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**CONTENT OF NUTRIENTS  
AND LIMITATION OF PHYTOPLANKTON PRIMARY PRODUCTION  
IN THE SPECIALLY PROTECTED NATURAL AREA “CAPE MARTYAN” (BLACK SEA)**

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The results are presented of studying the content of nitrogen compounds and mineral phosphorus, as well as phytoplankton primary production (PPP). The research was carried out in 2017–2019 in the marine area of the specially protected natural area “Cape Martyan” located on the southern coast of Crimea (Black Sea). As found, during summer in the surface seawater layer, PPP can be limited by both nitrogen and phosphorus. The dependence of PPP variation on the concentration of total nitrogen in water is not significant, while the dependence on the concentration of phosphorus is significant. It is shown that during the entire annual cycle, concentrations of nitrites, nitrates, ammonium, and mineral phosphorus vary but remain within the limits that do not lead to water hypereutrophication. A high ecological significance of precipitation was revealed: the related increase in PO<sub>4</sub> concentration caused a transition in PPP limitation mode from phosphorus to nitrogen one. Using theoretical concepts, it is substantiated that, under oligotrophic conditions, an increase in the concentration of the substrate limiting PPP in water results in an increase in the rate of its uptake from the environment in accordance with the negative feedback of natural regulation of ecosystem homeostasis. Under conditions of eutrophication, the effect of production processes on water conditioning by the factor of nutrients decreases.

**Keywords:** Black Sea, Cape Martyan, nitrogen compounds, phosphates, precipitation, plankton, primary production, limitation

The Crimean Black Sea coast is a zone of intensive natural resource management ([The Current State of the Crimean Coastal Zone, 2015](#)). The complex anthropogenic load on it is determined by the influx of a wide range of pollutants with wastewater and slope runoff, as well as urbanization and functioning of objects of transport infrastructure (*inter alia* intensive shipping), industrial centers, and recreational and tourist centers. According to classification of the marine environment quality, the Crimean coast is a critical zone ([Zaitsev & Polikarpov, 2002](#)), in which the content of pollutants can exceed both natural levels and maximum permissible concentrations established based on sanitary and hygienic requirements ([Egorov et al., 2013](#)). To date, one of the most urgent environmental issues is water hypereutrophication ([Vinogradov et al., 1992](#)). It is caused by the influx of excessive amounts of nutrients into the marine environment ([Yunev et al., 2019](#)) resulting in an increased phytoplankton primary

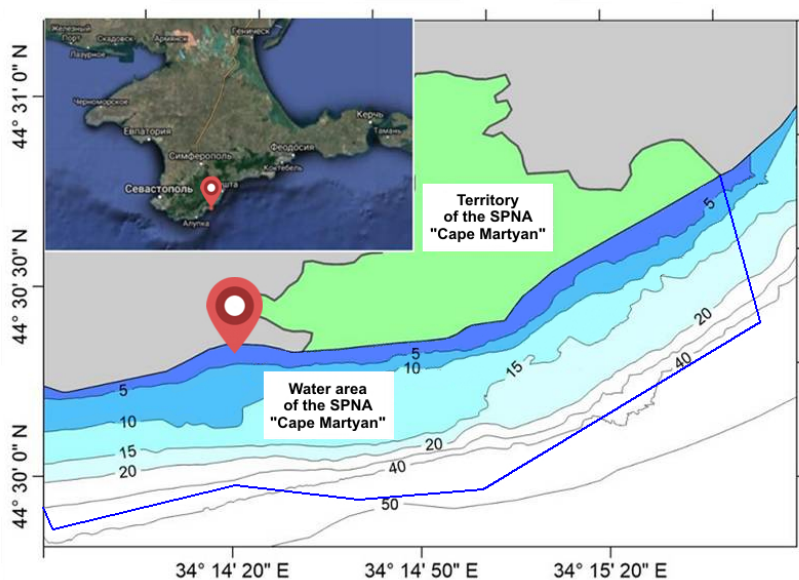
productivity. This leads to changes in structural and functional organization of marine ecosystems (Zaitsev, 1998) and to deterioration in seawater quality, that is both a habitat for hydrobionts and a recreational resource.

In 1973, in Crimea, on the basis of the Nikitsky Botanical Gardens, a specially protected natural area (hereinafter SPNA) was established: the “Cape Martyan” Nature Reserve (the Decree of the Council of Ministers of the Ukrainian SSR dated 20.02.1973, No. 84). Currently, it has the status of a natural park of regional significance (Ob utverzhdenii polozheniya, 2018). It is both a terrestrial and aquatic object since half of its total area of 2.4 km<sup>2</sup> falls on the Black Sea coastal waters. Comprehensive study of this object allows revealing ecological and biogeochemical peculiarities of the coastal water area, which is an integral part of the whole nature protection and recreational complex functioning in the coast – sea system.

The aim of this study was to assess the annual trends in the variation in primary production processes and the content of nitrogen mineral forms (nitrites, nitrates, and ammonium) and mineral phosphorus in the surface water layer of the SPNA “Cape Martyan” coast considering precipitation intensity and peculiarities of limitation of phytoplankton production by nutrients, as well as to give theoretical interpretation of the survey data.

#### MATERIAL AND METHODS

Sampling was carried out in 2017–2019 in the surface water layer at a distance of 60–70 m from the shoreline from a pier located within the boundaries of the economic zone of the SPNA “Cape Martyan” water area (the sampling point coordinates are 44°30′19.1″N, 34°14′19.5″E) (Fig. 1).



**Fig. 1.** Studied area localization and schematic map; 📍 denotes the sampling point

Tendencies in annual variation in the surface water temperature in the studied area are given according to the material from the website (Temperature, 2020); the amount of precipitation, according to the data provided by Nikitsky Botanical Gardens agrometeorological station. Hydrochemical indicators of the water samples were determined in a certified hydrochemical laboratory of the IBSS aquaculture and marine pharmacology department applying generally accepted methods (Rukovodstvo, 1977). The results of determining the concentrations of nutrients in water had ranges and mean

relative errors as follows: nitrate ions, 5 to 500  $\mu\text{g}\cdot\text{L}^{-1}$ , with an error of 2.7–7.39 %; nitrite ions, 0.5 to 1000  $\mu\text{g}\cdot\text{L}^{-1}$ , with an error of 1.53–18.02 %; ammonium nitrogen, 15 to 1500  $\mu\text{g}\cdot\text{L}^{-1}$ , with an error of 1.69–11.4 %; and phosphate ions, 5 to 100  $\mu\text{g}\cdot\text{L}^{-1}$ , with an error of 4.6 %. The data on phytoplankton primary production (hereinafter PPP) obtained by the radiocarbon method (Egorov et al., 2018b) were used, as well as the data on the concentration of nutrients in the SPNA “Cape Martyan” seawater in 2017–2018 (Egorov et al., 2018a).

To determine the limiting nutrient factor, the Redfield stoichiometric ratio ( $R_{at}$ ) (Redfield, 1958) was applied. With the dimension of included parameters in  $\mu\text{g}\cdot\text{L}^{-1}$ , the ratio had the following form:

$$R_{at}(N/P) = 1.53 (1.35NO_2 + NO_3 + 3.44NH_4)/PO_4, \quad (1)$$

where  $NO_2$ ,  $NO_3$ ,  $NH_4$ , and  $PO_4$  are the concentrations ( $\mu\text{g}\cdot\text{L}^{-1}$ ) of nitrogen (in nitrites, nitrates, and ammonium) and mineral phosphorus  $PO_4$  in the surface water, respectively.

According to the methodology of applying the Redfield ratio, at  $R_{at} > 16$ , PPP was limited by phosphorus, and at  $R_{at} < 16$ , by nitrogen (Zilov, 2009).

## RESULTS

The results of determining the concentration of nutrients in seawater, measuring of PPP, and calculating the Redfield ratio are given in Table 1.

**Table 1.** Results of measuring the concentration of nutrients and phytoplankton primary production and assessment of the Redfield ratio in the SPNA “Cape Martyan” water area

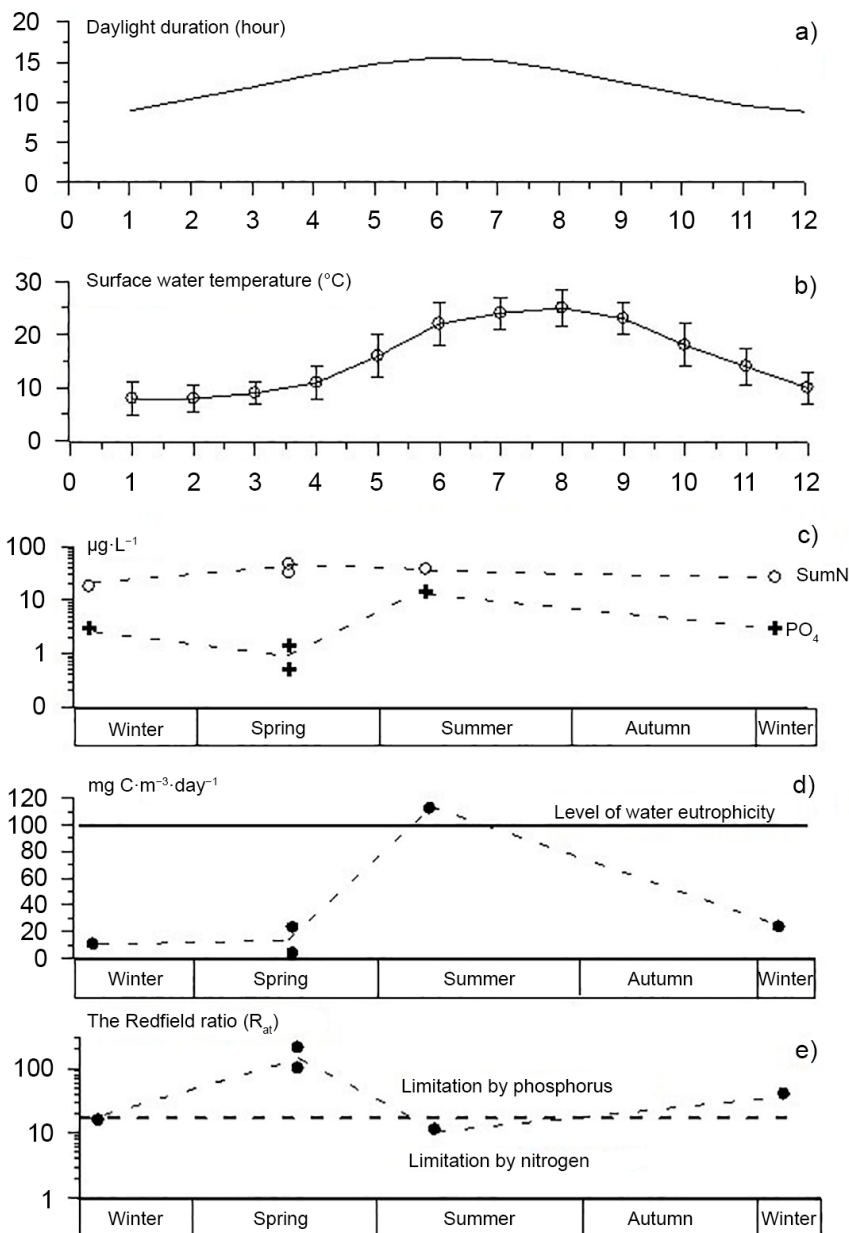
Date	Concentration					PPP, $\text{mg C}\cdot\text{m}^{-3}\cdot\text{day}^{-1}$ *	Redfield ratio ( $R_{at}$ )
	$NH_4 \pm SD$ , $\mu\text{g}\cdot\text{L}^{-1}$	$NO_2 \pm SD$ , $\mu\text{g}\cdot\text{L}^{-1}$	$NO_3 \pm SD$ , $\text{g}\cdot\text{L}^{-1}$	$\Sigma N$ , $\mu\text{g}\cdot\text{L}^{-1}$	$PO_4 \pm SD$ , $\mu\text{g}\cdot\text{L}^{-1}$		
2017							
19.04.2017	$15.00 \pm 0.70$	$0.50 \pm 0.10$	$17.00 \pm 0.50$	32.5	$0.50 \pm 0.10$	3.4	211.98
30.06.2017	$30.00 \pm 1.00$	$0.80 \pm 0.10$	$7.60 \pm 0.20$	38.4	$14.40 \pm 0.20$	112.8	11.28
14.12.2017	$21.00 \pm 1.00$	$0.40 \pm 0.10$	$6.50 \pm 0.20$	26.9	$3.00 \pm 0.20$	23.3	40.43
2018							
09.01.2018	$5.00 \pm 2.50$	$1.40 \pm 0.10$	$11.80 \pm 0.30$	18.2	$3.00 \pm 1.10$	10.2	15.75
20.04.2018	$18.00 \pm 0.86$	$0.40 \pm 0.01$	$29.20 \pm 0.87$	47.6	$1.40 \pm 0.10$	22.7	100.17
29.07.2018	$30.00 \pm 1.40$	$1.60 \pm 0.02$	$20.00 \pm 0.60$	51.6	$8.50 \pm 0.10$	n. d.	22.56
29.10.2018	$15.00 \pm 0.72$	$0.60 \pm 0.01$	$12.20 \pm 0.36$	27.8	$2.90 \pm 0.04$	n. d.	34.08
26.11.2018	$50.00 \pm 2.40$	$1.40 \pm 0.02$	$14.00 \pm 0.42$	65.4	$30.30 \pm 0.45$	n. d.	9.48
18.12.2018	$40.00 \pm 1.92$	$2.20 \pm 0.03$	$10.20 \pm 0.31$	52.4	$6.80 \pm 1.00$	n. d.	33.92
2019							
30.01.2019	$28.50 \pm 0.23$	$4.80 \pm 0.07$	$12.00 \pm 0.36$	45.3	$6.50 \pm 1.00$	n. d.	27.43
04.04.2019	$8.00 \pm 0.40$	$0.80 \pm 0.01$	$34.00 \pm 1.00$	42.8	$1.50 \pm 0.02$	n. d.	63.85
29.04.2019	$10.00 \pm 0.48$	$1.00 \pm 0.02$	$34.80 \pm 1.44$	45.2	$1.50 \pm 0.02$	n. d.	71.96
26.06.2019	$12.00 \pm 0.58$	$1.00 \pm 0.02$	$7.90 \pm 0.24$	20.9	$10.00 \pm 0.15$	n. d.	7.73
10.10.2019	$5.00 \pm 0.24$	$1.60 \pm 0.02$	$7.00 \pm 0.21$	13.6	$3.40 \pm 0.05$	n. d.	11.86
28.11.2019	$4.00 \pm 0.20$	$2.00 \pm 0.03$	$10.20 \pm 0.30$	16.2	$10.20 \pm 0.20$	n. d.	4.00
23.12.2019	$2.50 \pm 0.12$	$1.80 \pm 0.03$	$28.00 \pm 3.00$	32.3	$3.40 \pm 0.05$	n. d.	17.56

**Note:** SD denotes standard deviation; \* denotes data given according to (Egorov et al., 2018a); n. d. denotes no data available.

The results obtained show as follows: during the survey period, the concentration of nitrogen in water in the form of ammonium varied 2.5 to 50.0  $\mu\text{g}\cdot\text{L}^{-1}$ ; in the form of nitrites, 0.4 to 4.8  $\mu\text{g}\cdot\text{L}^{-1}$ ; in the form of nitrates, 6.5 to 34.8  $\mu\text{g}\cdot\text{L}^{-1}$ . The total concentration of mineral nitrogen compounds varied 13.6 to 65.4  $\mu\text{g}\cdot\text{L}^{-1}$ ; the concentration of phosphates was 0.5 to 30.3  $\mu\text{g}\cdot\text{L}^{-1}$ . In different seasons of the year, PPP varied within 3.4–112.8  $\text{mg C}\cdot\text{m}^{-3}\cdot\text{day}^{-1}$ . The value of the Redfield ratio varied 7.73 to 211.98, and this indicated PPP limitation by both nitrogen compounds and mineral phosphorus.

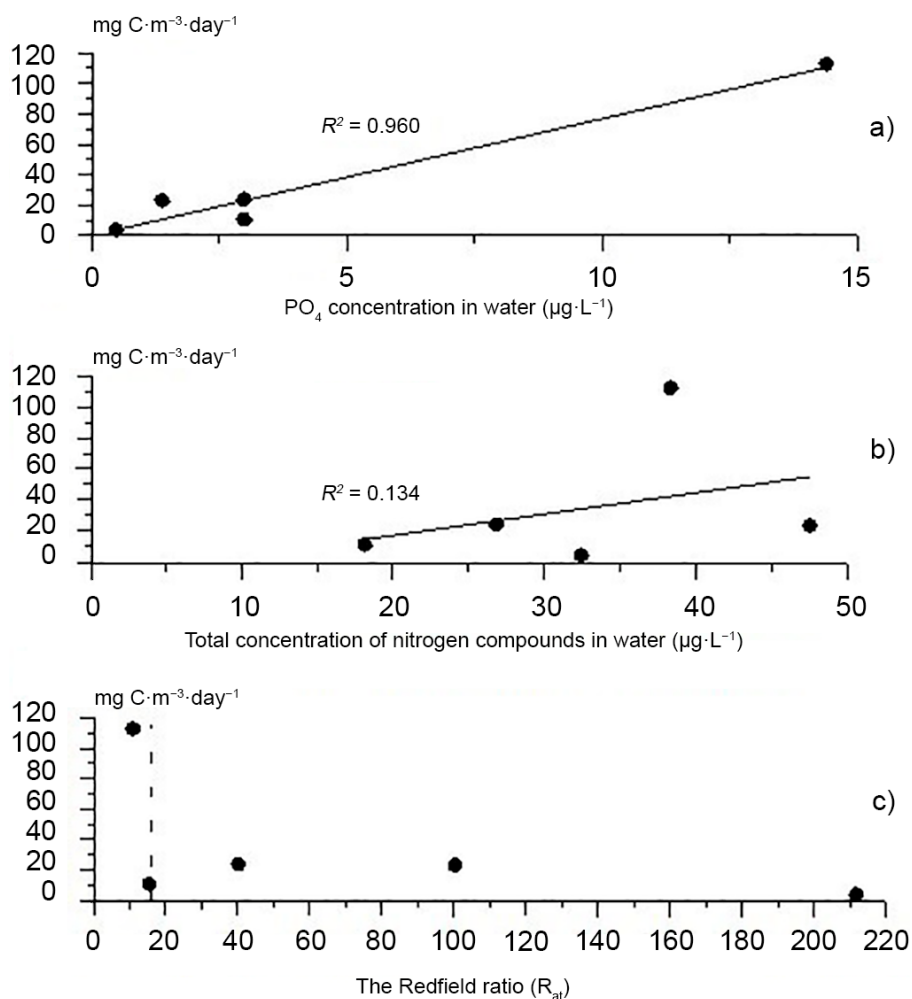
DISCUSSION

From 19.04.2017 to 20.04.2018, in the SPNA “Cape Martyan” water area, minimum PPP was recorded during the winter season, when the daylight duration was less than 10 hours, and the surface water temperature did not exceed +10 °C (Fig. 2a–2d). At the same time,  $R_{\text{at}} \approx 16$ , which indicated the absence of primary production processes limitation by nutrients (Fig. 2e).



**Fig. 2.** Annual dynamics of environmental indicators in the SPNA “Cape Martyan” and phytoplankton production indicators in its marine area according to 2017–2018 data: a) daylight duration; b) mean temperature of the surface seawater layer; c) concentration of the sum of nitrogen and mineral phosphorus compounds in the surface seawater layer; d) phytoplankton primary production; e) the Redfield ratio

Spring began under conditions of production processes limitation by phosphorus; PPP maximum level ( $112.8 \text{ mg C}\cdot\text{m}^{-3}\cdot\text{day}^{-1}$ ) exceeding the lower limit of water eutrophicity ( $100 \text{ mg C}\cdot\text{m}^{-3}\cdot\text{day}^{-1}$ ) was reached in summer under conditions of microalgae growth limitation by nitrogen. In general, in the water area studied, PPP variations were characterized by a statistically significant dependence ( $R^2 = 0.960$ ) on phosphorus concentration (Fig. 3a) and a dependence with a lower significance ( $R^2 = 0.134$ ) on nitrogen concentration (Fig. 3b). The recorded effects can be explained by the following fact: in 80 % of cases, during the survey period, PPP was limited by phosphorus concentration (Fig. 3c) at  $R_{\text{at}} \geq 16$ .



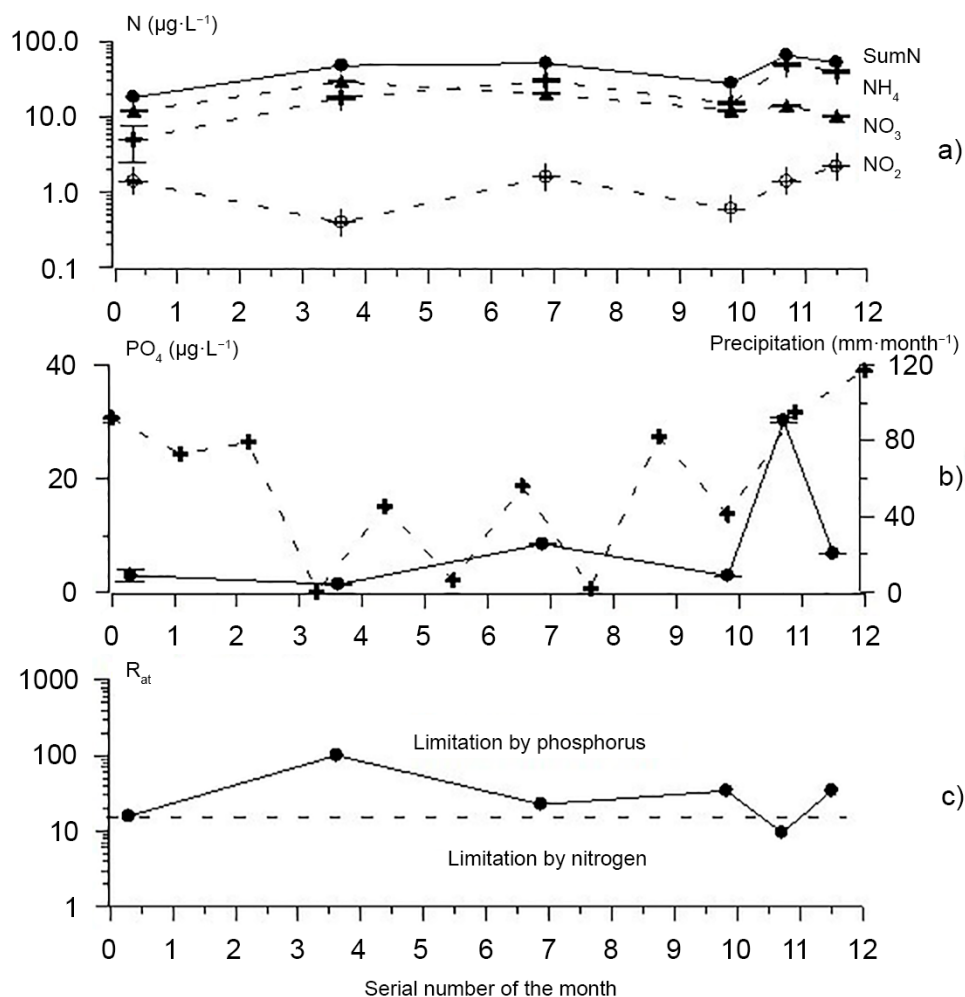
**Fig. 3.** Dependence of phytoplankton primary production in the surface seawater layer of the SPNA “Cape Martyan” marine area on the concentration of mineral phosphorus compounds (a) and the sum of nitrogen compounds (b), as well as on the value of the Redfield ratio (c)

The survey results showed as follows: in the spring of 2018 in the SPNA “Cape Martyan” water area, multidirectional simultaneous processes were observed: an increase in the concentration of nitrogen in the form of ammonium and nitrates and a decrease in the content of nitrites and mineral phosphorus (Fig. 4a, b).

During that period, the dilution of  $\text{NO}_2$  and  $\text{PO}_4$  concentration was likely to be due to intensive precipitation (Fig. 4b). In late spring and in summer, the concentration of the sum of nitrogen mineral forms (SumN) in water stabilized (Fig. 4a); this was probably caused by a relatively high

consumption of nitrates by phytoplankton under conditions of production processes limitation by phosphorus (Fig. 4c) against the backdrop of an increase in nitrites and ammonium content. No significant effect of precipitation on hydrochemical indicators of the surveyed water area (Fig. 4b) was revealed.

In the autumn of 2018, an increase in precipitation intensity was recorded (see Fig. 4b). It resulted in a slight rise in the concentration of all forms of mineral nitrogen and a significant increase in the content of mineral phosphorus in seawater, causing a transition in PPP limitation mode from phosphorus to nitrogen one (Fig. 4c).



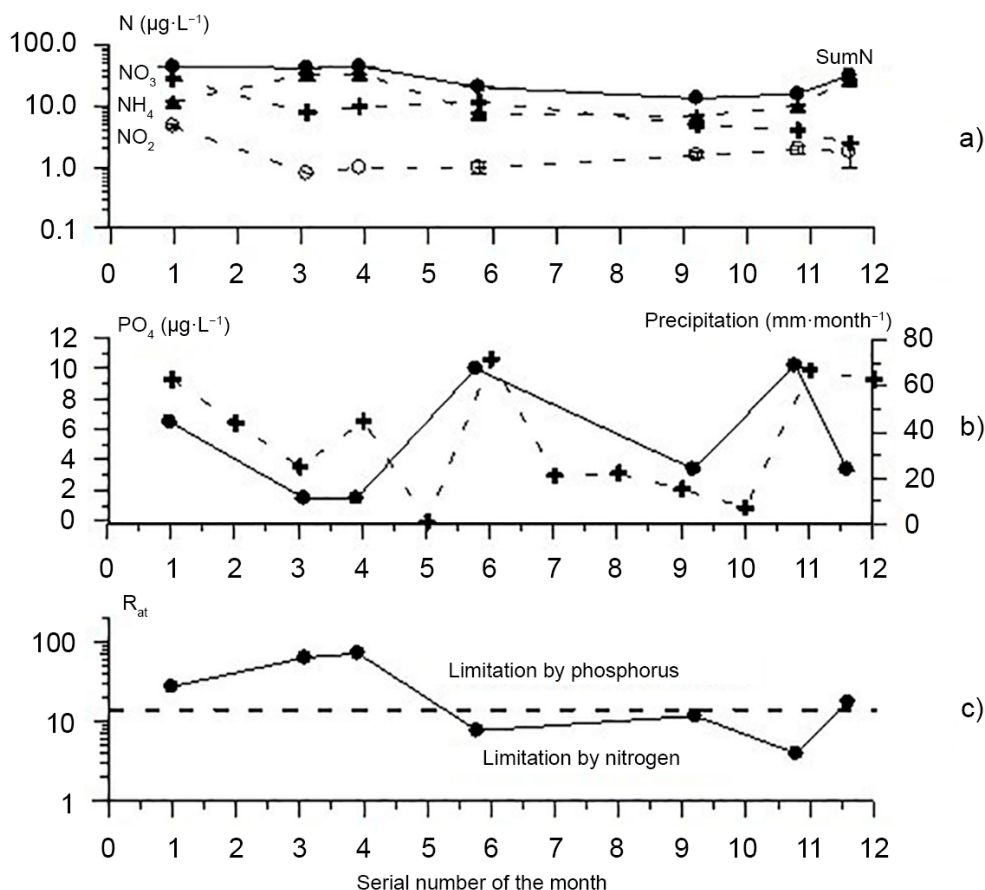
**Fig. 4.** Dynamics of environmental indicators in the SPNA “Cape Martyan” and content of nutrients in its marine area in 2018: a) concentration of nitrogen compounds in the surface water layer; b) concentration of mineral phosphorus compounds (●) in the surface water layer and precipitation volume (+) in the studied area; c) the Redfield ratio

In the spring of 2019, against the backdrop of a decrease in precipitation intensity in the SPNA “Cape Martyan” water area, an increase in ammonium concentration was recorded (Fig. 5b), with a simultaneous decrease in the content of nitrates, nitrites, and mineral phosphorus (Fig. 5a, b) under conditions of PPP limitation by phosphorus (Fig. 5c).

An increase in precipitation intensity [it peaked in late spring and early summer (see Fig. 5b)], almost did not change the content of nitrates and ammonium (see Fig. 5a) but resulted in a significant rise in the concentration of mineral phosphorus in the surveyed water area (see Fig. 5b). This caused



transition in phytoplankton mineral nutrition mechanism from limitation by phosphorus to limitation by nitrogen (Fig. 5c), accompanied by intense absorption of nitrates (see Fig. 5a) from aquatic environment. The autumn peak of precipitation (see Fig. 5b) coincided with a slight increase in the ammonium concentration and a significant rise in  $\text{PO}_4$  concentration in seawater, which resulted in an increase in the level of PPP limitation by nitrogen.



**Fig. 5.** Dynamics of environmental indicators in the SPNA “Cape Martyan” and content of nutrients in its marine area in 2019: a) concentration of nitrogen compounds in the surface seawater layer; b) concentration of mineral phosphorus compounds (●) in the surface seawater layer and precipitation volume (+) in the studied area; c) the Redfield ratio

In general, the survey carried out in 2017–2019 in the SPNA “Cape Martyan” coastal and marine area showed as follows: in summer, PPP can be limited by both nitrogen compounds and mineral phosphorus compounds. The observed phenomena set the task of theoretical interpretation and assessment of practical significance of the biochemical processes of PPP limiting factors’ transition.

For the first time, the dependence of the specific growth rate indicator of a microorganism culture ( $\mu$ , with the dimension inverse to time: 1 *per* time unit) on a weight concentration of the limiting substrate in the medium ( $C_v$ , concentration units *per* medium volume unit) was described by the Monod function (Monod, 1942):

$$\mu = \frac{\mu_{\max} C_v}{K_m + C_v}, \quad (2)$$

where  $\mu_{\max}$  is an indicator of the maximum physiologically possible specific growth rate of a cell culture (1 *per* time unit);

$K_m$  is an indicator (concentration units *per* medium volume unit), that characterizes the intensity of catalytic processes; it is numerically equal to  $C_v$  value, at which  $\mu = 0.5 \cdot \mu_{max}$ , and is usually called the Michaelis–Menten constant.

When using the Monod function to assess the level of PPP limitation, it seems reasonable to consider two biochemical situations with extreme values:  $C_v \ll K_m$  and  $C_v \gg K_m$ . In the first case ( $C_v \ll K_m$ ),  $C_v$  value in denominator of the expression (2) can be neglected. Therefore, the equation (2) turns into a linear function  $\mu = (\mu_{max} / K_m) \cdot C_v$ , in which  $\mu_{max} / K_m = \text{const}$ . That is, at  $C_v \ll K_m$ , which corresponds to oligotrophic conditions, the specific productivity of microalgae rises with increasing concentration of the limiting substrate in the environment. In the second case ( $C_v \gg K_m$ ),  $K_m$  value in the expression (2) can be neglected. Then,  $\mu \approx \mu_{max}$ . So, at  $C_v \gg K_m$ , which corresponds to eutrophic conditions, PPP is maximum and does not depend on the concentration of the limiting substrate in the environment.

Importantly, the results of many *ex situ* and *in situ* observations have shown that all living matter, including phytoplankton, can absorb different specific amounts of substrates depending on their content in the environment. For each substrate ( $C_f$ ) potentially limiting PPP, there is a minimum intracellular concentration  $q_{min}$ , which ensures microalgae viability. During the growing season, phytoplankton can accumulate limiting substrates up to  $C_f$  levels significantly exceeding  $q_{min}$ . As the stored substrates become depleted in the environment, they can be used by microalgae to continue cell division, which is accompanied by an increase in the level of limitation of the growth rate until their intracellular concentration ( $C_f$ ) decreases down to  $C_f = q_{min}$  level. For these conditions, the dependence of the indicator of the specific growth rate of a microorganism culture ( $\mu$ ) is described by the Droop equation (Droop, 1974):

$$\mu = \mu_{max}(1 - q_{min}/C_f) . \quad (3)$$

In the formula (3),  $q_{min}/C_f$  ratio refers to the substrate limiting PPP at present. When shifting limiting factors (see Figs 4 and 5), the expression (3) should take into account  $q_{min}/C_f$  ratio for the factor controlling the production process. In the equation (3), it is permissible to use not  $q_{min}/C_f$ , but an indicator limiting cell division by the effect of ecotoxicological factors. Therefore, to solve the problems of PPP processes limitation, it is necessary to assess the dependence of  $C_f$  on  $C_v$  considering modern concepts of sorption and metabolic interactions of phytoplankton with chemical elements, *inter alia* nutrients, of the marine environment (Polikarpov & Egorov, 1986).

In experimental studies with a  $^{32}\text{P}$  radioactive label, a differential equation was obtained for the kinetics of phosphorus metabolism in unicellular algae in time ( $t$ ), which had the following form (Egorov et al., 1982):

$$\frac{dC_f}{dt} = \frac{V_{max}C_v}{K_m + C_v} - [r + \mu_{max}(1 - q_{min}/C_f)]C_f , \quad (4)$$

where  $r$  is an indicator of the rate of phosphorus metabolism in unicellular algae (1/t);

$V_{max}$  is the maximum physiologically possible specific rate of the substrate intracellular absorption (concentration units *per* microalgae mass unit *per* time unit).

In (4), the first term on the right-hand side is the ratio proposed by Dugdale (1967) to determine the rate of nutrient absorption by algae in accordance with the Michaelis–Menten equation. The term  $r$  considers the metabolic peculiarities of intracellular phosphorus metabolism, and the second term in parentheses on the right reflects production processes limitation by a substrate  $C_f$  in accordance with the Droop equation (3).



Application of the equation (3) for oligotrophic stationary conditions, when  $C_v \ll K_m$ , showed that the dependence of  $C_f$  on the change in  $C_v$  value has the following form:

$$C_f = \frac{V_{max}}{K_m(r + \mu_{max})} C_v - \frac{q_{min}\mu_{max}}{r + \mu_{max}}. \quad (5)$$

It can be seen in the formula (5) that its parameters  $V_{max}$ ,  $K_m$ ,  $r$ ,  $\mu_{max}$ , and  $q_{min}$  are constant within the limits of the theoretical concepts used and at  $C_v \ll K_m$ . Hence, under oligotrophic conditions, the relationship between  $C_v$  and  $C_f$  is linear. Therefore, substitution into the equation (3) of  $C_v$  values from the expression (5) instead of  $C_f$  will not change the hyperbolic increase in the rate of microalgae cell division ( $\mu$ ) with an increase in the concentration of the primary production-limiting substrate ( $C_f$ ) in the environment.

At  $C_v \gg K_m$ , which corresponds to the conditions of water eutrophication, in the first term of the right-hand side of the equation (4),  $K_m$  value can be neglected. Considering this, under stationary conditions, the dependence of  $C_v$  on the indicators of (4) will have the following form:

$$C_f = \frac{\mu_{max}q_{min}}{r + \mu_{max}}. \quad (6)$$

When substituting  $C_f$  value from the formula (6) into the equation (3),  $\mu$  value will not depend on the change in the concentration of the limiting substrate in the environment ( $C_v$ ). This indicates as follows: under conditions of water eutrophication, the specific growth rate of microalgae ( $\mu$ ) reaches its maximum values, but with an increase in the concentration of the limiting substrate in the environment ( $C_v$ ), the relative rate of its extraction from water decreases.

As shown by the analysis, various theoretical approaches used to assess the limiting role of nutrients in PPP processes reveal the same physiological regularities. Both the Monod function (Monod, 1942) and Droop equation (Droop, 1974) show as follows: under oligotrophic conditions, a rise in the concentration of the limiting substrate in water results in an increase in the rate of its extraction from the environment. Thus, natural regulation of ecosystem homeostasis is carried out in accordance with the principle of negative feedback (Egorov, 2019). Under conditions of eutrophication, with an increase in  $C_v$ , the effect of production processes on water conditioning by the factor of nutrients decreases.

**Conclusion.** Research carried out in 2017–2019 in the SPNA “Cape Martyan” showed that in summer, phytoplankton primary production in its coastal and marine area can be limited by both nitrogen compounds and mineral phosphorus. As found, in the surface seawater, the dependence of PPP change on nitrogen concentration in water is less significant than the dependence on phosphorus concentration, which indicates the linear nature of the functional relationship. At the same time, during the entire annual cycle, the concentrations of nitrites, nitrates, ammonium, and phosphates vary but remain within the limits that do not lead to water hypereutrophication related to PPP. It was revealed that the variation in the concentration of nutrients in seawater correlates with precipitation volume. The influx of nutrients can occur directly with precipitation or with an increased slope runoff during precipitation. Survey shows that it is the slope runoff that has the greatest effect on the water composition of the studied water area in terms of nutrients. As found, summer and autumn peaks of precipitation to a greater extent increase the influx of mineral phosphorus into the water area than nitrogen compounds. The resulting increase in the concentration of mineral phosphorus in seawater leads to a transition in PPP limitation mode from phosphorus to nitrogen one. It was shown that, under oligotrophic conditions, an increase

in the concentration of the substrate limiting PPP in water results in a rise in the rate of its uptake from the environment in accordance with the principle of negative feedback regulating the natural homeostasis of the ecosystem. Under conditions of eutrophication, the effect of the production processes of microalgae on water conditioning by the factor of nutrients decreases.

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## СОДЕРЖАНИЕ БИОГЕННЫХ ЭЛЕМЕНТОВ И ЛИМИТИРОВАНИЕ ПЕРВИЧНОЙ ПРОДУКЦИИ ФИТОПЛАНКТОНА В АКВАТОРИИ ООПТ «МЫС МАРТЬЯН» (ЧЁРНОЕ МОРЕ)

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Представлены результаты изучения содержания соединений азота и минерального фосфора, а также первичной продукции фитопланктона (ППФ) в 2017–2019 гг. в морской акватории ООПТ «Мыс Мартьян», расположенной на Южном берегу Крыма (Чёрное море). Установлено, что в летний период в поверхностном слое морской воды ППФ может лимитироваться как по азоту, так и по фосфору. Зависимость изменения ППФ от концентрации общего азота в воде обладает малой значимостью, а зависимость от концентрации фосфора — высокой. Показано, что в течение всего годового цикла концентрации нитритов, нитратов и аммония, а также минерального фосфора изменяются, но остаются в пределах, не приводящих к гиперэвтрофикации вод. Выявлена высокая экологическая значимость атмосферных осадков: связанное с ними

повышение концентрации  $PO_4$  обуславливало изменение режима лимитирования ППФ с фосфорного на азотный. С использованием теоретических представлений обосновано, что в олиготрофных условиях увеличение концентрации лимитирующего ППФ субстрата в воде приводит к возрастанию скорости его извлечения из среды в соответствии с отрицательной обратной связью природного регулирования гомеостаза экосистем. В условиях эвтрофирования влияние продукционных процессов на кондиционирование вод по фактору биогенных элементов снижается.

**Ключевые слова:** Чёрное море, мыс Мартьян, соединения азота, фосфаты, атмосферные осадки, планктон, первичная продукция, лимитирование