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ORIGINAL PAPERS

The Influence of Phytoplankton Primary Production on the Cycle of Biogenic Elements in the Coastal Waters off Sevastopol, Black Sea

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Abstract—The phytoplankton primary production and the biogenic elements content of the coastal waters off Sevastopol have been studied as a result of 2-year monitoring. It has been found that mineral phosphorus is a key factor of chemical limitation of the production processes. During primary production of organic matter, the habitat conditions for phytoplankton in the photic layer are in accordance with the Le Chatelier–Braun principle of negative feedback.

Keywords: coastal waters, Sevastopol, primary production, phytoplankton, biogenic elements, Le Chatelier–Braun principle

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INTRODUCTION

One of the major environmental problems of the Black Sea is the hypereutrophication of waters [3]. The increase in the intensity of fluxes of biogenic elements into the marine environment with atmospheric precipitation, river waters, and terrestrial runoff caused an increased primary production of waters, a change in the species diversity of aquatic organisms in coastal ecosystems, [8] and, in a number of cases, a transformation of their functional and energy states from the resistant mode of homeostasis to the adaptive one [5].

Studies have shown that in the Black Sea the concentration of nitrates, which limits the primary production of waters, is 2 μg-at/L. At the same time, it was noted that the total nitrate and nitrite content in the range of 0.06–0.97 μg-at/L did not correlate with the value of primary production [2]. The 4- to 5-fold increase in the concentration of nitrates in the Black Sea at the first phase of eutrophication did not cause the concentration of chlorophyll *a* in water to increase, which indicated that the mineral nutrition of phytoplankton in the summer months occurs mainly due to regenerated biogenic elements [31]. According to the data on phosphorus metabolism, a quite high level of primary production of Black Sea waters, up to 100 mgC/(m^3 day), is provided even at an extremely low (not higher than 0.1 μg-at/L) phosphate concentration in water [24]. A conclusion was drawn that the light and biogenic elements, as a rule, weakly limit the rate of phytoplankton growth in the layer 0–1 m of coastal waters in the Black Sea [25]. However, it was found that in the areas of the Black Sea exposed to eutrophication there was a statistically significant decrease in the mean annual concentrations of mineral phosphorus in the photosynthetic layer and an increase in its level in the underlying waters at depths of 50–100 m [27].

As shown by studies of the metabolic mechanisms of mineral nutrition in algae, they are able to intensively and rapidly extract phosphorus from water and also to store it in cells in amounts that exceed their immediate needs [11]. In experiments with radioactive ^{32}P, it was found that the excess uptake of phosphorus by single-celled algae is caused by its intracellular absorption [6]. It should be noted that no explanation the above-mentioned patterns of interaction of phytoplankton with biogenic elements in the marine environment has been found as yet.

The goal of this work was to study the patterns of variations in primary phytoplankton production and intensity of biogenic elements cycle in coastal ecosystems of the Black Sea during a 2-year monthly monitoring at the reference station located near the city of Sevastopol.

MATERIALS AND METHODS

The experimental studies were conducted from May 2012 to May 2014 in the coastal waters of the Black Sea in the vicinity of the city of Sevastopol, off the eastern cape at the entrance to Karantinnaya Bay. The water temperature and illuminance (using a Yu-116 lux meter) were measured in the surface layer of water (0–0.5 m) at the reference station (44° 36.930′ N, 33° 30.177′ E) each month. The concentrations of mineral forms of nitrogen and phosphorus, the specific weight of suspended matter, and the primary production were also determined.

To study the primary production of organic matter (OM), we used the radiocarbon method based on the assumption that the labeled carbon (in the form of $Na_2{}^{14}CO_3$ or $NaH^{14}CO_3$) introduced in flasks becomes involved in the processes of OM photosynthesis at the same rate as the stable carbon isotope (^{12}C). Primary production was determined according to the standard protocol: water sampling, introduction of the isotope, exposure, filtration, and measuring the radioactivity of filters. When the experiments were set up, light and dark plastic flasks with 67-mL portions of water with ^{14}C added, were placed under conditions similar to those in situ (at the place of water sampling) for 1- to 3-day exposure; within this period, it is possible to obtain primary production close to the "pure" type. To calculate the rate of OM production, the following formula was used: $C_{ph} = C_K$ r/R, where C_{ph} is the value of photosynthesis (mgC/L); C_K is the total amount of carbon (mgC/L) in all forms of carbon dioxide in water (CO_2, HCO_3^-, CO_3^{2-}); r is radioactivity (kBq/L) received by phytoplankton; and R is the radioactivity (kBq/L) introduced into the experimental flasks and measured under the same conditions as r [13]. To calculate the primary production of OM by phytoplankton, a value of C_K equal to 36 mgC/L was used [10]; the initial radioactivity of ^{14}C in flasks (R) was 50 kBq/L and the relative error of determining the primary production was 18%. The radiometric measurements of ^{14}C in the water aliquots from the incubated flasks and in the suspended matter, precipitated into fractions on Sartorius membrane filters with a minimum pore size of 0.2–0.3 μm, were performed on a RackBeta-1219 beta spectrometer by using Opti-Phase-II scintillation liquid and periodically controlling the spectrometer operation by the ^{14}C-standard.

The concentration of suspended matter in the surface layer of water was determined by the method of membrane filtration [4]. For this, 1.0–1.5 L of water was filtered through pre-weighed nucleopore filters with a pore size of 0.45 μm; the filters were then dried and weighed on a Sartorius microanalytic scale with a measurement accuracy of 0.1 mg. The specific concentration of raw suspended matter in water [C_{SM}, mg wet weight/L] was calculated based on measurements of dry suspended matter [C_{SM}, mg wet weight/L] with a conversion coefficient of 12.5 [4]. The relative error of C_{SM} determination was 32% on average. The hydrochemical parameters of water samples were measured at a certified hydrochemical laboratory of the Department of Aquaculture and Marine Pharmacology, Kovalevsky Institute of Marine Biological Research, Russian Academy of Sciences, in accordance with published techniques [22]. The results of measurements of biogenic element concentration in water had mean relative errors as follows: nitrate ions, range 5–500 μg/L and error 2.7–7.39%; nitrite ions, range 0.5–1000 μg/L, error 1.53–18.02%; ammonium nitrogen, range 15–1500 μg/L, error 1.69–11.4%; and phosphate ions, range 5–100 μg/L, error 4.6%. In this regard, the confidence intervals of observations are not provided in the figures and the relative errors are not higher than those indicated above.

RESULTS

During the 2-year period of observations, the primary production of phytoplankton in the coastal waters off Sevastopol varied from 1.4 to 931.3 mgC/(m^3 day) (Fig. 1a); the dry suspended matter content of water varied from 0.3 to 3.0 mg/L with the maximum values in winter (Fig. 1b); the water temperature and the duration of daylight varied, respectively, from 7 to 26°C (Fig. 1c, curve *1*) and from 8.83 to 15.55 h (Fig. 1c, curve *2*) depending on the season; the concentration of nitrogen compounds in water (μg/L) varied within the ranges of 0.5–8.1 (NO_2), 7.5–653.0 (NO_3), and 1.4–424.2 (NH_4) but did not change significantly from seasons to season (Fig. 1d); the mineral phosphorus content (PO_4) had a winter–spring maxima and varied from 1.1 to 105.1 μg/L (Fig. 1e).

The highest values of primary production were observed in the spring–summer period; the lowest values occurred in autumn and winter. The primary production of over 100 mgC/(m^3 day) recorded in the summer of 2012 and 2013 indicated a hyper-eutrophication of waters [28]. The main biogenic elements that limit the primary production are nitrogen and phosphorus [29, 33]; for the cell protoplasm the normal ratio of weights of the main structural chemical elements is as follows:

$$1P : 7N : 40C \tag{1}$$

According to modern views [9], the ratio of nitrogen and phosphorus for photosynthesis and respiration can be described by the equation:

$$\begin{gathered}106CO_2 + 16NO_3^- + HPO_4^{-2} + 122H_2O + 18H^+ \\ \leftrightarrow C_{106}H_{263}O_{110}N_{16}P + 138O_2,\end{gathered} \tag{2}$$

from which it follows that each newly formed organic substance with a weight of 1000 g will require 80 g carbon, 2 g phosphorus, and 14 g nitrogen. Therefore, the limiting factor in phytoplankton primary production is a biogenic element, whose proportion in the aquatic environment is smaller than the stoichiometric ratio N : P = 16 : 1 in terms of molar concentration or 7 : 1 in terms of weight concentration. Exceeding of the value of this ratio indicates phosphorous limitation; a decreased value means nitrogen limitation. Different components of the nitrogen complex, that is, nitrites (NO_2), nitrates (NO_3), and ammonium (NH_4), were found in the studied water area. For this reason, we

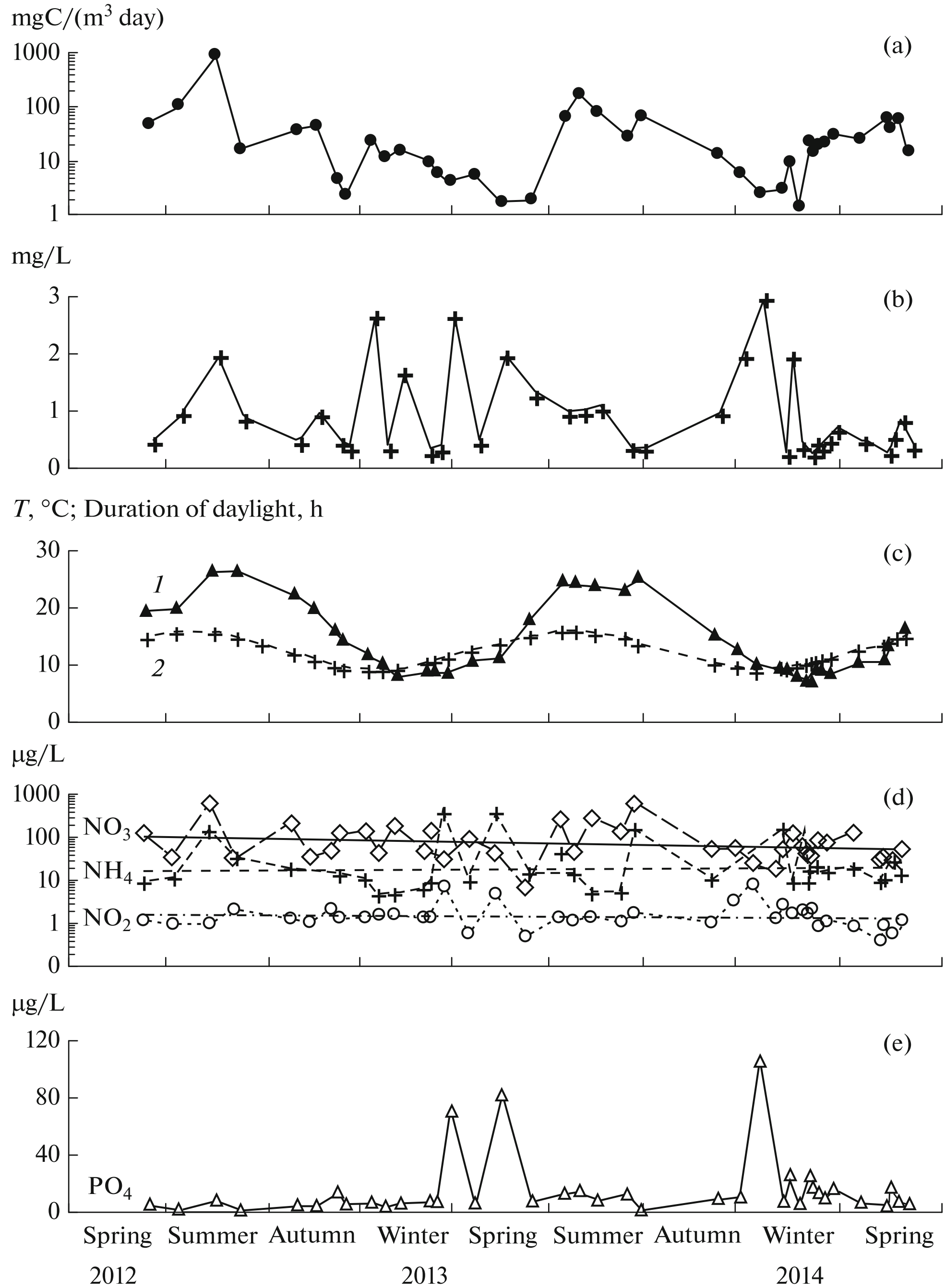

Fig. 1. Seasonal variations in the primary production (a), specific weight of dry suspended matter (b), water temperature (*1*) and duration of daylight (*2*) (c), the concentration of mineral forms of nitrogen (d) and phosphorus (e) in the coastal waters off the city of Sevastopol.

used Redfield's stoichiometric ratio (PR_{at}) to determine the limiting biogenic factor, which had the following form with the constituents (μg/L) included:

$$\begin{aligned}&Pr_{at}(N/P)\\&= 1.53(1.35NO_2 + NO_3 + 3.44NH_4)/PO_4.\end{aligned} \quad (3)$$

As follows from expression (3), when $PR_{at} > 16$, limitation for phosphorus is observed in the study area; when $PR_{at} < 16$, the limitation is for nitrogen. The results of calculations of Redfield's ratio by formula (3) provided a wide range of relative values ($PR_{at} = 1.7–886.5$) and showed (Fig. 2) that over the entire range of temperatures in the surface layer of the coastal waters off Sevastopol, the PR_{at} value, as a rule, was greater than 16. Consequently, the predominantly nitrogen limitation of primary production was not observed. However, the probability of phosphorus

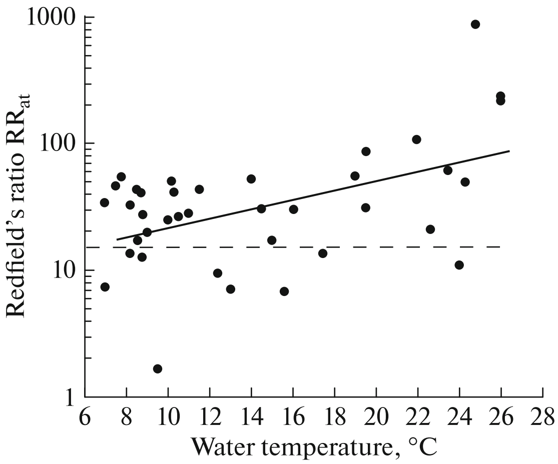

Fig. 2. The relationship between Redfield's stoichiometric ratio (PR_{at}) and water temperature (°C) in the coastal waters off Sevastopol.

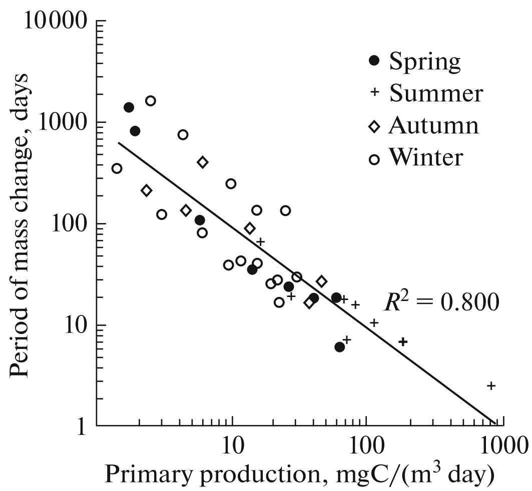

Fig. 3. The relationship of periods of mass change (days) in the coastal waters off Sevastopol with primary production of phytoplankton in the spring, summer, autumn, and winter seasons.

limitation of production process increased in all the seasons of year, especially in the spring–summer period.

The presented materials (Figs. 1a, 1b) indicate that the primary production of phytoplankton made some contribution to the suspended organic matter (SOM) content of water, and this caused its mass change in the photic layer. The periods of SOM mass change at a ratio of organic carbon to raw phytoplankton weight of 1 : 10 were estimated [21, 26]. An analysis of the relationship between the intensity of mass change and primary production of waters (Fig. 3) showed that in the spring and summer seasons the minimum period of SOM mass change was from 3 to 6 days, and in autumn and winter it varied within 18–1700 days. Consequently, in the spring–summer period, the productivity of phytoplankton was a significant factor in the cycle of suspended matter in surface waters of the coastal zone of the Black Sea.

As can be seen from the stoichiometric ratio (1), 1 mg $P{-}PO_4$ (phosphorus of phosphates) and 7 mg $N{-}\Sigma N$ (nitrogen of total mineral complex) is extracted from the aquatic environment per 40 mg organic carbon for phytoplankton production. Taking this into account, the specific fluxes of consumption of phosphate phosphorus [$P_{P-PO_4} = 0.025\ PP_{ph}$ (mg $P{-}PO_4$/(m^3 day)] and mineral nitrogen compounds [$P_{N-\Sigma N} = 0.175\ PP_{ph}$ (mg $N{-}\Sigma N$/(m^3 day)] for phytoplankton production were calculated. By comparing the concentrations of $P{-}PO_4$ and $N{-}\Sigma N$ in water with the corresponding fluxes of their consumption by phytoplankton (P_{P-PO_4} and $P_{N-\Sigma N}$), we found the relationship of periods of the biogenic element cycle (T_P and T_N) in the aquatic environment with primary production (Figs. 4a, 4c) and with water temperature (Figs. 4b, 4d).

It was established that the regression relationships of variations in T_P and T_N with primary production corresponded to straight-line equations on a logarithmic scale of the coordinate axes (Figs. 4a–4c) at a high degree of statistical significance ($R^2 = 0.775$ for $P{-}PO_4$ and $R^2 = 0.681$ for $N{-}\Sigma N$) and power-law behavior, which indicates a power trend in these relationships. The relationship between the periods of the cycle of phosphates and nitrogen compounds and water temperature became apparent at a lower statistical significance ($R^2 = 0.395$ for $P{-}PO_4$ and $R^2 = 0.182$ for $N{-}\Sigma N$). Figure 4 shows that in spring and summer the primary production of phytoplankton is the key factor that affects biogenic elements, mainly phosphates, in the aquatic environment. The essence of this process is that in the absence of chemical limitation the contribution of production processes to the cycle of biogenic elements in the aquatic environment is relatively small. Under conditions of chemical limitation, an acceleration of the biotic cycle of biogenic elements causes the flux of their remobilization in the photic layer to increase, which, in turn, facilitates an increase in the primary production of these waters.

DISCUSSION

Studies of mineral metabolism in aquatic species using radioactive tracers have shown that chemical elements are absorbed from the aquatic environment and can be removed from marine organisms during their lifecycle as a result of metabolic processes [1, 16]. The theoretical model of kinetics of biogenic-element metabolism by phytoplankton has the following form [6]:

$$\frac{dC_A}{dt} = \frac{V_m C_W}{K_m + C_W} - \left[p + \mu_{max}\left(1 - \frac{q_{max}}{C_A}\right)\right]C_A, \qquad (4)$$

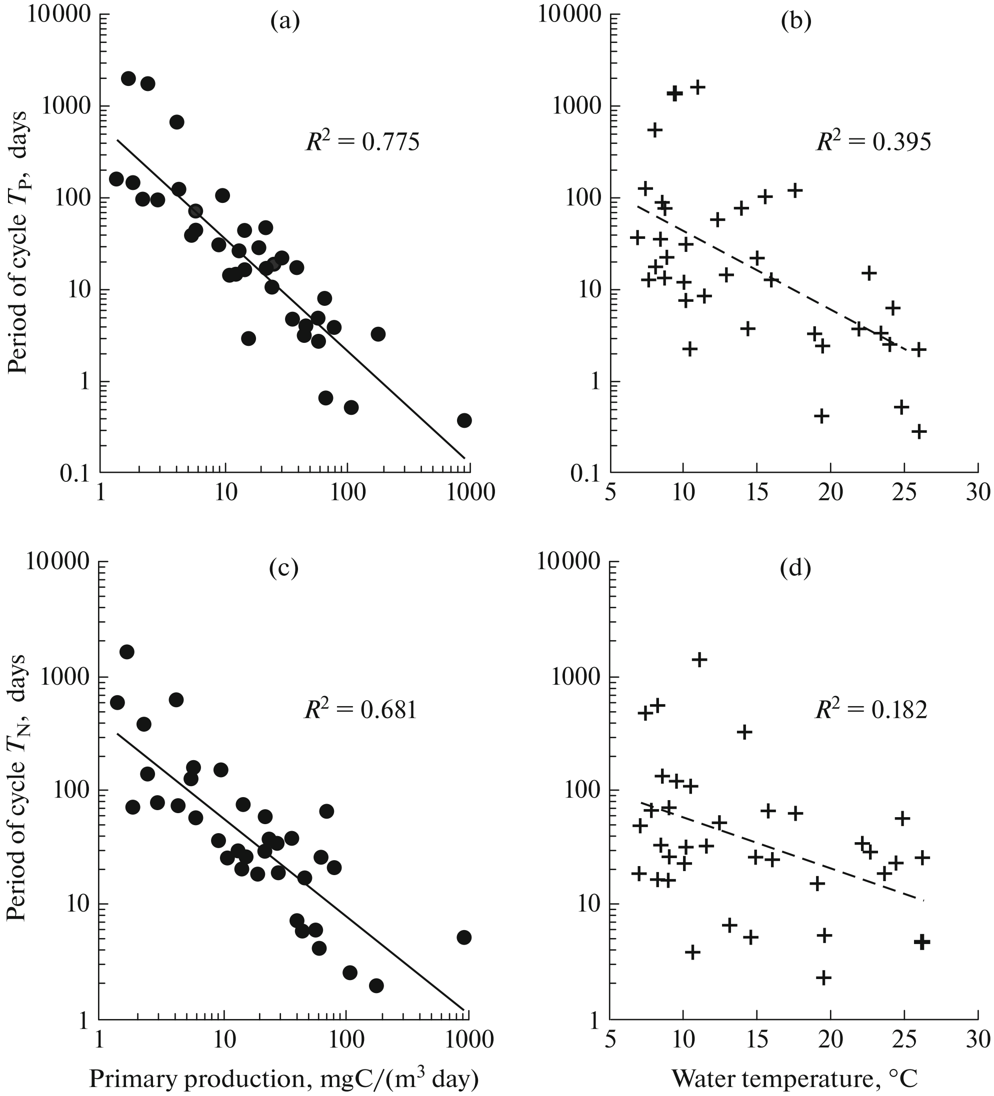

Fig. 4. The relationship between the periods of the cycle of phosphate phosphorus (T_P, days) (a, b) and total mineral nitrogen compounds (T_N, days) (c, d) and phytoplankton primary production (a, c) and water temperature (b, d).

where C_A and C_W are the intracellular concentration of biogenic elements in algae (μg/kg wet weight) and in water (μg/L); V_m is the maximum specific rate of uptake of biogenic elements by algae (μg/kg wet weight per day); K_m is the Michaelis–Menten constant [14], which is numerically equal to the concentration of biogenic elements in water (μg/L), at which the rate of its uptake by phytoplankton constitutes half of the maximum; p is the parameter of the rate of metabolism (i.e., intravital removal) of the elements from phytoplankton cells (1/day); μ_{max} is the maximum physiologically possible specific rate of phytoplankton growth (1/day); and q_{min} is the limiting concentration of biogenic elements in phytoplankton (μg/kg wet weight). The term $\mu_{max}(1 - q_{min}/C_A) = P_{sp}$, which is included in Eq. (4), characterizes the degree of chemical limitation of the specific rate of division of algal cells [32]. This equation shows that the growth rate is limited by the ratio q_{min}/C_A. When the intracellular concentration of the biogenic elements decreases to a value $C_A \approx q_{min}$, production processes cease. As it follows from Eq. (4), the production is limited from below by the element for which the value of q_{min}/C_A is close to 1. In this case, all the other elements can be accumulated by phytoplankton cells to levels that significantly exceed the q_{min}.

According to Eq. (4), at the stationary state of the biogenic elements in the marine environment–unicellular algae system, when $dC_A/dt = 0$ and P_{sp} = const, the coefficient of accumulation by phytoplankton is equal to:

$$K_a = \frac{V_m}{(K_m + C_W)(p - P_{sp})}. \quad (5)$$

As follows from Eq. (5), the accumulation coefficient (K_a) in a general case depends on the ratio of the values of the Michaelis–Menten constant (K_m) and on the concentration of the biogenic elements in water (C_W). At $C_W \ll K_m$, the value of C_W relative to K_m in expression (5) can be neglected and the accumulation coefficient is assumed to be equal to $K_a \approx K_{max}$, where K_{max} is the maximum possible relative level of concentration of the biogenic elements by phytoplankton. In case $C_W \gg K_m$, the value of K_m relative to C_W can be neglected; as well, as the concentration of the biogenic elements in water increases, the coefficient of accumulation by phytoplankton can be assumed to decrease in inverse proportion to the value of C_W.

A substantial number of experimental observations on parametrization of Eq. (5) using radioactive phosphorus (^{32}P) have been carried out [17–20]. It was shown in [20] that the Michaelis–Menten constant depends on salinity, the concentration of PO_4, and the concentration of chlorophyll *a* in water; the estimates of K_m from 1 to 22 μg P/L were obtained for different seasons of the year. In the complex experimental studies with suspended matter and ^{32}P, the following values for the Black Sea phytoplankton were obtained: K_m = 4.44 μg P/L; V_m = 6.45 μg P/(mg day); and p = 0.1–0.4 (1/day) [7]. Modeling of quasistationary states of marine waters in different seasons of the year showed that as the concentration of mineral phosphorus (P–PO_4) in water changed from 1.0 to 80 μg P/L, the specific production (P_{sp}) varied from 0.1 to 1.0 (1/day). By using these values in Eq. (5), the coefficient of accumulation of phosphorus by phytoplankton can be estimated at $K_{aP} = (0.05–16.1) \times 10^6$.

A comparison of the optimum levels of contents of the biogenic elements that limit the production processes in phytoplankton in the coastal waters off Sevastopol (80 g carbon, 2 g phosphorus, and 14 g nitrogen per 1000 g of organic matter) with the range of variation of their concentrations, that is, 1.1–105.1 μg/L for phosphates (PO_4) or 0.4–33.9 μg P/L for phosphorus of phosphates (P–PO_4) and 23.2–770.0 μg/L for the nitrogen complex (ΣN) of the mineral compounds (nitrites + nitrates + ammonium) we measured, or 13.6–341.6 μg N/L for nitrogen from this complex (N–ΣN), shows that during the observation period the coefficient of phosphorus accumulation (K_{aP}) in algae could vary within a range of $(0.06–5.0) \times 10^6$ and that of nitrogen compounds (K_{aN}) within a range of $(0.04–1.0) \times 10^6$. The data in the tables on distribution of the matter between aquatic organisms and water depending on the coefficients of accumulation of their biomass [15] are as follows: with a raw weight of phytoplankton of 10 g/m^3, which on average corresponds to an eutrophic level of waters [12], the pool of phosphorus in algae ranges from 37 to 98%, and the pool of nitrogen compounds ranges from 29 to 91% of its content in the seawater, with the upper estimates corresponding to the spring–summer values of primary production phytoplankton. Thus, the daily extraction of biogenic elements may reach 91–98% of their pool in the photic layer with a partial re-mobilization into the aquatic environment as a result of metabolic processes and mineralization of dead phytoplankton cells.

According to modern ideas, up to 70% of the primary production in the photic layer is consumed by microzooplankton, which is a trophic source of energy and mineral nutrition for the consuming and decomposing links of the ecosystem [34]. The results of experiments with diatoms [23] showed that the lifespan of phytoplankton cells can be measured on an hourly scale; thus, the return of biogenic elements due to re-mobilization processes can occur within hours or days.

At high concentrations of phosphorus and nitrogen in water (Figs. 5a, 5b) the intensity of their biotic cycle was low; at low concentrations it increased. These data indicate that relative to an element that limits the production processes the biogeochemical processes in the ecosystem develop as if they were under oligotrophic conditions; relative to a non-limiting element the biogeochemical processes in the ecosystem develop as if they were under eutrophic conditions. As follows from expressions (4) and (5), in the case of eutrophication of the marine environment (at $C_W \gg K_m$), phytoplankton accumulates biogenic elements up to a value of $C_A > q_{min}$. Therefore, the biogenic-element content of the sedimentation flux eliminated from the photic layer reaches its maximum, which leads to a relative increase in the intensity of de-eutrophication of waters. Under oligotrophic conditions (at $C_W \ll K_m$), the intracellular concentration of biogenic elements in the phytoplankton reaches its minimum ($C_A \approx q_{min}$), while the concentrating ability of phytoplankton towards the production-limiting element reaches its maximum: $K_a \approx K_{max}$. This provides the maximum possible supply of biogenic elements to the consuming and decomposing links of the ecosystem, which provide the return of the nutrients due to dying and mineralization to the photic layer under the conditions at which their concentration in the sedimentation flux is at its minimum.

In the present study, it was found that the primary production in the coastal waters off Sevastopol varied by three orders of magnitude during the year, reaching the level of hyper-eutrophication of waters in the spring–summer period. Mineral phosphorus was a key factor in the chemical limitation of the primary production of the phytoplankton, along with water temperature and duration of daylight. In the study area, the periods of mass change of SOM and the cycle of biogenic elements in the photic layer as a result of phytoplankton primary production varied from 0.1×10 to 1.7×10^3 days. The high intensity of the biogenic-element cycle in the spring–summer period was

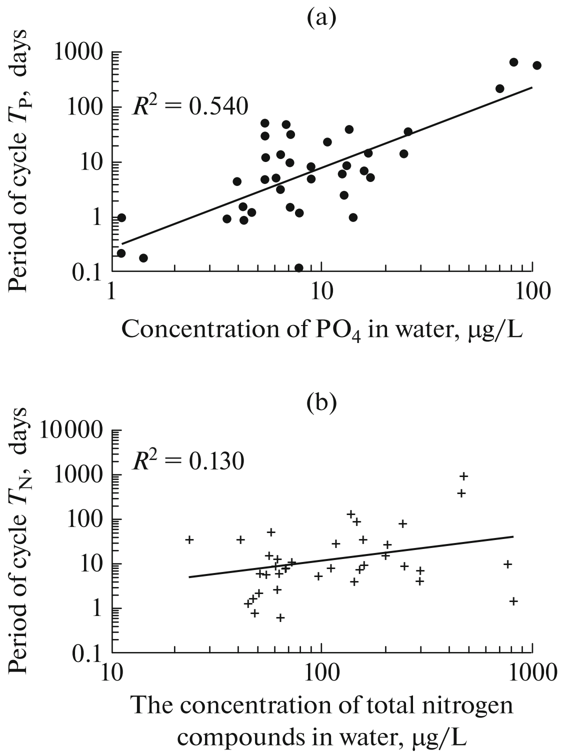

Fig. 5. The relationship between the periods of cycle of mineral phosphorus (a) and nitrogen (b) and their concentrations in the coastal waters off Sevastopol.

accompanied by their concentration by phytoplankton with an accumulation coefficient K_a equal to 10^4–10^6.

It has been established that a variation in the phytoplankton primary production causes an SOM mass change and causes the biogenic-element cycle within the photic layer to accelerate or slow down in such a way that the combined effect of the production and elimination processes would always be aimed at weakening the influence of the chemical limiting factor. These data indicate that the role of phytoplankton in the homeostasis of biogenic elements is determined by the Le Chatelier–Braun principle of negative feedback [30] in natural conditions, which increases the stability of the ecosystem both in the case of limitation of production processes by biogenic elements and in the case of hyper-eutrophication of waters.

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