Simulation of Chemical and Biological Processes of Seagrass Growth

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Abstract

Purpose. The paper is purposed at developing a seagrass growth simulation model to describe qualitatively and quantitatively the chemical and biological processes of seagrass interaction with the environment.

Methods and Results. The simulation model of the seagrass *Zostera* growth is represented. This species is a dominant one of seagrass phytocenoses in the Black Sea coastal areas. The model is based on the system of differential equations describing the processes of photosynthesis, uptake of nutrients (nitrogen and phosphorus) from the environment, production of organic matter, and release of oxygen and organic substances to the marine environment. The model control parameters are water temperature, intensity of photosynthetically active radiation, and concentrations of nitrates, ammonium and phosphates in the sea and pore waters. The model test calculations were carried out for the central part of the Donuzlav Bay that permitted to calculate the amounts of nitrogen and phosphorus uptake from the seawater and bottom, and those of oxygen, suspended and dissolved organic matter released to the environment from 1 sq. m area occupied by *Zostera*. In course of a year, from the 1 m depth, 1 kg of oxygen is released, 0.6 kg of carbon is produced, 64 g of nitrogen (47 g from water and 17 g from pore water) and 5 g of phosphorus are absorbed.

Conclusions. The proposed model makes it possible to estimate the growth rate of seagrass, the amount of the nutrients uptake, the released oxygen, the produced and released organic matter, and the nitrogen and phosphorus concentrations in plant tissues. The qualitative and quantitative assessments of the seagrass *Zostera* growth processes correspond to the field data represented in literature. It is shown that the developed model can be used as a block of an integrated ecological model, namely as a tool for quantitative assessing the intensity of chemical and biological processes in the coastal areas that are at risk of hypoxia.

Keywords: marine ecosystem, modeling, seagrasses, *Zostera*, photosynthesis, metabolic processes, Donuzlav

Introduction

Seagrasses are an area of interest for research for many reasons. Their extensive ubiquitous distribution allows them to be considered as a bioindicator of the marine environment state in the coastal zone. Thickets of grasses are a refuge for many marine organisms: benthic animals, some fish species, as well as the basis for the growth of microalgae – epiphytes [1]. In the coastal zone, seagrasses act as an

inorganic nitrogen and phosphorus accumulator, and when dying off they become a source of organic matter and biogenic elements. As a rule, the processes of growth and death of seagrasses are seasonal. In seas with low winter water temperatures, grasses shed leaves. Seas with strong coastal waves are characterized by uprooting, breaking off and destruction of plant foliage, and mass discharges of grasses onto the shore occur. The loose mass also sinks to the bottom, acting as an additional source of organic carbon and nutrients [2].

Ability of seagrasses to replenish dissolved oxygen in coastal areas is equally important. Shallow coastal areas are often at risk of conditions favorable for the development of hypoxia, which subsequently leads to anoxia. During photosynthesis seagrasses release significant amounts of oxygen, which is then used to oxidize excess organic matter and thereby prevent the development of hypoxia in shallow water, which in turn prevents the formation of hydrogen sulfide. On the other hand, in the dark, oxygen is consumed by grasses during respiration, which can contribute to the reducing environment development in the bottom area and pore waters.

One of the most common types of seagrass are members of *Zosteraceae* genus. *Zostera* communities are recognized as key links in coastal ecosystems according to the European BIOMARE program classification [3]. In view of the great importance of *Zostera* communities, the seasonal and annual dynamics of plant biomass is of undoubted scientific interest. Long-term observations of changes in *Zostera* phytocenoses make it possible to describe their dynamics for various water World Ocean areas, however, such studies do not provide information on the influence of external parameters, such as the concentration of nutrients in the environment, salinity, temperature, insolation and water transparency on biomass dynamics. Observations of *Zostera* complexes allow qualitative description of long-term changes in biomass. However, it is possible to achieve an understanding of the way how the processes of interaction of *Zostera* phytocenoses with the environment proceed and to give them a quantitative characteristic only with the help of mathematical modeling [4–7].

The work [4] presents a simulation model of *Zostera* growth in the Venetian Lagoon. The observed values are the biomass of roots, shoots and leaves. The influence of physical and chemical processes occurring in the environment on the plant is studied. According to the results of a number of test calculations with the model, the authors identified two main factors affecting *Zostera* growth in the Venetian Lagoon. These are temperature and illumination. In this work, much attention is paid to the effect of waves on *Zostera* biomass dynamics due to significant seasonal changes in the wind-wave regime of the lagoon. However, there is no significant seasonal change in the wave regime for the Black Sea in the areas of *Zostera* growth, so the model can be simplified. The sources of biogenic elements in the model are ammonium and phosphorus compounds, but nitrates, which make a significant contribution to the absorption of biogenic elements from the environment by grasses, are not taken into account.

The study [5] is aimed at simulation model development for photosynthesis and growth of *Zostera*. Dynamics of the biomass of *Zostera* leaves is described by functional dependencies on the following external parameters of the environment: illumination, water temperature and the concentration of biogenic elements.

The results of test calculations for one-year, four- and ten-year periods of modeling showed that *Zostera* growth is determined by a combination of temperature and solar regimes and the established regime violation leads to a significant decrease in productivity up to the complete death of leaf biomass. The model advantage is that it takes into account the many processes of interaction between a plant and the environment, however, the functional relationships between the parameters of the environment and the characteristics of the plant itself have been verified for the Chesapeake Bay (Virginia, USA), which causes difficulties when using the model for other water areas.

In [6], the processes of ammonium assimilation by *Zostera* are considered, and a numerical model is constructed. The authors studied the illumination effect on the intensity of nitrogen removal from the marine environment. It was shown that ammonium is more easily assimilated by *Zostera* than nitrates, and the amount of nitrogen obtained from the environment in the form of ammonium compounds is greater than with the assimilation of nitrates. In the presented model, the processes of nitrogen uptake by leaves and roots of a plant are described in sufficient detail, but there is no description of the process of the phosphate uptake.

Another model for *Zostera* biomass growth is presented in [7]. The biomass dynamics blocks of *Zostera* seagrass and *Ulva* macroalgae are included in the complex ecological model. The influence of the physical parameters of the environment on *Zostera* growth is shown, the processes of assimilation of nitrates, ammonium and phosphates are described. The paper demonstrates the effect of upwelling and intense advection, which are typical for the San Quintin Bay, Mexico, on the biogenic elements uptake. However, the influence of temperature and illumination on *Zostera* growth is not well described, although these two environmental parameters have a key effect on the dynamics of seagrass biomass.

An analysis of the literature on modeling the seagrass biomass dynamics showed the need to develop a mathematical model for *Zostera marina* growth for the Black Sea coast. The model should take into account the influence of the following environmental parameters: water temperature, illumination, concentrations of ammonium, nitrates and phosphates. This study presents such a development that can be used in an integrated ecological model of the ecosystem of the Black Sea coastal areas.

Materials and methods

In the coastal zone of the Black Sea, the most common species of sea grasses are *Zostera noltii* and *Zostera marina,* which are perennial flowering plants. In the Black Sea waters, the average biomass of *Zostera marina* ranges from $1–3$ kg/m^2 (wet weight), and in summer it sometimes reaches 5 kg/m^2 at a density of 916 ind./m^2 [3].

Zostera grows mainly on sandy silty soils, forming powerful rhizophyte root systems – mats. For the sandy soils of the Black Sea, *Zostera* is a carrying structural plant that forms coastal phytocenoses that are a place of refuge for benthic animals [8]. The role of *Zostera* in the biocenosis can hardly be overestimated, however, it is known that it is very sensitive to environmental pollution: in eutrophicated areas, its biomass decreases by $1.5–2$ times up to the complete degradation of thickets [9]. *Zostera* is an active bioconcentrator of heavy metals. Under their influence,

structural and functional changes in plant tissues are observed, which allows to use it as a bioindicator species [10].

Test calculations according to the model were carried out for the central part of Lake Donuzlav, which is located in the Black Sea region of Crimea and belongs to the Tarkhankut group of lakes. Today it is a man-made bay, as it is artificially connected to the Black Sea water area [11]. The Donuzlav Bay is an important object for studying the functioning of its ecosystem, since aquaculture of mussels and oysters is grown in a practically closed water area with low water exchange. Its impact on the ecosystem has not been studied, as well as the response effect of the environmental changes on the functioning of the plantation.

The bay is divided into three regions, different in their hydrological regime. Based on long-term hydrometeorological and hydrochemical data presented in [11], the annual variation of water temperature in the upper three-meter layer and the intensity of photosynthetically active radiation (PAR) on the surface was constructed. Interpolating average monthly data, series of seasonal variability of ammonium, phosphate and nitrate concentrations in water were also obtained. The ammonium concentration in the pore water for the Donuzlav Bay was assumed to be 100 µmol N/l. The prepared data series were used as external control variables for the mathematical model of *Zostera* growth.

The model description

Similarly to the mathematical model of macroalgae growth [12], we write the equation for the dynamics of *Zostera* biomass in the form of a balance relation

$$dB/dt = (P_r - eG_r - m)B, \tag{1}$$

where B is the biomass of all plant tissues: roots, rhizomes and leaves (g DW/m^2 or g DW/m^3); t is time (h); P_r is the specific rate of net primary production (1/h); G_r is the specific rate of gross primary production (1/h); $e = 10\%$ is the ratio of the released dissolved organic matter during the life of the alga to the gross production for the same time [13]; $m = 0.01$ 1/day is the coefficient of biomass loss due to mechanical damage, tissue death, grazing by marine animals [14].

Growth rate of plant tissues, or the rate of net primary production, depends on a variety of internal and external conditions. This value is affected by salinity, temperature, the rate of exchange processes with the environment and between parts of the plant, the concentration of nutrients both inside the plant and in the aquatic environment, illumination and intensity of waves. Growth rate is determined experimentally by the photosynthesis rate, most often measured by the amount of oxygen released by the plant in a certain period of time. The relationship between the photosynthesis rate and the external parameters of the environment is mathematically expressed by the photosynthesis curve, the so-called *PI*-curve. For each species of marine plants, the type of curve is individual and can be approximated by several expressions, based on empirical parameters. In the model, the photosynthesis curve for *Zostera* was approximated by a tangential function [8, 15, 16]

$$P_p = f(T)[P_{max}\tanh(\alpha I_k / P_{max}) - R_d], \quad I_k = I_0\exp(-\beta h), \tag{2}$$

where P_{max} is the maximum rate of photosynthesis (mg O_2/(g DW·h)); $\alpha = 0.07$ mg O_2/(g DW·h) is the slope of the *PI*-curve at low illumination [17]; R_d is dark respiration, i.e. the amount of absorbed oxygen that the plant spends on respiration and, accordingly, removes from the environment in the absence of photosynthesis (mg O_2/(g DW·h)); β is the light absorption coefficient in water, depending on the concentration of suspended matter (1/m).

The temperature effect on the growth rate of *Zostera* was approximated by dependences of *Zostera* maximum photosynthesis rate and dark respiration on temperature empirically obtained in the range of 10–27°C [18]:

$$P_{max}(T) = 1.3956\exp(0.073T), \quad R_d(T) = 0.6027\exp(0.074T), \quad (3)$$

where T is the water temperature (°C).

In addition to the influence of external physical factors, the growth rate of *Zostera* depends on the optimal ratio of nitrogen and phosphorus concentrations in tissues [7]. According to [19], the nitrogen content in *Zostera* tissues can vary in the range of 750–4500 µmol N/(g DW), the phosphorus content – in the range of 30–120 µmol P/(g DW). Plant growth does not occur if the content of one of the elements is below the specified minimum.

Let us introduce functions that limit the biomass growth at low concentrations of one of the biogenic elements [12]:

$$f(Q_N) = (Q_N - Q_N^{min}) / (Q_N^{max} - Q_N^{min}), \quad (4)$$

$$f(Q_P) = (Q_P - Q_P^{min}) / (Q_P^{max} - Q_P^{min}), \quad (5)$$

where Q_N and Q_P is the nitrogen and phosphorus content in plant tissues (µmol N(P)/(g DW)); Q_N^{min}, Q_P^{min}, Q_N^{max} and Q_P^{max} are the minimum and maximum values of valid nitrogen and phosphorus concentrations, respectively. Using these functions, a more accurate ratio for the photosynthesis rate depending on the water temperature, illumination and the content of biogenic elements in tissues can be written:

$$P_p = [P_{max}(T) \tanh(\alpha I_k / P_{max}) - R_d(T)] \min(f(Q_N), f(Q_P)). \quad (6)$$

The specific growth rate of *Zostera* P_r (1/h) can be estimated using the molar ratio of organic carbon produced and oxygen released during photosynthesis PQ (photosynthetic coefficient, mol O_2/mol C), and the carbon content in the dry mass of *Zostera* tissues Q_C (g C/(g DW)). Applying the relation for PQ [20], we write

$$P_C = 12 \cdot 10^{-3} P_p / 32 \, PQ, \quad (7)$$

where P_C is the organic carbon production (g C/(g DW·h)). Further, taking into account the carbon proportion in the dry mass of plant tissues, a formula for calculating the specific growth rate can be written: $P_r = P_C / Q_C$, or

$$P_r = 0.375 \cdot 10^{-3} P_p / (PQ \, Q_C). \quad (8)$$

Accordingly, the specific rate of gross production of a plant will be determined by the following ratios:

$$G_p = f(T) [P_{max} \tanh(\alpha I_k / P_{max})] \min(f(Q_N), f(Q_P),$$

$$G_r = 0.375 \cdot 10^{-3} G_p / (PQ \, Q_C). \quad (9)$$

Dynamics of nitrogen and phosphorus content in *Zostera* tissues is affected by the nutrients uptake rate and the rate of tissue growth. Uptake rates of nitrogen and phosphorus, on the one hand, depend on their concentration in the environment that can be approximated by the Michaelis–Menten law, and, on the other hand, are limited by the content of the element in tissues [12]. The maximum possible rates of removal of biogenic elements from the environment are determined by the morphological features of marine plants and may depend on the ambient temperature. Consequently, the equations for the content of nitrogen and phosphorus in *Zostera* tissues can be written as follows:

$$dQ_N / dt = V_N^{max}[1 - (Q_N - Q_N^{min}) / (Q_N^{max} - Q_N^{min})] \, [N] / (K_N + [N]) - P_r Q_N, \quad (10)$$

$$dQ_P / dt = V_P^{max}[1 - (Q_P - Q_P^{min}) / (Q_P^{max} - Q_P^{min})] \, [P] / (K_P + [P]) - P_r Q_P, \quad (11)$$

where V_N^{max} and V_P^{max} are the maximum possible rates of nitrogen and phosphorus uptake from the environment (μmol/(g DW·h)); the square brackets indicate the corresponding element concentration in the medium (μmol/l); K_N, K_P are half-saturation constants (μmol/l). Equations (10), (11) are valid for macroalgae, however, seagrasses have roots, and therefore it is necessary to take into account the assimilation of nitrogen and phosphorus from the pore water of the soil which they grow on.

The main nitrogen sources for *Zostera* are nitrates and ammonium dissolved in the water column and contained in bottom sediments. The withdrawal rates of these compounds vary. Let us take into account the contribution of each nitrogen source to the overall process. To do this, we rewrite equation (10) in the following form

$$dQ_N / dt = V^{max}_{NO3} [NO_3] / (K_{NO3} + [NO_3]) + V^{max}_{NH4(w)}[NH_{4(w)}] / (K_{NH4(w)} + [NH_{4(w)}]) + V^{max}_{NH4(b)}[NH_{4(b)}] / (K_{NH4(b)} + [NH_{4(b)}]) - P_r Q_N, \quad (12)$$

where V_{NO3}, $V_{NH4(w)}$, $V_{NH4(b)}$ – adjusted for internal content, the uptake rates of nitrate and ammonium from water (w) and pore water (b), respectively.

According to [7], we assumed that only one source, ammonium, makes a significant contribution to the processes of biogenic compounds uptake from pore water. Due to the small amounts of nitrates and phosphorus withdrawn from pore waters, their contribution can be ignored. To solve equations (1), (11) and (12), it is necessary to determine the values of photosynthetic (determining the type of *PI*-curve) and kinetic parameters – the maximum uptake rate of biogenic elements and the half-saturation constants. These characteristics for laboratory and natural conditions can be found in the literature. The quantities used in the calculations were chosen in a way to exclude extreme conditions that are not realized *in situ*. Model calculations were carried out at the following maximum nutrient uptake rates and half-saturation constants (according to [21, 22]):

$V^{max}_{NH4(w)} = 67.9$ μmol N/(g DW·h) [21],

$K_{NH4(w)} = 93.1$ μmol N [21],

$V^{max}_{NO3} = 4.9$ μmol N/(g DW·h) [21],

$K_{NO3} = 31.5$ μmol N [21],

$V_P^{max} = 8.5$ μmol P/(g DW·h) [22],

$K_P = 9.0$ μmol P [22],

$V^{max}_{NH4(b)} = 2.1$ μmol N/(g DW·h) [21],

$K_{NH4(b)} = 58.1$ μmol N [21].

At high concentrations of ammonium in water, a slowdown in the processes of its uptake from bottom sediments is observed [20]. However, for the species of *Ruppia maritima* seagrass, which is similar to *Zostera* in its morphofunctional characteristics, such an effect was not observed [23]. After analyzing the ammonium assimilation processes by seagrasses, we decided that it is not necessary to include the inhibition of ammonium uptake from sediments in the model, since its concentration in water when such an effect can be observed does not exist in the Black Sea coastal zone.

It was shown in [7, 8] that *Zostera* biomass loss coefficient due to dying off and grazing by marine organisms (*m* in equation (1)) varies in the range of 0.005–0.04 1/day. In the model, it was selected in such a way as to ensure the quasi-stationarity of the average seagrass biomass during the three-year period of model integration with the average seasonal dynamics of nutrient concentrations in water. Stable dynamics of *Zostera* biomass was obtained at the coefficient values 0.01 1/day for depths of 0.5 and 1 m, 0.007 1/day for depths of 2 m; these coefficients were used in the model.

The initial concentration of nitrogen and phosphorus in *Zostera* tissues is another control parameter. The range of possible concentrations is quite large, so a number of experiments was carried out to determine *Zostera* adaptation time to environmental conditions. According to the obtained results, it can be concluded that, regardless of the initial concentration of nitrogen and phosphorus in *Zostera* tissues, the internal content of these elements adapts to external conditions (temperature, illumination and concentrations of biogenic elements in the environment). The adaptation time increases with the plant growth depth: according to our calculations, it is 140 days for a growth depth of 0.5 m, 150 days for a depth of 1 m, and 160 days for a depth of 2 m (Fig. 1).
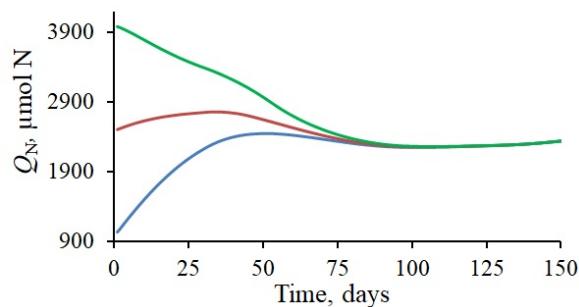

F i g. 1. Variability of nitrogen content in *Zostera* tissues in the process of establishing a stationary state at different initial conditions of the experiment

Discussion of the results

Test calculations on *Zostera* growth simulation model were carried out for the central part of the Donuzlav Bay. According to the average monthly values of environmental characteristics for 2015–2021 [11] the seasonal dynamics of water temperature PAR intensity, and concentrations of biogenic compounds in water and soil was modelled (Fig. 2). There were not enough observations to assess the seasonal variability in the total suspended matter (TSM) concentration, so an average value of 2.7 mg/l was chosen for the central part. To account for the oxygen respiration costs in the dark, a daily variation was superimposed on the seasonal variability of illumination. Test calculations were carried out for three depths – 0.5; 1 and 2 m. Deeper, as shown by our calculations, *Zostera* cannot normally photosynthesize due to the high content of TSM in water, which absorbs light. The light absorption coefficient β was calculated using the formula given in [24].
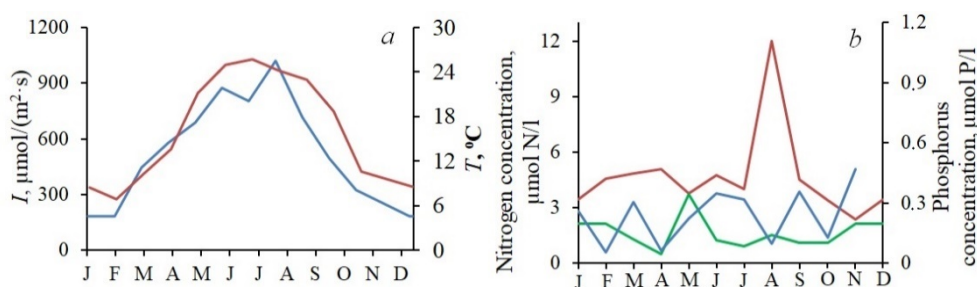

F i g. 2. Annual dynamics of the environment parameters: PAR (blue curve) and water temperature (red curve) intensities (*a*); concentration of the nutrient compounds in water: ammonium (red curve), nitrates (green curve) and phosphates (blue curve) based on the data for the Donuzlav Bay central part (*b*) [11]

The model input variables are illumination on the water surface, water temperature, concentrations of nitrogen and phosphorus compounds in water and soil. The initial values are *Zostera* biomass per m² of the bottom, the nitrogen and phosphorus content in the tissues. The integration step is 3 hours. Fig. 3 shows the annual dynamics of values characterizing *Zostera* growth and interaction processes with the marine environment. The inorganic carbon fixation and, accordingly, the oxygen release were calculated over an area of 1 m² using equations (6) and (7):

$$S_{O_2} = \int_0^{24} B(t) P_{\mathrm{p}}(t)\mathrm{d}t, \quad S_{\mathrm{C}} = \int_0^{24} B(t) P_{\mathrm{C}}(t)\mathrm{d}t,$$

where $B(t)$ – *Zostera* biomass (g DW/m²).

According to the simulation results, the maximum biomass is recorded at a depth of 0.5 m in September (Fig. 3, *a*). At depths of 0.5 and 1 m, *Zostera* biomass almost doubles in the summer season. The maximum illumination and temperature are recorded in summer, the maximum concentration of ammonium in water is observed in August. Intensive assimilation of nitrogen in the form of ammonium leads to a rapid increase in biomass, having its peak in September. On the curves

showing *Zostera* growth rates, the maximum is recorded in September (Fig. 3, *b*), which is due to an increased concentration of ammonium in water. In summer months, the rate remains approximately constant, since the light and temperature regimes, as well as the concentrations of nitrogen and phosphorus in the water, provide optimal conditions for *Zostera* growth. The maximum flux of oxygen released by *Zostera* thickets starts in the second half of summer – September, i.e., during the period of maximum growth (Fig. 3, *c*). *Zostera* at a depth of 2 m in winter months does not release, but absorbs oxygen due to the almost complete cessation of photosynthesis processes due to insufficient PAR intensity at this depth.
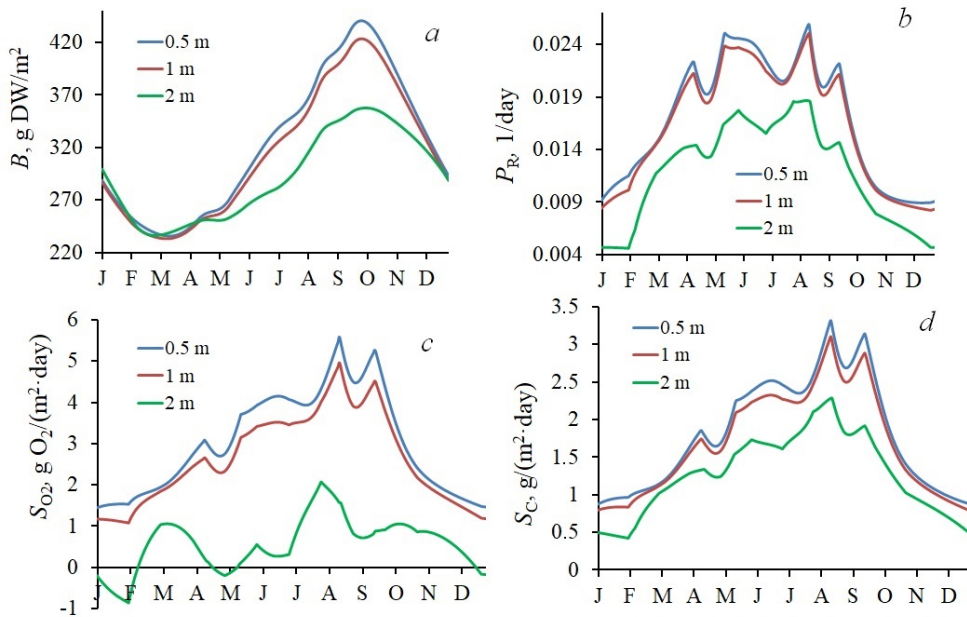

F i g. 3. Seasonal variability of *Zostera* growth and the related processes for three depths of growth: 0.5; 1 and 2 m
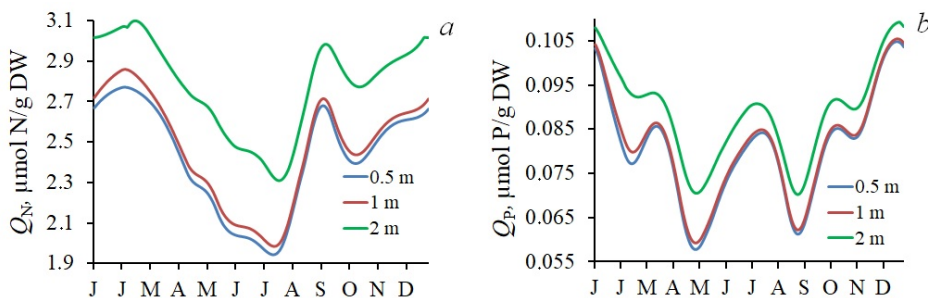

F i g. 4. Annual dynamics of the nitrogen Q_N (*a*) and phosphorus Q_P (*b*) contents in *Zostera* tissues

When carrying out test calculations, the concentrations of nitrogen and phosphorus in *Zostera* tissues were determined (Fig. 4). In winter and early spring,

Zostera accumulates nutrients in its tissues. Since there is no active growth during this period, nitrogen and phosphorus obtained from the environment are slowly consumed, the uptake rates decrease as biogenic elements accumulate in the tissues. In summer period, with an increase in the growth intensity, the plant needs more nutrients, so the nitrogen uptake rate increases during this period (Fig. 5).

Model simulations allow to quantify the processes of *Zostera* interaction with the environment. The volumes of nitrogen and phosphorus withdrawn by seagrass from an area of 1 m^2 during a day (Fig. 5) were calculated. Formulas (10) and (11) were used to obtain the following estimates:

$$S_{N(water)} = \int B(t)(V^{max}_{NO3} [NO_3] / (K_{NO3} + [NO_3]) + V^{max}_{NH4(w)} [NH_{4(w)}] / (K_{NH4(w)} + [NH_{4(w)}]))dt,$$

$$S_{N(bottom)} = \int B(t) V^{max}_{NH4(b)} [NH_{4(b)}] / (K_{NH4(b)} + [NH_{4(b)}])dt,$$

$$S_P = \int B(t) V^{max}_P [P] / (K_P + [P]) \, dt.$$

Zostera most intensively removes ammonium dissolved in the water column and pore waters of the soil, nitrates are absorbed worse. The maximum fluxes correspond to the maximum values of external concentrations and are recorded during the period of the greatest growth (second half of summer – September). At all depths, an increase in the flux of nutrients in February and a decrease in December are recorded. Both effects are due to photosynthesis: in early January, under the influence of low temperatures and low PAR intensity, *Zostera* photosynthesizes weakly, so there is no need for active uptake of nutrients, but as soon as the light and water temperature reach the values necessary for photosynthesis, *Zostera* actively begins to remove biogenic elements necessary for tissue growth from the environment. In December, the reverse process occurs: photosynthesis stops, absorption processes fade.
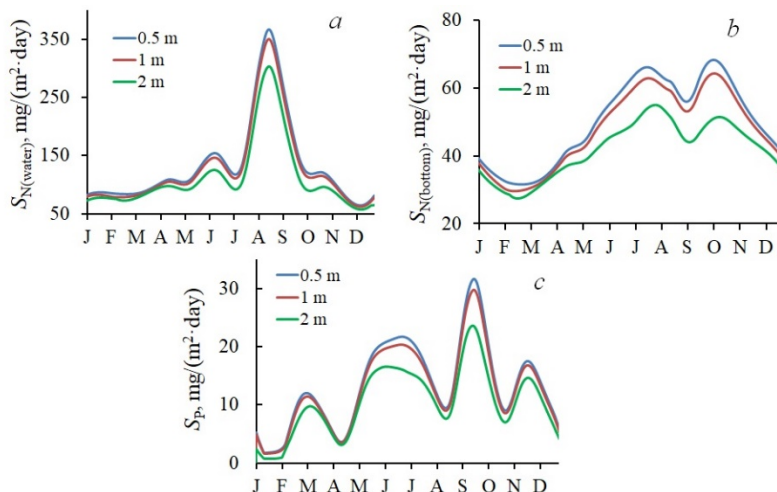

F i g. 5. Nutrient fluxes from the 1 sq. m area occupied by *Zostera* thickets: S_N (water) – ammonium and nitrates of the water column (*a*); S_N (bottom) – ammonium of pore water (*b*); S_P – phosphates (*c*)
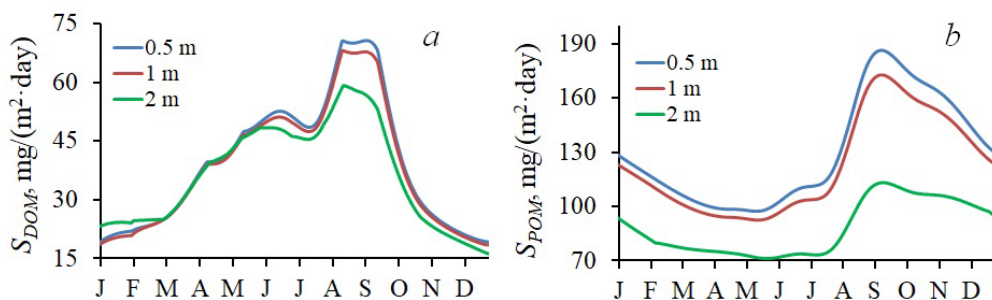
F i g. 6. Fluxes of the released dissolved S_{DOM} (*a*) and suspended organic S_{POM} (*b*) matters from the 1 sq. m area in the units of nitrogen

Another process of *Zostera* interaction with the environment is the dissolved (DOM) and particulate (POM) organic matter release, which accompanies its growth. Dissolved organics are released during metabolic processes; particulate matter is formed due to the death of plant parts, partial destruction of leaves under dynamic impact (the model does not take into account the beaching, gradual decomposition and mineralization of dead plant parts in bottom sediments). Fig. 6 shows the seasonal variability of the released POM and DOM. The maximum values of DOM and POM fluxes are recorded in the second half of summer and September, which corresponds to the maximum growth rate of *Zostera*.

A quantitative assessment of the substance fluxes allows to calculate the mass of absorbed nitrogen and phosphorus, as well as the oxygen released during photosynthesis from 1 m^2, occupied by *Zostera* thickets. At a depth of 1 m, 1 kg of oxygen is released during the year, 0.6 kg of carbon is produced, 64 g of nitrogen is absorbed (47 g from water and 17 g from pore water) and 5 g of phosphorus. The values obtained were compared with the available similar estimates [25, 26]. The data on productivity per dry weight are in good agreement with the estimates [26] for macroalgae.

Conclusions

The simulation model of seagrass growth presented in the paper enables to describe the chemical and biological processes of seagrasses' interaction with the environment at a qualitative and quantitative levels. Using the developed model, the growth rates of seagrasses at three depths of the basin, the mass of absorbed biogenic elements, released oxygen, formed and released organic matter and the internal content of nitrogen and phosphorus in plant tissues were calculated. Comparison of the obtained characteristics with the values presented in the literature shows a good agreement between the model and field data.

Thus, the proposed model of *Zostera* growth is the basis for developing a block of functioning of the bay bottom phytocenosis, an important component of the future integrated ecological model of this water area. In general, based on the results of test calculations, we can conclude that they are reliable and adequate for the simulation model proposed.

REFERENCES

1. Moore, K.A. and Short, F.T., 2007. Zostera: Biology, Ecology, and Management. In: A. Larcum, R. Orth and C. Duarte, eds., 2006. *Seagrasses: Biology, Ecology and Conservation*. Dordrecht: Springer. Chapter 16, pp. 361-386. https://doi.org/10.1007/978-1-4020-2983-7_16

2. Rasmussen, J.R., Olesen, B. and Krause-Jensen, D., 2012. Effects of Filamentous Macroalgae Mats on Growth and Survival of Eelgrass, Zostera Marina, Seedlings. *Aquatic Botany*, 99, pp. 41-48. https://doi.org/10.1016/j.aquabot.2012.01.005

3. Milchakova, N.A., 2008. Marine Weeds of Eurasia Southern Seas: Composition, Distribution and Structural-Functional Features (Review). In: B. N. Panov, ed., 2008. *Main Results of Complex Research in the Azov-Black Sea Basin and the World Ocean (Jubilee Issue)*. Kerch: YugNIRO Publishers. Vol. 46, pp. 93-101 (in Russian).

4. Zharova, N., Sfriso, A., Voinov, A. and Pavoni, B., 2001. A Simulation Model for the Annual Fluctuation of Zostera Marina Biomass in the Venice Lagoon. *Aquatic Botany*, 70(2), pp. 135-150. doi:10.1016/S0304-3770(01)00151-6

5. Wetzel, R.L. and Neckles, H.A., 1986. A Model of Zostera Marina L. Photosynthesis and Growth: Simulated Effects of Selected Physical-Chemical Variables and Biological Interactions. *Aquatic Botany*, 26, pp. 307-323. doi:10.1016/0304-3770(86)90029-X

6. Zimmerman, R.C., Smith, R.D., and Alberte, R.S., 1987. Is Growth of Eelgrass Nitrogen Limited? A Numerical Simulation of the Effects of Light and Nitrogen on the Growth Dynamics of Zostera Marina. *Marine Ecology – Progress Series*, 41, pp. 167-176. doi:10.3354/meps041167

7. Aveytua-Alcázar, L., Camacho-Ibar, V.F., Souza, A.J., Allen, J.I. and Torres, R., 2008. Modelling Zostera Marina and Ulva Spp. in a Coastal Lagoon. *Ecological Modelling*, 218(3–4), pp. 354-366. https://doi.org/10.1016/j.ecolmodel.2008.07.019

8. Duarte, C.M., Martínez, R. and Barrón, C., 2002. Biomass, Production and Rhizome Growth near the Northern Limit of Seagrass (Zostera Marina) Distribution. *Aquatic Botany*, 72(2), pp. 183-189. doi:10.1016/S0304-3770(01)00225-X

9. Zenkina, V.G. and Pavlova, A.V., 2016. Zostera Marina Is an Informative Indicator of Ecological Status of Marine Waters. *International Journal of Experimental Education*, (10-2), pp. 190-192. Available at: https://expeducation.ru/ru/article/view?id=10630 [Accessed: 11 November 2022] (in Russian).

10. Mokievsky, V.O., Tsetlin, A.B., Azovskiy, A.I., Naumov, A.D., Kosobokova, K.N., Kuzishchin, K.V., Sapozhnikov, F.V., Vedenin, A.A., Gavrilo, M.V. [et al], 2020. [*Species are Biological Indicators of the State of Arctic Marine Ecosystems*]. Moscow: Foundation "NIR", 383 p. Available at: https://www.rosneft.ru/upload/site1/attach/0/10/22/Biologicheskie_indikatory.pdf [Accessed: 11 November 2022] (in Russian).

11. Dyakov, N.N. and Fomin, V.V., eds., 2021. [*Modern Hydrological and Hydrochemical Regimes of the Donuzlav Bay*]. Sevastopol, 464 p. (in Russian).

12. Vasechkina, E.F. and Filippova, T.A., 2019. Modeling of the Biochemical Processes in the Benthic Phytocenosis of the Coastal Zone. *Physical Oceanography*, 26(1), pp. 47-62. doi:10.22449/1573-160X-2019-1-47-62

13. Barrón, C., Apostolaki, E.T. and Duarte, C.M., 2012. Dissolved Organic Carbon Release by Marine Macrophytes. *Biogeosciences Discussion*, 9, pp. 1529-1555. https://doi.org/10.5194/bgd-9-1529-2012

14. Kraemer, G.P. and Alberte, R.S., 1993. Age-Related Patterns of Metabolism and Biomass in Subterranean Tissues of Zostera Marina (Eelgrass). *Marine Ecology Progress Series*, 95, pp. 193-203. doi:10.3354/meps095193

15. Jassby, A.D. and Platt, T., 1976. Mathematical Formulation of the Relationship between Photosynthesis and Light for Phytoplankton. *Limnology and Oceanography*, 21(4), pp. 540-547. doi:10.4319/LO.1976.21.4.0540

16. Goodman, J.L., Moore, K.A. and Dennison, W.C., 1995. Photosynthetic Responses of Eelgrass (Zostera Marina L.) to Light and Sediment Sulfide in a Shallow Barrier Island Lagoon. *Aquatic Botany*, 50(1), pp. 37-47. https://doi.org/10.1016/0304-3770(94)00444-Q

17. Dennison, W.C. and Alberte, R.S., 1982. Photosynthetic Responses of Zostera Marina L. (Eelgrass) to In Situ Manipulations of Light Intensity. *Oecologia*, 55(2), pp. 137-144. https://doi.org/10.1007/BF00384478

18. Hansen, A.B., Pedersen, A.S., Kühl, M. and Brodersen, K.E., 2022. Temperature Effects on Leaf and Epiphyte Photosynthesis, Bicarbonate Use and Diel O_2 Budgets of the Seagrass Zostera Marina L. *Frontiers in Marine Science*, 9, 822485. https://doi.org/10.3389/fmars.2022.822485

19. Atkinson, M.J. and Smith, S.V., 1983. C:N:P Ratios of Benthic Marine Plants. *Limnology and Oceanography*, 28(3), pp. 568-574. https://doi.org/10.4319/lo.1983.28.3.0568

20. Thursby, G.B. and Harlin, M.M., 1982. Leaf-Root Interaction in the Uptake of Ammonia by Zostera Marina. *Marine Biology*, 72, pp. 109-112. doi:10.1007/BF00396910

21. Sandoval-Gil, J.M., Camacho-Ibar, V.F., Ávila-López, M.C., Hernández-López, J., Zertuche-González, J.A. and Cabello-Pasini, A., 2015. Dissolved Inorganic Nitrogen Uptake Kinetics and $\delta^{15}N$ of Zostera Marina L. (Eelgrass) in a Coastal Lagoon with Oyster Aquaculture and Upwelling Influence. *Journal of Experimental Marine Biology and Ecology*, 472, pp. 1-13. https://doi.org/10.1016/j.jembe.2015.06.018

22. Pérez-Lloréns, J.L. and Niell, F.X., 1995. Short-Term Phosphate Uptake Kinetics in Zostera Noltii Hornem: A Comparison between Excised Leaves and Sediment-Rooted Plants. *Hydrobiologia*, 297, pp. 17-27. https://doi.org/10.1007/BF00033498

23. Thursby, G.B. and Harlin, M.M., 1984. Interaction of Leaves and Roots of Ruppia Maritima in the Uptake of Phosphate, Ammonia and Nitrate. *Marine Biology*, 83, pp. 61-67. https://doi.org/10.1007/BF00393086

24. Latushkin, A.A., Artamonov, Yu.V., Skripaleva, E.A., and Fedirko, A.V., 2022. The Relationship of the Spatial Structure of the Total Suspended Matter Concentration and Hydrological Parameters in the Northern Black Sea According to Contact Measurements. *Fundamental and Applied Hydrophysics*, 15(2), pp. 124-137. doi:10.48612/fpg/4heu-kxbn-gg7t

25. Pedersen, M.F. and Borum, J., 1992. Nitrogen Dynamics of Eelgrass Zostera Marina during a Late Summer Period of High Growth and Low Nutrient Availability. *Marine Ecology Progress Series*, 80, pp. 65-73. https://doi.org/10.3354/meps080065

26. Littler, M.M., 1980. Morphological Form and Photosynthetic Performances of Marine Macroalgae: Tests of a Functional/Form Hypothesis. *Botanica Marina*, 22, pp. 161-165. doi:10.1515/botm.1980.23.3.161

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