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Comparative Analysis of Nitrogen and Phosphorus Assimilation Rates by Macroalgae and Seagrasses according to Simulation Data

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Abstract
The paper considers assimilation and release of nitrogen and phosphorus compounds by sea macroalgae and grasses during primary production synthesis in a coastal euphotic zone. To reproduce the processes of aquatic plant functioning under competition for resources among themselves and phytoplankton, a mixed type benthic phytocenosis simulation model was used. The object-oriented concept of the model allows reproducing random spatial distribution of plant species in the computational domain. Plant biomass dynamics is calculated using an individual-based approach. The rates of physiological processes depend on temperature, light, nutrient concentrations in water and soil as well as the content of these elements in plant tissues. The empirical coefficients of the model are based on published data from laboratory experiments. Quantitative estimates of the efficiency of nutrient accumulation in the tissues of various plant groups were obtained. It is shown that brown and red macroalgae having coarser thallus structure as well as sea grasses have the highest bioremediation potential. For the coastal zone of Crimea these are species of cystoseira, phyllophora and seagrass zostera. Benthic phytocenoses, where these species predominate, support the health of coastal marine ecosystems under increased anthropogenic pressure.

Keywords: benthic phytocenosis, phytocenosis, bioremediation, object-oriented modelling, primary production

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Сравнительный анализ скоростей ассимиляции азота и фосфора макроводорослями и морскими травами по данным имитационного моделирования

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Аннотация
Рассматриваются ассимиляция и выделение соединений азота и фосфора морскими макроводорослями и травами в процессе синтеза первичной продукции в прибрежной эвфотической зоне. Имитационная модель донного фитоценоза смешанного типа использована для воспроизведения процессов функционирования водных растений в условиях конкуренции за ресурсы между ними и с фитопланктоном. Объектно-ориентированная концепция модели позволяет воспроизвести в расчетной области произвольное пространственное распределение видов растений. Динамика биомассы растений рассчитывается с использованием индивидуум-ориентированного подхода. Скорости протекания физиологических процессов зависят от температуры, освещенности, концентрации биогенных элементов в воде и грунте, а также уровня накопления этих элементов в тканях растения. Эмпирические коэффициенты модели базируются на опубликованных данных лабораторных экспериментов. Получены количественные оценки эффективности накопления биогенных элементов в тканях различных групп растений. Показано, что наибольшим потенциалом биоремедиации обладают бурые и красные макроводоросли, имеющие более грубое строение талломов, а также морские травы. Для прибрежной зоны Крыма это виды цистозиры, филлофоры и морская трава зостера. Донные фитоценозы, в которых эти виды доминируют, поддерживают здоровье морских экосистем прибрежной зоны в условиях повышенной антропогенной нагрузки.

Ключевые слова: донный фитоценоз, фитоценоз, биоремедиация, объектно-ориентированное моделирование, первичная продукция

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Introduction

Macrophytobenthos has a decisive influence on the biochemical state of coastal waters. Benthic macroalgae and seagrasses compete with phytoplankton for inorganic resources, being a significantly better reservoir for the accumulation of carbon and other biogenic elements [1]. Phytobenthos, in contrast to phytoplankton, is characterized by high levels of biomass and a turnover time of about a year, comparable to terrestrial photosynthetic systems. For phytoplankton, the turnover time is of about a week. Thus, estuaries, bays, shallow coastal areas of the seas play an important role in the processes of the global carbon cycle.

According to the authors of [2], in the 1990s the net primary production of macroalgae and seagrasses growing in the shallow euphotic zone was approximately $3\cdot10^9$ t·year^{-1}, at least 10 % of all primary production produced in the World Ocean. The area of the coastal zone under consideration, corresponding to the width of the algae growth band down to depths of 50 m, was estimated at 1.9 % of the area of the World Ocean [2]. In relation to the annual volumes of carbon emissions into the atmosphere as a result of fuel combustion (~ $5.4\cdot10^9$ tC·year^{-1} in 1990), the primary production of macroalgae and seagrasses was 55 %. In specific terms, the primary production of macrophytobenthos in the coastal zone exceeded the production of phytoplankton by an order of magnitude, varying within 500–2000 gC·m^{-2}·year^{-1} against 50–300 gC·m^{-2}·year^{-1}.

As is known, in recent decades, the coastal areas of the seas have experienced an unprecedented anthropogenic impact, which often results in their eutrophication with the development of negative phenomena, one of which is degradation of benthic phytocenoses. The main reasons are: a decrease in water transparency, as a result of which the width of the band of benthic vegetation decreases; and wastewater emissions with a high content of nutrients, leading to structural changes in the phytocenosis. Degradation and reduction of areas occupied by benthic vegetation is an extremely negative phenomenon, since it is benthic plants that prevent the development of hypoxia and deaths in shallow water during periods of summer stagnation. A number of studies record these negative phenomena in different areas of the World Ocean and the Black Sea in particular [3, 4].

According to modern estimates [5, 6], the average net primary production of macroalgae has noticeably decreased and varies within 91–738 gC·m^{-2}·year^{-1}. The growth band width of macroalgae and seagrasses has decreased as a result of raising the lower boundary of benthic vegetation distribution. For a rough estimate, it can be taken as no more than 1 % of the width of the shelf of the World Ocean, which corresponds to the thickness of the photosynthesis zone near the coast (25–30 m). Accordingly, the net primary production of macroalgae and seagrasses can be estimated at $1.5\cdot10^9$ tC·year^{-1}, which amounts to 18 % of the total carbon emissions into the atmosphere in 2020 (against 55 % in 1990).

In the Black Sea, a noticeable decrease in the photosynthesis zone has been recorded in recent decades. The lower boundary of macroalgae distribution on the North Caucasian and Crimean coasts runs at a depth of 10–15 m, in rare cases up to 20 m. According to the authors of the work 1), over the past 30 years, macrophyte biomass has decreased almost tenfold on the coast of the North Caucasus.

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1) Oguz, T., ed., 2008. *State of the Environment of the Black Sea (2001-2006/7)*. Istanbul, Turkey : BSC, 448 p. Available at: http://blacksea-commission.org/Downloads/SOE27032009-1_compressed.pdf [Accessed: 04 September 2022].

The width of the *Cystoseira* growth belt decreased from 1.5 km to 300–500 m. The structure of benthic phytocenoses changed significantly. The biomass of *Cystoseira* and *Phyllophora* (dominants of the corresponding benthic phytocenoses) noticeably decreased, while the biomass of associated algae and epiphytes increased, among which green algae predominate. Such changes are characteristic of a situation of excessive anthropogenic load, when native vegetation is replaced by associations of unproductive species, representatives of the genera *Ulva*, *Cladophora*, *Polysiphonia*, and others, and spatial and hierarchical structure of the community is simplified [7]. Regular blooms of seawater, caused by massive development of green algae, on the beaches of Anapa is a natural consequence of such changes [8].

It was shown in [9] that the diversity of green algae is currently increasing in the coastal zone of the Black Sea. At the same time, it is typical that "mesosaprobic communities of macroalgae displace oligosaprobic ones and become dominant almost throughout the entire length of the Russian coast, including open areas" [9, p. 29].

Restoration of destroyed benthic phytocenoses is a complex task that requires a long time and significant financial costs. The following are the known methods of such reconstruction:

– use of aquaculture of macroalgae and molluscs to reduce the concentration of biogenic elements in water, to reduce the concentration of suspended organic matter and, accordingly, to increase water transparency [10, 11];

– creation of artificial reefs inhabited by filter-feeding mollusks and macroalgae to improve water quality in the near bottom layer [12–14];

– reconstruction of seagrass fields by implanting rather large areas of benthic vegetation with its subsequent rooting (for an analysis of modern methods of such reconstruction, see [2]).

In this regard, modeling studies of the dynamics of processes occurring in benthic phytocenoses, studying the response of the macroalgae and seagrass community to abrupt changes in environmental conditions, and elucidating specific reactions of various components of phytocenoses to these changes are relevant. In a practical sense, it is useful to assess the potential efficiency of the use of various macroalgae for the purpose of biological treatment of coastal waters with an excess supply of biogenic elements with wastewater.

In [15], using a two-layer model of the ecosystem of a semi-enclosed reservoir, the dynamics of dissolved oxygen concentration in the upper mixed and near-bottom layers was analyzed as a response to the release of wastewater with a high concentration of biogenic compounds; the contribution of individual genera of micro- and macroalgae to the process of self-purification of the reservoir was evaluated. This work is a continuation and development of this study, in which we are going to consider the processes of self-purification of a reservoir by analyzing the rates

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[2] Clark, D. and Berthelsen, A., 2021. *Review of the Potential for Low Impact Seagrass Restoration in Aotearoa New Zealand*. Nelson, New Zealand, 55 p. Available at: https://envirolink.govt.nz/assets/2146-NLCC119-Review-of-the-potential-for-low-impact-seagrass-restoration-in-Aotearoa-New-Zealand.pdf [Accessed: 04 September 2022].

of accumulation of nitrogen and phosphorus compounds in plant tissues. The paper uses an extended version of the model, which includes a procedure for calculating the dynamics of seagrass biomass. A semi-enclosed reservoir is considered, the bottom of which is composed of stony-sandy soils. For rocky soil, we are going to consider the *Cystoseira* phytocenosis as the main component in terms of biomass, for sandy soils – the *Zostera* phytocenosis.

Materials and methods

The object-oriented model of the ecosystem of a semi-enclosed reservoir, including phytoplankton and phytobenthos, is described in detail in [15, 16], therefore, we are not going to dwell on this model in detail here. An addition to it is a block describing the dynamics of seagrass biomass. In the coastal zone of Crimea, areas with rocky and sandy bottoms alternate, so a complete ecological model must include blocks for both types of benthic phytocenosis. The object-oriented approach to building the model makes it possible to use different blocks in different parts of the computational domain and to flexibly switch the model from one mode to another. To do this, it is only necessary to have data on the nature of phytocenosis in a particular section of the bottom, which must be specified in the model as control variables. For shallow-water areas of the coast, it is possible to remotely determine the type of dominant species in a particular area of the bottom and an approximate determination of the composition of associated algae and epiphytes characteristic of this phytocenosis. The mapping of benthic vegetation of the Kruglaya Bay was carried out, for example, in [17]. Using these data, it is possible to set the spatial distribution of model objects corresponding to the main species growing on each particular section of the bottom.

The main differences between the two types of benthic phytocenoses are that seagrasses grow on the sandy bottom, while macroalgae phytocenosis is characteristic of the rocky bottom. The associated seagrass species may be algae, so the model must be flexible enough to reflect the observed vegetation biodiversity in the coastal zone. Such flexibility is provided in the model by specifying the field of benthic vegetation in the form of a set of objects with different characteristics and describing the growth of different types of algae and seagrasses. As an example, let us present the composition of benthic vegetation of the Kruglaya Bay, according to [17], where the following plant complexes were recorded:

– Cystoseira species (*C. crinita* and *C. barbata*) on block-boulder substrate and bedrock exposures;

– *Phylophora cripsa* on gravel-sand deposits with broken shells;

– community of seagrasses: *Zostera noltei, Stuckenia pectinata,* and *Ruppia* species on silt-sand deposits;

– community of seagrasses and green algae, represented mainly by *Cladophora* species on muddy sediments.

For the modeler, the main difference between algae and grasses is that grasses have roots that provide additional nutrients to their tissues, unlike algae, which extract the necessary nutrients directly from sea water. This entails the need for a mathematical description of this additional flow with the corresponding characteristics of the consumption rate and its dependence on the internal state of the tissues and concentration of nutrients in the soil. Accordingly, it is required to introduce two new classes into the previously developed object-oriented model – "Seagrasses" and "Seagrass species". Fig. 1 shows a block diagram of the biological block of the ecosystem model, which includes classes of both macroalgae and seagrasses.

The components of the bottom phytocenosis compete for light and mineral resources. Nitrogen and phosphorus circulate in the system, passing through the turnover from inorganic forms through plant tissues (phytoplankton, macroalgae, seagrasses), particulate (POM) and dissolved (DOM) organic matter and returning to the inorganic form. Hydrodynamic factors also have a significant effect

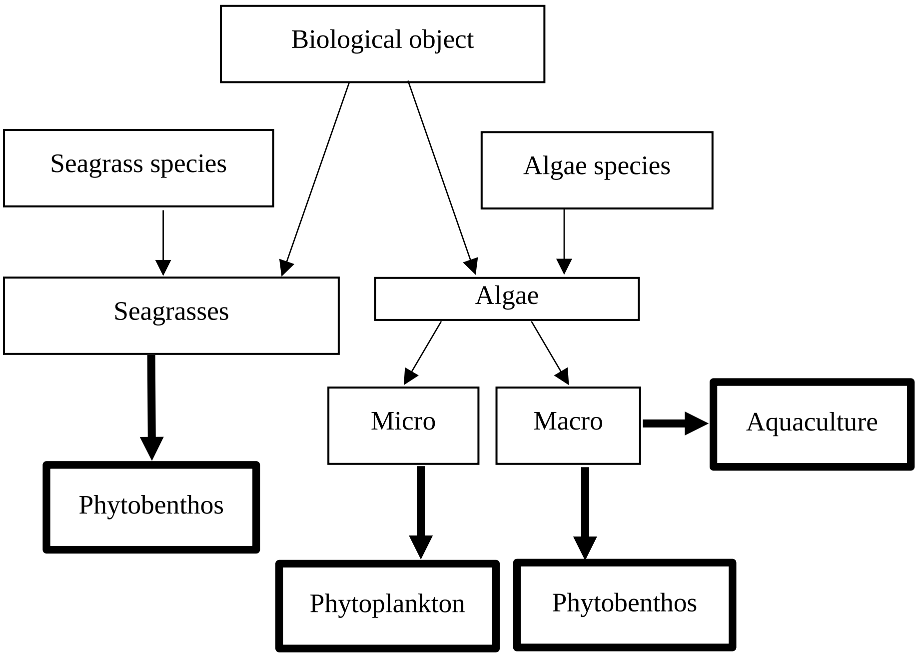

Fig. 1. Diagram of classes and relationships between them in the biological block of the object-oriented simulation model for describing the mixed macroalgae and seagrasses phytocenosis dynamics

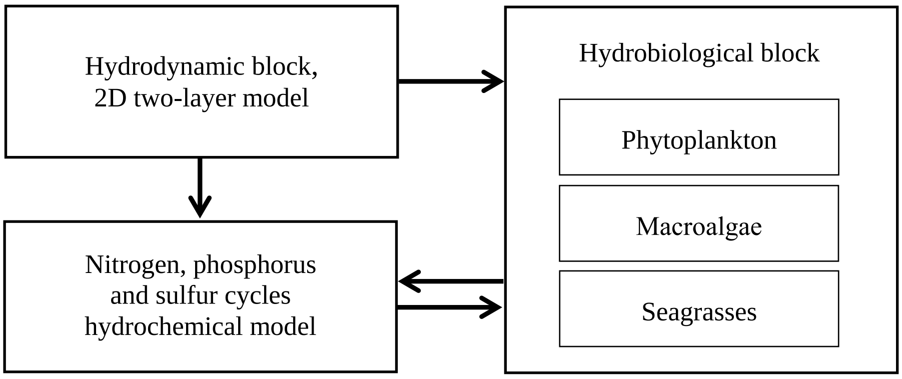

Fig. 2. Block diagram of the object-oriented model of a mixed-type benthic phytocenosis

on the rate of circulation of matter in the system. To account for all these processes, the biological model is coupled with hydrochemical and hydrodynamic blocks, as shown in Fig. 2.

Additional parameters in the class “Seagrass species” are the coefficients in the Michaelis-Menten formulas for calculating the rate of removal of inorganic forms of nitrogen and phosphorus from the soil. The main method of the new “Seagrasses” class is a seagrass growth model, which is largely similar to the previously developed algae growth model, but also contains significant differences. When developing it, the works [18, 19] have been used, which provide the necessary parametrizations based on the data of laboratory experiments.

Let us move on to the consideration of the developed mathematical model of seagrass growth. The extraction of mineral resources necessary for plant growth is carried out both through the roots and through the leaves directly from seawater. These fluxes can provide the plant with necessary substances in approximately equal proportions [20, 21]. The rhizosphere of a plant is usually characterized by reducing conditions, but the roots of the plant require oxygen, which the plant generates during photosynthesis and delivers to the roots. In the absence of light, the roots cannot absorb nutrients from the soil. Thus, the local illumination of the bottom area has a noticeable effect on the supply of plants with nitrogen and phosphorus.

As follows from the analysis of the energy balance of a plant cell and the equations of the growth model based on it, the rate of biogenic element uptake depends on the internal state of the tissues (intracellular reserves of the corresponding element), concentration of biogenic elements in water and soil, water temperature, and irradiance. In the process of vital activity, plant cells release DOM. The release rate in the model is proportional to the gross production in the process of photosynthesis in the light and the respiration rate in the dark, and the proportionality coefficient depends on the taxonomy of the plant. The model equations are based on these postulates and have the following form:

$$\frac{dB}{dt} = (\mu - E - m)B, \tag{1}$$

$$P_p = \left\{ P_{\max} \tanh\left(\alpha \frac{1}{P_{\max}} \right) - R_d \right\} f(T),\ I = I_0 \mathrm{e}^{-\varepsilon h}, \tag{2}$$

$$\mu = P_p \min\bigl(f(Q_\mathrm{N}), f(Q_\mathrm{P}) \bigr), \tag{3}$$

$$f(Q_\mathrm{P}) = \frac{Q_\mathrm{P} - Q_\mathrm{P}^{\min}}{Q_\mathrm{P}^{\max} - Q_\mathrm{P}^{\min}}, \qquad f(Q_\mathrm{N}) = \frac{Q_\mathrm{N} - Q_\mathrm{N}^{\min}}{Q_\mathrm{N}^{\max} - Q_\mathrm{N}^{\min}}, \tag{4}$$

$$\begin{aligned} \frac{dQ_\mathrm{N}}{dt} = {} & V_{\mathrm{NH4}} \frac{[\mathrm{NH}_{4w}]}{K_{\mathrm{NH4}} + [\mathrm{NH}_{4w}]} + V_{\mathrm{NO3}} \frac{[\mathrm{NO}_{3w}]}{K_{\mathrm{NO3}} + [\mathrm{NO}_{3w}]} + \\ & + V_{r\mathrm{NH4}} \frac{[\mathrm{NH}_{4b}]}{K_{r\mathrm{NH4}} + [\mathrm{NH}_{4b}]} - \mu Q_\mathrm{N}, \end{aligned} \tag{5}$$

$$\frac{dQ_\mathrm{P}}{dt} = V_\mathrm{P} \frac{[\mathrm{P}]}{K_\mathrm{P} + [\mathrm{P}]} + V_{r\mathrm{PO4}} \frac{[\mathrm{PO}_{4b}]}{K_{r\mathrm{PO}_4} + [\mathrm{PO}_{4b}]} - \mu Q_\mathrm{P}, \tag{6}$$

$$\begin{gathered} V_{\mathrm{NO}_3} = V_{\mathrm{NO}_3}^{\max}\bigl(1 - f(Q_\mathrm{N})\bigr), \qquad V_{\mathrm{NH}_4} = V_{\mathrm{NH}_4}^{\max}\bigl(1 - f(Q_\mathrm{N})\bigr), \\ V_\mathrm{P} = V_\mathrm{P}^{\max}\bigl(1 - f(Q_\mathrm{P})\bigr), \\ V_{r\mathrm{NH}_4} = V_{r\mathrm{NH}_4}^{\max}\bigl(1 - f(Q_\mathrm{N})\bigr), \qquad V_{r\mathrm{PO}_4} = V_{r\mathrm{PO}_4}^{\max}\bigl(1 - f(Q_\mathrm{P})\bigr). \end{gathered} \tag{7}$$

Here B is biomass of the object in units of dry weight, consisting of biomass of roots and leaves, g/m^3; μ is specific plant growth rate, 1/h; E is specific release rate of dissolved organic matter during the life of a plant, proportional to gross production, 1/h; m is mortality rate, 1/h; I is photosynthetically active radiation, μmol photons/(m^2·s); P_p is photosynthesis rate, mgO$_2$·g^{-1} DW·h^{-1}; $P_{\max}$ is maximum photosynthesis rate, mgO$_2$·g^{-1} DW·h^{-1}; α is slope of PI curve at low light outputs; R_d is respiration rate in the dark, mgO$_2$·g^{-1} DW·h^{-1}; ε is extinction coefficient depending on the concentration of phytoplankton and POM in the water; I_0 is irradiance on the water surface, depending on the time of day and season of the year; Q_P and Q_N are phosphorus and nitrogen concentrations in plant tissues, μmol·g^{-1}; $Q_\mathrm{P}^{\min}$, $Q_\mathrm{N}^{\min}$, $Q_\mathrm{P}^{\max}$ and $Q_\mathrm{N}^{\max}$ are minimum and maximum concentrations of phosphorus and nitrogen in plant tissues, μmol·g^{-1}; T is water temperature, ºC; $V_{\mathrm{NO}_3}^{\max}$, $V_{\mathrm{NH}_4}^{\max}$, $V_\mathrm{P}^{\max}$ are maximum possible uptake rates of nitrogen and phosphorus compounds at a sufficiently high concentration of biogenic element in water, μmol·g^{-1} DW·h^{-1}; K_P, K_{NO_3}, K_{NH_4} are half-saturation constants in the Michaelis-Menten ratios for describing the processes of assimilation of nitrogen and phosphorus compounds from seawater, μmol·l^{-1}; $V_{r\mathrm{NH}_4}^{\max}$, $V_{r\mathrm{PO}_4}^{\max}$ are maximum rates of ammonium and phosphate assimilation by plant roots; $K_{r\mathrm{NH}_4}$, $K_{r\mathrm{PO}_4}$ are half-saturation constants for this process; letter “w” denotes concentration of the corresponding compound in water, letter “b” – in soil.

It should be noted that all the “constants” of the model (maximum rates of physiological processes, half-saturation constants, etc.) are variables that depend on water temperature and irradiance. In the first approximation, they can be set as constant values based on the published data of laboratory experiments, however, for more accurate calculation results, additional studies are needed to find these dependences and formalize them for inclusion in the model.

Numerical experiments, results and discussion

The ecosystem model was used to study the processes of assimilation of nitrogen and phosphorus compounds by various species of macroalgae and seagrasses that are part of benthic phytocenosis. The task of planning and analyzing the results of simulation experiments was to establish differences in the efficiency of water purification from excess nutrients by different types of macroalgae and seagrasses. At the same time, all objects of benthic vegetation had to function in conditions of competition for resources, the main of which in this case is light.

The model also included three main groups of microalgae for the Black Sea: Diatoms, Dinoflagellates, and Coccolithophores, represented by species that have maximum abundance in the coastal waters of Crimea. Thus, phytobenthos and phytoplankton competed for mineral resources (nitrogen and phosphorus), in addition, phytoplankton, multiplying, increased water turbidity, which led to a decrease in illumination at the lower boundary of computational area, where phytobenthic objects were located.

Consuming inorganic components of nitrogen and phosphorus from seawater and accumulating them in their tissues, macrophytes purify seawater from excess nutrients, thereby slowing down the growth of phytoplankton and preventing formation of an excessively large amount of rapidly dying organic matter. However, situations are well known when eutrophication of a water body leads to rapid development of macroalgae rather than phytoplankton [8, 22]. More often these are green macroalgae (*Cladophora*, *Ulva*, *Enteromorpha*, etc.). Repeated mass development of macroalgae can lead to a change in the species composition of benthic phytocenosis. As a result of eutrophication, the dominant species of benthic vegetation is replaced: rapidly growing green macroalgae replaced the seagrasses. With a further increase in the volumes of biogenic substances entering the reservoir under the influence of other factors aggravating the situation, it is possible for macroalgae to be replaced by phytoplankton [23].

In the process of life, plant cells release DOM. According to estimates [24–27], from 50 to 70 % of the gross primary production is released into the environment in the form of DOM. Dissolved organics, the source of which is phytobenthos, can amount to 20 % of the total DOM in coastal areas and estuaries [28]. The mechanisms of DOM release for macroalgae and seagrasses are much less studied than for phytoplankton. It is believed that marine algae release DOM using the same mechanisms as microalgae, plus an additional significant amount of DOM is released through leakage during tissue fragmentation caused by dynamic processes [27]. There are active (exudation) and passive (diffusion) mechanisms of DOM release. The chemical composition of the released organic matter is important for assessing the amount of biogenic substances that enter the environment during macroalgae growth in the form of organic compounds. According to estimates [29], up to half of all particulate organic matter can be polysaccharides. In [26], based on the data of laboratory experiments, the elemental composition of DOM and POM released by different types of macroalgae is considered in detail. 11 species of macroalgae were studied: 4 red, 6 brown and 1 species of green algae, which stood out significantly from the group in terms of growth rate and other indicators. The average ratio C:N for DOM and POM was 4.46 ± 2.43 and 5.44 ± 0.75 respectively; ratio N:P for DOM and POM was recorded within 24.29 ± 18.00 and 20.00 ± 7.84 respectively. The experiments confirmed dependence of the DOM release rate on the growth rate, however, quantitative characteristics of such a dependence for different groups of algae were not given due to the small sample size.

When developing the model, we relied on the data of works by K. M. Khailov et al. [7, 24], who studied the intensity of organic matter release by algae growing in the coastal regions of the Crimea. Thus, according to the results of laboratory experiments, green algae have, on average, a lower percentage of lifetime release of dissolved organic matter – 23 % of gross production versus 38 % for red and 39 % for brown algae. The release of DOM by seagrasses, according to [25], was estimated as 10–15 % of the gross production. These estimates were used in the model to select the empirical parameters that govern the DOM release process.

POM during the growing season is usually released in a much smaller amount, but this is unfair for fast growing green algae with a fine structure [26]. Dead or defragmented algae tissues in the process of decomposition partially pass into DOM and POM. The destruction of thalli and their death in the model is parameterized using mortality rate, which is applied to the biomass of the algae. Since there are no subsequent links in the trophic chain in the model, this coefficient also takes into account the consumption of algae by marine hydrobionts. For fast growing green algae, it is about 0.002 (1/day), for slow growing brown and red algae it is 0.0001 (1/day). Model variables DOM, POM are taken into account in units of nitrogen (µmol N).

The growth dynamics is also significantly affected by the ability of algae to accumulate reserves of biogenic elements in order to maintain viability in conditions of deficiency of nutrients necessary for growth. This ability is numerically characterized by the possible maximum and minimum values of the intracellular content of the corresponding element. Having analyzed a number of works [30, 31], the intervals of variability of the intracellular content of nitrogen and phosphorus for red, brown and green macroalgae were established, and they are given in Table 1.

Table 1. Minimum ($Q_{\min}$) and maximum ($Q_{\max}$) nitrogen (N) and phosphorus (P) tissue content of different macroalgae groups (μmol·g^{-1} DW)

Macrophyte group	$Q^{\mathrm{N}}_{\min}$	$Q^{\mathrm{N}}_{\max}$	$Q^{\mathrm{P}}_{\min}$	$Q^{\mathrm{P}}_{\max}$
Macroalgae:				
brown	457	3711	15	113
red	853	3453	14	80
green	552	3789	15	96
Seagrasses	755	4507	30	119

To conduct research by analyzing the results of simulation experiments to assess the effectiveness of the nitrogen and phosphorus uptake from seawater, eight species of macroalgae growing on the rocky soil of the coastal zone of Crimea (*Cystoseira barbata, Ulva lactuca, Ceramium tenuicorne, Cladophora glomerata, Polysiphonia nigrescens, Gracilaria gracilis, Phyllophora truncata, Enteromorpha prolifera*), and two seagrass species dominating on sandy areas (*Zostera marina, Ruppia maritima*) were selected. The phytoplankton community included three groups of the most abundant microalgae in the area under consideration. The initial average concentrations of chemical and biological components of the ecosystem model, simulating conditions for the water outlet with high concentration of nitrogen compounds into the reservoir, are presented in Table 2. Fluctuations of concentrations in the computational grid nodes were set using a random number generator with a given dispersion and a mean. Irradiance changed during the model day along a sinusoid with zeroing of negative values corresponding to the night time. The light regime was 15 hours of light time and 9 hours of dark time.

At the initial moment, the nitrogen content in the algae tissues was 1000 μmol·g^{-1} DW, phosphorus – 40 μmol·g^{-1} DW. The simulation experiment lasted for one month of model time; during this period, the initially high concentration of biogenic elements significantly decreased due to their assimilation by aquatic plants (Fig. 3, *b*). Fluctuations in the concentration of nitrates and ammonium in the lower layer are associated with fluctuations in the thickness of the upper mixed layer (UML) caused by wind variability (Fig. 3, *a*). The rates of nitrogen and phosphorus assimilation, which were high at the beginning of the calculation, decreased as tissues became saturated, and the rates of photosynthesis and DOM release behaved accordingly (Fig. 4).

The average specific rates of physiological processes in the light and dark for the period of the most intensive growth of algae (the first 15 days of model time) were compared. Averaging was performed over the objects of each species of benthic algae and seagrasses separately. Daily average net production

Table 2. Initial mean values of the ecosystem model components in the experiments of the evaluation of nitrogen and phosphorus uptake efficiency

Model component	Unit of measurement	Initial value	
		upper layer	lower layer
[O$_2$]	mg/L	7	6
[DOM]	µmolN/L	1	1
[POM]	µmolN/L	1	1
[NO$_3$]	µmolN/L	50	50
[NH$_4$]	µmolN/L	10	10
[NO$_2$]	µmolN/L	1	1
[PO$_4$]	µmolP/L	2	2
Water temperature	°C	22	15
Mixed layer thickness	m	10	
Illumination at water surface	µmolphoton/(m^2·s)	0–800	
Testing area average plankton biomass	mg DW/m^3	110	
Testing area average phytobenthos biomass	g DW/m^2	360	

in oxygen units (*NetP*), respiration rate (*R*), specific rates of nitrogen (*N_up*) and phosphorus uptake (*P_up*), release of dissolved (DOM) and particulate (POM) organic matter, measured in units of nitrogen, were analyzed (Table 3).

The maximum specific rates of all physiological processes were observed for green algae (*Ulva, Enteromorpha*), the minimum ones were observed for *Phyllophora.* Several dependencies with significant coefficients of determination were found for the averaged rates. Linear dependences of nitrogen and phosphorus uptake rates on net production (*NetP*) were revealed, and the ratios differed

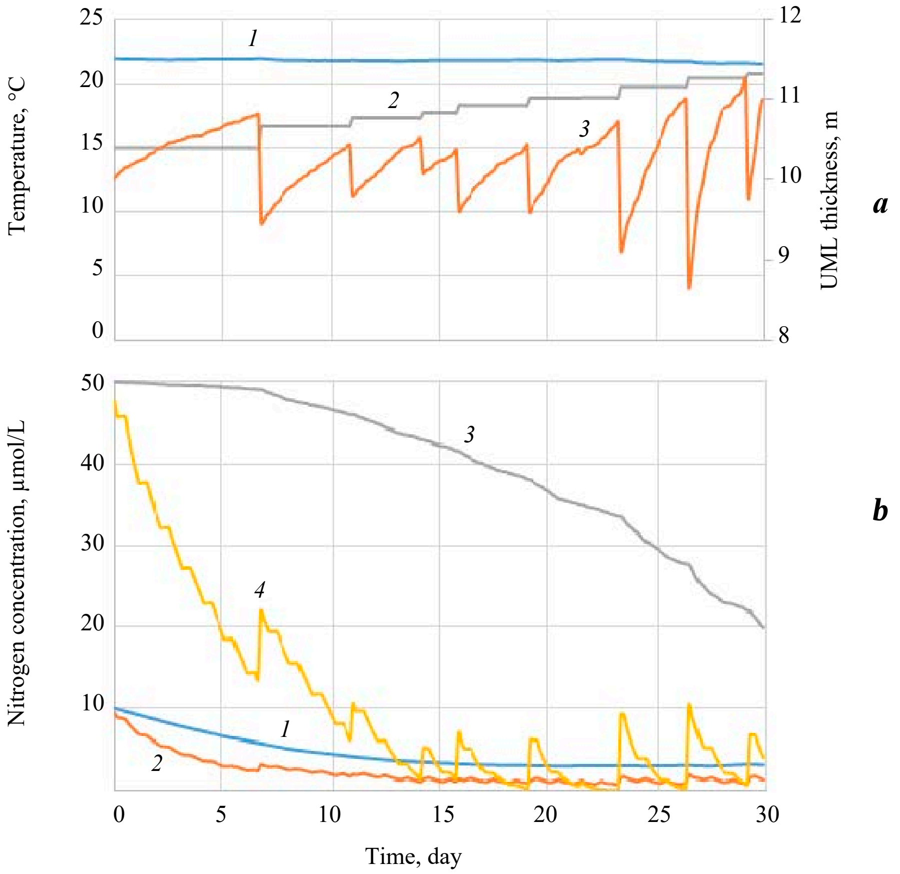

Fig. 3. Model conditions for the phytocenosis functioning: *a* – water temperature of the upper (*1*) and lower (*2*) layers, upper mixed layer (UML) thickness (*3*); *b* – concentration of ammonium (*1*, *2*) and nitrates (*3*, *4*) in the upper (*1*, *3*) and lower (*2*, *4*) layers of the computational domain

significantly for macroalgae and grasses. Fig. 5 shows the found dependencies.

The flows of the main biogenic elements at the boundary between a biological object and the environment are interconnected with each other. A plant cell consumes inorganic and releases organic compounds containing carbon, nitrogen and phosphorus. Clear relationships are observed between the averaged specific rates of uptake and release (Fig. 6), established as a result of simulation experiments with different initial conditions. Thus, a significant dependence of the DOM release rate on the respiration of macroalgae and seagrasses was revealed (Fig. 6, *a*). The release rates of DOM and POM are related to the photosynthesis process intensity, which is confirmed by the dependence of these values on the rate of nitrogen assimilation (Fig. 6, *b*).

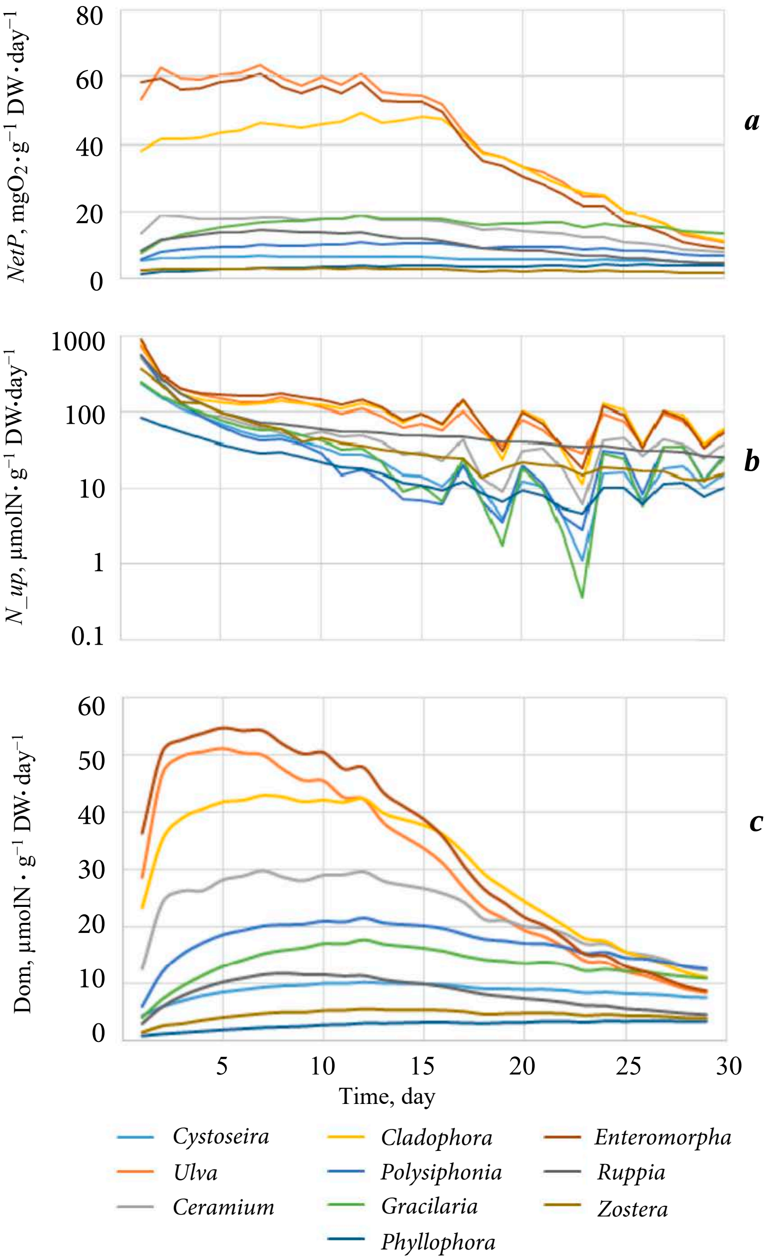

Fig. 4. Specific rates of the macroalgae and sea grasses physiological processes according to the model experiment data: primary production (*a*); nitrogen compounds assimilation (*b*); dissolved organic matter release (*c*)

Table 3. Averaged net production in the units of oxygen *NetP* (mg $O_2 \cdot g^{-1}$ DW$\cdot$day^{-1}), specific respiration rate *R* (mg $O_2 \cdot g^{-1}$ DW$\cdot$day^{-1}), nitrogen assimilation *N_up*, dissolved (Dom) and particulate (Pom) organic matter release rates (μmolN$\cdot g^{-1}$ DW$\cdot$day^{-1}), phosphorus assimilation (μmol P$\cdot g^{-1}$ DW$\cdot$day^{-1}) rate, relative characteristics of the efficiency of nutrients removal from the environment

Species	*NetP*	*R*	*N_up*	*P_up*	Dom	Pom	$\frac{N\_up}{\text{Dom}+\text{Pom}}$	$\frac{P\_up}{\text{Dom}+\text{Pom}}$
Cystoseira	3.89	0.86	40.24	1.29	5.28	1.44	6.00	0.19
Ulva	35.23	3.33	109.05	2.88	26.37	7.15	3.25	0.09
Ceramium	10.69	1.88	63.52	1.46	16.14	1.43	3.61	0.08
Cladophora	26.82	2.29	111.19	2.77	23.72	11.44	3.16	0.08
Polysiphonia	5.74	1.33	54.72	1.59	11.00	4.30	3.58	0.10
Gracilaria	9.53	0.62	44.16	1.36	8.37	1.43	4.50	0.14
Phyllophora	1.85	0.22	20.16	0.68	1.39	1.44	7.14	0.24
Enteromorpha	34.00	2.82	127.35	2.83	29.14	11.43	3.14	0.07
Ruppia	7.82	0.94	75.60	2.37	5.91	2.86	8.62	0.27
Zostera	1.78	0.83	57.76	1.60	2.66	2.87	10.46	0.29

Macroalgae and seagrasses cleanse the environment of excess nutrients by accumulating them in their tissues. At the same time, in the process of photosynthesis and production of organic matter, part of the assimilated compounds is released into the environment through various mechanisms (diffusion, exudation). The ratios of the rates of assimilation and release of nitrogen and phosphorus in the composition of organic matter (the last two columns of Table 3) can be considered as an assessment of the efficiency of removing excess nutrients during self-purification of a reservoir (bioremediation). It has been found that these indicators depend on the morphometric characteristics of macroalgae.

The fastest growing green algae with a fine structure are characterized by a significantly lower ability to remove nutrients from seawater than red and brown algae, which have a coarser structure. By introducing the specific surface index, which is often used in biology and defined as the ratio of the surface area of an alga to its volume *SA/V* (cm^{-1}), one can quantify this dependence. Fig. 7, *a* shows graphs illustrating the revealed dependence of the efficiency indicator of the use of macroalgae for the purpose of bioremediation on its morphometric characteristic *SA/V*. This dependence is stable, obtained in many numerical experiments with different initial conditions and mass ratios between the biological components of the marine ecosystem. Maximum performance indicators were

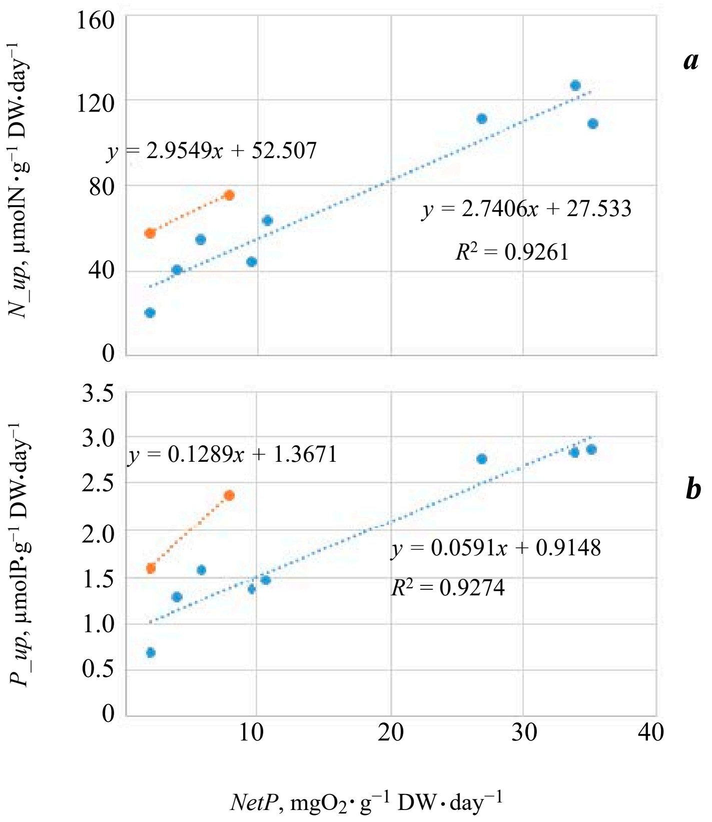

Fig. 5. Linear relationships between nitrogen (*a*) and phosphorus (*b*) assimilation rates and net plant production expressed in the units of oxygen for macroalgae (blue); seagrasses (orange)

obtained for the brown alga Cystoseira and red Phyllophora. Both species are dominant in the structure of benthic phytocenoses growing on rocky soils in the coastal zone of Crimea.

Unfortunately, reliable estimates of *SA/V* for seagrasses in the literature were not be found, so the function in Fig. 7, *a* was built only for macroalgae. The normalized values of the efficiency indicator for all model marine plant species are shown in Fig. 7, *b*. *Phyllophora* and *Cystoseira* have the highest potential for bioremediation among the considered macroalgae. Seagrasses have comparatively better properties than macroalgae phytocenosis in general.

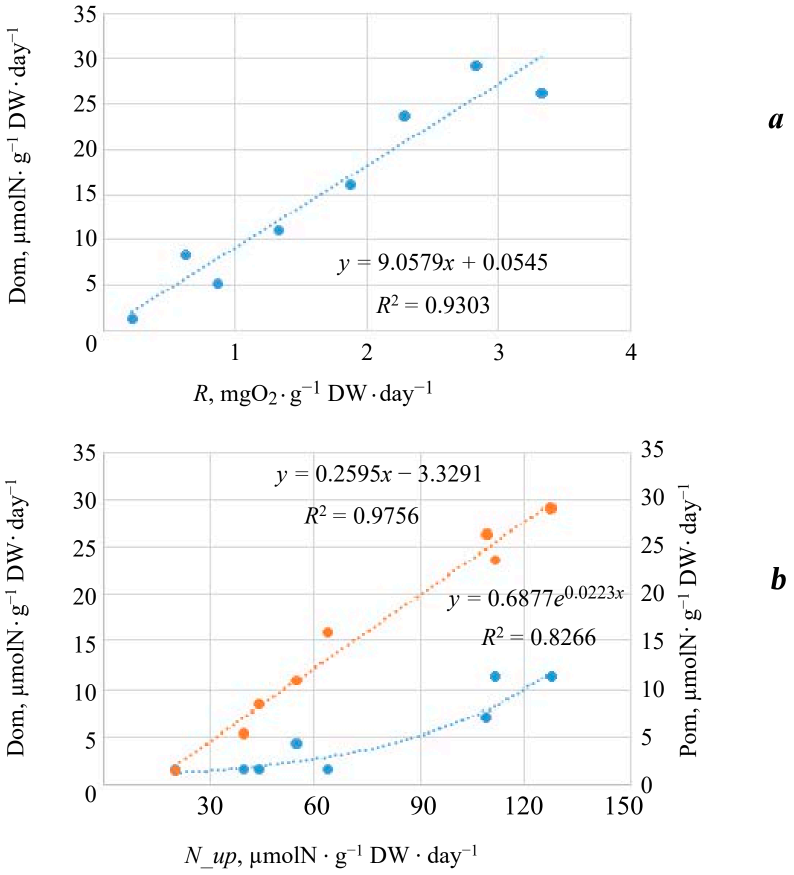

Fig. 6. Identified relationships between uptake and release rates during macroalgae functioning: release of dissolved organic matter as a function of a respiratation rate (*a*); release of particulate (blue) and dissolved (orange) organic matter as a function of nitrogen assimilation rate (*b*)

The leader is *Zostera marina*, which is also the dominant species of benthic phytocenoses on sandy soils in the coastal zone of Crimea. It is noteworthy that the efficiency of nitrogen and phosphorus assimilation by plants differs.

The efficiency indicator of the uptake of nutrients from the environment characterizes the response of the system to a sharp impact in the form of a discharge of polluted waters with a high concentration of nitrogen and phosphorus.

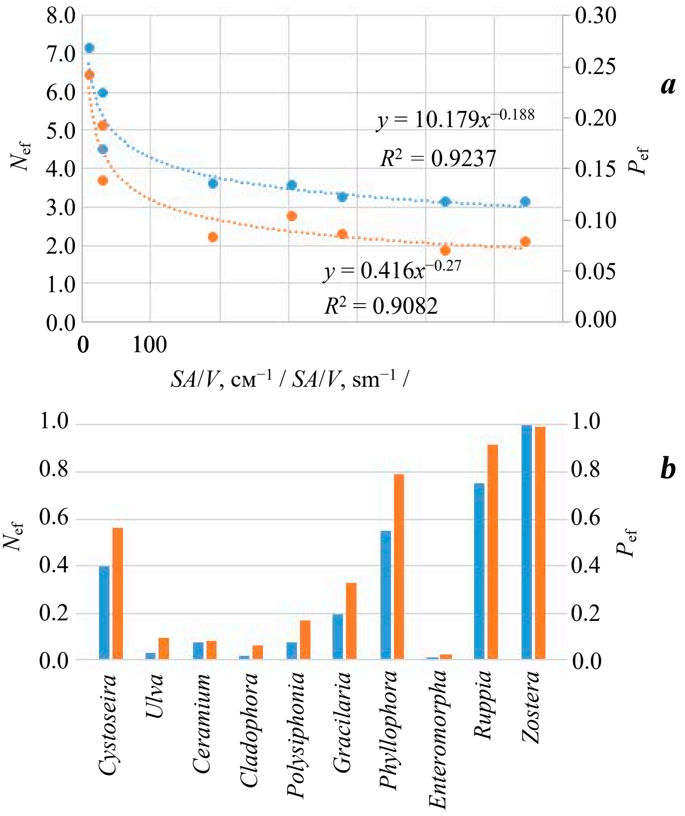

Fig. 7. Nitrogen $N_{ef} = N\_up/(\text{Dom} + \text{Pom})$ (blue) and phosphorus $P_{ef} = P\_up/(\text{Dom} + \text{Pom})$ (orange) assimilation efficiency indicators as a function of morphometric characteristic of macroalgae *SA/V* (*a*); normalized efficiency indicators for macroalgae and sea grasses (*b*)

During the first day, there is an active consumption and accumulation of biogenic elements in algae tissues, after which their concentration in water decreases and the system stabilizes. In a stable state, the efficiency indicators for various algae converge, although they do not level out. Clear dependences on the morphometric characteristics of *SA*/*V* manifest themselves precisely in the process of rapid growth of the alga under conditions of an increased concentration of biogenic substances, accompanied by their intensive removal and synthesis of primary production.

Conclusion

In recent decades, in the coastal zone of the Black Sea (as well as in many other areas of the World Ocean), there has been a restructuring of benthic phytocenoses with significant changes in their structure. With a decrease in the dominant species biomass and an increase in the proportion of fine-structured green algae species (which have the ability to grow rapidly at elevated nitrogen concentrations in water), the bioremediation potential of bottom phytocenoses sharply decreases, and, accordingly, the possibilities of self-purification of the reservoir decrease. The growth of anthropogenic pressure on the coastal area in the form of growing volumes of nutrient discharges leads to the gradual replacement of seagrasses as the dominant producer of organic carbon by macroalgae by rapidly growing green algae that have competitive advantages compared to brown and red algae species with coarser thalli structure. Further degradation of phytocenoses could lead to the development of stagnant phenomena in the water basin with transition to the mass phytoplankton development and displacement of macroalgae.

The simulation experiments performed under the conditions of competitive relationships between phytoplankton, macroalgae, and seagrasses made it possible to obtain visual confirmation of the well-known statements about the importance of preserving the structure of benthic phytocenoses, typical for the era of low anthropogenic loads, and restoring this structure to maintain a healthy state of the coastal zone ecosystems. A comparative analysis of the efficiency of nutrients accumulation in the tissues of marine plants clearly showed the advantages of seagrasses, brown and red macroalgae with a relatively coarse thalli structure in the process of self-purification of a water basin under stress loads.

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Tatiana A. Filippova – computational experiment running, result analysis, article text preparation

All the authors have read and approved the final manuscript.