surface chlorophyll a (Chl_0) and assimilation activity (AN_m) showed that only 12% of the variability of the integrated PP_{int} was determined by the variability of Chl_0, whereas the correlation between PP_{int} and AN_m was strong ($R^2 = 0.635$). Thus, in autumn, PP_{int} values in the Kara Sea depended primarily on the activity of phytoplankton assimilation. At the end of the vegetative season, high (close to or above 1 mg/m^3) Chl_0 values did not reflect phytoplankton production within the entire photosynthetic layer, where organic matter was synthesized at a low rate. In turn, PP_{int} and AN_m depended primarily on the intensity of insolation and was weakly related to the content of dissolved forms of nitrogen and phosphorus. In autumn, at the end of the vegetative season, insolation apparently is the main factor in the determination of the formation of primary production in the Kara Sea.

DOI: 10.1134/S0001437015040037

INTRODUCTION

Among all the seas of the Arctic basin, the Kara Sea occupies a unique place due to specific processes of synthesis of organic matter. The runoff of the Ob and Yenisei rivers reaches, on average, approximately 1100 km^3/year [57], which is approximately 55% of the total riverine runoff to all Arctic seas of Russia and more than one-third of the total freshwater runoff to the Arctic basin [35]. The interaction between fresh and salt waters contributes to both horizontal and vertical differentiation of structural and functional characteristics of pelagic plankton communities [8, 17, 19, 39, 44, 48]. Another characteristic feature of the Kara Sea is the shallow nature of a considerable part of its water areas, which determines the specific supply of the euphotic layer with main biogenic elements. Approximately 40% of the bottom areas are less than 50 m in depth; 64% are less than 100 m; and only 2% are deeper than 500 m (data available at http://www.dic.academic.ru/). The average depths of the sea and the shelf are approximately 110 m [29] and 56 m [41], respectively.

The formation of sharp gradients of the physicochemical properties of water masses (especially salinity and the concentrations of particulate and dissolved matter) determines the specific features of the abiotic and biotic factors that determine the conditions of phytoplankton primary phytoplankton production. These features include, first of all, low temperature and low water transparency throughout the year and, as a result of the latter, the small (on average, 22 m) thickness of the photosynthetic layer and a higher (on average, >1 mg/m^3) chlorophyll content in the layer above the pycnocline [3, 14]. At the end of the vegetative season (September–October), factors limiting the primary production (PP) in the Kara Sea include low content of dissolved forms of nitrogen and phosphorus in the surface layer and the lower insolation. On the basis of this, in the previous study we concluded that main abiotic factors limit primary production in the Kara Sea in autumn [3].

From the standpoint of the consideration of the biomass as a basis of primary production, the inconsistency of the low PP_{int} values in the Kara Sea in September obtained by experimental methods (primarily using the radiocarbon modification of the flask method), and the high chlorophyll a concentration (Chl a) in the upper mixed layer (UML) (>1 mg/m^3), which is characteristic of the phytoplankton bloom, seems paradoxical [58]. For this reason, the main objective of this study was to assess the influence of various abiotic and biotic factors on primary production in the Kara Sea, which determines the notion of the adequacy of the value of PP_{int} in this water body. Emphasis was placed on the investigation of the dependence of production characteristics of phytoplankton on the variability of parameters of the surface layer. The analysis of the influence of the peculiarities of the vertical distribution of the chlorophyll concentration, subsurface irradiance, and content of biogenic elements on the PP_{int} value is beyond the scope of this work. The aim of this study is relevant in the light

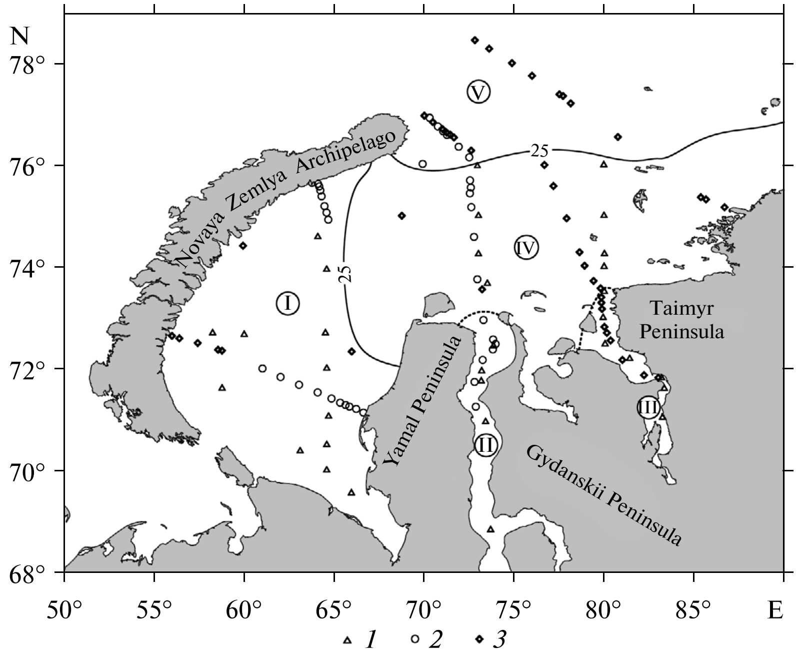

Fig. 1. Location of sampling stations for the determination of the primary production and chlorophyll a content in different parts of the Kara Sea: (*1*) 49th voyage of the RV *Dmitrii Mendeleev* (August–September 1993), (*2*) 54th voyage of the RV *Akademik Mstislav Keldysh* (September 2007), and (*3*) 59th voyage of the RV *Akademik Mstislav Keldysh* (September–October 2011). Designations: I—southwest region (southwestern water mass), II—Ob River Estuary, III—Yenisei River Estuary, IV—Ob and Yenisei runoff area (river plume water mass), and V—western and eastern slopes of the St. Anna Trough (northern water mass).

of climate changes in the Arctic basin, which have been observed in the last decades and affect both the conditions of the synthesis of organic matter and the level of productivity of seas in this region [23, 24, 49].

MATERIALS AND METHODS

Data sources and zoning of the Kara Sea. The database analyzed in this study was created on the basis of the results of three complex ecosystem expeditions to the Kara Sea: voyage 49 of the RV *Dmitrii Mendeleev* (August–September 1993) and voyages 54 and 59 of the RV *Akademik Mstislav Keldysh* (September 2007 and September to October 2011, respectively). The study area and the location of stations were described earlier [3, 14, 15]. Figure 1 provides a summary picture of the location of sampling sites in these expeditions. The total content of Chl a was studied at 113 stations, and primary production was measured at 85 stations.

The Kara Sea can be divided into areas with different hydrophysical and biogeochemical conditions. These differences are determined primarily by the differential influence of riverine runoff on the areas located at different distances from Ob and Yenisei estuaries. Taking into account the fact that the main characteristics of water masses (WM) of the Kara Sea, which allow the influence of the riverine runoff to be determined, are the surface salinity (S_0) and the content of dissolved silicon (Si_0), these indices can be considered as indicators for the zoning of its water areas. Phytoplankton communities living in different WMs of the Kara Sea should differ in the production characteristics.

On the basis of the previously developed classification of WMs [51], in the study area we have identified the Southwestern outflow area (I), the Ob Estuary (II), the Yenisei Estuary (III), the Ob and Yenisei region of riverine runoff (IV), and the areas of the eastern and western slopes of St. Anna Trough (V) (Fig. 1). The border between areas I, IV, and V was drawn along the average long-term position of isohaline 25 psu on the surface [51]. According to one of the famous classification, the boundary between the brackish water and seawater approximately follows this isohaline [11]. The Ob and Yenisei estuaries are considered separately because of previously found differences in the conditions of formation of primary production in these water areas [3]. The northern boundary of estuaries was drawn along the averaged position of isohaline 10 psu, recorded according to the results of our expeditions, which is close to the geographic boundary (Fig. 1). Salinities of 2–10 psu are characteristic of estuarine regions and estuaries of rivers (so-called mixohaline areas) [20]. The formation of WMs in the major area of the southwestern part of the Kara Sea is only slightly affected by the riverine runoff (S_0 = 28–32 psu, $Si_0 < 5$ μM). The St. Anna Trough is located in the northern water mass, the characteristic features of which are a salinity of 30–32 psu and a low content of dissolved silicon ($Si_0 < 10$ μM) [51].

Sampling and methods for determination of the primary production and chlorophyll a content. The location of the stations was chosen on the basis of the results of hydrophysical and hydro-optical surveys, performed using a Rybka multiparametric scanning probe and a flow fluorometer developed at the Institute of Oceanology, Russian Academy of Sciences. The locations of stations were selected so as to ensure the maximum coverage of the studied water area with experimental points and to provide the most comprehensive characterization of narrow gradient frontal zones. Sampling horizons were determined after preliminarily probing the temperature, conductivity, and fluorescence with SBE-19 and SBE-32 CTD probes (Seabird Electronics).

To determine Chl content, water samples were collected with plastic bathometers of the Carousel Water Sampler complex from six to nine horizons of the upper 100-m layer. The sample from the subsurface layer at these stations was taken with a plastic bucket simultaneously with the closure of bathometers near the surface.

On the 49th voyage of the RV *Dmitrii Mendeleev*, primary production in three stations was measured in situ. At other stations, primary production was determined using samples from the surface, vertical profiles of Chl and subsurface irradiance, and the light curves obtained in situ. On the 54th voyage of the RV *Akademik Mstislav Keldysh* (2007), samples for the determination of the primary production were collected from the horizons with irradiances of the following percentages of subsurface irradiance in the PAR range (I_0), namely: 100, 75, 50, 25, 10, 5, and 2. In the 59th voyage of the RV *Akademik Mstislav Keldysh* (2011), sampling was performed from horizons in which light conditions approximately corresponded to the nominal transmittance of flasks with neutral density filters of the following percentages of I_0, namely: 100, 78.7, 63.9, 48.7, 24.3, 5.8, 3.2, and 2.2; these filters came with the ICES laboratory incubator.

On all expeditions, primary production was measured by the radiocarbon modification of the flask method [56], using different experimental schemes [3, 14, 15]. Chl a content was determined spectrophotometrically [3] or fluorometrically [14, 15].

Methods for the determination of surface and subsurface irradiance. The intensity of the surface irradiance was measured with a pyranometer [3] or a LI-190SA [14, 15] incident radiation sensor (LI-COR) in the PAR range. Measurement results were automatically integrated into the LI-1400 unit for 5-min intervals (Ein/m^2) during the day and were stored in the internal memory unit. Subsequently, these values were used to calculate integrated incident radiation for the period of exposure of the experimental flasks in determining the primary production and for the entire light period for a certain date.

The index of vertical attenuation of irradiance (k_d) was measured using an alpha meter. In the absence of subsurface hydro-optical measurements, k_d values were calculated by empirical dependence of the diffuse light attenuation coefficient on relative transparency by Secchi depth, which was obtained in August to September 1993 [3].

Methods for determination of hydrochemical parameters. Immediately after collection, samples were fixed to determine dissolved oxygen and ammonia nitrogen. Samples for determination of pH, nutrients (silicates, phosphates, and nitrogen forms) and alkalinity were collected in 0.5-L plastic flasks without conservation. When working with waters abounding in particulate matter (water in bays and inlets, in zones of the mixing of river and sea waters), samples for determination of biogenic elements were preliminarily filtered through a lavsan nuclear filter (mesh, 1 μm) manufactured at the Joint Institute for Nuclear Research (Dubna). In samples with a visually noticeable color of water, colorimetric determination of mineral phosphorus and silicates was performed by the appropriate procedure [16, 18].

The total alkalinity (Alk) was determined by direct titration according to Bruevich with a visual determination of the end point of titration [18]. Dissolved inorganic and total phosphorus (phosphates), dissolved inorganic silicon (silicates), nitrite nitrogen (nitrites), nitrate nitrogen (nitrates), and ammonium nitrogen (ammonium ion) were determined colorimetrically as described in [16, 18].

The content of dissolved carbon dioxide and various forms of dissolved inorganic carbon was calculated by the pH-Alk method with thermodynamic equations of carbonate equilibrium using the Roy concentration dissociation constants for carbonic acid [46] with corrections for the waters whose properties differed from the properties of the sea water [1, 45].

Statistical data analysis. Before calculations, the production characteristics and environmental parameters were transferred to logarithmic values to approximate their distribution to the normal, so that the data arrays could be processed by parametric statistics methods. The normality of distribution was verified using the Kolmogorov–Smirnov test. For the main parameters studied, the null hypothesis was accepted at $p > 0.20$.

The correlations between the production characteristics of phytoplankton as such and between the production characteristics of phytoplankton and abiotic factors were studied by regression analysis. Linear regression equations of the form $y = a + bx$ were calculated, where y is the dependent variable, x is the independent variable, and a and b are the regression coefficients.

The degree of correlation between variables was estimated by the coefficient of determination (R^2), the standard error for the individual function definitions (m), and coefficient F [10, 31]. Coefficient F shows how strongly the dependent variable y can differ from the independent variable x and how adequately the standard error of regression m shows the maximum possible deviation (along the Y axis) of experimental

Table 1. Mean production characteristics of phytoplankton in different areas of the Kara Sea

Parameter	Southwestern water mass			Ob Estuary			Yenisei Estuary			River plume water mass			Northern water mass		
	M	cv	*N*	*M*	cv	*N*	*M*	cv	*N*	*M*	cv	*N*	*M*	cv	*N*
PP_0	9.83	93	14	27.04	60	7	53	62	12	25.17	186	28	3.84	56	18
PP_{int}	82	51	14	38	59	7	145	74	12	69	98	28	32	64	18
Chl_0	0.83	55	29	4.47	132	11	3.25	40	12	1.18	58	34	0.64	47	20
Chl_{phs}	19.56	36	14	21.52	71	7	31.22	58	12	11.91	47	28	12.08	53	18
Chl_{av}	0.49	50	15	5.53	133	7	2.72	51	12	0.76	56	28	0.50	38	18
AN_0	1.10	36	14	0.72	32	7	1.29	55	12	1.49	151	28	0.51	58	18
AN_m	1.81	122	14	0.72	32	7	1.29	55	12	1.57	142	28	0.57	56	18
ψ	0.56	73	11	2.14	47	4	0.80	33	12	0.80	88	24	0.59	36	13
Z_{phs}	47	51	14	6	77	7	12	27	12	18	40	28	25	38	18

M—arithmetic mean value, cv—coefficient of variation, *N*—number of measurements.

points from the regression line, thus being an indicator of the scatter.

RESULTS

The mean values of primary production and Chl a content, calculated for different regions of the Kara Sea (Table 1, Fig. 2), allow determination of their trophic status. According to Chl a content on the surface [21], the Ob and Yenisei estuaries and the riverine runoff area in autumn are classified among eutrophic water areas (Chl_0 > 1 mg/m^3), whereas the southwestern region and waters of the St. Anne trough (northern WM) are classified as typically mesotrophic water areas (Chl_0 0.1–1 mg/m^3). Judging by primary production on the surface (PP_0) [12], the Ob and Yenisei estuaries and the riverine runoff area can be classified as intermediate between mesotrophic and eutrophic water areas (10–100 mg C/m^3 per day), the southwestern WM is characterized as a mesotrophic water area (5–10 mg C/m^3 per day), and the northern WM is intermediate between the oligotrophic and mesotrophic water areas (2–5 mg C/m^3 per day). Judging by the PP_{int} values [13], only the Yenisei Estuary can be classified with the mesotrophic water areas (100–500 mg C/m^2 per day), whereas the remaining areas of the Kara Sea are typically oligotrophic with primary production values in the water column below 100 mg C/m^2 per day.

Table 2 shows regression equations obtained for the entire dataset for the Kara Sea, which link the phytoplankton production indices to biotic and abiotic factors. As follows from Table 2 and the regression dependence shown in Fig. 3, the correlation between chlorophyll content on the surface and depth-integrated primary production is very weak (R^2 = 0.115). As can be seen in Table 2 and Fig. 4, PP_{int} values were correlated much more strongly with the maximum assimilation number (AN_m) and the Chl a content in the photosynthetic layer (Chl_{phs}) (R^2 = 0.635 and 0.340, respectively). At the same time, we found a sufficiently strong correlation between the surface values of the primary production, Chl a content, and assimilation number (R^2 = 0.494 and 0.582, respectively) (Table 2).

The analysis of the relationship between PP_{int} values and abiotic factors showed the absence of a dependence on surface temperature (T_0), a weak positive correlation with the content of phosphate (PO_4) and the sum of nitrite and nitrate nitrogen ($NO_2 + NO_3$) (R^2 = 0.216 and 0.133, respectively). A stronger correlation was found between the PP_{int} value and the Si content (R^2 = 0.352) (Table 2). Interestingly, the strongest correlation was found between PP_{int} and the level of insolation (I_0) (R^2 = 0.569) (Fig. 5), which apparently indicates the key role of incident solar radiation in the limitation of the integrated primary production in autumn. A similar pattern was obtained when correlations between AN_m and abiotic factors were analyzed. The AN_m values strongly depended on the surface irradiance level (R^2 = 0.560) (Fig. 5), were much less correlated with the content of basic biogenic elements, and hardly depended on the T_0 value (Table 2). It should be noted that the high values of the standard error of individual function definitions (*m*) and coefficient F (data scatter index) indicate strong spatiotemporal variability in the production characteristics of phytoplankton in the Kara Sea and abiotic factors (Table 2).

DISCUSSION

The dependence of the primary production on the content of Chl a on the surface and assimilation activity. According to the results of previous studies of spatial changes in Chl_0 in the Kara Sea in autumn, the content of this pigment varies in a wide range. It reaches a maximum value in Ob and Yenisei estuaries (>3 mg/m^3) and is, on average, 1–3 and 0.2–1 mg/m^3 on the Ob–Yenisei shelf and in the southwestern region, respectively. Relatively low average Chl_0 values were detected in the northern WM of the St. Anna Trough (0.5–0.7 mg/m^3) [2, 5, 6, 14, 15, 48]. The results of calculations of the Chl_0 concentration, presented in modern

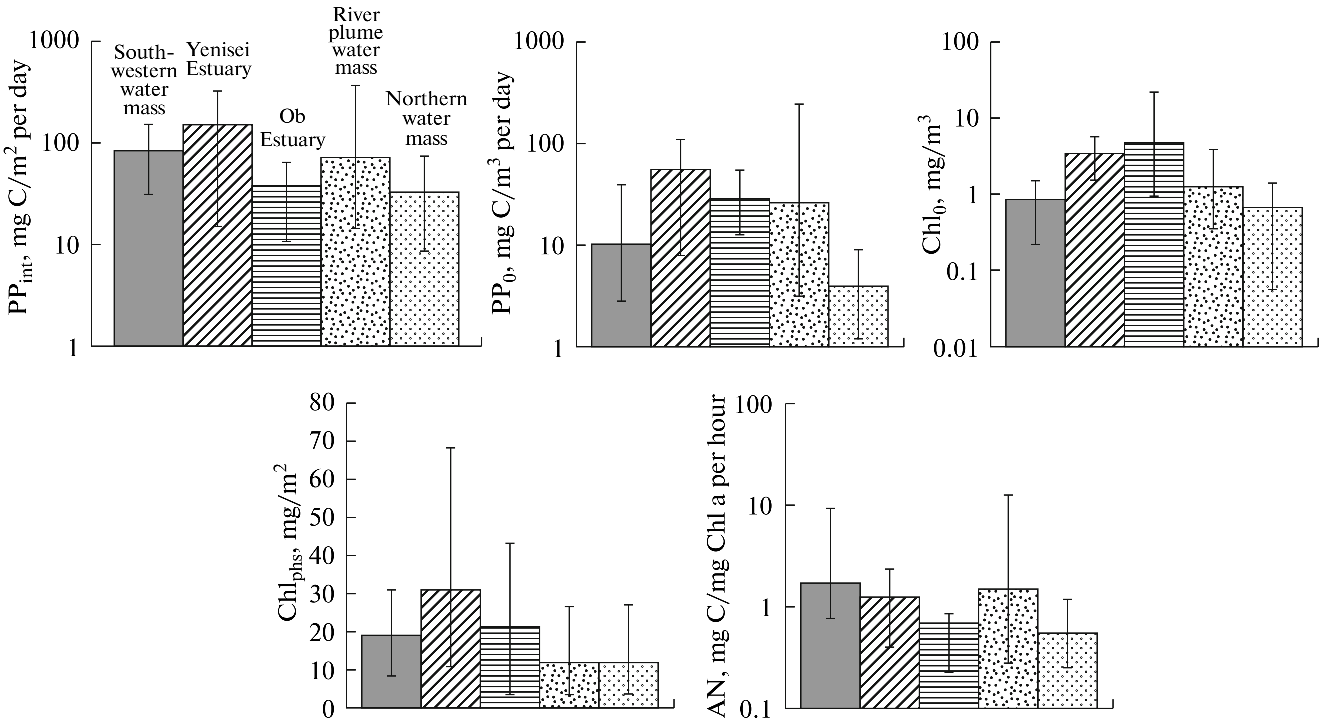

Fig. 2. Mean values of production characteristics of phytoplankton in different areas of the Kara Sea. Designations: PP_{int}—depth-integrated primary production, PP_0—primary production on the surface, Chl_0—chlorophyll a (Chl a) content on the surface; Chl_{phs}—Chl a content in the photosynthetic layer, AN_m—maximum assimilation number. Bars show the limits of variability of the index.

satellite maps, need to be adjusted, especially for the areas under the influence of riverine runoff. However, in general, they correspond to the range of variability and the overall picture of Chl a distribution in the Kara Sea [6, 49, 62].

In the simplest algorithms used to calculate the integrated primary production, surface Chl a content is considered as the only input parameter, which makes it possible to estimate the level of productivity of seas as well as individual regions and the entire World Ocean [7, 9, 25]. In this regard, it is important to assess the degree to which Chl_0 content determines depth-integrated primary production. The results of our regression analysis of the correlation between Chl_0 and PP_{int} showed that only 12% of the variability of the integrated PP depends on the variability of the Chl a content on the surface ($R^2 = 0.115$). It is believed that, for the entire World Ocean, Chl_0 determines < 50% of integrated primary production [25]. Figure 3 shows the results of the comparison of Chl_0–PP_{int} regression lines for the Kara Sea and the regions of the World Ocean with similar climatic conditions [4, 5, 9, 49]. Analysis showed that the Chl_0–PP_{int} dataset for the Kara Sea differs from that for other Arctic seas and cold-water regions of the World Ocean. The difference consists in the fact that, for the same Chl_0 concentrations, the integrated primary production values in the Kara Sea were 2–3 times lower than in the Barents and Pechora seas [4, 5] and 8–12 times lower than in the Chukchi and Beaufort seas [49] and in World Ocean regions more polar than 40° N and S [10].

At present, it is generally assumed that the main parameter of PP_{int} models is the photosynthesis rate under optimal light conditions—the maximum assimilation number (AN_m). The accuracy of the AN_m estimation largely determines the adequacy of the simulation of primary production in the water column [25, 27]. Regression analysis showed a strong correlation between PP_{int} values in the Kara Sea and AN_m values ($R^2 = 0.635$). In addition, PP_{int} values correlated better with Chl_{phs} than with Chl_0 (Fig. 4). It was noted earlier that the variability of the integrated values of the primary production in the World Ocean depends mainly on the Chl a content in the photosynthetic layer and the spatial variability of AN [25].

Thus, depth-integrated primary production in the Kara Sea in autumn was determined primarily by the level of assimilation activity of phytoplankton rather than by its biomass, if Chl a content on the surface is taken as an index of biomass. At the same time, the primary production on the surface depended both on Chl_0 and the surface assimilation number (AN_0) ($R^2 =$ 0.494 and 0.582, respectively) (Table 2). Therefore, the high (close to 1 mg/m^3 or more) Chl a concentration on the surface of the Kara Sea at the end of the vegetative season did not reflect the level of functioning of the phytoplankton community of the

Table 2. Statistical parameters characterizing the linear ($y = a + bx$) relationships of logarithms of the production characteristics of phytoplankton in the Kara Sea with biotic and abiotic factors

y	x	a	b	N	R^2	p	m	F
$\log PP_{int}$	$\log Chl_0$	1.623	0.398	85	0.115	0.001	0.425	7.08
$\log PP_{int}$	$\log AN_m$	1.712	0.999	85	0.635	0.000	0.274	3.53
$\log PP_{int}$	$\log Chl_{phs}$	0.575	0.935	85	0.340	0.000	0.367	5.42
$\log PP_{int}$	$\log PP_0$	1.007	0.645	85	0.621	0.000	0.278	3.59
$\log PP_{int}$	$\log T_0$	1.628	−0.007	85	0.000	0.976	0.453	8.05
$\log PP_{int}$	$\log I_0$	0.831	1.104	69	0.569	0.000	0.310	4.17
$\log PP_{int}$	$\log PO_4$	1.248	0.530	81	0.216	0.000	0.399	6.28
$\log PP_{int}$	$\log Si$	0.494	0.518	85	0.352	0.000	0.395	6.17
$\log PP_{int}$	$\log(NO_2 + NO_3)$	1.360	0.240	85	0.133	0.001	0.421	6.95
$\log PP_{int}$	$\log UML$	1.491	0.157	85	0.009	0.395	0.451	7.98
$\log PP_{int}$	$\log Z_{phs}$	1.331	0.236	85	0.028	0.129	0.489	9.51
$\log Chl_0$	$\log T_0$	−0.482	0.753	113	0.195	0.000	0.338	4.74
$\log PP_0$	$\log Chl_0$	0.954	1.007	85	0.494	0.000	0.392	6.08
$\log PP_0$	$\log AN_0$	1.116	1.166	85	0.582	0.000	0.396	6.19
$\log AN_m$	$\log T_0$	−0.009	−0.139	85	0.007	0.462	0.359	5.22
$\log AN_m$	$\log I_0$	−0.708	0.899	69	0.560	0.000	0.255	3.24
$\log AN_m$	$\log PO_4$	−0.358	0.385	81	0.171	0.000	0.335	4.68
$\log AN_m$	$\log Si$	−0.793	0.323	85	0.214	0.000	0.319	4.35
$\log AN_m$	$\log(NO_2 + NO_3)$	−0.236	0.135	85	0.066	0.018	0.349	4.99
$\log Z_{phs}$	$\log Chl_0$	1.240	−0.543	85	0.432	0.000	0.277	3.58

y—Dependent variable, x—independent variable, a and b—regression coefficients, N—number of observations, R^2—coefficient of determination, p—regression equation accuracy, m—standard error of regression, F—index of y variability at a given x.

entire photosynthetic layer, in which the organic matter was formed at a low rate.

Dependence of primary production and assimilation activity of phytoplankton on the insolation level. It is known that the main abiotic factors limiting the primary production of Arctic seas are the content of the main biogenic elements, the level of surface and subsurface irradiance, and temperature [54]. However, it is not clear which factor is the key factor limiting PP_{int} in the Arctic in a given season [52].

Previous studies have shown that, on the scale of the entire World Ocean, the level of incident solar radiation has little effect on the PP_{int} value due to, on the one hand, the development of photoadaptive mechanisms and, on the other hand, the inhibition of photosynthesis at high I_0 values [25]. A priori it can be assumed that, in the Arctic seas, the influence of light conditions on the level of primary production should be more substantial, especially at the end of the vegetative season, due to the low level of daily PAR, associated with the low angle of the sun above the horizon and a decrease in daylight hours [54]. In riverine runoff areas, in addition to incident radiation, PP_{int} is limited by subsurface irradiance due to low water transparency [3, 55].

In the period from the end of August to the beginning of October, I_0 values ranged from 1.56 to 32.07 Ein/m^2 per day. The wide range of values of this index revealed the significant dependence of the depth-integrated primary production and the maximum assimilation number on the level of incident solar radiation (Table 2). We have shown a linear relationship between the logarithms of PP_{int} and AN_m, on the one hand, and the I_0 value, on the other hand, with a high coefficient of determination ($R^2 = 0.569$ and 0.560, respectively) (Fig. 5). Earlier, a linear relationship between AN and I_0 was found in summer in some areas of the Canadian Arctic [50]. The low level of insolation largely determined the generally low (<100 mg C/m^2 per day) PP_{int} values in the major part of the Kara Sea water area.

In a number of studies, light conditions, together with the content of biogenic elements, are considered a key factor limiting the primary production in the Arctic seas in spring and summer [22, 40, 43]. In autumn, at the end of the vegetative season, the level of insolation apparently becomes crucial in determining the conditions for the formation of the primary production [26, 34, 50, 63]. In September 1993, the low level of insolation in the Kara Sea limited PP_{int} in the Ob Estuary [3]. In the second half of September 2011, I_0 values did not exceed 12 Ein/m^2 per day; the lowest (2–7 Ein/m^2 per day) value of incident solar radiation was recorded in the area of the St. Anna Trough and near the Novaya Zemlya archipelago in late September to early October [15]. These extremely low I_0 values, together with the low water transparency in these areas (on average, 10 m according to Secchi depth), limited the depth of the photosynthetic layer and led to a decrease in PP_{int}.

Dependence of primary production and assimilation activity of phytoplankton on the content of main biogenic elements. In this work, we studied the relationship of the production characteristics of phytoplankton with the

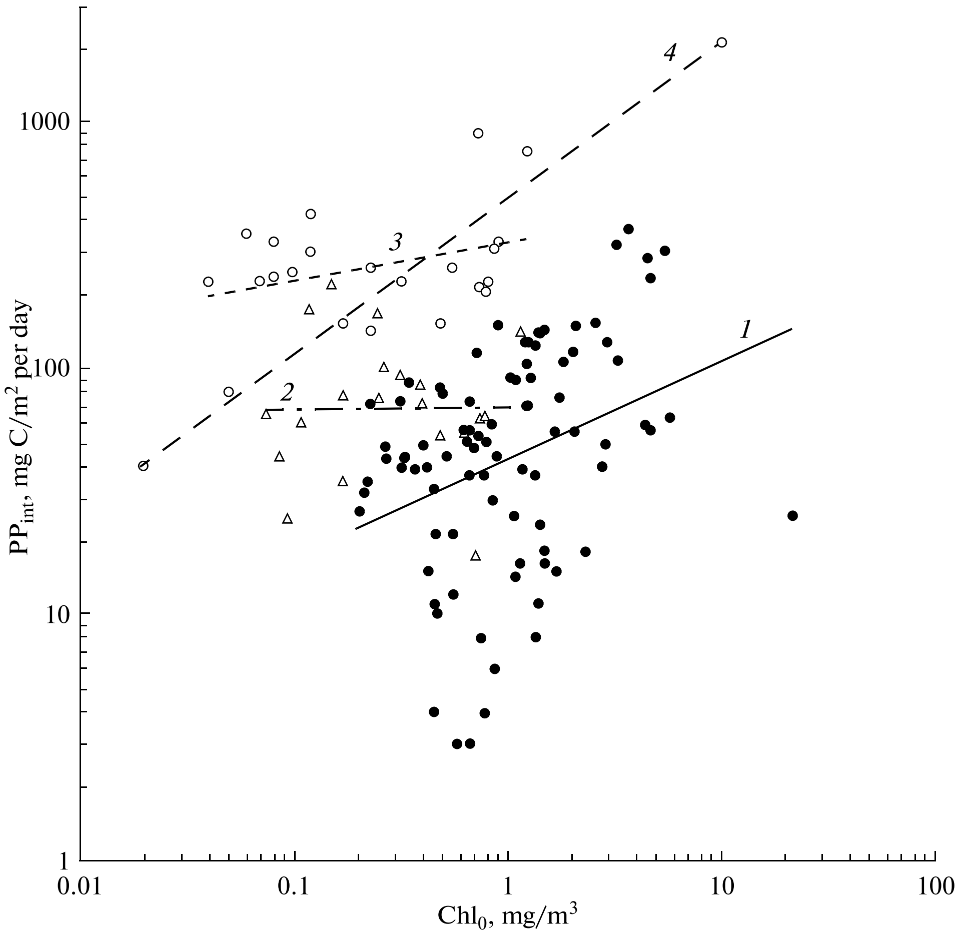

Fig. 3. Datasets and regression lines characterizing the dependence of the depth-integrated primary production (PP_{int}) on chlorophyll a content on the surface (Chl_0) in different cold-water areas of the World Ocean: (*1*) the Kara Sea (present study); (*2*) Barents and Pechora seas [4, 5]; (*3*) Chukchi and Beaufort seas [49]; (*4*) areas of the World Ocean polarward 40° [10].

mean concentrations of biogenic elements (PO_{4av}, $NO_2 + NO_{3av}$, NH_{4av}, and Si_{av}) in the photosynthetic layer. Correlation analysis showed a closer correlation of these indices with PP_{int} and AN_m than with the content of biogenic elements on the surface.

In autumn, the content of PO_{4av} in the Kara Sea varied from 0.04 to 2.08 μM; the concentration of $NO_2 + NO_{3av}$ varied from 0.04 to 7.79 μM; the content of dissolved silicon varied from 0.38 to 112.62 μM; and the content of ammonia nitrogen varied from 0.09 to 4.37 μM. The average concentrations of biogenic elements in different areas indicate the limitation of the growth and photosynthesis of phytoplankton by dissolved nitrogen forms in September and early October in almost the entire water area of the Kara Sea, except for the Ob estuary (Table 3). The concentration of phosphates in the photosynthetic layer was slightly higher than the limiting values in the southwestern area (0.23 μM), 2.2–6.2 times higher in the Ob and Yenisei estuaries and in the riverine runoff area, and slightly lower than the limiting values in the northern WM (0.18 μM) [32]. The content of dissolved Si may be a limiting factor for phytocene development in the southwestern region and in the waters of the St. Anna Trough, despite its mean concentrations in these areas (2.74–4.77 μM), exceeding the upper limit of the limiting concentrations [32]. It is known that, at low water temperatures in the Arctic and Antarctic, low silicon-regeneration rates can limit photosynthesis even for high Si content [36, 61].

The N/P ratio was less than 16 [53] in all studied areas of the Kara Sea (Table 3). This result was in agreement with the notions of the basic role of nitrogen as the limiting element in the phytoplankton development in the Arctic seas [30, 59, 60]. The analysis of the variability in the Si/N ratio also shows preferential depletion of dissolved nitrogen forms as compared to silicon in the subsurface layer of the Kara Sea in autumn (Si/N > 1.44).

It is known that riverine runoff in Arctic seas is enriched in dissolved forms of nitrogen and silicon as compared to phosphates [33, 47]. Therefore, it can be assumed that the growth and photosynthesis of phytoplankton in the estuarine brackish-water areas of the Kara Sea will be limited by PO4 [54]. On the other hand, it was noted that the dissolved phosphorus is

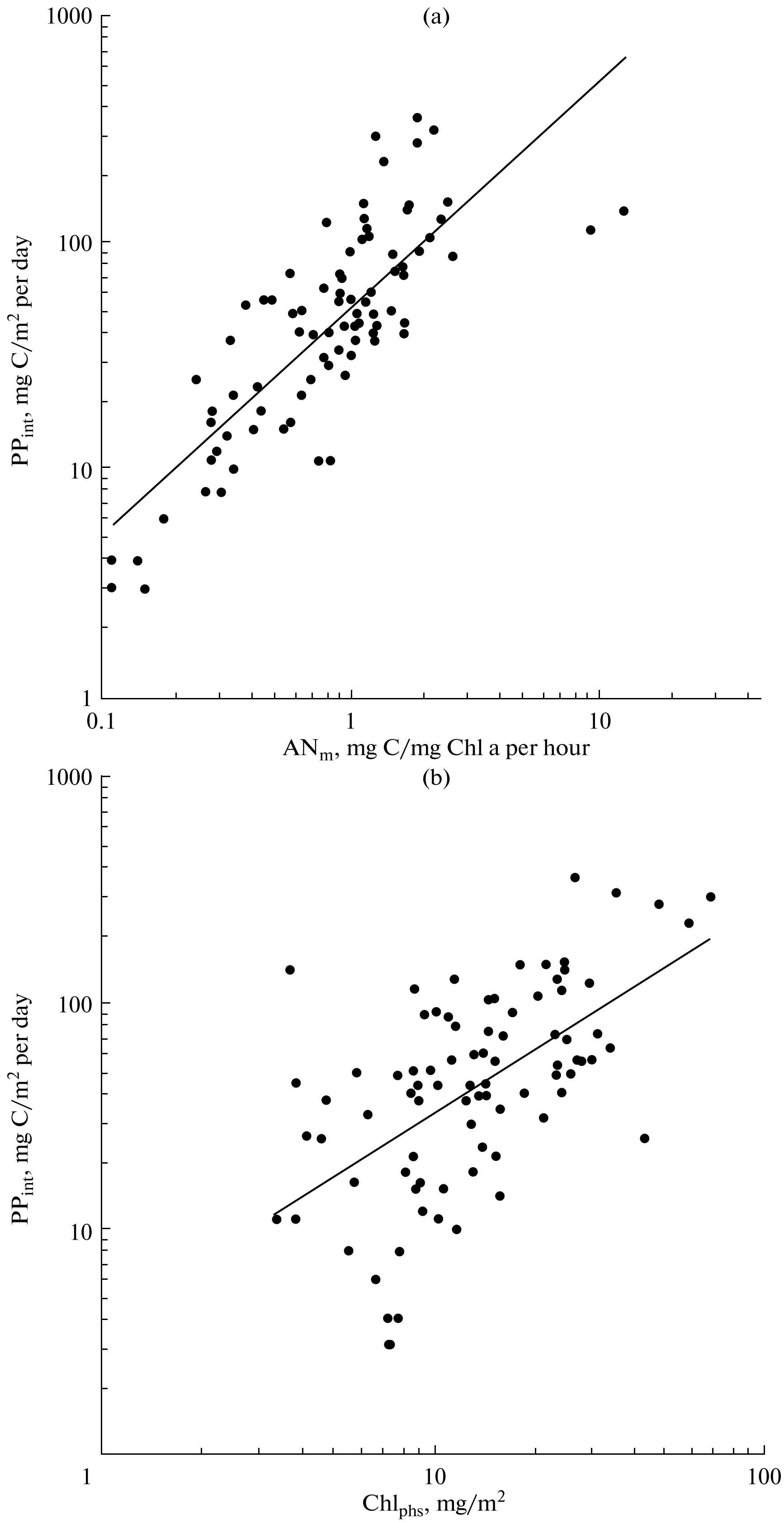

Fig. 4. Dataset and regression lines characterizing the dependence of the depth-integrated primary production (PP_{int}) on the values of (a) maximum assimilation number (AN_m) and (b) Chl a content in the photosynthetic layer (Chl_{phs}) in the Kara Sea.

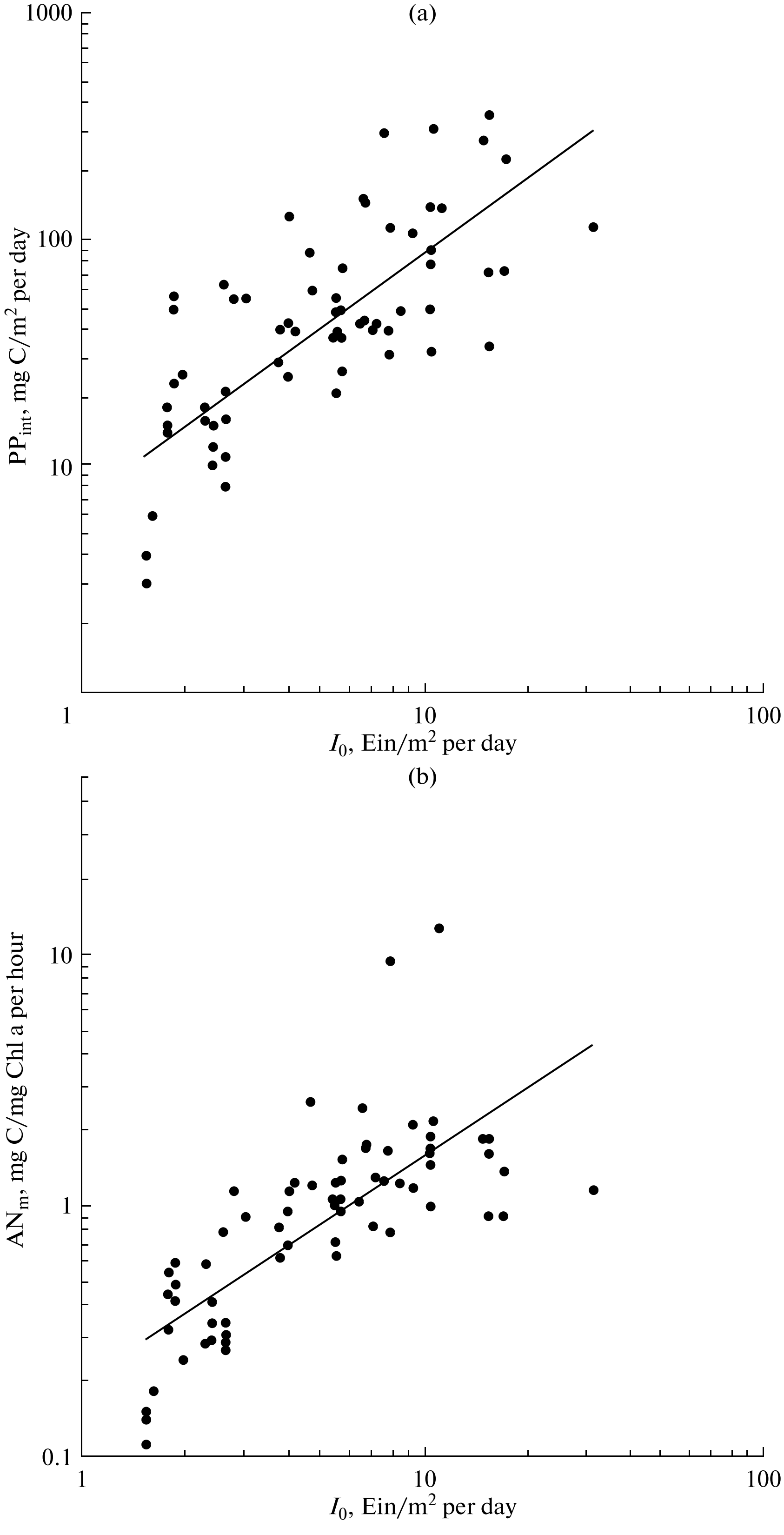

Fig. 5. Dataset and regression lines characterizing the dependence of (a) depth-integrated primary production (PP_{int}) and (b) maximum assimilation number (AN_m) on the level of subsurface solar radiation in the PAR range (I_0).

Table 3. Variability of abiotic factors in different regions of the Kara Sea

Parameter	Southwestern water mass			Ob Estuary			Yenisei Estuary			Ob–Yenisei riverine runoff area			St. Anna Trough (northern water mass)		
	M	cv	*N*	*M*	cv	*N*	*M*	cv	*N*	*M*	cv	*N*	*M*	cv	*N*
T_0	4.84	19	29	5.29	29	11	7.59	25	12	3.99	44	34	3.31	35	20
S_0	24.93	28	29	2.90	102	11	3.47	115	12	19.10	23	34	31.11	9	20
I_0	10.76	35	11	2.87	27	4	7.37	73	12	6.53	94	28	3.81	43	13
PO_{4av}	0.23	30	11	1.24	34	7	0.43	95	12	0.52	60	27	0.18	71	18
$NO_2 + NO_{3av}$	1.84	91	14	3.04	34	7	1.57	104	12	1.36	113	28	1.00	121	18
NH_{4av}	0.54	56	6	2.11	51	4	1.75	67	12	0.81	57	24	0.67	47	18
Si_{av}	4.77	93	14	36.60	54	7	64.57	61	12	19.75	56	28	2.74	97	18
Si/N	28.90	204	14	15.02	49	7	90.43	101	12	68.89	197	28	8.46	131	18
Si/P	25.45	99	11	33.73	24	7	316.92	102	12	54.31	123	27	16.88	99	18
N/P	6.96	66	11	3.91	63	7	12.79	92	12	4.36	50	27	9.85	30	18
$NH_4/\Sigma N$	0.61	53	6	0.39	26	4	0.55	47	12	0.48	62	24	0.56	55	18
UML	9	52	29	10	72	11	10	78	12	7	34	34	7	63	20
$\Delta\sigma_t$	6.90	108	29	9.62	53	7	24.38	73	9	23.46	96	30	19.54	101	20

present in excess in the surface waters of Arctic seas even in summer, when its concentrations are minimal [36]. The analysis of the generalized data for the content of biogenic elements in the Kara Sea in autumn led us to conclude that the content of PO_4 in the photosynthetic layer was a weaker limiting factor in the development of the phytoplankton community than the concentration of $NO_2 + NO_3$.

It is of interest to consider the variability of the ratio of ammonium nitrogen to the sum of its dissolved forms ($NH_4/\Sigma N$) as an index of possible compensation for mineral nutrition with the regenerative forms of N. The $NH_4/\Sigma N$ ratio increased, on average, by 1.6: from 0.39 in the Ob Estuary to 0.61 in the southwestern region (Table 3). This ratio and the relatively high content of NH_4 (on average, 0.54–2.11 μM in different areas) indicate the major role played by NH_4 as a buffer preventing the nitrogen starvation of phytoplankton in autumn. The great importance of the reduced forms of nitrogen in the mineral nutrition of phytoplankton has been repeatedly noted earlier for other Arctic areas [37, 42].

Regression analysis showed that PP_{int} and AN_m directly depended on the content of phosphates in the photosynthesis layer at low coefficients of determination ($R^2 = 0.216$ and 0.171, respectively). A weak correlation was also found between PP_{int} and AN_m, on the one hand, and $NO_2 + NO_3$, on the other hand ($R^2 =$ 0.150 and 0.083, respectively). It is known that a direct relationship between production characteristics and biogenic elements in Arctic often cannot be established [28, 36, 38]. This phenomenon can be explained by differences at the time of enrichment of the euphotic zone with mineral elements and processes of intensive synthesis of organic matter, the use of reduced forms of biogenic elements by phytoplankton, as well as by the successional changes in its species and size composition. The closest correlation was observed between PP_{int}, AN_m, and the content of dissolved silicon ($R^2 = 0.352$ and 0.214, respectively), which is indicative of the dominant role of diatom assemblages in the phytoplankton community at the majority of stations of the Kara Sea [17, 48].

The comparison of the degree of correlation of PP_{int} and AN_m with the level of incident PAR and the content of the main biogenic elements in the photosynthetic layer showed that, in September and early October, the value of the productive parameters of phytoplankton in the Kara Sea were largely determined by I_0 values. The weak correlation with the phosphate concentration and the sum of nitrite and nitrate nitrogen can be explained by the low assimilation activity of phytoplankton at the end of the vegetative season, when possible additional supply of biogenic elements to the euphotic layer, due to local upwelling and vertical turbulent mixing, does not significantly increase depth-integrated primary production.

ACKNOWLEDGMENTS

This study was supported by the Russian Foundation for Basic Research (project no. 13-05-00029 a) and the Russian Science Foundation (projects nos. 14-17-00681 (field studies) and 14-50-00095 (office studies)).

REFERENCES

1. A. S. Bychkov, G. Yu. Pavlova, and V. A. Kropotov, "Carbonate system," in *Chemistry of the Sea Water and Autogenic Mineral Formation* (Nauka, Moscow, 1989), 49–111 [in Russian].
2. Yu. A. Bobrov, V. M. Savinov, and P. R. Makarevich, "Chlorophyll and primary production," in *Ecology and Bioresources of the Kara Sea* (Kola Scientific Cen-

ter, Academy of Sciences of USSR, Apatity, 1989), pp. 45–50 [in Russian].

3. V. I. Vedernikov, A. B. Demidov, and A. I. Sud'bin, "Primary production and chlorophyll in the Kara Sea in September 1993," Okeanologiya (Moscow) **34** (5), 693–703 (1994).

4. V. I. Vedernikov and V. I. Gagarin, "Primary production and chlorophyll in the Barents Sea in September–October, 1997," Okeanologiya (Moscow) **38** (5), 642–649 (1998).

5. V. I. Vedernikov, V. I. Gagarin, and V. I. Burenkov, "Features of distribution of primary production and chlorophyll in the Pechora Sea in August–September 1998," Okeanologiya (Moscow) **41** (1), 64–74 (2001).

6. A. A. Vetrov, "Chlorophyll, primary production, and organic carbon fluxes in the Kara Sea," Oceanology (Engl. Transl.) **48** (1), 33–42 (2008).

7. M. E. Vinogradov, V. I. Vedernikov, E. A. Romankevich, and A. A. Vetrov, "Components of the carbon cycle in the Russian Arctic seas: primary production and flux of corg from the photic layer," Okeanologiya (Moscow) **40** (2), 204–215 (2000).

8. M. E. Vinogradov, E. A. Shushkina, L. P. Lebedeva, et al., "Mesoplankton of the eastern Kara Sea and Ob' and Yenisei estuaries," Okeanologiya (Moscow) **34** (5), 716–723 (1994).

9. M. E. Vinogradov, E. A. Shushkina, O. V. Kopelevich, and S. V. Sheberstov, "Photosynthetic productivity of the World ocean from satellite and expeditionary data," Oceanology (Engl. Transl.) **36** (4), 531–540 (1996).

10. M. E. Vinogradov, E. A. Shushkina, N. P. Nezlin, V. I. Vedernikov, and V. I. Gagarin, "Correlation between different parameters of the ecosystem of the epipelagic zone of the World ocean," Oceanology (Engl. Transl.) **39** (1), 54–63 (1999).

11. N. M. Knipovich, *Hydrology of Seas and Saline Waters* (Pishchepromizdat, Moscow, 1938) [in Russian].

12. O. I. Koblents-Mishke, "Primary production," in *Pacific Ocean*, Vol. 7: *Biology of the Pacific Ocean*, Book 1: *Plankton* (Nauka, Moscow, 1967), pp. 86–97 [in Russian].

13. O. I. Koblents-Mishke and V. I. Vedernikov, "Primary production," in *Biology of an Ocean*, Vol. 2: *Biological Productivity of an Ocean* (Nauka, Moscow, 1977), pp. 183–209 [in Russian].

14. S. A. Mosharov, "Distribution of the primary production and chlorophyll a in the Kara Sea in September of 2007," Oceanology (Engl. Transl.) **50** (6), 884–892 (2010).

15. S. A. Mosharov, A. B. Demidov, and U. V. Simakova, "Specific processes of primary production in the Kara Sea by the end of vegetation period," Okeanologiya (Moscow) (in print).

16. *Handbook on Chemical Analysis of the Sea Water, RD 52.10.242-92* (Gidrometeoizdat, St. Petersburg, 1993) [in Russian].

17. I. N. Sukhanova, M. V. Flint, S. A. Mosharov, and V. M. Sergeeva, "Structure of the phytoplankton communities and primary production in the Ob River estuary and over the adjacent Kara Sea shelf," Oceanology (Engl. Transl.) **50** (5), 743–758 (2010).

18. *Modern Hydrochemical Analysis Methods of an Ocean*, Ed. by O. K. Bordovskii and V. N. Ivanenkov (Shirshov Scientific Research Institute of Oceanology, Academy of Sciences of USSR, Moscow, 1992) [in Russian].

19. M. V. Flint, T. N. Semenova, E. G. Arashkevich, I. N. Sukhanova, V. I. Gagarin, V. V. Kremenetskiy, M. A. Pivovarov, and K. A. Soloviev, "Structure of the zooplankton communities in the region of the Ob River's estuarine frontal zone," Oceanology (Engl. Transl.) **50** (5), 766–779 (2010).

20. V. V. Khlebovich, *Maximum Salinity for Biological Processes* (Nauka, Leningrad, 1974) [in Russian].

21. D. Antoine, J.-M. André, and A. Morel, "Oceanic primary production 2. Estimation at global scale from satellite (coastal zone color scanner) chlorophyll," Global Biogeochem. Cycles **10** (1), 57–69 (1996).

22. M. Ardyna, M. Gosselin, C. Michel, et al., "Environmental forcing of phytoplankton community structure and function in the Canadian High Arctic: contrasting oligotrophic and eutrophic regions," Mar. Ecol.: Progr. Ser. **442**, 37–57 (2011).

23. K. R. Arrigo, G. L. van Dijken, and S. Pabi, "Impact of a shrinking Arctic ice cover on marine primary production," Geophys. Res. Lett. **35**, 19603 (2008). doi 10.1029/2008GL035028

24. K. R. Arrigo and G. L. van Dijken, "Secular trends in Arctic Ocean net primary production," J. Geophys. Res., C: Oceans Atmos. **116**, 09011 (2011). doi 10.1029/2011JC007151

25. M. J. Behrenfeld and P. G. Falkowski, "A consumer's guide to phytoplankton primary productivity models," Limnol. Oceanogr. **42** (7), 1479–1491 (1997).

26. S. Brugel, C. Nozais, M. Poulin, et al., "Phytoplankton biomass and production in the southeastern Beaufort Sea in autumn 2002 and 2003," Mar. Ecol.: Progr. Ser. **377**, 63–77 (2009).

27. M.-E. Carr, M. A. M. Friedrichs, M. Schmeltz, et al., "A comparison of global estimates of marine primary production from ocean color," Deep Sea Res., Part II **53** (5–7), 741–770 (2006).

28. G. F. Cota, L. R. Pomeroy, W. G. Harrison, et al., "Nutrients, primary production, and microbial heterotrophy in the southeastern Chukchi Sea: Arctic summer nutrient depletion and heterotrophy," Mar. Ecol.: Progr. Ser. **135**, 247–258 (1996).

29. E. C. Carmack, D. Barber, J. Christensen, et al., "Climate variability and physical forcing of the food webs and the carbon budget on panarctic shelves," Progr. Oceanogr. **71** (2–4), 145–181 (2006).

30. E. C. Carmack, R. W. Macdonald, and S. Jasper, "Phytoplankton productivity on the Canadian shelf of the Beaufort Sea," Mar. Ecol.: Progr. Ser. **277**, 37–50 (2004).

31. F. E. Croxton, *Elementary Statistics with Applications in Medicine and Biological Sciences* (Dover, New York, 1959).

32. T. R. Fisher, E. R. Peele, J. W. Ammerman, and L. W. J. Harding, "Nutrient limitation of phytoplankton in Chesapeake Bay," Mar. Ecol.: Progr. Ser. **82**, 51–63 (1992).

33. V. V. Gordeev, J. M. Martin, I. S. Sidorov, and M. V. Sidorova, "A reassessment of the Eurasian river input of water, sediment, major elements and nutrients to the Arctic Ocean," Am. J. Sci. **296** (6), 664–691 (1996).

34. E. N. Hegseth, "Phytoplankton of the Barents Sea—the end of a growth season," Polar Biol. **17** (3), 235–241 (1997).
35. D. Hanzlick and K. Aagaard, "Freshwater and Atlantic water in the Kara Sea," J. Geophys. Res., C: Oceans Atmos. **85** (9), 4937–4942 (1980).
36. W. G. Harrison and G. F. Cota, "Primary production in the polar waters: relation to nutrient availability," Polar Res. **10** (1), 87–104 (1991).
37. W. G. Harrison, B. Irwin, and T. Platt, "Primary production and nutrient assimilation by natural phytoplankton population of the eastern Canadian Arctic," Can. J. Fish. Aquat. Sci. **39** (2), 335–345 (1982).
38. W. G. Harrison and T. Platt, "Photosynthesis-irradiance relationships in polar and temperate phytoplankton populations," Polar Biol. **5** (3), 153–164 (1986).
39. H. J. Hirche, K. N. Kosobokova, B. Gaye-Haake, et al., "Structure and function of contemporary food webs on Arctic shelves: a panarctic comparison the pelagic system of the Kara Sea – communities and components of carbon flow," Progr. Oceanogr. **71** (2–4), 288–313 (2006).
40. V. Hill and G. Cota, "Spatial patterns of primary production on the shelf, slope and basin of the Western Arctic in 2002," Deep Sea Res., Part II **57** (24–26), 3344–3354 (2005).
41. M. Jakobsson, A. Grantz, Y. Kristoffersen, and R. Macnab, "Bathymetry and physiography of the Arctic Ocean and its constituent seas," in *The Organic Carbon Cycle in the Arctic Ocean*, Ed. by R. Stein and R. W. Macdonald (Springer-Verlag, Berlin, 2004), pp. 1–6.
42. S. Kristiansen and B. A. Lund, "Nitrogen cycling in the Barents Sea – I. Uptake of nitrogen in the water column," Deep Sea Res., Part I **36** (2), 255–268 (1989).
43. S. H. Lee and T. E. Whitledge, "Primary and new production in the deep Canada basin during summer 2002," Polar Biol. **28** (3), 190–197 (2005).
44. P. R. Makarevich, N. V. Druzhkov, V. V. Larionov, and E. I. Druzhkova, "The freshwater phytoplankton biomass and its role in the formation of a highly productive zone on the Ob-Yenisei shallows (southern Kara Sea)," in *Siberian River Run-Off in the Kara Sea*, Ed. by R. Stein, et al. (Elsevier, Amsterdam, 2003), pp. 185–193.
45. P. N. Makkaveev, "The total alkalinity in the anoxic waters of the Black sea and in sea-river mixture zones," in *Joint IOC-JGOFS CO_2 Advisory Panel Meeting, Seven Session, Annex V* (Intergovernmental Oceanographic Commission, UNESCO, 1998).
46. F. J. Millero, "Thermodynamics of the carbon dioxide system in oceans," Geochim. Cosmochim. Acta **59** (4), 661–677 (1995).
47. R. W. Macdonald, C. S. Wong, and P. E. Erickson, "The distribution of nutrients in the southeastern Beaufort Sea: Implication for water circulation and primary production," J. Geophys. Res., C: Oceans Atmos. **92** (3), 2939–2952 (1987).
48. E.-M. Nöthig, Y. Okolodkov, V. V. Larionov, and P. R. Makarevich, "Phytoplankton distribution in the inner Kara Sea: a comparison of three summer investigations," in *Siberian River Run-Off in the Kara Sea*, Ed. by R. Stein, et al. (Elsevier, Amsterdam, 2003), pp. 163–183.
49. S. Pabi, G. L. van Dijken, and K. R. Arrigo, "Primary production in the Arctic Ocean, 1998–2006," J. Geophys. Res., C: Oceans Atmos. **113**, 08005 (2008). doi 10.1029/2007/JC004578
50. T. Platt, W.G. Harrison, E. P. W. Horne, and B. Irwin, "Carbon fixation and oxygen evolution by phytoplankton in the Canadian High Arctic," Polar Biol. **8** (2), 103–113 (1987).
51. S. Pivovarov, R. Schlitzer, and A. Novikhin, "River runoff influence on the water mass formation in the Kara Sea," in *Siberian River Run-Off in the Kara Sea*, Ed. by R. Stein, et al. (Elsevier, Amsterdam, 2003), pp. 9–25.
52. E. E. Popova, A. Yool, A. C. Coward, et al., "What controls primary production in the Arctic Ocean? Results from an intercomparison of five general circulation models with biogeochemistry," J. Geophys. Res., C: Oceans Atmos. **117**, 00D12 (2012). doi 10.1029/2011JC007112
53. A. C. Redfield, B. H. Ketchum, and F. A. Richards, "The influence of organisms on the composition of sea water," in *The Sea, Ideas, and Observation* (Interscience, New York, 1963), Vol. 2, pp. 26–77.
54. E. Sakshaug, "Primary and secondary production in the Arctic Seas," in *The Organic Carbon Cycle in the Arctic Ocean*, Ed. by R. Stein and R. W. Macdonald (Springer-Verlag, Berlin, 2004), pp. 57–81.
55. Yu. I. Sorokin and P. Yu. Sorokin, "Plankton and primary production in the Lena River estuary and in the south-eastern Laptev Sea," Estuarine, Coast. Shelf Sci. **43** (4), 399–418 (1996).
56. N. E. Steemann, "The use of radioactive carbon (C^{14}) for measuring organic production in the sea," J. Cons. Perm. Ins. Explor. Mer, No. 18, 117–140 (1952).
57. R. Stein, "Circum Arctic river discharge and its geological record," Int. J. Earth Sci. **89**, 447–449 (2000).
58. C. W. Sullivan, K. R. Arrigo, C. R. McClain, et al., "Distribution of phytoplankton blooms in the Southern Ocean," Science **262**, 1832–1837 (1993).
59. J.-E. Tremblay, C. Michel, and K. A. Hobson, "Bloom dynamics in early opening waters of the Arctic Ocean," Limnol. Oceanogr. **51** (2), 900–912 (2006).
60. J.-E. Tremblay and J. Gagnoon, "The effect of irradiance and nutrient supply on the productivity of Arctic waters: a perspective on climate change," in *Influence of Climate Change on the Changing Arctic and Sub-Arctic Condition*, Ed. by J.C.J. Nihoul (Springer-Verlag, New York, 2009), pp. 73–94.
61. P. Treguer, A. Kamatani, S. Gueneley, and B. Queguiner, "Kinetics of dissolution of Antarctic diatom frustules and the biogeochemical cycle of silicon in the Southern Ocean," Polar Biol. **9** (6), 397–403 (1989).
62. A. A. Vetrov and E. A. Romankevich, "Primary production and fluxes of organic carbon to the seabed in the Russian arctic seas as a response to the recent warming," Oceanology (Engl. Transl.) **51** (2), 255–266 (2011).
63. M. S. Yun, K. H. Chung, S. Zimmermann, et al., "Phytoplankton productivity and its response to higher light levels in the Canada basin," Polar Biol. **35** (2), 257–268 (2012).

Translated by M. Batrukova